



## Time allocation by a deep-diving bird reflects prey type and energy gain

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Central-place foragers must decide how to trade off travel time with foraging time when energy costs and gains differ between available prey types. Oxygen consumption places a fundamental constraint on the available options for deep-diving birds. Dives exceeding the aerobic dive limit (ADL) are considered costly because they extend the interdive surface time. Nevertheless, dives exceeding ADL, combined with short surface pauses, may be an efficient strategy if (1) prey density or (2) the probability of losing contact with ephemeral prey is high. We examined surface pause duration, dive duration and dive depth during dive bouts of Brünnich's guillemots, *Uria lomvia*, immediately before prey delivery. Surface pauses were more strongly related to dive depth than to duration and were both 'anticipatory' (of short dives) and 'reactive' (to long dives). Surface pauses decreased weakly, but significantly, with prey mass and were not shorter for ephemeral than for benthic prey once prey mass was accounted for. Dive duration was a decelerating function of dive depth and was unaffected by prey type (benthic versus pelagic). Dive duration (as a function of depth), bottom time (as a function of depth and duration) and an index for prey acquisition rate based on these parameters all increased with prey mass. Thus, surface pause duration was not reduced during dive bouts for ephemeral prey and only slightly reduced during dive bouts for larger prey, suggesting that guillemots alter other components of the dive cycle (bottom time, transit time) to accommodate differences in prey type and energy gain.

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Early theoretical formulations of foraging behaviour characterized animals as naïve foragers, randomly encountering prey items while foraging (MacArthur & Pianka 1966; Ward & Zahavi 1973). Recent empirical results, however, have shown that predators specializing on specific prey types ('specialists') actively search out prey encounters by returning to locations known to have abundant prey (Davoren et al. 2003a, b; Wilson et al. 2005). None the less, it is unclear whether predators that prey on a variety of prey types ('generalists') also actively

change their behaviour to search for and capture specific prey items, or whether they move randomly through a habitat, and consume prey items as they are encountered (Barrett 2002; Woehler et al. 2003; Tremblay et al. 2005). Foraging strategy is especially important in the marine environment, where many predators are generalists, and where, for breath-hold divers, access to air limits foragers to brief and intermittent contact with their prey (Thompson & Fedak 2001; Gaston 2004).

Dive duration among aquatic birds and mammals scales with body mass (Schreer & Kovacs 1997; Watanuki & Burger 1999). Thus, small pursuit-diving birds, such as auks, are especially constrained and, hence, are under strong selection to improve underwater performance (Gaston 2004). Adaptation to underwater foraging may be morphological (e.g. improved hydrodynamics), physiological (e.g. increased oxygen storage capacity), or

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behavioural (e.g. dive spacing and depth). Behavioural strategies need to be optimized to account for morphological and physiological constraints.

Surface pause duration is closely correlated with both dive depth and duration, either because divers anticipating a deep dive remain at the surface for a longer period to obtain sufficient oxygen stores and/or because divers surfacing from a deep dive remain at the surface for a longer period to remove lactate and carbon dioxide from the blood (Carbone & Houston 1996; Costa et al. 2001; Wilson et al. 2003). Surface pause duration increases rapidly once oxygen stores are exhausted because of the slow rate of lactate metabolism following anaerobic dives (Carbone et al. 1996; Kooyman & Ponganis 1998; Butler 2006). Therefore, to maximize time spent foraging at depth ('bottom time'; here defined as time spent within 90% of maximum depth), breath-hold divers are anticipated to dive within their aerobic dive limit (ADL), which is the maximum time a diver can remain submerged without resorting to anaerobic respiration (Kooyman & Ponganis 1998; Butler 2006). In support of this, most marine animals do not regularly exceed their ADL (Kooyman & Ponganis 1998; Costa et al. 2001; Butler 2006).

None the less, it may be beneficial to increase bottom time by exceeding ADL once prey items are encountered (Ydenberg & Clark 1989; Croll et al. 1992). Exceeding ADL might be cost-effective if (1) prey encounter rates are high enough to outweigh the costs associated with longer surface pauses, or (2) the probability of losing contact with a current, ephemeral prey source during transit to the surface is high, especially if locating a new prey source is time-consuming (Ydenberg & Clark 1989; Jodice & Collopy 1999). Increasing bottom time to maximize time spent pursuing ephemeral, schooling fish has been a common explanation for why some deep-diving birds routinely exceed their ADL (Ponganis et al. 1997; Kooyman & Ponganis 1998; Nagy et al. 2001). For example, Mori (1998a, b, 1999) developed a model that suggests that extending surface pause duration can be an 'optimal' strategy if the rate of prey acquisition is high in a given 'patch' (e.g. fish school). The model is based partly on the premise that divers are only expected to dive deep if prey density increases with depth (Mori 1998a, b; Gaston 2004).

