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Specialization in Murres: The Story of Eight Specialists

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Abstract.—Prey items fed to chicks of eight individually-marked and known specialist Thick-billed Murres (*Uria lomvia*) were watched over a 15-year period at Coats Island, Nunavut, and time-depth recorders attached to eight birds in two separate years. Two males were amphipod specialists, one male a cod specialist and another male a shanny specialist; two females were sculpin specialists and two capelin specialists. Although there was likely some gender-related component to diet, there were clear specializations within each gender. Specialization in diet was mirrored by specialization in foraging behavior: amphipod specialists made V-shaped dives and had short foraging ranges, shanny/cod specialists made many shallow dives, sculpin specialists made deep, U-shaped dives, while capelin specialists made V- or W-shaped dives to moderate depths. There was no clear pattern between specialties and age or reproductive success. The use of longitudinal studies in foraging behavior, as long-term studies of individuals can complement existing knowledge of the flexibility or specialization of waterbirds, is encouraged. *Received 27 November 2008, accepted 10 February 2009.*

Key words.—Thick-billed Murre, *Uria lomvia*, Hudson Bay, specialization.

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Ornithologists are increasingly aware that understanding fundamental processes requires a comprehensive understanding of variation among individuals, rather than trends followed by the population mean (Áraujo *et al.* 2007, 2008; Sargeant 2007). The importance of individual-based behavior is especially true in studies of foraging behavior, as "generalist" predators are usually composed of individual specialists (Bolnick *et al.* 2002, 2003, 2007; Ropert-Coudert *et al.* 2003).

Waterbirds have been model organisms for studying specialization in foraging and diet, with several pioneering studies involving waterbirds (Pierotti and Annett 1990; Watanuki 1992; Wanless *et al.* 1992; Goss-Custard *et al.* 1995). In many cases, specialists have keyed into successful strategies, which they then repeat (Voslamber *et al.* 1995; Annett and Pierotti 1999; Golet *et al.* 2000). Specialists are sometimes older birds that have learned particularly successful strategies (Goss-Custard and Durell 1987; Restani *et al.* 2000; Elliott *et al.* 2006). In other cases, there are no apparent differences in fitness of specialists versus generalists, and they appear to be using merely different, but equivalent, strategies (Votier *et al.* 2004; Katzner *et al.* 2005). Indeed, some long-term datasets suggest different specialization strategies are successful in different years; short-term studies may report a certain strategy as being "optimal" as an artifact of that strategy being most successful in the particular year of study (Woo *et al.* 2008).

A recent study examined dietary specialization by Thick-billed Murres (*Uria lomvia*) over a 15-year period (Woo *et al.* 2008). These authors found that independent of age or gender, birds were more specialized in diet and behavior over short time-scales (days) than long time-scales (years), but specialists and generalists were largely equivalent in terms of fitness. About a third of the sample could be considered specialists across years, and more than half were considered specialists within a given season, among the highest proportion of any animal studied so far (within-year trends would be equivalent for comparison to most other studies which are <1 yr).

Although the complex statistics used by Woo *et al.* (2008) (e.g. Monte Carlo simulations) were essential to demonstrate specialization in rigorous terms, the generalizations involved obscured some features of the data. Here, we examine the degree of specialization in murres by examining eight birds chosen from the Woo *et al.* (2008) dataset because

many feeds were recorded and they showed a range of specializations. We chose four males and four females to illustrate that specialization occurs within each gender. Rather than developing our study in a hypothesis-testing framework, we present the data separately for each individual in an attempt to develop a "story" for each bird. The hypothesis-testing framework relies on disproving or failing to disprove a series of dichotomous (or, rarely, polychotomous) statements. Such statistical tests necessarily oversimplify the behavior of an individual into a few simple and quantifiable traits. These traits are then often separated into a priori (or supposedly a priori) selected groups for statistical comparisons. Alternative approaches, such as the information-theoretic paradigm, avoid some of the pitfalls of hypothesis-testing, but also involve pooling individuals (Anderson and Burnham 2002). Both approaches work best for large sample sizes and result in broad generalizations among or between groups. Our approach presents representative data for a given individual, allowing the reader to view each datapoint (each individual) as unique.

