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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).

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

attendance (Paredes et al. 2005), mass loss (Croll et al. 1992; Falk et al. 2000, 2002; Watanuki et al. 2001) and dive depth and duration (Elliott et al. 2007), our leg-mounted TDRs had no impact on provisioning rates, trip duration or mass loss (Elliott et al. 2007, in press).

We obtained dive depth, duration and surface pause interval for all dives during the final dive bout preceding each prey delivery using a custom-built MS Excel macro that corrected for device drift and determined bouts based on sequential differences (Mori et al. 2001; difference criterion = 37.4 m or 63.4 s). Only dives to depths greater than 3 m were analysed. Dive duration was calculated based on the number of TDR records that exceeded 3 m, and then adding an additional interval assuming a constant descent rate to the first depth recorded and a constant ascent rate from the last depth recorded that increased with maximum depth (Elliott et al. 2007). We defined bottom time as the time from when the bird first reached 90% of maximum depth to the time when the bird last left 90% of maximum depth. We used the definition for the index of patch quality (IPQ) from Mori et al. (2002) and Elliott et al. (2008).

To examine whether dive depth and duration varied within a dive bout, we calculated the difference in dive depth and duration between subsequent dives for all dive bouts with at least three dives. We only used data for unhandicapped, chick-rearing guillemots. Because final dives tend to be shorter than average (Elliott et al., in press), presumably because they reflect dives during which a prey item was captured and the dive subsequently terminated, we also completed these analyses with the final dive removed. Differences were averaged over each dive bout. We used Z tests on these averages to determine whether dive depth and duration increased significantly during dive bouts.

To test whether oxygen uptake rate is biphasic (Walton et al. 1998), we examined dive-to-surface ratios for unhandicapped, chick-rearing guillemots ($N = 2866$ dives). We set the minimum surface interval at 1 s ($N = 6$ dives fit into this category) because shorter intervals provided large bias in our data (dividing by a number close to zero gave large ratios) and appeared to represent dives where a surface interval was identified because the guillemot was above our threshold for a dive (3 m), but in fact the guillemot never surfaced. Dive-to-surface ratios were ln-transformed to meet normality assumptions.

During chick rearing (5–16 August 2005), we attached neutrally buoyant wooden blocks with cross-sectional areas of 2.8 or 5.6 cm^2 to guillemots at 'Z Plot' for 24–48 h. The blocks (38.3 or 19.2 g) were made of plywood and were effectively neutrally buoyant after 30 min of submersion in saltwater. We attached the handicaps to the back feathers of selected birds using cable ties and duct tape. Every effort was made to attach the handicaps parallel to the back and posterior to the wings. Each bird was monitored with a TDR for an equivalent period (~ 24 h) with and without a handicap, and therefore, paired statistical tests were used to remove the effect of individual variation on dive behaviour. Order of attachment (e.g. 'control' versus 'handicap' period) was randomized by flipping a coin. To minimize any bias associated with the diel

light cycle, all dives between 2100 and 0400 hours were excluded (Croll et al. 1992). To determine whether surface pause duration covaried with handicap treatment, we used ANCOVA with surface pause duration ln-transformed; to determine whether dive duration covaried with handicap treatment, we used ANCOVA with both dive duration and dive depth ln-transformed.

RESULTS

Handicapped individuals reduced both dive duration and depth (Table 1). There was no difference in surface pause duration or number of dives per bout (Table 1). There was no significant change in surface pause duration, despite a decrease in dive depth and dive duration (Table 1), because handicapped individuals paused longer at the surface for a given dive depth and duration (Fig. 1). The 'behavioural' aerobic dive limit (upswing in surface pauses for a given dive duration) appeared to occur at about 60 and 40 s for the 2.8 and 5.6 cm^2 drag handicaps, respectively (Fig. 1). The relationships between surface pause duration and dive depth (ANCOVA: $F_{2,1636} = 53.80$, $P < 0.0001$) and surface pause duration and dive duration (ANCOVA: $F_{2,1636} = 41.96$, $P < 0.0001$) covaried significantly with handicap type. In contrast, the relationships between dive duration and dive depth (ANCOVA: $F_{2,2198} = 2.05$, $P = 0.13$) and bottom time and dive duration (ANCOVA: $F_{2,2198} = 2.45$, $P = 0.09$) did not covary with handicap type (Fig. 1).

