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Underwater and above-water search patterns of an Arctic seabird: reduced searching at small spatiotemporal scales

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Abstract How predators vary search patterns in response to prey predictability is poorly known. For example, marine invertebrates may be predictable but of low energy value, while fish may be of higher energy value but unpredictable at large (pelagic schools) or small (solitary benthics) spatial scales. We investigated the search patterns of the thick-billed murre (*Uria lomvia*), an Arctic seabird feeding on invertebrates, pelagic fish, or benthic fish. Foraging ranges at the Coats Island colony are generally smaller (<240 min per trip) than at larger colonies, and many birds specialize in foraging tactics and diet. Underwater search times for benthic fish were higher than for pelagic fish or invertebrates while above-water search times for pelagic fish were higher than for benthic fish or invertebrates. There were few stops during trips. Total trip time, flying time, number of flights, and number of dives were intercorrelated and increased with prey energy content, suggesting that longer trips involved fewer prey encounters due to selection of higher-quality, but rarer, prey items. Flight times were not Lévy-distributed and seabirds may have used area-restricted searches. The high degree of specialization, apparent absence of information center effects, and reduced above-water searching times may be linked to the relatively small colony size and the resulting short commuting distances to feeding areas, leading to greater prey predictability. We concluded that prey predictability over various scales affected predator search patterns.

Keywords Predator–prey interactions · Ecological scale · Lévy search pattern · Information Center Hypothesis · Thick-billed murre · *Uria lomvia*

Introduction

Predators are continually presented with choices for how to move (or not move) to maximize prey capture rates (Ropert-Coudert et al. 2004; Ohashi et al. 2007; Garthe et al. 2007; Catania et al. 2008). These choices form the "search pattern" of the predator. Search patterns are particularly important in marine ecosystems, where predators must search in three dimensions (Sjoberg and Ball 2000; Simpkins et al. 2001; Davoren et al. 2003a, b) and where prey items (e.g., fish) are patchily distributed, meaning that search patterns represent decisions on whether to search a given patch or move on to another patch (Mori et al. 2002, Grémillet et al. 2004; Weimerskirch et al. 2005a, b). During the breeding season, search patterns may be under particularly strong selection, as adult marine mammals and birds minimize time away from offspring while maximizing energy delivered to offspring (Wilson et al. 2005; Garthe et al. 2007; Jaquemet et al. 2007).

Search patterns will be partially dependent on the spatial and temporal predictability of prey aggregations. Marine

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animals searching over small spatial and temporal scales, where prey aggregations are likely to persist between foraging bouts, may use memory to return to the same patches that were successful on previous foraging bouts (Davoren et al. 2003a, b; Weimerskirch 2007; Woo et al. 2008). Marine animals searching over larger spatial and temporal scales, where prey aggregations are unlikely to persist between foraging bouts, are less likely to return to the same patches and require other sources of information to locate prey items (Fauchald et al. 2000; Weimerskirch et al. 2005a, b; Weimerskirch 2007; Mallory et al. 2008). For example, unsuccessful or naïve foragers may obtain information about food sources by following successful foragers (Information Center Hypothesis or ICH, *sensu* Ward and Zahavi 1973; Birkhead 1985; Buckley 1997a, b), providing an explanation for why colonial breeding increases foraging efficiency only when food occurs in a few dense but ephemeral patches (Barta and Szép 1992). Information transfer may occur away from the colony because animals often gather some distance from a colony before departing on foraging flights ("information halo" *sensu* Burger 1997) because outgoing birds can cue to the directions of incoming birds (Gaston and Nettleship 1981) or because outgoing birds cue in on the location of actively foraging animals far away from the colony ("local enhancement"). To illustrate, murres usually descend to the water within a 1-km area of the colony ("splashdown area") after a brooding shift and time spent in this area may be an opportunity for information transfer ("information halo"; Burger 1997).

Because animals are able to locate prey or feeding aggregations that occur within visual range, predators are expected to move directly to patches that are within this fixed radius ("local enhancement") but randomly if there are no visible patches within that radius. Search patterns obeying this concept could result in a Lévy search pattern, characterized by flight distances that follow an inverse-square power law (Reynolds 2005; Bénichou et al. 2006). Animals as diverse as albatrosses (Viswanathan et al. 1996), bumblebees (Viswanathan et al. 1999), monkeys (Ramos-Fernández et al. 2004), whales (Austin et al. 2004), plankton (Bartumeus et al. 2003), fishing fleets (Bertrand et al. 2005, 2007), and deer (Viswanathan et al. 1999, Mårell et al. 2002) have been reported to obey Lévy search patterns. However, reanalysis of the data from three studies showed that flight times actually followed an exponential distribution, implying that food patches were encountered randomly (Edwards et al. 2007).

Excluding animals feeding on sessile prey (Halsey et al. 2003; Heath et al. 2006, 2007), predators on pelagic and benthic prey have very different search patterns (Womble and Sigler 2006; Gende and Sigler 2006; Elliott et al. 2008c). Pelagic prey items congregate in enormous con-

centrations, but these concentrations may be extremely dispersed and their location may vary over large spatial and temporal scales (Gende and Sigler 2006; Womble and Sigler 2006; Cotté et al. 2007). Thus, for pelagic foragers, locating patches may be difficult, but once a patch is located capturing prey items is easy (Irons 1998; Weimerskirch et al. 2005a, b; Weimerskirch 2007). Benthic prey items often occur in much smaller concentrations, but they persist at the same location owing to habitat requirements (e.g., reefs, sandy bottoms, kelp forests) over large spatial and temporal scales (Davoren et al. 2003a, b; Womble and Sigler 2006; Gende and Sigler 2006). Thus, for benthic foragers, locating patches may be easy, but once a patch is located finding an accessible prey item may be difficult. Spawning pelagic fish, which may be both highly abundant and highly predictable, creating "hot spots" (Davoren et al. 2003a, b, 2006; Womble and Sigler 2006; Gende and Sigler 2006), are an exception to this generalization.