The relationship between time allocation during the dive cycle and prey type and/or 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; Halsey et al. 2003; Heath et al. 2007). To address this issue, we combine information from visual observations of parental prey deliveries to nestling Brünnich's guillemots with information on surface pause duration, dive duration and dive depth during the dive bout immediately preceding prey delivery. First, we examined whether guillemots often exceeded their ADL using previously described values (Croll et al. 1992); were guillemots unlikely to be limited by oxygen availability, there would be little reason for them to show to the behavioural mechanisms described above. Next, we tested the following hypotheses: (1) dive duration will correlate better with

the preceding than the succeeding surface pause duration, and this relationship will depend on location in the water column (e.g. pelagic versus benthic; Jodice & Collopy 1999); (2) surface pause duration will be shorter when guillemots are (a) capturing larger prey items (e.g. large fish ~10 g) than when they are capturing smaller prey items (e.g. invertebrates ~0.4 g) and (b) capturing ephemeral prey items (e.g. schooling fish) than when they are capturing stationary prey items (e.g. benthic fish); and (3) bottom time and Mori's (1999) index of patch quality will increase with prey mass.

## 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. 2005a, b) during the chick-rearing season in 2004 ( $N = 23$ ), 2005 ( $N = 33$ ) and 2006 ( $N = 57$ ). 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 weighing 14–35 g affect 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 smaller, leg-mounted TDRs had no effect on provisioning rates, trip duration or mass loss (Elliott et al. 2007, in press a).

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. The macro subdivided dives into bouts using a bout-ending criterion equal to a difference of 37.4 m or 63.4 s between sequential dives (Mori et al. 2001). Chick-provisioning bouts were considered to be the final bouts before prey delivery. Only dives that exceeded depths of 3 m were analysed. Dive duration was calculated based on the number of TDR records greater than 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 time from when the bird first arrived at 90% of maximum depth to the time when bird last left 90% of maximum depth, so that if a bird rose above 90% of maximum depth in between these two points, this was still considered part of bottom time. We defined behavioural ADL (sensu Kooyman & Ponganis 1998) as the point at which surface pause duration began to increase rapidly relative to dive duration. We defined 'short' dives as less than 150 s and 'long' dives as greater than 150 s, which is the behavioural ADL given by Croll et al. (1992) and confirmed by our data (see Fig. 2a).

We defined the calculated ADL (maximum oxygen stores divided by oxygen consumption rate during diving) as 48 s, which is the value given by Croll et al. (1992). To eliminate pseudoreplication, we examined the relationships between surface pause duration and dive depth and duration averaged across each individual separately (Jodice & Collopy 1999). Because averaging obscured the actual relationships between these variables, we also examined the relationships on a per-dive basis.

To determine whether surface pause duration covaried with another variable (e.g. prey type, handicap treatment), we used ANCOVA with surface pause duration ln-transformed; to determine whether dive duration covaried with another variable, we used ANCOVA with both dive duration and dive depth ln-transformed. To compare among models, we used the following formula for AIC:

$$\text{AIC} = 2k + n \ln\left(\frac{\sigma}{n}\right) \quad (1)$$

where  $k$  is the number of parameters,  $n$  is the number of observations and  $\sigma$  is the explained sum of squares. To meet assumptions of normality for AIC calculations, surface pause duration was ln-transformed.

### Prey Type and Energy Gain

In conjunction with deployment of the TDRs, continuous 24 or 48 h observations ('feeding watches') were also carried out from blinds within 6 m of the birds to determine prey type (20–45 focal sites observed simultaneously). We did not conduct feeding watches when it was too dark to see deliveries because chicks are rarely fed at this time (Gaston et al. 2003). Fish length was estimated by reference to the white streak on the upper mandible of the adult birds' bill (~5 cm). Length was then converted to mass using taxon-specific length–mass relationships for fish from fresh prey collected on ledges between 1988 and 2006 (Elliott & Gaston, in press). For invertebrates, we used average mass across all samples collected because there is little variation in size. We classified sandlance (*Ammodytes* sp.) and Arctic cod (*Boreogadus saida*) as ephemeral (schools likely to persist within a dive bout but not between dive bouts; Gaston et al. 2003) and sculpin (mostly *Triglops* sp.), shannies (*Stichaeus punctatus* and *Leptoclinus maculatus*), fish doctor (*Gymnelus* sp.), poacher (*Leptagonus decagonus*) and snakeblenny (*Eumesogrammus praecisus*) as stationary (unlikely to persist within a dive bout; Gaston et al. 2003). We did not classify capelin (*Mallotus villosus*) as ephemeral because they can persist in large aggregations for long periods (Davoren et al. 2003a, b, 2006), and therefore are not always ephemeral on the temporal scale of guillemot dive bouts. Invertebrates included shrimp (*Lebbeus* sp., *Pandalus* sp.), squid (*Gonatus* sp.) and amphipods (*Parathemisto libellula*), and along with capelin were not included in analyses comparing ephemeral and stationary fish, but were included as pelagic prey items in comparisons between benthic and pelagic prey items.

We assumed that the final dive bout before delivery of a prey item represented foraging behaviour typical for that prey item. This idea is supported by the observation that

most individual guillemots specialize on a given prey item during each feeding watch (Elliott et al., in press), suggesting that foraging behaviour is continually tailored towards the given prey item. Furthermore, average dive depth and duration throughout the final bout were strongly correlated with final dive depth and duration (Elliott et al., in press).

To examine the effect of prey mass on dive behaviour, we calculated a single best-fit equation across all prey items for each relationship (e.g. surface pause and dive duration, surface pause and dive depth, etc.). For each dive during each dive bout preceding the delivery of a prey item, we calculated the residual relative to the best-fit equation. We averaged the residual across all dives for a given dive bout, and then calculated the linear regression between the average residual and estimated prey mass.

