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Do activity costs determine foraging tactics for an arctic seabird?

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Abstract How energy costs affect foraging decisions is poorly understood for marine animals. To provide data relevant to this topic, we examined the relationship between activity levels and foraging behavior by attaching activity recorders to 29 chick-rearing wing-propelled diving birds (thick-billed murres, *Uria lomvia*) in 1999–2000. We connected the activity during the final dive bout with the prey item we observed being fed to the chicks. After accounting for changes in activity level with depth, activity was highest during the final dive of a dive bout, reflecting maneuvring during prey capture. Pelagic prey items, especially invertebrates (amphipods), were associated with higher depth-corrected activity, leading to shorter dives for a given depth (presumably due to higher oxygen consumption rates) and, thus, shorter search times (lower bottom time for a given depth). Pelagic prey items were likely captured during active pursuit, with the birds actively seeking and pursuing schooling mid-water prey. In contrast, benthic prey involved low activity and extended search times, suggesting that the birds slowly glided along the bottom in search for prey hidden in the sediments or rocks. We concluded that activity levels are important in determining the foraging tactics of marine predators.

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Introduction

In the marine environment, predators encounter prey items that vary considerably in their predator-avoidance tactics (e.g., speed, density, movement in three dimensions). To facilitate prey capture, many marine predators specialize on a single-prey type, necessitating only a single-prey capture tactic (Watanuki et al. 1993; Davoren et al. 2003; Wilson et al. 2005). In contrast, generalist marine predators must modulate their prey-capture strategies depending on the energy gain available from a given prey type and the energy expenditure required to capture the prey type (Schluter 1995; Svanbäck and Eklöv 2003; Svanbäck and Bolnick 2005). For example, breath-hold divers may extend dive duration when ephemeral fish schools are encountered (Ydenberg and Clark 1989; Houston and Carbone 1992) or allocate time and activity differentially between transit and bottom time depending on whether prey items are pelagic or benthic (Wilson et al. 2002; Ropert-Coudert et al. 2006a, b; Elliott et al. 2008b, c). Although there is a growing body of literature showing that marine predators modulate their prey-capture tactic (dive depth, dive shape, foraging distance) for different prey types (Garthe et al. 2000; Estes et al. 2003; Tremblay et al. 2005), there is little information on the activity levels associated with different tactics although it is known that penguins are more active when feeding on krill than fish (Wilson et al. 2002).

Activity, as measured by stroke frequency or dynamic acceleration, is a useful proxy variable for underwater energy costs, where direct measurement is difficult, and activity recorders attached to wild animals can estimate energy expenditure during underwater activity (Williams et al. 2004; Wilson et al. 2006) and fine-scale activity budgets (Ropert-Coudert et al. 2004a, b, 2006a, b). Yet, because most seabirds and marine mammals make relatively long foraging trips and return with many prey items, it is difficult to link activity patterns and dive characteristics to specific prey items (Wanless et al. 1993; Simeone and Wilson 2003; Tremblay et al. 2005; Wilson et al. 2005). Thick-billed murres (*Uria lomvia*, hereafter “murres”) provide an opportunity for overcoming some of these difficulties because they return to the colony with a single prey item (“single prey loaders”, except when capturing invertebrates) and yet are sufficiently large that recording equipment can be deployed with limited impact on dive behavior (Croll et al. 1992; Jones et al. 2002; Mori et al. 2002; Paredes et al. 2006; Takahashi et al. 2008b). Murres in the Low Arctic are particularly well suited for these comparisons because individuals here have an especially diverse diet (Gaston and Bradstreet 1993).

To determine whether murre foraging tactics differ when searching for and capturing different prey types, with particular emphasis on underwater activity, we combined identification of prey deliveries at the colony with information on foraging behavior from activity recorders attached to adult birds during the chick-rearing season. We made the assumptions that the last dive represented the dive during which prey was captured for the chick and that the last dive bout represented foraging behavior typical for searching for that prey item. Support for these assumptions is provided by the observation that the final dive prior to prey delivery tends to be shorter, but no deeper, than other dives, suggesting that the final dive represents a premature abortion following a successful prey-capture event (Elliott et al. 2008a, c). Here, we examine how murre activity patterns vary among prey types. Specifically, we ask (1) Does activity during different dive phases vary among prey types? and (2) Is activity highest on the final dive during a dive bout, when prey capture presumably happens?