The search patterns of marine predators tend to be characterized by long travel times interspersed by area-restricted searches over small spatial scales (Weimerskirch et al. 2005a, b; Pinaud and Weimerskirch 2007; Cotté et al. 2007), potentially resulting in Lévy search patterns (Plank and James 2008). Foraging site fidelity is greater for those seabirds feeding at relatively small spatial and temporal scales because prey is more predictable at smaller scales (Weimerskirch 2007). For example, Grémillet et al. (2004, 2005) showed that prey encounter rates are exceptionally high for a seabird foraging on benthic prey over small spatial scales, suggesting little need for searching. Many high-latitude seabirds show a high degree of foraging site fidelity (Irons 1998; Hamer et al. 2001; Garthe et al. 2007).

Here, we investigate the search patterns of an arctic seabird, the thick-billed murre (*Uria lomvia*), at a colony where it feeds on both pelagic and benthic prey items (Gaston and Bradstreet 1993; Gaston et al. 2003; Hipfner et al. 2006). Most individuals forage relatively close to the colony relative to other colonies (<40 km; Elliott et al. 2008c). Consistent with the idea that birds foraging over small spatial scales have greater specialization, murres at this site show a high degree of fidelity to foraging strategies (dive depth, flight time, dive shape), locations, and prey types regardless of whether the prey items are consumed by adults or chicks (Woo et al. 2008). At large colonies (foraging ranges >100 km), murres stop periodically on the outbound trip to sample the environment (Benvenuti et al. 1998; Falk et al. 2000, 2002). In contrast, due to the smaller spatial scale of our study colony, we predicted that there would be few stops on outbound trips. As previous investigators had shown an inverse power law frequency distribution for total trip times (Davoren and Montevecchi 2003; Davoren et al. 2003a, b), we predicted that flight

times would follow a power law distribution. We also predicted that birds returning with pelagic prey items would have more flight bouts and less bottom time than birds returning with benthic prey items, reflecting more above-water search time and less underwater search time. Finally, we examine the importance of an ICH-type mechanism for information exchange at this colony by describing behavior in splashdown areas relative to at-sea searching behavior as well as the synchrony of departures and arrivals of adults at the colony, the latter suggesting the type of following behavior predicted by the ICH (Ward and Zahavi 1973; Birkhead 1985; Götmark 1990). Another approach is to assess whether incoming directions were significantly clumped over time (see Davoren et al. 2003a,b), but this was not possible as virtually all birds feed to the west of the colony (Elliott et al. 2008c).

Materials and methods

Our observations were made at the Coats Island thick-billed murre (*U. lomvia*) colony (30,000 breeding pairs; 62° 57′ N, 82° 00′ W), Nunavut, Canada (Gaston et al. 2003, 2005; Hipfner et al. 1997; Gaston and Hipfner 2006a, b) during the breeding seasons 2000–2007. At least three continuous (24 or 48 h) observational sessions of breeding sites were carried out from a blind situated on the Q study plot, within 5 m of the birds (Hipfner et al. 2006). We did not conduct feeding watches when it was too dark to see deliveries (roughly 0100–0200 hours in late July; 2300–0400 in mid-August) because chicks are rarely fed at this time (Gaston and Bradstreet 1993; Gaston et al. 2003). During these observation sessions, prey items delivered to chicks were identified whenever possible.

Time–depth–temperature recorders

In conjunction with these observations, murres were caught with a noose pole (2004: *n*=23; 2005: *n*=33; 2006: *n*=80; 2007: *n*=37; total foraging trips=729). Handling time was always less than 10 min and usually less than 5 min. We secured LOTEK 1100LTD time–depth–temperature recorders (TDRs; Lotek Marine Technology, St. John's, Newfoundland, Canada) with duct tape to plastic bands that were attached to the legs of murres (murres do not use their legs for underwater propulsion). The TDRs were cylindrical (mass=4.5 g; diameter=1 cm; length=3.3 cm; sampling interval=3 s; absolute error±2 m) and attached parallel to the leg with the rounded end facing toward the body and the pressure sensor facing toward the foot. We corrected for drift using a custom-built Excel macro and dives shallower than 3 m were ignored (Elliott and Gaston 2009). Whereas back-mounted TDRs are known to impact murre provisioning

rates, trip duration, mass loss, and dive behavior (Tremblay et al. 2005; Hamel et al. 2004; Paredes et al. 2004; Elliott et al. 2007, 2008b), our smaller leg-mounted devices had no measurable effect on any of these parameters (Elliott et al. 2007, 2008b, c). We used the temperature log from the TDR to determine whether the bird was on the water, in the air, or at the colony (Tremblay et al. 2005; Elliott et al. 2007, 2008c). Because we also knew when the bird arrived at the colony from the continuous watches, we were able to calibrate the temperature log in many cases. A summary date file of TDR trips appears as ESM Fig. S1.

Prey type

During feeding watches, prey items delivered to chicks were visually identified whenever possible. Size was estimated in relation to the length of the white streak on the bill (approximately 5 cm, Gaston et al. 2003; Hipfner et al. 2006). Prey energy content was calculated from species-specific energy densities and mass–length regressions developed at Coats Island (Elliott and Gaston 2008). By assuming that the last dive or dive bout prior to a prey delivery represented the foraging behavior associated with that prey item, we were able to determine dive depth, dive shape, and flight time associated with each prey item. Support for the assumption that prey items were captured on the final dive 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, b, c). We categorized prey items into pelagic (Arctic cod *Boreogadus saida* and sand lance *Ammodytes* sp.), benthic (sculpin, shannies, blennies, and poachers), or invertebrate (shrimp, squid, and amphipods) groupings. Sand lance were considered to be pelagic because they were generally captured after u-shaped dives (Fig. 2b in Elliott et al. 2008c—mislabeled as "U-shaped" in the legend), and because they were almost always zero- or one-age class, which are usually captured in pelagic schools (Robards et al. 1999; Elliott et al. 2008c; Elliott and Gaston 2008). Fish captured during u-shaped dives would also be considered pelagic based on classification schemes using wiggles (Halsey et al. 2007). We separated invertebrates from fish because invertebrates are superabundant, requiring little above-water or underwater searching compared with fish (Elliott et al. 2008c; Elliott and Gaston 2008). Capelin (*Mallotus villosus*) was not categorized because they can occur as either benthic or pelagic schools (Davoren et al. 2003a, b; Hedd et al. 2009). Furthermore, both capelin and invertebrates were usually captured after V-shaped dives, meaning that searching presumably also occurs during transit to and from the surface and that our values for bottom time likely

underestimate total underwater search time; auks sometimes capture pelagic prey from below (Burger et al. 1993).