METHODS

Observations were made at the Coats Island Thick-billed Murre (*Uria lomvia*) colony (Q-Plot, 62°57'N, 82°00'W), Hudson Bay, Canada (Gaston *et al.* 2003, 2005) during the breeding seasons 1993-2007. Band combinations of site-holders and, usually, metal band numbers, were recorded using binoculars each year, so birds could be identified individually. In addition, most birds on Q-Plot were eventually captured, so the metal band numbers field-read for most birds observed during feeding watches were verified in the hand. Reproductive success was measured by observing each plot daily from July 14-August 16. Chicks disappearing after 14 days old were considered to have fledged successfully.

In each year, at least three continuous (24 or 48 h) observation sessions were carried out from a blind situated, within 5m of the birds (Hipfner *et al.* 2006; Elliott *et al.* 2008d). We did not conduct feeding watches when it was too dark to see deliveries (approximately 01:00-02:00 in late July; 23:00-0:400 in mid August) because chicks are rarely fed at that time (Elliott *et al.* 2008d). During these observation sessions, prey items delivered to chicks were identified whenever possible. Size was estimated assuming the length of the white streak on the bill is 5 cm (Elliott *et al.* 2008d; Hipfner *et al.* 2006). Data are provided in Appendix 1.

In conjunction with these observations, murres were caught with a noose pole to attach LOTEK 1100LTD time-depth-temperature recorders (TDRs; Lotek Marine Technology, St. John's, Newfoundland, Canada) with duct tape to plastic bands placed on the legs. (2004: n = 23; 2005: n = 33; 2006: n = 80; 2007: n = 37). Handling time was always less than ten minutes. The TDRs were cylindrical (mass = 4.5g; diameter = 1 cm; length = 3.3 cm) and attached parallel to the leg with the pressure sensor facing toward the foot. The gauges sampled temperature and pressure every 3 s. They were calibrated by the company prior to the field season and we corrected for drift using a custom-built Excel macro. The macro calculated pressure during the previous ten measurements prior to the dive to determine a drift value (pressure at the surface), which was subtracted from the dive depth. Total absolute error was likely to be about ±2 m due to unsteady effects (e.g. Bernoulli effect, short-term electronic drift) underwater; dives shallower than 3 m were ignored. These small devices had no measurable effect on murre provisioning rates, trip duration, body mass and dive depth (Elliott *et al.* 2008 a,b,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.* 2003; Elliott *et al.* 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.

Foraging behavior can be described in terms of prey depth (measured as dive depth), benthic or pelagic foraging (dive shape) and distance from the colony (flight time). All other foraging variables are closely correlated with one of the three parameters, so we could monitor variability in foraging behavior by measuring dive depth, dive shape and flight time. The representative graphs shown are the first dive traces available outside of the period of reduced light availability (2100-0400) that were followed by a prey delivery (and were therefore known to be for foraging). We present the same axis size (4 and 45 minutes and 110 m) for each bird. We estimated the location of prey capture for each benthic prey item assuming all birds flew to the west, that benthic prey items were captured at maximum dive depth and that birds flew directly back from the foraging location at 75 km/hr (Elliott and Gaston 2005; Elliott *et al.* 2008a).

RESULTS

We obtained information for two separate years from eight specialists. A summary of the dive and diet data each individual is included below. For the benthic specialists, foraging locations tended to clump into a relatively small area for each individual (Fig. 9). Specialization in foraging behavior was not correlated with specialization in prey type (TNW/WIC measures; $R^2 = 0.00$, $P = 0.32$), showing that all birds specialized in foraging behavior but this resulted in prey type specialization for only some birds.

1. Male, banded as an adult in 2005, delivered almost exclusively amphipods, with only one other prey item recorded; a capelin (Table 1). The male often returned to the colony from its short forays

Table 1. Summary of typical feeding data for eight individuals. Birds in bold were banded as chicks. Rearing dates for birds banded as adults (non-bold) were estimated by subtracting seven years from the date of banding. Once they commenced breeding all individuals attempted to breed in every year. Birds in italics were followed only for part of their life, so breeding attempts are a minimum. Periods of darkness (2100-0400) excluded from analyses. Speciality codes follow those presented in the Appendix.