### Index of Patch Quality

We completed all calculations and statistics in Mathematica 3.0 (Wolfram Media, Inc., Champaign, IL, U.S.A.). Following Mori et al. (2002), we assumed that: (1) within each dive cycle, guillemots selected a dive duration that maximized the ratio of energy gain to energy expended (efficiency, sensu Ydenberg et al. 1994); (2) energy gain was an increasing function of bottom time (dive duration minus travel time), and that this relationship could be approximated by a power function; (3) energy expenditure was proportional to the total duration of the dive cycle (dive duration plus surface time); and (4) travel time  $\tau$  to depth  $d$  was fixed. Mori et al.'s (2002) definition of  $G$  as rate (energy intake/time expended, i.e.  $\beta = 1$ ) results in the same final equation as our definition, which maintains the same units in the numerator as the denominator. A conversion coefficient  $\alpha$  arises from the assumption that energy gain is a power function of time spent at the bottom: energy gain =  $\alpha(\text{bottom time})^x$ . The coefficient  $\beta$  is the average energy expended per time spent in the dive cycle. The coefficients  $\alpha$  and  $\beta$  convert time units into energy units and are assumed to be fixed. The exponent,  $x$ , is the rate at which energy gain increases relative to bottom time; when  $x$  is high, energy is accumulated quickly for a given bottom time. The constants  $b$  and  $c$  are derived empirically from the relationship between surface pause duration  $s$  and dive duration  $u$ :  $s = be^{cu}$ . Thus, we determined an index of patch quality (IPQ) by assuming that guillemots maximize efficiency,  $G$ , which is energy gained (numerator; proportional to dive duration minus travel time) per energy expended (denominator; proportional to surface pause duration plus dive duration) by solving the following equations:

$$G = \frac{\alpha(u - \tau)^x}{\beta(u + be^{cu})} \quad (2)$$

$$\frac{dG}{du} = 0 \quad (3)$$

$$\frac{\alpha x(u - \tau)^{x-1} \beta(u + be^{cu}) - \alpha(u - \tau)^x \beta(1 + bce^{cu})}{(\beta(u + be^{cu}))^2} = 0 \text{ (quotient rule)} \quad (4)$$

$$x(u - \tau)^{x-1}(u + be^{cu}) - (u - \tau)^x(1 + bce^{cu}) = 0 \quad (5)$$

$$x(u + be^{cu}) = (1 + bce^{cu})(u - \tau) \quad (6)$$

$$x = \frac{(1 + bce^{cu})(u - 1.321d)}{be^{cu} + u} \quad (7)$$

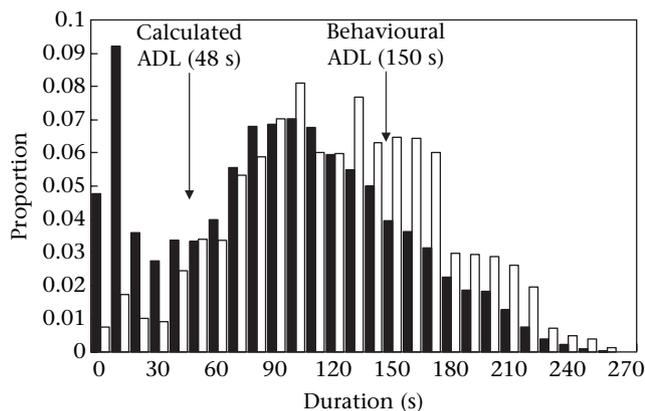
$$\text{IPQ} = \ln x \quad (8)$$

where  $\alpha$  and  $\beta$  are conversion coefficients that do not affect the final result. We defined our IPQ as the natural logarithm of IPQ calculated by Mori et al. (2002) to satisfy normality requirements for statistical tests (in our data set,  $x$  was log-normally distributed).

We assumed that surface pauses were a reaction to dive duration (higher  $R^2$  value, following Mori et al. 2002; see Results), and we derived the relationship between surface pause and dive duration from all foraging dives pooled (data as in Fig. 1a;  $b = 3.18$ ,  $c = 0.0191$ ). Based on observations of 100 randomly selected dives and because ascent and descent rates appear to be highly constrained (Lovvorn et al. 1999, 2004; Watanuki et al. 2003, 2006; Elliott et al. 2007), we used  $\tau = 1.321d$  for relating transit time (time in ascent plus time in descent) to depth  $d$  (Mori et al. 2002).

## RESULTS

Approximately 94% of the chick-provisioning dives that we observed were greater than the calculated ADL (48 s; Croll et al. 1992) and 34% were greater than the behavioural ADL (Fig. 1). For all dives pooled, 78% exceeded the calculated ADL and 21% exceeded the behavioural ADL



**Figure 1.** Proportion of all dives (■) and all dives from dive bouts that ended in a prey delivery ('provisioning dives'; □) for each duration in Brünnich's guillemots. Duration represents the start of each 10 s increment (e.g. 0 = 0–10 s). Few dives were shorter than 10 s because we included only dives that were deeper than 3 m, and most of these occurred in more than 10 s.