Synchrony of arrivals and departures and splashdown behavior

To test the ICH, we examined arrival, departure, and splashdown behavior. We put more emphasis on arrival synchrony than departure synchrony because most birds depart on foraging trips from the splashdown area rather than the colony and, thus, synchrony of departures from the colony may not reflect synchrony of departures for feeding (Gaston and Nettleship 1981; Burger 1997). To test for synchrony of arrivals and departures, we used the 4-h period between 0600 and 1000 hours because no autocorrelation occurred during this interval. Time intervals between successive arrivals and successive departures were calculated for plot Q during 1997–2007. The frequencies of occurrence of time intervals were plotted against the interval lengths to give the simulated distributions of time intervals between successive arrivals and time intervals between successive departures. To determine if these distributions showed some clumping of arrivals or departures, a computer model simulating random arrivals and departures was created using Visual Basic. This model generated random numbers between zero and 240 representing bird arrival or departure times in a 4-h period (240 min in 4 h). The model generated a specific number of random numbers set as the mean number of events (either arrivals or departures) observed to occur within a 4-h period. These numbers were ordered ascendantly and the intervals between successive simulated arrivals or departures were calculated. This procedure was repeated 200 times to generate the expected distribution of intervals between arrivals or departures, assuming independent behavior. We also calculated the dispersion (ratio of standard deviation to the mean) for feeding intervals for individual murres (Hipfner et al. 2006).

To test whether birds were lingering in the splashdown area to obtain information on likely feeding areas, we compared the duration of the splashdown period with the subsequent outbound flight duration, number of flights, and duration of between-dive flights, assuming that uncertainty in prey location increases with these parameters and that they are therefore indices for above-water searching. For example, birds accessing predictable food sources (e.g., invertebrates) would not need information transfer during the splashdown period and, thus, would remain in this area for much shorter durations than those accessing unpredictable sources (e.g., pelagic fish). We also compared time in the splashdown area between birds whose breeding sites were located below other birds (and which therefore become dirtier and presumably require longer periods of cleaning) and those breeding on sites where they generally remained unsoiled.

Searching metrics

In contrast with other studies showing that genders eat different prey (Jones et al. 2002, Lewis et al. 2002, Paredes et al. 2006), chick prey items are usually larger than adult prey items (Hobson 1993; Davoren and Burger 1999; Wilson et al. 2004) leading to bimodal foraging distributions (Ropert-Coudert et al. 2004; Steen et al. 2007), murres at Coats Island show few gender differences, no difference between adult and chick prey items and have highly specialized foraging behavior across trips (Woo et al. 2008), meaning that we did not need to distinguish between searching for self-feeding and searching for chick provisioning. Nonetheless, self-feeding dives are shorter than chick-provisioning dives (Elliott et al. 2008b). Foraging behavior of thick-billed murres is stereotyped for a given prey item and occurs along three major axes (Elliott et al. 2008c), representing prey depth (measured as dive depth), benthic or pelagic foraging (dive shape), and distance from the colony (flight time). As all other foraging variables are closely correlated with one of these parameters, variability in foraging behavior can be monitored by including only these three measures. Metrics for underwater searching were bottom time per dive and number of dives per bout (Table 1). Bottom time per dive was defined as time spent within 90% of maximum depth. Unlike murres that catch invertebrates and capelin, those taking Arctic cod and sand lance usually have u- or U-shaped dives, with a clear bottom phase, so it is unlikely that searching occurs during transit (Elliott et al. 2008c). Metrics for above-water searching were outbound flight time, number of flights per trip, total trip time, total flying time,

Table 1 Underwater search parameters (±SE) for different thick-billed murre prey types at Coats Island 2004–2007 ($N=729$)

Prey type (N)	Bottom time per dive (s)	Number of dives per final dive bout[a]
Pelagic (71)	53.1 ± 4.6[b]	6.6 ± 0.8
Benthic (160)	67.2 ± 2.4	8.9 ± 0.8
Invertebrate (116)	49.8 ± 1.2	3.0 ± 0.4
Capelin (229)[c]	51.0 ± 0.9	10.0 ± 1.0
Average	53.2 ± 3.4	7.5 ± 0.4
$F_{2, 364}$	101.7[d]	16.7
P	<0.0001	<0.0001

"All types" includes trips where deliveries were unidentified

[a] Capelin occurs as planktonic larvae, pelagic schools, and benthic spawners and are therefore excluded from statistical analyses

[b] Statistics represent analyses of variance (ANOVAs) on each value, after correcting for prey energy content, among the three prey types

[c] Number of dives in the final dive bout prior to prey delivery

[d] Groupings that are homogenous (do not differ from one another at the Bonferroni-corrected α value) for post hoc t tests with Bonferroni corrections are shown in italics

the percentage of trips with flights between dive bouts, the duration of flights between dive bouts, and the difference between outbound and inbound flight times (Table 2). For both searching metrics, we used the residual of the metric on energy content for all statistical analyses to control for the effect of prey energy value.