Bird	Reared	Sex	Breeding attempts	Successful breeding attempts	Specialty	Typical dive depth (m)	Shape	Typical return flight distance (km)
1	1998	M	2	2	AMP	65	V	3
2	1989	M	12	5	AMP	72	V	5
3	1997	F	4	4	CAP	70	V	21
4	1984	F	**3**	2	CAP	65	W	14
5	1979	M	**15**	14	STI/GYM	21	U	26
6	1989	M	10	7	COD	39	U	41
7	1988	F	12	9	SCU	91	U	26
8	1988	F	13	13	SCU	82	U	26

involving a single, V-shaped dive (Fig. 1). The male provided a possible example of a poor specialization strategy, as the male only reared offspring for two years before disappearing. A similar strategy was pursued by a nearby bird of unknown sex which also brought back large numbers of amphipods, and successfully reared young in four out of the 15 years the male was present.

2. Male, banded as an adult in 1996. The male produced a fledgling in five of 12 years. The male specialized on amphipods, occasionally bringing back other pelagic prey such as squid and small capelin. As 1, the male often returned from short forays involving a single, V-shaped dive (Fig. 2). In earlier, failed breeding attempts the male brought back very few prey items and no amphipods; so specializing on amphipods appeared to trigger a successful strategy for this bird. Although specializing on amphipods brought back little energy per trip, the large number of trips with multiple amphipods added up to roughly the same energy content per trip (9.0 kJ per hour for that bird) as a single, long trip (10.1 kJ per hour) for the same bird.
3. Female, banded as a chick in 1997. The female produced its first young in 2005, at age eight. A capelin specialist, the female had an unusual strategy, bringing back two capelins at a time, held crosswise in the bill—typically murres deliver single prey held with the head inside the gape (Gaston and Jones 1998). In this way, the female specialized on the commonest prey item, showing that specialization is not only restricted to rare prey items. The female used primarily several V- or W-shaped dives to variable depths (Fig. 3). The female was still a relatively young bird during the observations presented here. Her partner, ever since the female first bred on the plot, was also a capelin specialist.
4. Female banded as a chick in 1984. The site was colonized during the study period and was not included in our feeding watches until 2005 (the site was immediately underneath our blind, and the chick soon disappeared when an Arctic fox *Alopex lagopus* appeared on the colony, as in 2007). This bird was never observed bringing back any prey other than capelin. The female was one of only two birds observed bringing back at least ten items over the course of the study, but which delivered only one prey type. The female generally captured prey items during a deep, U-shaped dive, with a defined but not constant bottom period (Fig. 4). Dive bouts were usually about ten dives, to variable depths. The within- and between-dive variation in dive depth suggests the female captured capelin during forays into pelagic water.
5. Male banded as an adult with nestling in 1986; assuming the male was at least seven years old at banding, it was at least 28 years