Methods

Our observations were made at the Coats Island west colony (62°57′N, 82°00′W), Nunavut, Canada (Gaston et al. 2003, 2005a, b) during the 1999 ($n = 24$) and 2000 ($n = 5$) breeding seasons. Adult murres were caught at their nest sites using a noose pole (Hipfner et al. 2003, 2006). We used activity recorders identical to those described by Falk et al. (2000, 2002) and Benvenuti et al. (1998, 2002): length, 80 mm; width, 23 mm (tip) to 30 mm (base); depth, 13–18.5 mm; mass, 28 g (3% of body mass and 4% of body cross-sectional area), containing a pressure sensor and two motion recorders (in case one failed). The motion recorders were made of a metal ball (modified microphone) within a case and the activity (three-dimensional movement of the ball as measured by vibrations within the microphone) was averaged over the 8-s interval and converted into bits between 0 and $2^8 - 1 = 255$. Because calibrations may have been slightly different between activity recorders, we included individual devices (which were reused up to five times) as a covariate in analyses. The pressure sensors sampled every 4 s and recorded to a maximum depth of 76 m. We assumed that activity (e.g., wingbeat frequency) and energy costs are correlated, so that the activity recorders provide an index of activity, wingbeat frequency and energy costs (Sato et al. 2003; Watanuki et al. 2003, 2006; Kato et al. 2006; Ropert-Coudert et al. 2006a, b). Although activity recorders measuring at a finer scale (32 Hz) are available, we used devices that recorded at 0.125 Hz because we were interested in larger sample sizes and in showing broad differences in activity among prey type rather than the detailed kinematics of single wingbeats, which has already been studied in detail (e.g., Lovvorn et al. 2004; Watanuki et al. 2003, 2006); even high-frequency devices are improved by smoothing over longer intervals when linking dynamic acceleration with behavior (Shepard et al. 2008). Back-mounted devices are known to affect murre provisioning rates, trip duration, mass loss and dive parameters (Croll et al. 1992, Watanuki et al. 2001, Tremblay et al. 2003, Hamel et al. 2004, Paredes et al. 2004; Elliott et al. 2007, 2008a, c). To minimize these effects, the devices were attached along the midline of the lower back by means of cable ties and tape around several dorsal feathers (Bannasch et al. 1994). Handling time was always less than 10 min and usually less than 5 min.

Continuous observations of breeding sites were carried out in conjunction with the deployment of the devices (Elliott et al. 2008d). All observations were made from blinds situated on the study plots, within 6 m of the birds. Three 48 h continuous feeding watches were conducted during 1999 (28–30 July, 7–9 August, 12–14 August) and one in 2000 (30–31 July). We did not conduct feeding watches when it was too dark to see deliveries (roughly 01:00–02:00 in late July, 23:00–0:400 in mid August) because nestlings are rarely fed at this time (Gaston et al. 2003). During these observation sessions, prey items delivered to the colony for chick provisionings were identified whenever possible. Arctic cod (*Boreogadus saida*), sand eels (*Ammodytes* sp.) and capelin (*Mallotus villosus*) were classified as pelagic prey items, while all other fish, including blennies, shannies and sculpin, were classified as benthic prey items (Elliott and Gaston 2008; Elliott et al. 2008b, c). We considered capelin to be pelagic because they were often captured after V-shaped dives and sand eels to be pelagic because they are generally captured after W- or u-shaped dives. U-shaped dives have a flat bottom with at least three identical consecutive measurements, while u-shaped dives have a rounded bottom (definite bottom phase) but without at least three identical consecutive measurements (see Fig. 4b in Elliott et al. 2008c; their legend should read "u-shaped" rather than "U-shaped"). However, sand eels and capelin are caught during benthic dives by some predators (Davoren et al. 2003, 2006; Watanuki et al. 2008), and although we are confident that most pelagic prey items were caught in the water column, some of our "pelagic" prey items may have been captured during benthic dives. Including a few benthic dives in our analyses should make our statistics more conservative as it would reduce our ability to detect a difference; any statistically-significant differences are therefore likely to be biologically relevant. Invertebrates (amphipods, shrimp) were also classified separately.