To examine whether murres followed a Lévy search pattern, we examined the shape of the log-frequency and log-flight time relationship (Reynolds 2005; Bénichou et al. 2006). Specifically, we used the maximum likelihood method presented by Edwards et al. (2007) to compare the statistical support (ΔAIC value) for a linear versus shifted gamma distribution with exponential tail. Considering the tail to start at a (e.g., for $x \geq a$), the power law $f(x)$ and exponential $g(x)$ tails have probability density functions:

$$f(x) = (\mu - 1)a^{\mu-1}x^{-\mu}$$

$$g(x) = \lambda e^{-\lambda(x-a)}$$

Maximum likelihood estimators for λ and μ can be solved using Eqs. 5 and 6 from Edwards et al. (2007). We used the methodology presented therein on both all data pooled and only the data within a single individual, for all individuals with at least 30 recorded flights.

Results

Splashdown behavior and arrival/departure synchrony

Most brooding shifts were followed by a period on the water with no diving activity (Fig. 1). The majority (97%) of shifts longer than 120 min were followed by splashdown periods, while no shift shorter than 30 min was followed by splashdown. Thus, splashdown duration increased with shift duration ($t_{146}=4.93$, $p<0.0001$, $r^2=0.17$, ESM Fig. S2), but not for shifts longer than 120 min ($t_{98}=0.90$, $p=0.37$, $r^2=0.01$); birds did not use the splashdown after foraging trips without at-colony shifts. Time spent in the splashdown area was generally short (8.0 ± 0.4 min) and duration was not related to above-water search behavior, such as number of flight bouts ($t_{146}=0.85$, $p=0.40$, $r^2=0.00$), duration of between-dive flight bouts ($t_{146}=0.39$, $p=0.83$, $r^2=0.00$), and outbound flight duration ($t_{146}=0.79$, $p=0.43$, $r^2=0.00$). Birds on ledges with no birds above them had significantly shorter splashdown durations (6.5 ± 2.9 min) than birds on ledges with birds above them (8.9 ± 2.8 min, $t_{135}=-3.05$, $p=0.001$). We also found that 25% of birds returned to the colony for 3–98 min (24 ± 19 min) following splashdown. Birds that spent less time in the splashdown were not more likely to return to the colony ($t_{22}=0.72$, $p=0.51$).

Arrival ($\chi^2=17,042$, $df=49$, $p<0.00001$) and departure times ($\chi^2=9,302$, $df=49$, $p<0.00001$) were significantly different from the associated Poisson distribution, with many more close arrival and departure times than anticipated from the Poisson distribution. Nonetheless, arrivals ($\chi^2=54.4$, $df=49$, $p=0.28$, ESM Fig. S3a) and departures ($\chi^2=60.1$, $df=49$, $p=0.13$, ESM Fig. S3b) were not significantly different from the randomly generated function. Arrivals ($\chi^2=56.8$, $df=49$, $p=0.24$) and departures ($\chi^2=63.2$, $df=49$, $p=0.10$, ESM Fig. S3b) were also not significantly different from the exponential distribution. This was also true for arrivals with benthic ($\chi^2=10.1$, $df=6$, $p=0.12$) and pelagic prey items ($\chi^2=14.0$, $df=6$, $p=0.03$) at

Table 2 Mean above-water search parameters ($\pm$SE) in minutes for different thick-billed murre prey types at Coats Island 2004–2007 ($N=729$). Capelin occur as planktonic larvae, pelagic school, and benthic spawners and are therefore excluded from statistical analyses

Prey type	Inbound flight	Outbound flight	Inbound− outbound	Number of stops per trip[a]	% trips with flights between dives	Flight duration between dives	Total flight time
Pelagic	26.0±1.9	*17.5±1.2*[b]	*8.5±2.1*	2.8±0.3	*59.2%*	*7.8±5.6*	57.0±4.0
Benthic	21.6±0.8	*15.2±0.7*	*6.6±0.9*	2.1±0.1	*55.6%*	*7.6±5.9*	45.2±13.1
Invertebrate	5.7±0.5	5.1±0.4	0.6±0.4	1.1±0.1	12.1%	*5.7±3.0*	11.3±0.9
Capelin	20.0±0.5	14.2±1.0	6.1±0.9	2.1±0.1	47.0%	11.2±0.5	43.1±1.9
All types	17.2±12.7	12.6±0.3	4.5±0.4	1.9±0.1	42.4%	7.9±6.7	36.9±1.0
$F_{2,335}$	118.3[c]	79.6	15.2	29.1		1.81[d]	139.2
P	< 0.0001	< 0.0001	< 0.0001	< 0.0001		0.16	< 0.0001

"All types" includes trips where deliveries were unidentified

[a] One stop implies a single outbound and inbound flight; two stops imply one flight apart from the inbound and outbound flights; etc.

[b] Groupings that are homogenous (do not differ from one another at the Bonferroni-corrected α value) for post hoc t tests with Bonferroni corrections are shown in italics

[c] Statistics represent ANOVAs on each value, after correcting for prey energy content, among the three prey types
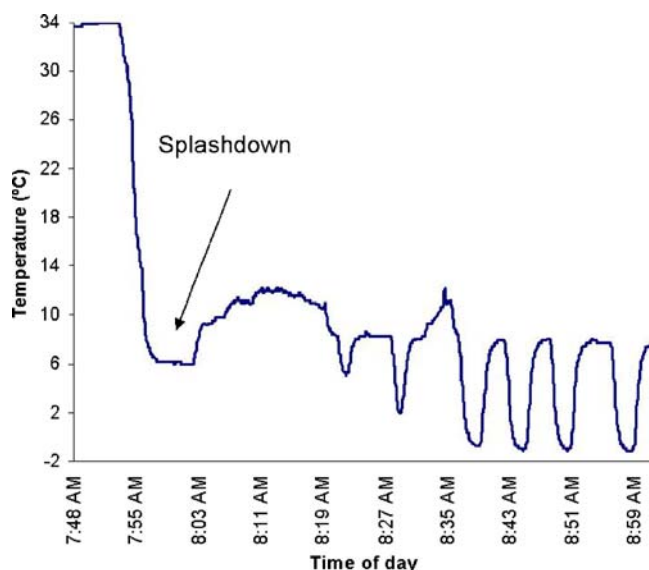
[d] Degrees of freedom=2, 288

Fig. 1 Typical at-sea behavior following a brooding shift, showing the splashdown followed by an outbound flight

the Bonferroni-corrected α value of 0.01. Across all feeding watches 1999–2007, the average dispersion in feeding intervals $= \sigma{:}\mu = 0.63 \pm 0.02$.