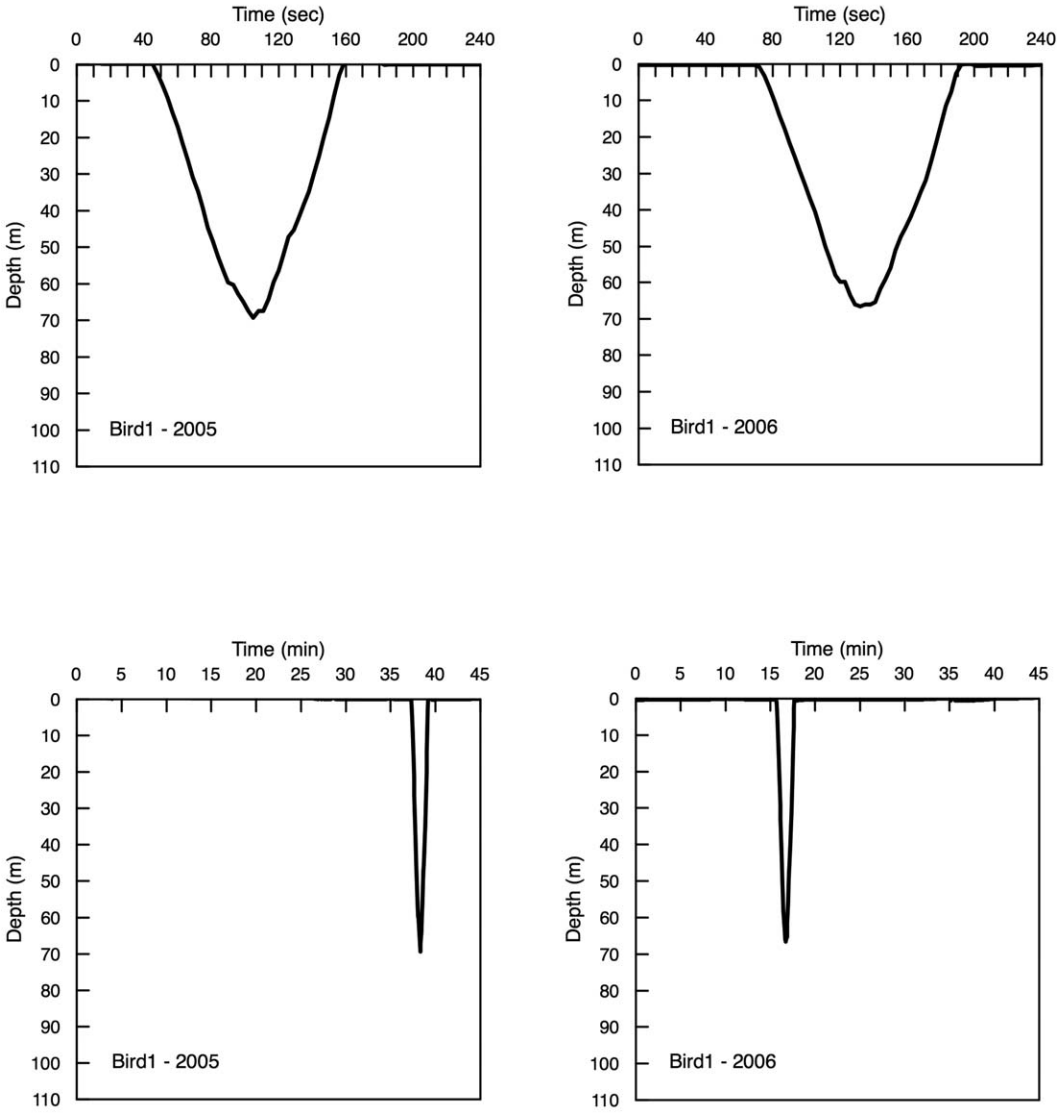

Figure 1. Typical V-shaped dive profile of Bird 1, a male who delivered almost exclusively amphipods.

old in 2007. The male successfully reared a chick in every year except 2003. The male was a benthic specialist, with *Gymnelus* and *Stichaeus* accounting for nearly half of prey delivered (and in all but three years), and cod for nearly one-third. Capelin, the dominant prey item at the population-wide level, was never recorded in the first five years and only made up 9% of total deliveries. The male used many short, shallow, flat-bottomed dives with little surface time (Fig. 5).

6. Male banded as a breeding adult in 1996 and at least 16 years old in 2007. The male produced young in 8/12 years. Despite reproducing primarily in the "post-cod" years (late 1990s onwards, Gaston *et al.* 2003), the male was a cod specialist, switching to benthics in the years when capelin was most dominant at the population-wide level and cod disappeared almost completely from the population-wide diet (2004-06). Cod were captured in