(150 s; Croll et al. 1992). The distribution for chick-provisioning dives was unimodal, with a mean duration of 120 s, whereas the distribution for all dives pooled together was bimodal, with peaks at 15 s and 100 s.

## Are Surface Pauses Anticipatory or Reactive?

There was a strong, exponential relationship between surface pause duration and both dive depth and dive duration (Tables 1, 2, Fig. 2a, b). The relationship was stronger with dive depth than dive duration, although a multivariate analysis suggested that both variables contributed significantly to the observed variance in surface pause duration (Tables 1, 2). On a per-dive basis, the relationship was consistently stronger between the preceding surface pause and dive depth (i.e. surface pauses were 'anticipatory') while on a per-individual basis, the relationship was stronger between the succeeding surface pause and dive depth (i.e. surface pauses were 'reactive'); a multivariate analysis suggested that there was both a reactive and anticipatory component to all dives (Tables 1, 2). When only dives less than 150 s were included, surface pauses were anticipatory, whereas when only dives greater than 150 s were included, surface pauses were reactive (Tables 1, 2). There was a strong relationship between dive depth and duration across all prey items (Fig. 2c; Table 3), and it was not related to prey lifestyle (e.g. pelagic prey items showed a similar relationship to benthic prey items).

## Energy Gain (Influence of Prey Type)

The relationship between surface pause duration and dive duration was similar across all prey items except for amphipods (Fig. 2a). Surface pause duration also varied exponentially with dive depth for all prey items, with little variation among prey items (Fig. 2b). Sandlance and cod, the two ephemeral prey items, had shorter surface pause duration for a given dive depth (Fig. 2b), but this difference was not significant once prey mass was accounted for (Table 4). Surface pause duration decreased with prey mass (Fig. 3a, b), although these trends were weak. Dive duration was a decelerating power function of dive depth (Fig. 2c). For a given depth, dive duration increased with prey mass (Fig. 3c). Bottom time increased steeply with dive depth for the first 60 m (Fig. 2d). Beyond this depth, bottom time changed only slightly with dive depth. In contrast, bottom time increased rapidly and linearly with dive duration and dive cycle time for all prey items (Fig. 2e, f). For a given depth or dive duration, bottom time increased with prey mass (Fig. 3e, f). IPQ showed a similar relationship with prey mass (Fig. 3d), which is not surprising as IPQ is derived from the relationship between dive depth, bottom time and duration.

Once corrected for mass, IPQ and dive duration, corrected for depth were significantly greater for stationary than for ephemeral prey items (Table 1). There was no difference in surface pause duration in response to dive duration or depth (Table 1). As found by Mori et al. (2002), IPQ was higher for multitime bouts

**Table 1.**  $\Delta$ AIC values (correlation coefficients,  $R^2$ , in parentheses) between surface pause duration and untransformed dive duration and depth for (1) chick-provisioning dives (dives during the final dive bout preceding prey delivery), (2) chick-provisioning dives less than and greater than 150 s, (3) all dives pooled and (4) chick-provisioning dives from the final dive bout preceding the delivery of various prey items ( $N > 10$ )

	N	Duration		Depth	
		Anticipatory	Reactive	Anticipatory	Reactive
Foraging dives	2866	1666.1 (0.702)	1797.8 (0.715)	1565.5 (0.753)	1425.8 (0.773)
Multivariate*	2866	35.8 (0.839)	<b>0.0 (0.841)</b>	35.8 (0.839)	<b>0.0 (0.841)</b>
Multivariate†	2866	1020.4 (0.773)		643.1 (0.801)	
<150 s	1873	367.2 (0.457)	664.5 (0.375)	<b>0.0 (0.591)</b>	242.4 (0.501)
>150 s	935	667.6 (0.406)	607.0 (0.470)	22.3 (0.681)	<b>0.0 (0.689)</b>
All dives	27 823	2831.9 (0.545)	4493.1 (0.536)	<b>0.0 (0.604)</b>	950.5 (0.611)
Benthic	872	319.8 (0.794)	234.1 (0.813)	<b>0.0 (0.857)</b>	73.9 (0.844)
Capelin	1581	190.5 (0.652)	310.0 (0.677)	<b>0.0 (0.695)</b>	102.3 (0.714)
Invertebrate	115	26.2 (0.510)	33.9 (0.446)	<b>0.0 (0.610)</b>	7.2 (0.562)
Ephemeral	220	53.5 (0.719)	68.8 (0.699)	<b>0.0 (0.780)</b>	34.9 (0.742)

Note that  $\Delta$ AIC values are valid only for comparisons within data sets (within the first three rows; otherwise only within each row). Best models (lowest AIC) for each data set are shown in bold. Sample sizes ( $N$ ) are the number of dives included in each analysis.

\*Multiple regression provided: subsequent (reactive) surface pause =  $1.44 \pm 0.47e^{(0.017 \pm 0.001)\text{duration}} + 11.0 \pm 1.2e^{(0.022 \pm 0.001)\text{depth}}$ ; previous (anticipatory) surface pause =  $1.06 \pm 0.38e^{(0.018 \pm 0.001)\text{duration}} + 12.1 \pm 1.1e^{(0.022 \pm 0.001)\text{depth}}$ .