Underwater searching

Bottom time per dive and the number of dives in the final dive bout increased with prey energy content (Fig. 2). After accounting for prey energy content, bottom time per dive was higher for benthic than for pelagic ($t_{34} = -3.67$, $p = 0.0004$) and invertebrate prey items ($t_{174} = -6.51$, $p < 0.0001$, Table 1). The number of dives during the final bout was also higher for benthic than for pelagic ($t_{22} = 2.17$, $p = 0.02$) and invertebrate ($t_{285} = 9.25$, $p < 0.0001$, Table 1) prey items. In total, birds spent 88% more bottom time per dive bout when searching for benthic prey items than when searching for pelagic prey items and four times more bottom time per dive bout searching for benthic prey items than when searching for invertebrate prey items.

Above-water searching

Over all foraging trips, the outbound trip was ~13 min, followed by a 17-min inbound trip, with 42% of trips having at least one flight between dive bouts (average of one between-dive flights per trip), which averaged about 8 min (Table 2). Overall, the total duration of flight per trip was 37 min (Table 2). Once invertebrates were excluded, typical foraging trips consisted of a 15-min outbound trip, followed by a 20-min inbound trip, with 55% of trips having at least one flight between dive bouts for a total flight time per trip of 44 min. Virtually all (>99%) stops were followed by diving, showing that underwater search-

ing usually followed above-water searching. Total flight time, inbound and outbound flight time, number of stops per trip, number of dives in the final dive bout, and total trip time were all highly correlated (Fig. 3; Table 3). The weakest relationships were between outbound flight time and other parameters (Table 3). All parameters except outbound flight time also increased with prey energy content, but the best correlation was with inbound flight time (Fig. 2).

After accounting for prey energy content, the following measures varied among prey types: inbound flight time, outbound flight time, the difference between inbound and outbound flight time, the number of flights per trip, the percent of trips with flights between dives, and total flight time (Table 2). The duration of flight bout between dive bouts did not vary among prey types. In all cases where above-water searching parameters varied among prey type, search times were greater for pelagic and benthic fish than for invertebrates. Furthermore, after accounting for prey energy content, total flight time was higher for pelagic than benthic ($t_{34} = 3.11$, $p = 0.007$) and invertebrate prey items ($t_{44} = -13.06$, $p < 0.0001$, Table 2). The number of stops per trip was also higher for pelagic than benthic ($t_{34} = 2.61$, $p = 0.01$) and invertebrate prey items ($t_{44} = 6.71$, $p < 0.0001$, Table 2). Similarly, inbound flight time was greater for pelagic than benthic ($t_{34} = 2.77$, $p = 0.009$) and invertebrate prey items ($t_{44} = 137.57$, $p < 0.0001$, Table 2).

There was no difference in the number of flights (within-individual paired $t_{52} = 1.48$, $p = 0.15$), total trip duration ($t_{52} = 0.80$, $p = 0.43$), inbound flight duration ($t_{52} = 1.05$, $p = 0.30$), or total flight duration ($t_{52} = 1.89$, $p = 0.07$) between trips that were taken after short stays at the colony (<10 min) and those taken following extended periods at the colony (>2 h). Flight durations ($\mu = 2.66$, $\lambda = 0.090$, $\Delta AIC = 12.0$, $N = 2{,}083$) followed a shifted gamma distribution with exponential tail and there was no support for a Lévy search pattern (Fig. 4). ΔAIC values were higher for an exponential tail rather than power law tail for all individual murres considered separately. An exponential distribution implies random distribution of flight durations with constant low probability for long enough flight durations.