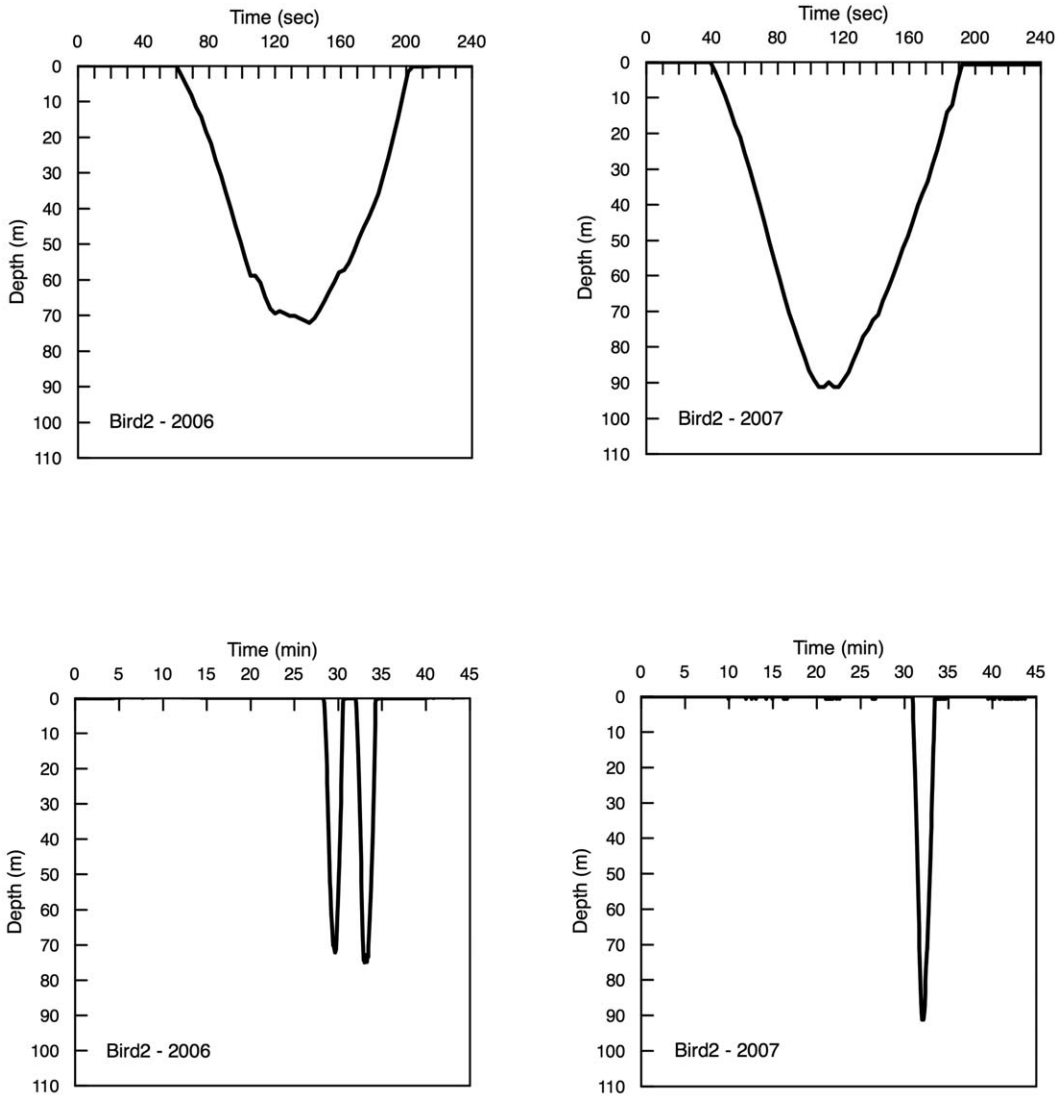

Figure 2. Dive pattern of Bird 2, a male who delivered mostly amphipods (V-shaped dives) with occasional other pelagic prey.

shallow, flat-bottomed dives during long dive bouts (Fig. 6). They were usually collected far from the colony, as shown by long (30+ min) return flight times.

7. Female, banded as a chick in 1988; reared its first young in 1996. The female produced a chick in 9/12 years. The female was another benthic specialist, bringing back deep water sculpins in the genus *Triglops*. The female was the colony record-holder for longest dive (278 s), and used a deep-diving tactic resulting in long dives and relatively short dive bouts (1-5 dives; Fig. 7); presumably the female was unable to maintain this deep-diving activity for long.
8. Female, banded as a chick in 1988, first raised an offspring in 1995, and every year since then. The female was another sculpin specialist, with sculpins making up over half of the diet, and represented in every year but two. The female mostly delivered deep water sculpins (*Triglops*), using very deep, long dives with several