†Multiple regression provided: duration =  $-13.2 \pm 1.6 + (20.8 \pm 1.2)\ln(\text{previous surface pause}) + (19.0 \pm 1.2)\ln(\text{subsequent surface pause})$ ; depth =  $-48.7 \pm 1.0 + (13.3 \pm 0.7)\ln(\text{previous surface pause}) + (13.5 \pm 0.7)\ln(\text{subsequent surface pause})$ .

( $-0.004 \pm -0.001$ ) than for single-dive bouts ( $-0.660 \pm 0.002$ ;  $t_{60} = 8.89$ ,  $P < 0.00001$ ).

## DISCUSSION

Dive duration for Brünnich's guillemots was exceptionally long, with a substantial proportion exceeding previously estimated ADLs. This was especially true for chick-provisioning dives, which tended to be longer than all dives pooled together, as also found by Jones et al. (2002) for guillemots in Labrador. Almost all of the chick-provisioning dives that we observed were greater than the calculated ADL, and over one-third were greater than the behavioural ADL (Fig. 1). For all dives pooled, most exceeded the calculated ADL and one-fifth exceeded the behavioural ADL. Thus, our results suggest that guillemots, like other deep divers, must have exceptional abilities to

deal with low oxygen levels at the end of the dive (Knower Stockard et al. 2005) and therefore are good candidates to examine behavioural strategies associated with deep diving. Although the ADL is poorly known in guillemots, these benchmarks provide support for our contention that guillemots dive for exceptionally long times relative to their oxygen stores, as most marine animals do not regularly exceed either the calculated or behavioural ADL (Kooyman & Ponganis 1998; Butler 2006). The exceptional dive bout noted by Croll et al. (1992), involving a series of dives for 200 s to depths of 60–90 m with a mean surface pause duration of 130 s, is actually fairly typical of thick-billed murrelets at Coats Island (Fig. 2a, b).

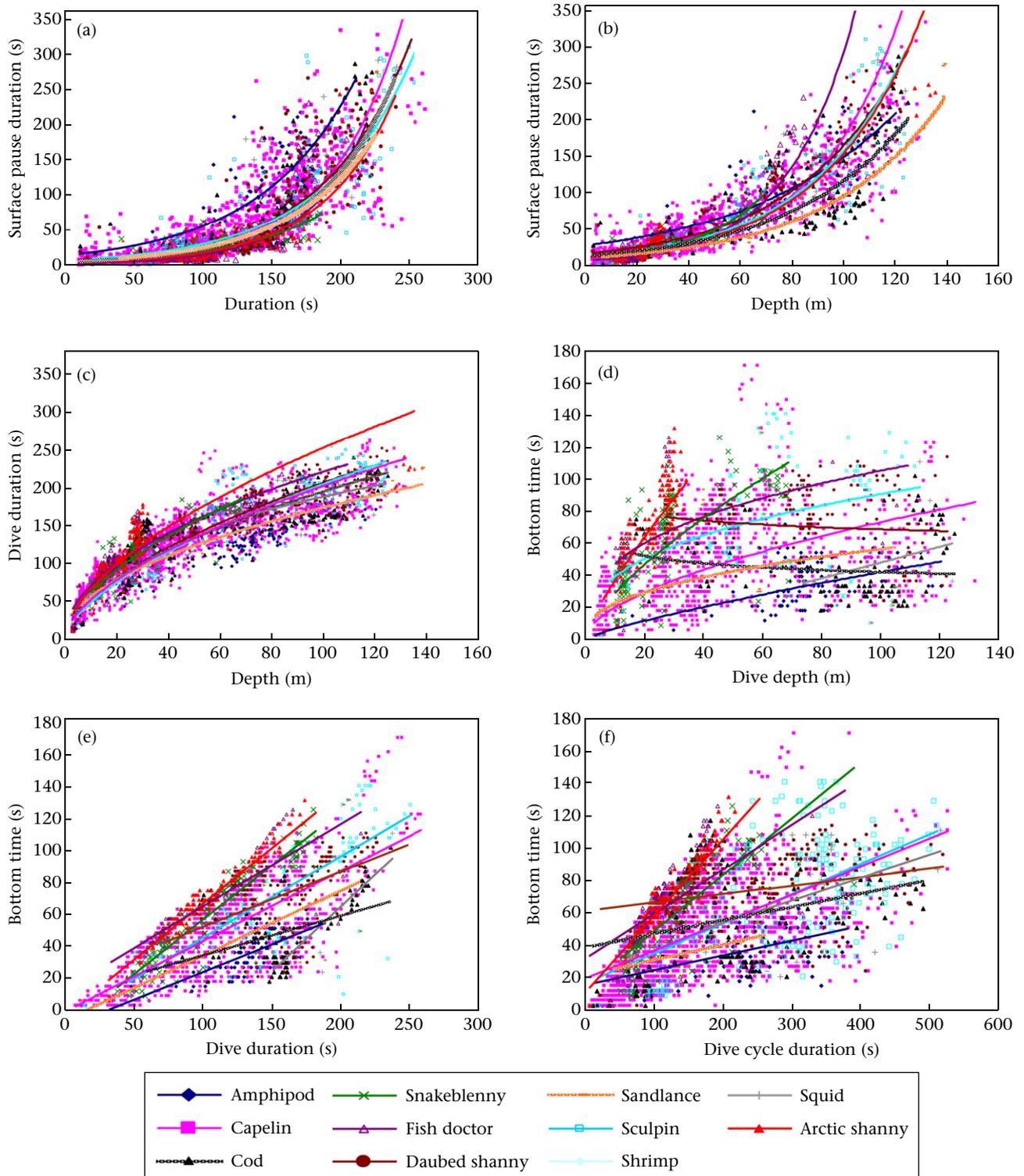
The unimodal, approximately bell-shaped distribution in dive duration for chick-provisioning dives suggests that prey suitable for chicks are continuously distributed in such a way that the most common dive duration lies between 100 and 170 s. These dive durations represent