Discussion

Search patterns varied among birds collecting different prey types, with birds increasing both above-water and under-water search effort for more energetically profitable items (Fig. 2). Longer foraging trips involved more underwater and above-water search time (Fig. 3). Presumably, trips were extended to increase the opportunity for encountering more energetically profitable, but less predictable, prey
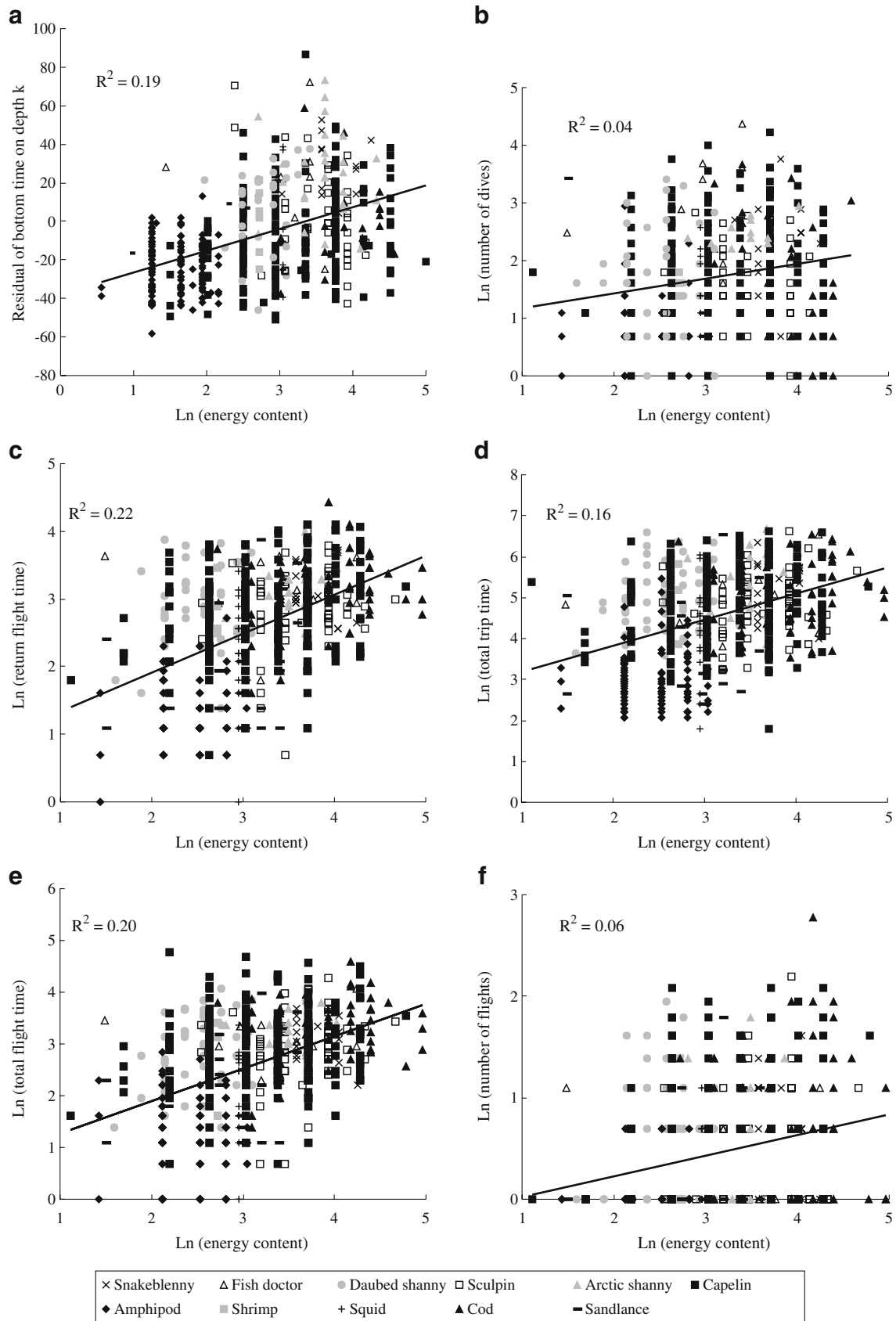
Fig. 2 **a** Bottom time for a given dive depth, **b** number of dives, **c** return flight time, **d** total trip duration, **e** total flying time, and **f** number of flights increased with prey energy content for thick-billed murres (*n*=579 deliveries) at Coats Island (2004–2007)

Fig. 3 Relationship between total trip time (min) and **a** inbound flight time (min), outbound flight time (min), total flying time (min), **b** number of dives, and number of flights for thick-billed murres ($N=729$ trips) at Coats Island 2004–2007
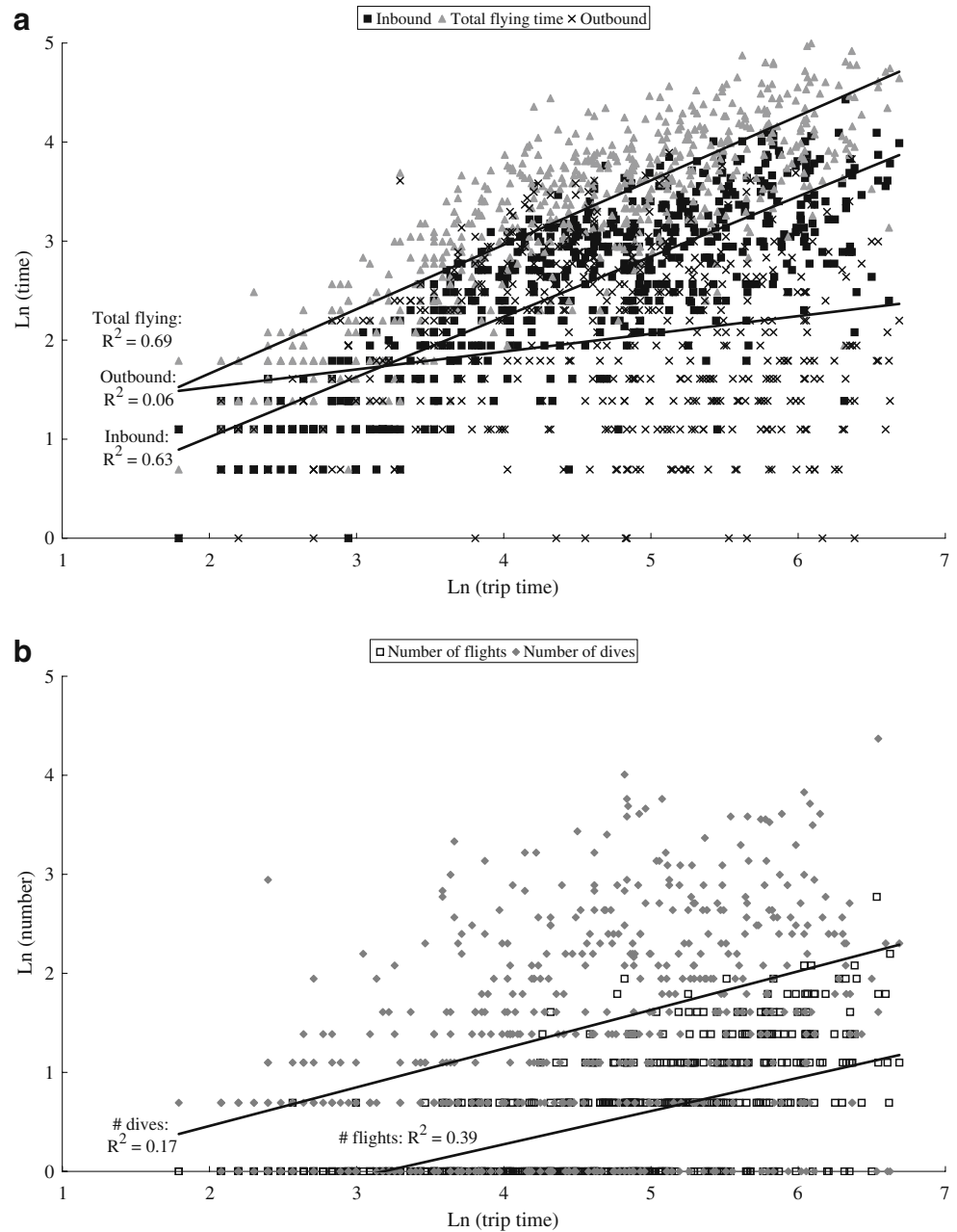
items (Figs. 2 and 3). On longer trips, birds apparently spent more time and covered a larger area both underwater and above-water, increasing the opportunity for encounters with prey that were spatially and temporally unpredictable. Inbound flight duration, and presumably foraging radius, increased with trip time across the entire range of trip times, in contrast to other seabirds (cf. Hamer et al. 2000; Daunt et al. 2002; Weimerskirch et al. 2005a, b). Longer trips meant higher time and energetic costs. Consequently, on longer trips, birds presumably pursued only more valuable prey items and were less likely to give up and return to the colony, leading to extended underwater and above-water search times.