We used sequential differences analysis to define final dive bouts (Mori et al. 2001; bout defined when sequential dives differed by either 37 m or 63 s). To increase the likelihood that dives were directed towards a given prey item, we only included the final ten dives in dive bouts with more than ten dives (<5% of dive bouts had more than 10 dives). We excluded dives that were shallower than 3 m because of device resolution. Because activity was only recorded every 8 s, we only analyzed dives at least 24 s in length, excluding <5% of all final dives as too short (Elliott et al. 2008a, b). We partitioned each dive into three phases: descent, bottom time and ascent. We defined bottom time as from the first reading below 90% of maximum depth to the last reading below 90% of maximum depth (Elliott et al. 2008a, b). The definition of bottom time was appropriate because even most pelagic prey items (excluding invertebrates, which tended to show high activity during both descent and ascent) had a clear bottom phase, although for pelagic prey items this bottom was often ragged. We ignored the first and last activity reading during each phase to avoid the possibility that activity from another phase was included in the analyses (e.g., we excluded the first and last reading from each dive as it may include periods not included in the dive).

For murres, surface pauses are more closely related to dive depth than duration, presumably because dive depth better reflects energy expenditure for these deep-diving birds, and surface pauses for a given dive depth increase with increasing energy expenditure but are independent of prey type (Elliott et al. 2008a, b). For short, likely aerobic dives, birds used the surface interval to optimize oxygen stores and buoyancy for the subsequent dive while for long, likely anaerobic dives, birds used the surface interval to metabolize lactate from the previous dive (Elliott et al. 2007, 2008a, b). It is possible that predictions of surface intervals could be refined by the inclusion of activity measurements.

All statistical analyses were completed in R 2.4.1. To examine how activity (output from a custom-built program that converted binary data into digital readout in bits) changed with depth and maximum depth, we created a general linear model for each phase (descent, bottom and ascent) with depth, maximum depth and prey type as independent variables and individual and device as covariates. Only dives prior to the final dive (non-feeding dives) were included; a separate analysis included feeding dives as a covariate. To avoid pseudoreplication due to individual specialization (Elliott et al. 2008c; Woo et al. 2008), we randomly selected a single prey item for each individual–prey type combination and reran all analyses. As this did not change the significance of any results, we included all data in the analyses. To examine the role of activity in predicting surface intervals, we created a general linear model with ln (surface interval) as the dependent variable, depth, activity and dive duration as independent variables and individual and device as covariates. We used AIC values to create forward stepwise regressions. Models with ΔAIC >2.0 were considered to be unsupported.

Results

In 1999, median dive duration was 74 s and median dive depth was 18 m, with 20 out of 24 birds having at least one dive that exceeded 76 m (maximum depth recorded by device; Table 1). Out of 10,404 dives, 541 (5.2%) exceeded 76 m. In 2000, median dive duration was 104 s and median dive depth was 32 m, with 4 out of 5 birds having at least one dive that exceeded 76 m. Out of 1,742 dives, 188 (10.8%) exceeded 76 m.