The mean ± SE difference in depth between subsequent dives within a dive bout was 0.86 ± 0.21 m ($N = 327$), whereas the difference in duration was -5.47 ± 0.51 s ($N = 327$), although the difference in duration was only due to the final dive. Once the final dive was removed, the difference in depth averaged 0.68 ± 0.23 m ($N = 278$) and duration averaged -0.53 ± 0.53 s ($N = 278$). The mean difference in dive depth across a given dive bout decreased with IPQ (ΔDepth $= (-6.19 \pm 0.89)$IPQ -3.33 ± 0.62; $t_{276} = -6.93$, $P < 0.0001$, $R^2 = 0.149$) and with the natural logarithm of the number of dives in the bout (ΔDepth $= (-0.60 \pm 0.29)$ln(number of dives) $+ 2.05 \pm 0.64$; $t_{268} = -2.06$, $P = 0.04$, $R^2 = 0.016$). There was no relationship between the mean difference in dive duration across a given dive bout and IPQ ($t_{276} = -0.62$, $P = 0.53$) or ln(number of dives) ($t_{268} = 0.81$, $P = 0.42$). Dive-to-surface ratios peaked at about 50 s (Fig. 2). The highest dive-to-surface ratio was 62.

DISCUSSION

As predicted by Houston & Carbone (1992), dive duration decreased, whereas surface pause duration did not change, when foraging costs increased (Table 1). This occurred because increased drag resulted in surface pauses increasing for a given dive duration or depth (Fig. 1a, b). Carbone & Houston (1994) also tested some of the predictions made by Houston & Carbone (1992) by manipulating the costs and benefits of foraging by pochards. Their results agreed qualitatively with the model. In contrast, Halsey et al. (2003) found that captive tufted ducks increased foraging time when the energetic costs of foraging

Table 1. Dive parameters for handicapped guillemots, excluding dives between 2100 and 0400 hours

| Variable	No handicap	Handicap 2.8 cm^2		Handicap 5.6 cm^2	
		Mean ($\pm$SD)	Paired difference	Mean ($\pm$SD)	Paired difference
N	14	8	**8**	6	**6**
Dive duration (s)	132$\pm$13	93$\pm$10	**16$\pm$7 (1.93, 0.04)**	85$\pm$11	**43$\pm$17 (2.48, 0.02)**
Dive depth (m)	72$\pm$14	49$\pm$6	**12$\pm$5 (2.40, 0.02)**	29$\pm$4	**27$\pm$11 (2.45, 0.02)**
Surface pause (s)	64$\pm$12	59$\pm$12	−22$\pm$74 (0.74)	58$\pm$12	14$\pm$22 (0.64)
Number of dives	6.2$\pm$1.0	3.9$\pm$0.8	0.4$\pm$3.4 (0.81)	8.0$\pm$3.9	−0.1$\pm$6.1 (0.96)

Paired columns show mean differences in pairwise comparisons between the same individuals with and without handicaps (paired *t* test value, followed by *P* values in parentheses). Significant relationships are shown in bold.

increased, although optimal surface duration did not change. Their results agreed quantitatively with Carbone & Houston's (1994) predictions for surface times. When Cornick & Horning (2003) increased foraging costs by attaching drag harnesses to Steller sea lions, *Eumetopias jubatus*, the sea lions decreased dive duration, bottom time and foraging efficiency. Similarly, when Webb et al. (1998) increased foraging costs in elephant seals, *Mirounga angustirostris*, using Styrofoam floats, the seals decreased dive duration, although these results were not statistically significant. There was no change in surface interval for the elephant seals (Webb et al. 1998).

Handicapped guillemots showed no change in bottom time or dive depth as a function of dive duration (Fig. 1c, d).

Thus, increasing energy expenditure did not appear to affect time allocation within a dive. Handicapped guillemots appeared to maintain similar time budgets within a foraging trip (dive), but altered the time budgets over the entire dive cycle by decreasing dive duration relative to surface pauses.