For animals with widely spaced and dispersed prey items, prey encounters occur randomly (e.g., some albatrosses; Weimerskirch et al. 2005a, b). However, for most animals, prey occurs in patches and the optimal strategy is to conduct an area-restricted search following prey encounters (Weimerskirch 2007). For murres, benthic specialists return to the same habitat features repeatedly while pelagic foragers use local enhancement to locate pelagic fish schools (Fauchald and Erikstad 2002; Davoren et al. 2003a,b; Woo et al. 2008). As pelagic fish schools do not persist over short time scales, murres feeding on pelagic schools likely use area-restricted searches based on memory of past prey encounters to find feeding flocks, leading to

Table 3 R^2 values for thick-billed murre searching metrics at Coats Island 2004–2007 ($N=729$)

	Trip	Outbound	# flights	Total	# dives
Inbound	0.63	0.12	0.19	0.90	0.30
# dives	0.17	0.06	0.13	0.39	
Total	0.69	0.17	0.17		
# flights	0.39	0.03			
Outbound	0.06				

longer above-water search times than for birds returning to known habitat features (Fauchald et al. 2000; Davoren et al. 2003a,b). Many birds may have "chosen" a single foraging location and probable prey type prior to leaving the colony, as evidenced by the relatively small number of stops per trip (Table 2). In support, there is a high degree of individual specialization diet, foraging behavior, and foraging location (Elliott et al. 2008c; Woo et al. 2008).

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; Ropert-Coudert et al. 2006; Tinker et al. 2006; Yeates et al. 2007; Zavalaga et al. 2007; Deagle et al. 2008; Paredes et al. 2008; Enstipp et al. 2007; Miller and Trivelpiece 2008). For example, European shags (*Phalacrocorax aristotelis*) feeding on gunnels in rocky habitats swam solitarily and rapidly along the bottom while

shags feeding on sand lance in sandy habitats foraged in groups and slowly probed the ground (Watanuki et al. 2008). For murres, pelagic specialists were more likely to give up on a given patch, while benthic specialists were more likely to remain at the same patch and extend each visit (dive, dive bout) at the same patch (Tables 1 and 2). Foraging trips preceding deliveries of benthic prey items were characterized by more underwater (many dives per bout, more bottom time per dive) and less above-water (many flights per trip, more total flying time) searching than those preceding the delivery of pelagic prey items (Tables 1 and 2). We suggest that it may be difficult to locate patches of pelagic prey but once the patch is located it is easy to capture prey items while for benthic prey, it may be easy to locate patches, but once a patch is located it may be difficult to capture prey (Womble and Sigler 2006; Gende and Sigler 2006; Hedd et al. 2009). For pelagic capelin and invertebrates, differences in underwater searching include searching throughout the descent or ascent phase, as shown by the V-shaped dive shape and slower descent rate (Elliott et al. 2008c). The differences in search patterns between pelagic and benthic items extends the dichotomy between these two prey types apparent in foraging behavior, with pelagic prey items associated with V-shaped dives, slower descent rates, more variable dive depths within a bout and shorter dives for a given depth (Elliott et al. 2008b, c).

Whereas Coats murres averaged two or fewer stops (one or fewer between-dive flights) during foraging (Table 2), murres at larger colonies showed many more stops during foraging (Benvenuti et al. 1998; Falk et al. 2000, 2002). For example, at a large colony in Iceland (>650,000 pairs of seabirds including >400,000 pairs of murres, compared with 30,000 pairs of murres and fewer than 100 other seabirds at Coats Island) where foraging radii and trip durations were large, trips averaged 7.8 stops and varied between four and 12 stops (Benvenuti et al. 1998; excluding data without inbound trip information). Similarly, the dispersion of feeding rates ($\sigma{:}\mu=0.63$) is similar to that found in the past ($\sigma{:}\mu = 0.60$; Hipfner et al. 2006). Feeding rates are underdispersed at Coats Island compared to a nearby large colony (Digges Island, 300,000 breeding pairs; $\sigma{:}\mu = 0.67$), meaning that adults are better able to regulate feeding rates (presumably because searching is less time-consuming) at Coats Island compared to larger colonies (Hipfner et al. 2006).