Table 1 Summary data for deployments

	1999	2000
Number of TDRs deployed	24	5
Number with feeds	21	5
Feeds per bird	3.3 ± 0.6	2.8 ± 1.2
Number of dives per bird	434 ± 29	348 ± 68
Maximum dive duration	192 ± 8 s (max = 249 s)	193 ± 24 s
Average dive duration	93 ± 7 s	107 ± 19 s
Median dive duration	74 s	104 s
Maximum dive depth	72 ± 2 m	71 ± 6 m
Average dive depth	32 ± 3 m	38 ± 8 m
Median dive depth	18 m	32 m

Table 2 Average residual activity from best fit general linear models including depth, maximum depth, individual and device

	N	Descent	Bottom	Ascent
All taxa (no residual)	88	203 ± 44	106 ± 56	48 ± 62
Benthic fish	24	**−8 ± 1**	−15 ± 2	**−19 ± 4**
Pelagic fish	58	**−6 ± 1**	0 ± 2	**−12 ± 4**
Pelagic invertebrate	6	29 ± 11	99 ± 11	78 ± 15

Values are ± SE; AIC values are described n the text. Values that are not significantly different from one another within each column are shown in bold

After accounting for depth and maximum depth, average activity varied among prey types (Table 2; Fig. 1). During all phases, activity was greater when pursuing pelagic invertebrates (Table 2). During ascent and descent, there was no difference among fish prey types (Table 2), whereas in bottom phase activity was greater for pelagic than for benthic fish or capelin. After accounting for depth, average activity was higher during the bottom phase of final dives than for the remainder of the dives during the dive bout (final dive = 115, other dives = 98, $z_{28} = 2.21$, $P = 0.02$), as was the variance (final dive = 7,000 ± 450; other dives = 5,550 ± 355, $P = 0.01$). There was no difference ($P > 0.50$) in activity during the ascent and descent phases of final dives, compared to the remainder of dives during the dive bout. The relationship for surface pauses with dive depth was considerably stronger than with dive duration (ΔAIC = 64), and both were considerably stronger than with activity (ΔAIC = 1,093). When considered together, dive depth and duration factored into the loglinear model for surface pauses but activity, individual and device did not (ΔAIC > 6.0).

Discussion

Activity levels had a strong relationship with prey type. Pelagic prey items, especially invertebrates (amphipods), were associated with high depth-corrected activity, while benthic prey items were associated with low depth-corrected activity. Activity was high during descent as birds