**Table 2.**  $\Delta$ AIC values (correlation coefficients,  $R^2$ , for exponential regressions in parentheses) between surface pause duration and dive duration and depth averaged across each individual for (1) chick-provisioning dives, (2) chick-provisioning dives less than and greater than 150 s, (3) all dives pooled and (4) chick-provisioning dives from the final dive bout preceding the delivery of various prey items ( $N > 5$ )

	N	Duration		Depth	
		Anticipatory	Reactive	Anticipatory	Reactive
Provisioning	98	68.1 (0.783)	62.4 (0.770)	18.5 (0.862)	14.4 (0.867)
Multivariate*	98	<b>0.0 (0.885)</b>	0.8 (0.884)	<b>0.0 (0.885)</b>	0.8 (0.884)
<150 s	87	59.7 (0.470)	66.2 (0.310)	<b>0.0 (0.733)</b>	55.8 (0.391)
>150 s	68	47.3 (0.431)	59.0 (0.607)	14.0 (0.797)	<b>0.0 (0.835)</b>
All dives	127	44.5 (0.844)	41.3 (0.835)	17.6 (0.874)	<b>0.0 (0.880)</b>
Benthic	24	26.0 (0.813)	28.6 (0.797)	6.4 (0.899)	<b>0.0 (0.917)</b>
Capelin	71	9.3 (0.748)	5.9 (0.760)	2.8 (0.816)	<b>0.0 (0.823)</b>
Invertebrate	12	0.7 (0.734)	0.6 (0.732)	8.7 (0.559)	<b>0.0 (0.743)</b>
Ephemeral	13	0.8 (0.881)	2.0 (0.860)	<b>0.0 (0.895)</b>	1.2 (0.876)

Note that  $\Delta$ AIC values are valid only for comparisons within data sets (within the first two rows; otherwise only within each row). Best models (lowest AIC) for each data set are shown in bold. Sample sizes ( $N$ ) are the number of dives included in each analysis.

\*Multiple regression provided: subsequent (reactive) surface pause =  $2.19 \pm 0.10 + (0.0047 \pm 0.0013)\ln(\text{duration}) + (0.019 \pm 0.002)\ln(\text{depth})$ ; previous (anticipatory) surface pause =  $2.11 \pm 0.11 + (0.0059 \pm 0.0014)\ln(\text{duration}) + (0.018 \pm 0.002)\ln(\text{depth})$ .



**Figure 2.** Relation between (a) subsequent surface pause duration and dive duration, (b) subsequent surface pause duration and depth, (c) dive duration and dive depth, (d) bottom time and dive depth (e) bottom time and dive duration and (f) bottom time and total time in the dive cycle (dive duration + surface pause duration) in Brunnich's guillemots. Solid symbols denote ephemeral prey.

depths of roughly 30–90 m. The bimodal distribution for all dives pooled together results from a large number of very short dives. The shorter dives are presumably used for socialization, preening, searching or self-feeding on

shallow prey items. The symmetrical distribution of dive durations corresponds to that provided by Thompson & Fedak (2001) for deep-diving seals. Thus, for deep-diving animals (such as guillemots), where travel time is high

**Table 3.** Correlation coefficients,  $R^2$ , between dive duration and depth per delivery and per individual

	Individual		Delivery	
	<i>N</i>	$R^2$	<i>N</i>	$R^2$
Provisioning dives	98	0.807	3397	0.725
All dives	127	0.834	40 045	0.828
Benthic	26	0.773	998	0.815
Capelin	72	0.850	1831	0.743
Invertebrate	12	0.880	222	0.867
Ephemeral	15	0.864	257	0.750

relative to bottom time, it pays to maximize bottom time for each dive, whereas when travel time is low, it is relatively inexpensive to abort a dive when no prey items are encountered.