Our results have implications for the potential effect of devices on measurements of surface pauses and dive durations. Specifically, the cross-sectional areas of the handicaps we used were similar to those of early time−depth recorders (e.g. 3.8 cm^2: Croll et al. 1992; 4.2 cm^2: Falk et al. 2000, 2002; Benvenuti et al. 2002; 4.5 cm^2: Jones et al. 2002). Our results suggest that the relationships between surface pauses and dive durations reported by early researchers may be partially
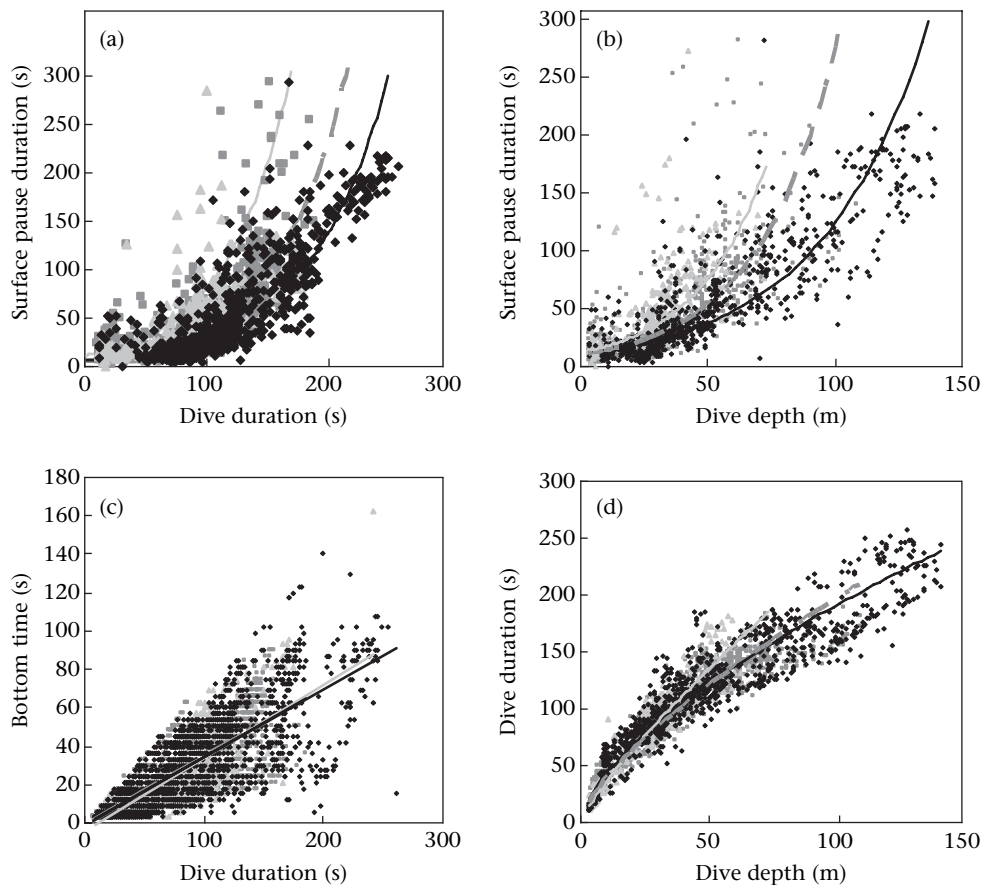
Figure 1. Relation between dive duration and (a) surface pause duration and (c) bottom time, and the relation between dive depth and (b) surface pause duration and (d) dive duration in Brünnich's guillemots that were handicapped (■: 2.8 cm^2; ■: 5.6 cm^2) and unhandicapped (■).
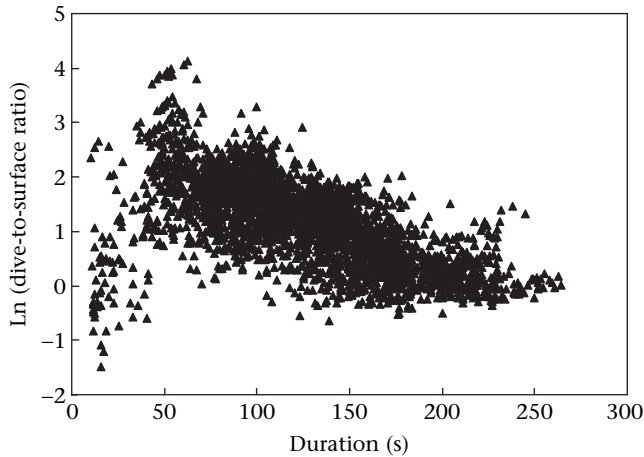
Figure 2. The dive-to-surface ratios at different dive durations for Brünnich's guillemot.

an artefact of increased energy expenditure associated with the time–depth recorder. For example, Croll et al. (1992; see their Figure 9); highlighted a 'unique' dive bout to show that surface pauses in guillemots were sometimes very short for the measured dive duration, suggesting that guillemots sometimes use anaerobic metabolism. In fact, the highlighted dive bout was an average dive bout within our data set. Future testing of empirical results against theory should consider the potential effect of the time–depth recorder on the measurement of the relationship between surface pauses and dive duration.