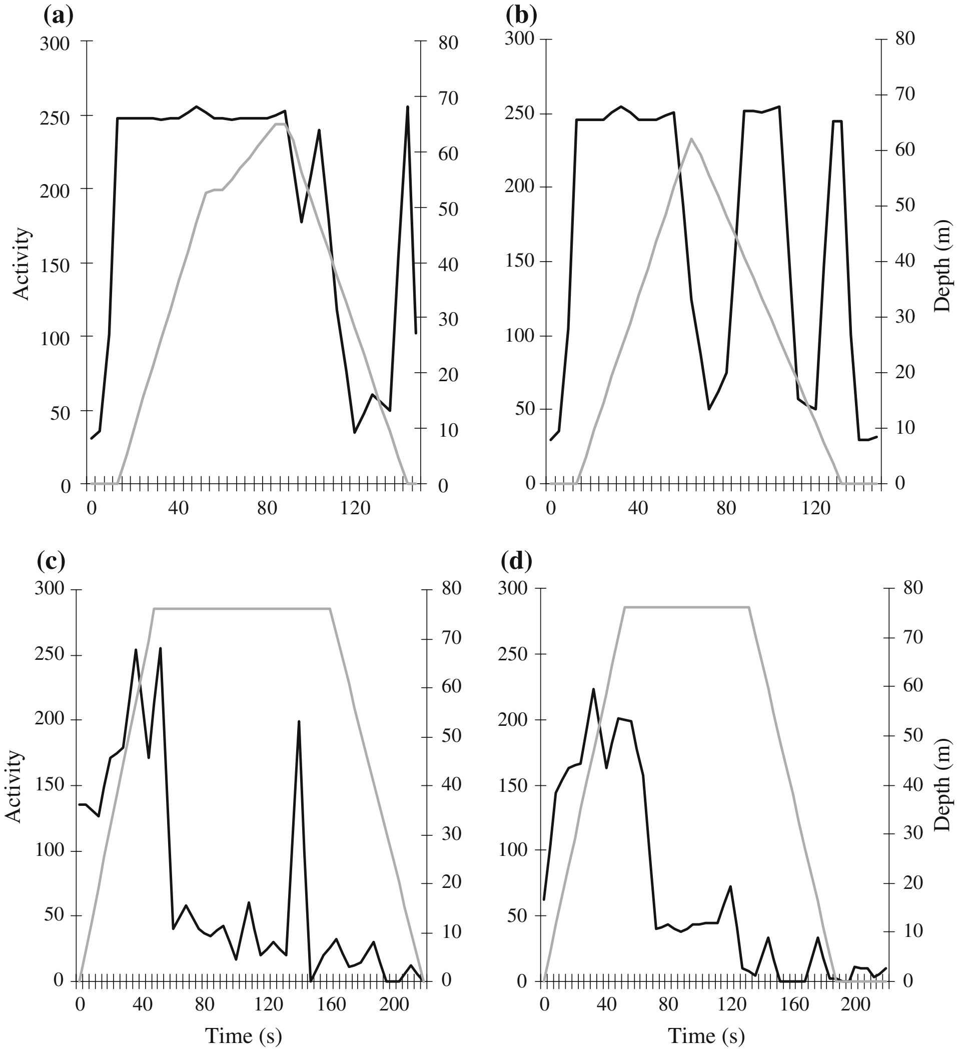

Fig. 1 Activity (*black*) and depth (*grey*) profiles for a typical dive prior to the delivery of pelagic (**a**, **b** amphipods) and benthic (**c**, **d** sculpin) prey. The pelagic graphs show high activity until the final portion of ascent, whereas the benthic graphs show high activity during descent, reduced activity during the bottom phase and low activity during ascent. Graph (**c**) was the final dive of a dive bout, and shows the characteristic increase in activity (presumed prey capture) just before ascent

overcame high surface buoyancy and low during passive ascent (Fig. 1, Lovvorn et al. 1999, 2004; Watanuki et al. 2003, 2006). Thus, as the bird descended it worked hard near the surface to overcome buoyancy, but wingbeat frequency decreased as air stores were compressed and the bird became closer to neutrally buoyant (Lovvorn et al. 1999, 2004; Watanuki et al. 2003, 2006). The exact point of neutral buoyancy is likely irrelevant as there is a zone of neutral buoyancy (sensu Cook et al. 2008) where murres are effectively close enough to neutrally buoyant that they neither need to expend great amounts of energy to overcome buoyancy, nor are able to use buoyancy to ascend in a timely manner (Lovvorn et al. 1999, 2004; Elliott et al. 2007).

For a given depth, pelagic prey items required greater activity during the bottom phase than benthic prey items (Fig. 1; Table 2). Presumably, pelagic prey items were likely captured during active pursuit, with the birds actively seeking and pursuing schooling mid-water prey (cf. Takahashi et al. 2008a). The high rate of turning, coupled with repeated accelerations and decelerations would all be measured as higher activity by the devices. For amphipods, multiple prey items are caught in a single dive—birds return with multiple amphipods after completing only a single dive away from the colony—and there may be multiple accelerations and decelerations associated with capturing multiple amphipods (Wilson et al. 2002). Bite marks on the underside of prey and videography of auks (e.g., rhinoceros auklets, common murres; Burger et al. 1993; Gaston 2004; Morelle 2009) suggest that auks feeding on pelagic prey herd them towards the surface or attack them when they are silhouetted against the surface, although herding may occur less often in thick-billed murres, which tend to forage in smaller groups (Gaston 2004). Herding, and avoiding being eaten incidentally by competitors at large fish schools, requires a high level of activity, but presumably results in a high rate of energy gain. The schooling nature of pelagic prey items combined with the high activity needed to capture them likely led to a faster rate of oxygen depletion. This may be why pelagic prey items involved shorter dive durations for a given dive depth and less bottom time during the dive (Elliott et al. 2008b). Cormorants feeding on mobile prey also show higher energy expenditure, longer pursuit durations and shorter dive durations than cormorants feeding on sedentary prey (Enstipp et al. 2006, 2007; Halsey et al. 2007).