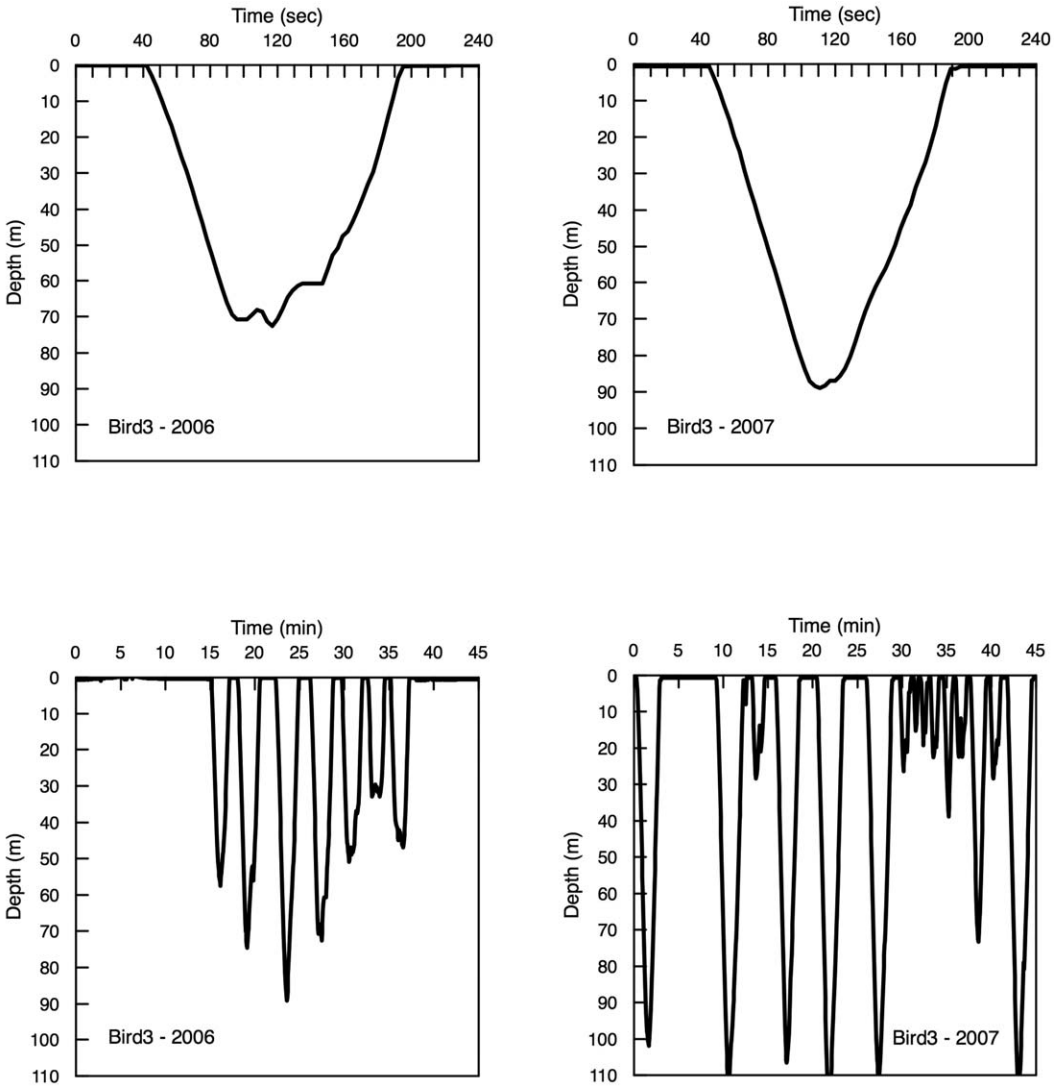

Figure 3. Successive, variable depth V- or W-shaped dive pattern of Bird 3, a female specializing on capelin.

dives per bout (Fig. 8). The sculpin strategy has paid off for this bird, resulting in consistent successful breeding (Table 1).

DISCUSSION

Several strategies were evident at the colony, with these strategies reflecting parallel differences in diet and foraging behavior (Table 1). Specifically, individual benthic specialists tended to forage repeatedly at the same location (Fig. 9), suggesting that repeated, stereotyped foraging behavior represents birds returning to the same location. There was no clear pattern between specialties and age or reproductive success, although amphipod specialists tended to have fewer successful breeding attempts. Apparently, site and/or mate quality, were much more important in determining reproductive success than foraging strategy. If there was any relation between strategy and success it could be as a symptom of quality, with preferred feeders winning better sites (Moody *et al.* 2004; Lewis *et al.* 2006).