Green et al. (2003, 2005a, b) noted that a drop in core body temperature during diving, observed for penguins (Culik et al. 1996; Handrich et al. 1997; Bevan et al. 2002) and shags (Kato et al. 1996; Bevan et al. 1997), reduces metabolic rate. Thus, a drop in core body temperature through the dive bout could result in increased aerobic dive limit and, thus, dive duration. Green et al. (2003) found that dive duration did not increase during dive bouts of macaroni penguins. These authors suggested that this effect may be more likely in species that exceed their aerobic dive limit regularly, and thus, could be applicable to guillemots. Nevertheless, we found that dive duration did not change during the dive bout, although dive depth increased slightly through the bout. We propose two explanations for this observation. First, Niizuma et al. (2007) found that Brünnich's guillemots do not reduce core body temperature during diving, presumably because the higher cost of transport per unit of body mass results in heat generated by muscles being greater than that lost to the water. However, guillemots may reduce diving metabolic rate in other ways, thereby increasing maximal dive duration. The calculated aerobic dive limit (maximum oxygen stores/diving metabolic rate, DMR) is about one-third the behavioural aerobic dive limit (Croll et al. 1992), despite accurate measurements of oxygen stores (Croll et al. 1992), suggesting that DMR, which was measured for shallow dives in a laboratory (Croll & McLaren 1993), is decreased during longer dives. As buoyancy costs are low (Lovvorn et al. 1999, 2004), it is unlikely that reduced DMR is entirely due to reduced

buoyancy costs. Rather, guillemots may reduce blood flow to metabolically expensive tissues. Second, any reduction in diving metabolic rate during a dive bout will result in increased metabolic rate after the dive bout to warm or reoxygenated tissues (Green et al. 2005a, b). Thus, guillemots may be balancing their oxygen stores over a longer timescale than a single dive (e.g. Heath et al. 2007), resulting in no change in dive duration over the course of a bout.

In fact, dive duration tended to decrease through the dive bout because final dives tended to be exceptionally short, but to the same depth. We interpret this as an indication that final dives usually involved prey capture and were, therefore, aborted prematurely. In another single-prey loader, the otter, *Lutra lutra*, dives resulting in prey capture are also shorter than the average dive duration (Nolet et al. 1993). In our study, differences in dive depth tended to decrease with IPQ and the number of dives in a bout. This result suggests that when high-quality prey patches are discovered, guillemots tend to dive sequentially to the same depth. In general, we found that sequential dives were influenced by prey capture rate ('patch quality') rather than internal physiology.

As shown by Walton et al. (1998) for shags, *Phalacrocorax aristotelis*, black guillemots, *Cepphus grylle*, and common guillemots, *Uria aalge*, we found a peak in the dive-to-surface ratio at intermediate dive durations (Fig. 2). Thus, our results are consistent with a biphasic oxygen uptake curve in Brünnich's guillemots. Nevertheless, a peak in dive-to-surface ratio is also an inevitable result whenever the relationship between dive duration and surface pause duration is exponential. Consider the dive-to-surface ratio, R:

$$R = \frac{u}{a\,e^{bu}}$$

where u is dive duration and a and b are experimentally derived values expressing the relationship between dive duration and surface pause duration. R is maximized when:

$$\frac{dR}{du} = 0$$

$$\frac{uab\,e^{bu} - a\,e^{bu}}{(a\,e^{bu})^2} = 0$$

$$uab\,e^{bu} = a\,e^{bu}$$

$$u = \frac{1}{b}.$$

For the case of guillemots, where $b = 0.0191$, R is maximized when $u = 1/0.0191 = 52$ s, which agrees with the results shown in Fig. 2. Thus, although the dive-to-surface ratio for guillemots peaks at an intermediate value, this is a necessary result of the exponential relationship between

surface interval and dive duration and is not necessarily due to a biphasic oxygen uptake curve. As Houston & Carbone (1992) assume an exponential relationship between surface interval and dive duration, our results satisfy their assumptions.

Conclusions

In agreement with our initial predictions, handicapped individuals reduced dive duration but did not alter surface pauses. Handicapped individuals showed no change in bottom time or depth as a function of dive duration. Thus, increasing energy expenditure for a central-place forager altered the relationship between the time spent at the central place and the time spent at and travelling to the foraging patch, but did not alter how time was allocated at the patch. In contrast, increasing energy intake for a central-place forager altered bottom time and depth as a function of dive duration, with little impact on surface pauses (Elliott et al. 2008). The final dive in each dive bout tended to be shorter than the average dive duration. Once the final dive was excluded, and in contrast to our initial expectations, dive depth tended to decrease and there was no relationship with dive duration. Because the relationship between surface pauses and dive depth and duration changed with increased energy expenditure, these parameters may be useful proxies for monitoring whether energy expenditure increases with changing environmental conditions (Wanless et al. 1993; Monaghan et al. 1994; Davoren & Montevecchi 2003; Davoren et al. 2003; Mori et al. 2005).

Acknowledgments

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