The relatively small amount of above-water searching at Coats Island, where foraging trips are short in both distance and duration, is consistent with the idea that foraging site fidelity is greater for seabirds that feed at relatively small spatial and temporal scales because prey are more predictable over smaller scales, at least in nontropical environments (Weimerskirch 2007). Specialization in diet and
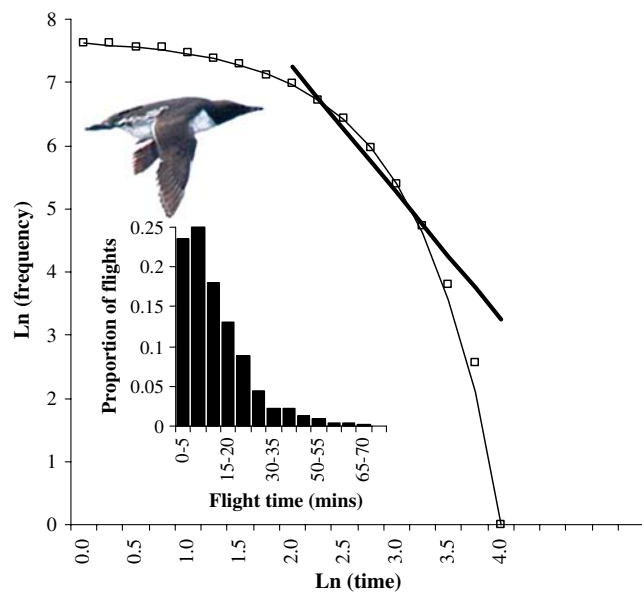

Fig. 4 Frequency distributions for ln-transformed flight durations (all flights, including outbound and inbound; subset: all flight durations) for thick-billed murres at Coats Island 2004-2007 ($N=2083$ flights). The thin line represents the maximum likelihood shifted gamma function and the thick line represents a potential Lévy search pattern for comparison

foraging strategy is high for many high-latitude seabirds (Irons 1998; Hamer et al. 2001; Garthe et al. 2007; Elliott et al. 2008c, Woo et al. 2008), including murres at another small colony in Svalbard (Mehlum et al. 2001), due to high prey encounter rates (Grémillet et al. 2004). Nonetheless, our observation of periodic sampling of the environment (stops), which has also been observed for murres elsewhere (Benvenuti et al. 1998, 2002; Falk et al. 2000, 2002), showing that some above-water searching does occur and that specialization does not mean complete foraging site fidelity. Outbound flights were generally shorter than inbound flights (Fig. 3), suggesting that stops must occur progressively further out on the outbound journey. Virtually all stops were followed by diving. Thus, as with other marine predators, search patterns were characterized by long travel times interspersed by area-restricted searches over small spatial scales (Weimerskirch et al. 2005a, b; Pinaud and Weimerskirch 2007; Cotté et al. 2007) but where, in this case, the area-restricted searches were dives.

We did not find any evidence for a Lévy search pattern (Fig. 4). Lévy search patterns are characterized by flight distances following a power law relationship between log-frequency and log-flight time (Reynolds 2005; Bénichou et al. 2006; cf. ESM Fig. S3). Many marine animals have been reported to obey Lévy search patterns (Viswanathan et al. 1996; Bartumeus et al. 2003; Austin et al. 2004; but see Edwards et al. 2007). An exponential distribution, such as we observed, implies random distribution of flight durations with constant low probability for long enough flight durations (Edwards et al. 2007). Theoretical models show that a distribution very similar to what we observe can occur when birds use small steps if prey is found and large steps if prey is not found ("area-restricted search"; Plank and James 2008).

Information transfer appeared to be relatively unimportant at the Coats Island colony because (1) foraging site fidelity was high (Woo et al. 2008); (2) naïve birds (birds leaving the colony for the first time) did not require more above-water search time than experienced birds; (3) time spent in the splashdown area did not reduce above-water searching time, with 25% of birds returning to the colony before making a final departure from the area; (4) there was no evidence of synchronized arrivals or departures. Earlier studies showing synchronization of arrivals in seabirds (e.g., Götmark 1990; Burger 1997) may have incorrectly applied the Poisson distribution instead of the exponential distribution. Rather than being a major site of information transfer, the main purpose of the splashdown period appeared to be to cleanse the feathers, as birds occupying sites that were likely to be soiled by feces spent 37% longer at the splashdown area than birds occupying sites where they were less likely to be soiled. Although we suggest that birds locate prey largely by returning to known locations or

by searching at small spatial scales, either independently, via network foraging or by local enhancement, there are still several ways that information transfer could play a role at our colony (Burger 1997). For example, Gaston and Nettleship (1981) estimated that outgoing flocks would encounter incoming flocks every 280 m and Davoren et al. (2003a, b) reported that commuting paths of murres at sea were obvious, possibly keeping murres on track to food sources, and the splashdown may aid in the selection of commuting route while also playing a role in cleansing (Burger 1997). Presumably, at larger colonies where foraging ranges are greater, especially at colonies where rapidly changing ice conditions mean that the location of food sources change over a time scale of hours or where increased presence of fog means that visibility is low (Gaston and Nettleship 1981), ICH effects—as well as greater above-water searching—may be more important and reduced ability to buffer changes in prey abundance (Harding et al. 2007).

In conclusion, thick-billed murres varied their search strategies in response to the predictability of the target prey item. Underwater search times for benthic fish were 90% higher than for pelagic fish and 300% higher than for invertebrates while above-water searching for pelagic fish involved 20% more flights and total flying time than for benthic fish and 90% more flights and 180% more total flying time than for invertebrates. The absence of dietary differences between adult and chick prey items (Woo et al. 2008) and the unimodal distribution of trip durations suggest that birds searched for similar targets during both self-feeding and chick provisioning. The presence of a high degree of specialization in diet and foraging behavior and the lower above-water searching compared to larger colonies suggest that less energy may be spent searching at small spatial and temporal foraging scales due to greater predictability of prey items. At large (between colonies), medium (above-water), and small (underwater) scales, the predictability of prey items plays a strong role in determining the search patterns of a marine predator.

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