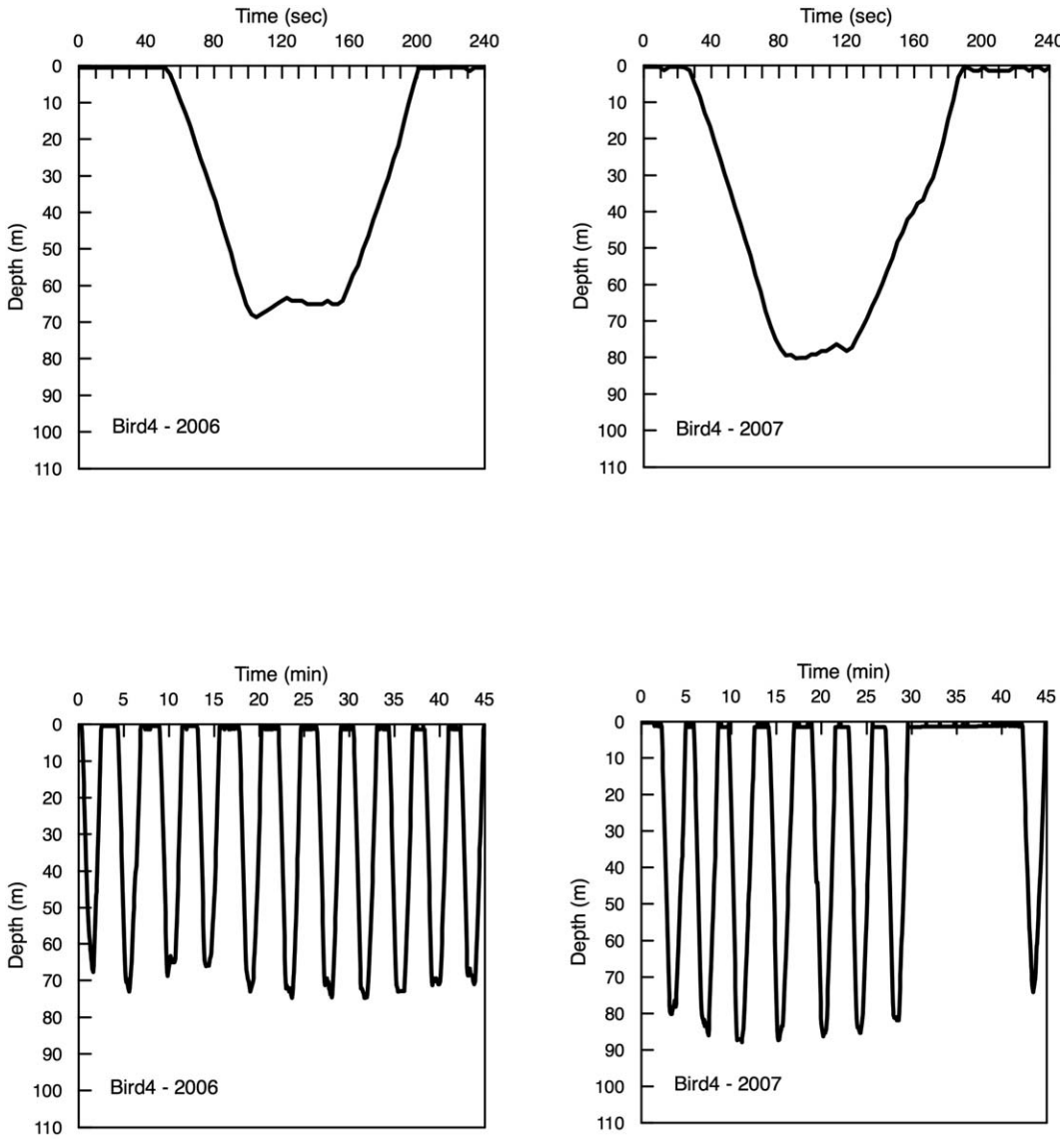

Figure 4. Dive pattern of Bird 4, a female specializing entirely on capelin—exemplified by successive deep, U-shaped dives with a defined but variable bottom period.

Two major changes have taken place over the period of the study: diet has shifted from Arctic (cod) to Sub-arctic (capelin) fish species since 1981 (Gaston *et al.* 2003, 2005), and the opportunity to observe older birds increased as our banded population aged. Increasing proportions of older birds during the study period potentially confounds our observations of age-related trends because older birds tend to appear to "specialize" on capelin because the only birds known to be old occurred during the most recent years. Nonetheless, individuals tended to maintain specializations across many years, including the Arctic cod specialist presented here. Thus, the switch from cod to capelin represents a switch in the diet of generalists (which represent about two-thirds of the population; Woo *et al.* 2008), with specialists not showing the switch. As the repeatability of foraging behavior was high for generalists and specialists alike, we sug-