Other studies have focused on the difference in energy density between pelagic and benthic prey items as a possible reason for the preference of pelagic over benthic prey (Litzow et al. 2004; Österblom et al. 2008). Although pelagic prey items have higher energy density than benthic prey at our study site, the difference (1.5-fold) is much smaller than differences in prey mass (>100-fold; Elliott and Gaston 2008) and, as with differences in flight time and time allocation with the dive (Elliott et al. 2008b, 2009), differences in prey mass (e.g., energy quantity) is likely more important in determining activity levels than energy quality. Rather than selecting prey based on energy intake, birds may select prey items based on energy output. For example, birds may select benthic over pelagic prey because they require less searching (i.e., occur at known geographic features, such as rocky outcrops) or are nearer to the colony (Baird 1991; Elliott et al. 2009).

In contrast to pelagic prey items, benthic prey involved low activity and extended search times. Slowly gliding along the bottom in a single direction to surprise prey hidden in the sediments or between rocks would result in low measures of activity. This is consistent with the notion that benthic prey items require greater underwater search time, and therefore more bottom time, than pelagic prey items (Elliott et al. 2008a, b). Swim speeds during the bottom phase were lower during benthic than pelagic dives for cormorants and penguins feeding on pelagic invertebrates used slower swim speeds than those feeding on schooling fish but remained at an optimum in terms of net energy gain (Wilson et al. 2002; Ropert-Coudert et al. 2006a). Shags feeding on benthic gunnels usually fed solitarily and swam rapidly over rocky bottoms, whereas shags feeding on sand eels usually fed in groups and sifted carefully through sandy bottoms (Watanuki et al. 2008). Similarly, murres feeding on deep water capelin, encountered at below-zero temperatures where the fish would be very slow-moving, were able to have extended dive times and depths, presumably because they required low levels of activity during capture (Hedd et al. 2009). Our results add to the growing body of literature showing that marine predators modulate their prey-capture strategy for different prey types (Garthe et al. 2000; Estes et al. 2003; Tremblay et al. 2005; Elliott et al. 2008b, c; Deagle et al. 2008; Paredes et al. 2008; but see Ropert-Coudert et al. 2002) and suggest that certain individuals specialize on active prey pursuit while others specialize on less active prey-capture tactics (Woo et al. 2008).

Higher and more variable activity during the final dive of a bout is consistent with our assumption that the final dive represents prey capture. Thus, as with most single-prey loaders, dive bouts are terminated once a prey item is captured (Nolet et al. 1993; Watanuki et al. 2008). Higher activity during prey-capture dives suggests that an index of prey-capture rate, or at least prey pursuit, may be obtainable during the self-feeding portion of the dive schedule by examining activity during the bottom phase of non-final dive bouts. A similar approach was successful in determining prey encounter rates for benthic-feeding penguins (Ropert-Coudert et al. 2006b) and shags (Sato et al. 2008). In larger penguins, “wiggles” in dive profiles represent prey captures

(Simeone and Wilson 2003; Bost et al. 2007; Wilson et al. 2005). Although this method does not seem to work in murres, which show few wiggles during diving, activity profiles may provide a useful alternative. Additional work confirming this method using beak opening sensors would be critical (Simeone and Wilson 2003; Wilson et al. 2005). Activity was a worse predictor of surface pause interval than either depth or duration. This is presumably because our devices only crudely estimated activity costs, or because other factors (e.g., thermoregulatory costs) might obscure the relationship between activity level and energy expenditure during diving (Niizuma et al. 2007).

In conclusion, activity levels were directly related to foraging decisions, with high activity associated with midwater, pelagic prey pursuit and low activity associated with benthic prey pursuit. Thus, activity was an important part of the foraging tactics of marine predators.

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