### Were Surface Pauses Reactive or Anticipatory?

Dive depth and duration are similar throughout the dive bout (Elliott et al., in press a), so guillemots can probably anticipate the target depth of foraging before each dive (e.g. can 'anticipate' oxygen requirements). Indeed, recent evidence has shown that surface pause duration may be anticipatory in seabirds (Jodice & Collopy 1999; Mori et al. 2002; Wilson 2003). In our case, there was only weak support for one model over the other, and a multivariate approach suggested that all dives have both an anticipatory and reactive component (Tables 1, 2). This is unsurprising because birds (1) adjust inhaled air volume (and thus preceding surface pause duration), presumably to optimize air stores and buoyancy for a given dive depth and duration (Sato et al. 2002; Wilson et al. 2003; Wilson & Quintana 2004) and (2) react to high lactate levels following dives exceeding ADL by increasing surface pause duration (Ponganis et al. 1997). Heart rate (and presumably oxygen intake) is high both before and after dives (Green et al. 2003). Perhaps shallow dive bouts (<150 s) are more likely to be anticipatory because regulating buoyancy through inspired air volumes is more important at shallow depths, whereas deep dive bouts are more likely to be reactive because they are close to or exceed the ADL, and, therefore, result in significant levels of lactate build-up while inhaled oxygen stores are already maximal. There was also a tendency for AIC values to select anticipatory relationships more frequently than  $R^2$  values, as AICs were calculated on ln-transformed data, which removed the emphasis on higher values. We found no evidence

for the hypothesis that anticipatory surface pauses should be found in benthic foragers or those handling the prey at the surface, whereas reactive surface pauses should be found in pelagic foragers or those consuming prey underwater (Lea et al. 1996; Jodice & Collopy 1999). We found the opposite trend; all dives pooled (including self-feeding, when prey was consumed underwater) tended to be anticipatory, whereas chick-provisioning bouts (where prey may have been manipulated at the surface to improve aerodynamics on the return flight) were reactive (all dives versus provisioning; Tables 1, 2). There was little variation in the role of preceding and succeeding surface pauses among prey items, and this did not reflect a pelagic–benthic dichotomy.

### Energy Gain

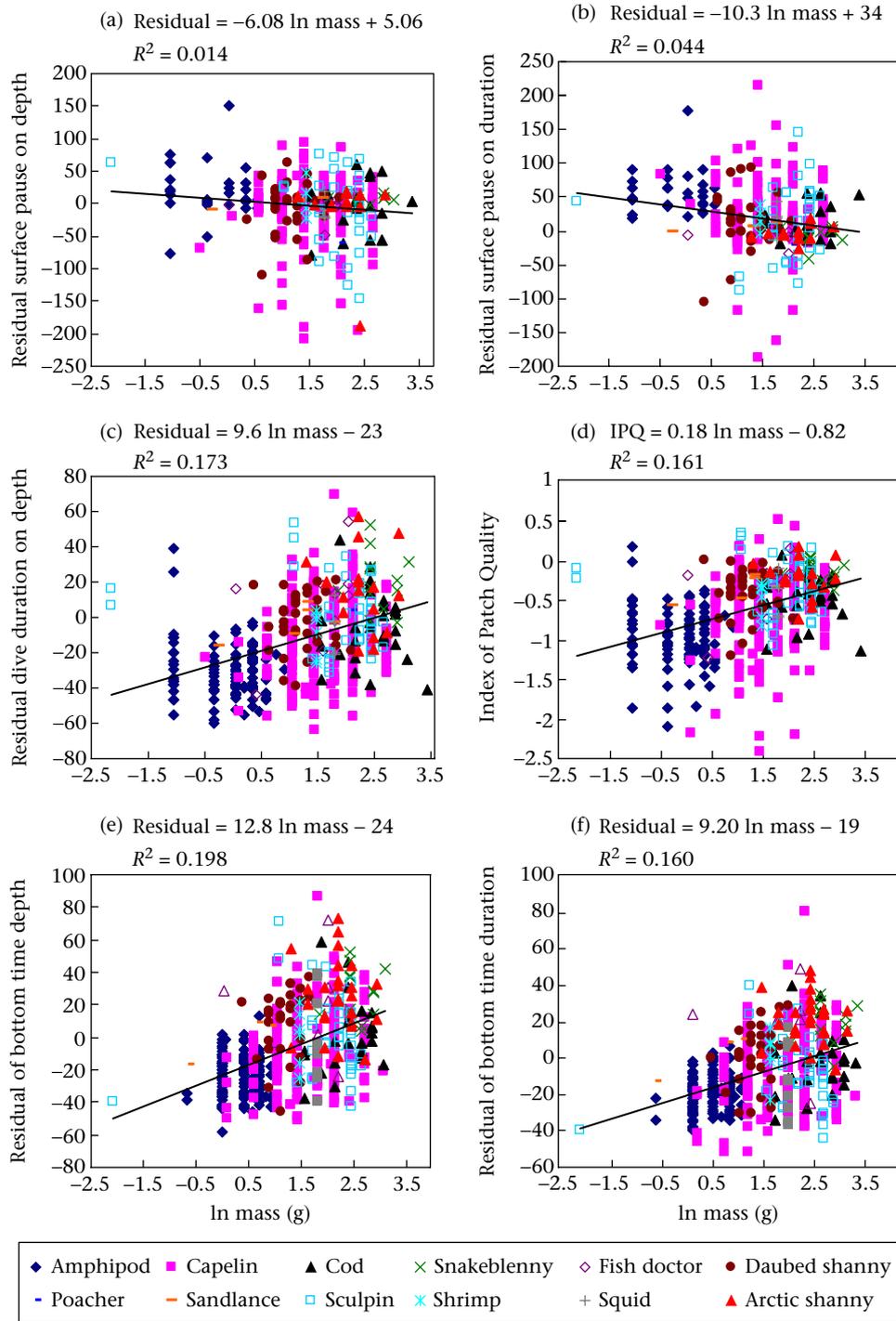
The relationship between surface pause duration, dive duration and dive depth varied among prey items (Fig. 2). As expected, IPQ increased with anticipated gain (prey mass; Fig. 3d), as did dive duration and bottom time for a given dive depth (Fig. 3c, e) and bottom time for a given dive duration (Fig. 3f). In general, our estimates of patch quality were higher than those of Mori et al. (2002); roughly 20% of our dive bouts had mean  $x > 1.0$  or IPQ  $> 0$ , whereas Mori et al. (2002) never recorded any bouts above these thresholds. This may reflect differences in prey abundance or guillemot dive behaviour between Svalbard and Hudson Bay. In our study, as at Svalbard (Mori et al. 2002), IPQ was higher for multidive bouts than for single-dive bouts. Because differences in sequential dive depths were lower when IPQ and the number of dives in the bout were high, we concluded that these dive bouts represented prey encounter events, and consequently, repeated dives to the same depth (Elliott et al. 2008). As expected, and implicit in the IPQ model, bottom time increased with dive duration (Fig. 3e), suggesting that longer dives increase time spent foraging. In contrast, bottom time did not increase with dive depth beyond shallow depths (Fig. 3d). Thus, it would only be profitable for birds to dive deep if prey density increased with depth.

Surface pause duration decreased with prey mass, although these relationships were very weak (Fig. 3a, b). The clearest relationship, and the one primarily responsible for the relationship between surface pause residual and prey mass, was that surface pauses tended to be longer, for a given dive duration, when birds were preying on amphipods (Fig. 2). These small invertebrates weigh only about 0.35 g and are presumably unable to migrate out of the area in the timescale of a guillemot dive bout. As the

**Table 4.** Comparison of dives and surface pauses of Brünnich's guillemots that resulted in the capture of stationary and ephemeral prey

Variable	Ephemeral	Stationary	<i>t</i> ( <i>df</i> )	<i>P</i>
IPQ (mass corrected)	−0.01±0.05	0.19±0.03	3.28 (59)	0.002
Dive duration (depth corrected)	−2.8±3.3 s	11.0±1.8 s	3.51 (60)	<0.001
Surface pause duration (duration corrected)	0.5±4.3 s	−9.6±3.8 s	1.48 (60)	0.14
Surface pause duration (depth corrected)	5.3±3.3 s	12.6±1.8 s	1.62 (60)	0.11

Values were 'corrected' by using residuals on relationships outlined for pooled data in Fig. 1, which includes both invertebrates and capelin (and explains why the residuals do not sum to zero).



**Figure 3.** Natural logarithm of prey mass and (a) surface pause duration for a given dive depth ( $t_{326} = -2.14$ ,  $P = 0.03$ ), (b) surface pause duration for a given dive duration ( $t_{326} = -3.87$ ,  $P < 0.0001$ ), (c) dive duration for a given dive depth ( $t_{499} = 10.2$ ,  $P < 0.0001$ ), (d) an index of patch quality (IPQ;  $t_{499} = 9.76$ ,  $P < 0.0001$ ), (e) bottom time for a given dive depth ( $t_{499} = 10.7$ ,  $P < 0.0001$ ) and (f) bottom time for a given dive duration ( $t_{499} = 9.52$ ,  $P < 0.0001$ ) in Brünnich's guillemots.

relationship appeared to be anticipatory (Table 1), we suggest that the birds were reducing effort (increasing surface pause duration) in anticipation of a low-value, non-ephemeral prey item, rather than reacting to high energy costs associated with searching and capturing these small items in the water column. Otherwise, we found no

support that surface pause duration differed between stationary and ephemeral fish. In contrast to our initial expectations, dive durations for stationary fish were longer and had a higher IPQ than those for ephemeral fish (Table 4). This result may reflect high dive costs when foraging for ephemeral prey items, as foraging for benthic prey

items appears to be a 'sit and wait' strategy (S. Benvenuti, personal communication). Dive duration and depth were strongly correlated for all prey items, including ephemeral prey items (Fig. 2c, Table 3); we found no support for the idea that this correlation was poorer for birds returning with pelagic prey items than for birds returning with benthic prey items (Jodice & Collopy 1999).

In agreement with our initial predictions, surface pause duration for a given dive depth and duration tended to decrease with prey mass. None the less, the relationship between residual surface pause duration and prey mass explained very little of the variation. Furthermore, dive bouts directed towards ephemeral fish did not have longer surface pause duration than dive bouts directed towards stationary fish. In contrast, IPQ, bottom time relative to dive depth, and duration and dive duration relative to dive depth all increased with prey mass and were higher for stationary than for ephemeral items. Thus, in response to energy intake, guillemots appeared to adjust components within a dive, instead of adjusting the relationship between surface pause and dive duration. In contrast, in response to changes in energy expenditure, guillemots adjusted the relationship between surface pause and dive duration, but did not adjust components within a dive (Elliott et al., 2008). As the relationship between surface pause, bottom time, dive depth and dive duration varies with prey quality and type, we suggest that these parameters may be useful indicators of prey abundance (Wanless et al. 1993; Monaghan et al. 1994; Mori et al. 2005).

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