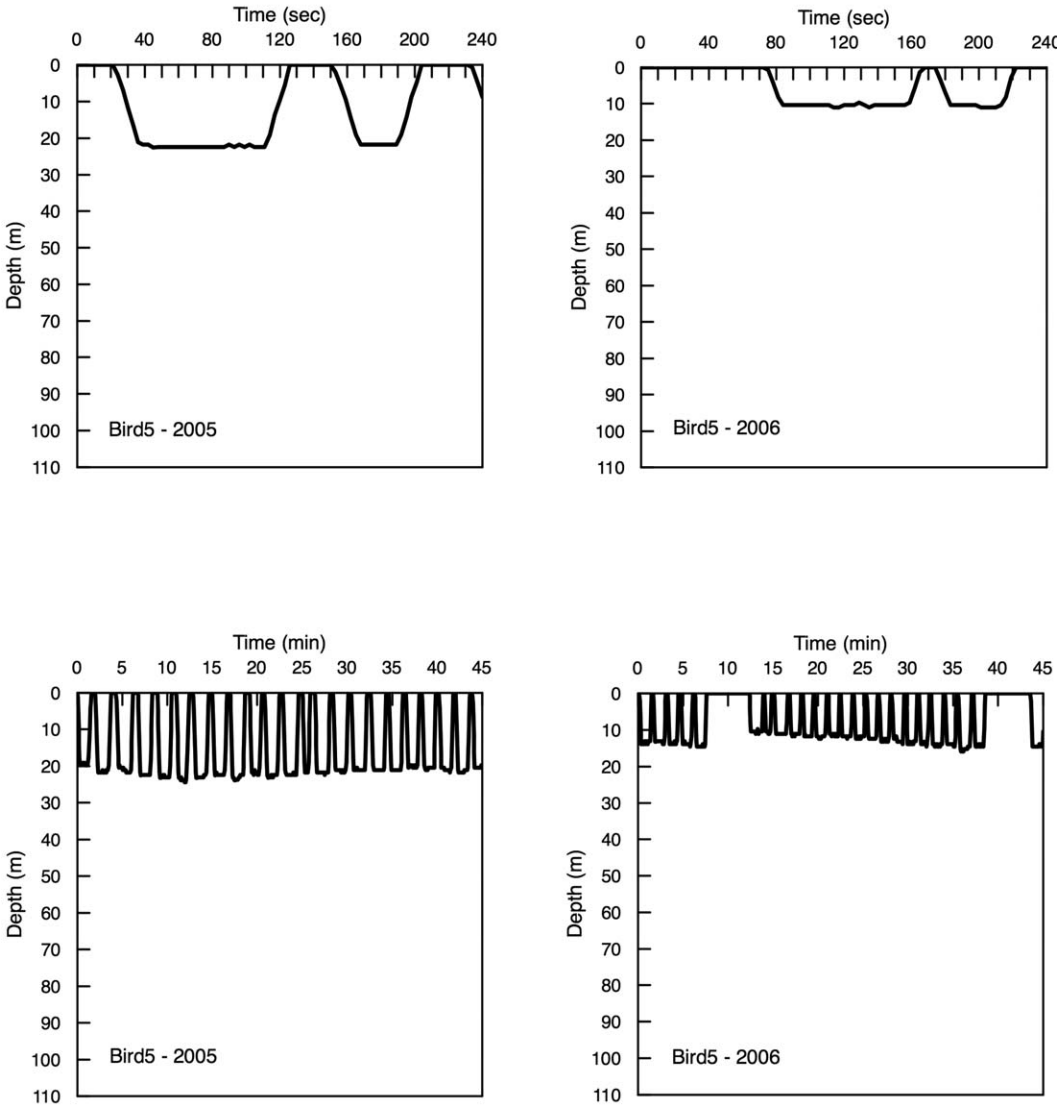

Figure 5. Short, shallow, flat-bottomed dive pattern of Bird 5, a male specializing primarily on shallow benthic prey items.

gest all birds have highly repeatable foraging behavior (dive depth, flight time, distance from colony, habitat selection, foraging location), but the particular foraging behavior used by generalists intersects the habitat of several prey items while specialists use habitat where only one prey item dominates.

Much can be learned from focusing on telling the stories of a few individuals, rather than getting a little information from a large number of individuals (Warren *et al.* 1996; Pepperberg 2000). For example, although our birds fit into a few simple categories (benthic, pelagic), there was individual variation in alternative prey types, dive behavior and life history consequences (see Ropert-Coudert *et al.* 2003). By presenting only statistical means, we would be obscuring much of the variation that makes each individual unique. The variation represents the flexibility of an individual to adapt to changing environmental conditions and, therefore, may play an important part of its life history. Past studies at Coats Island have

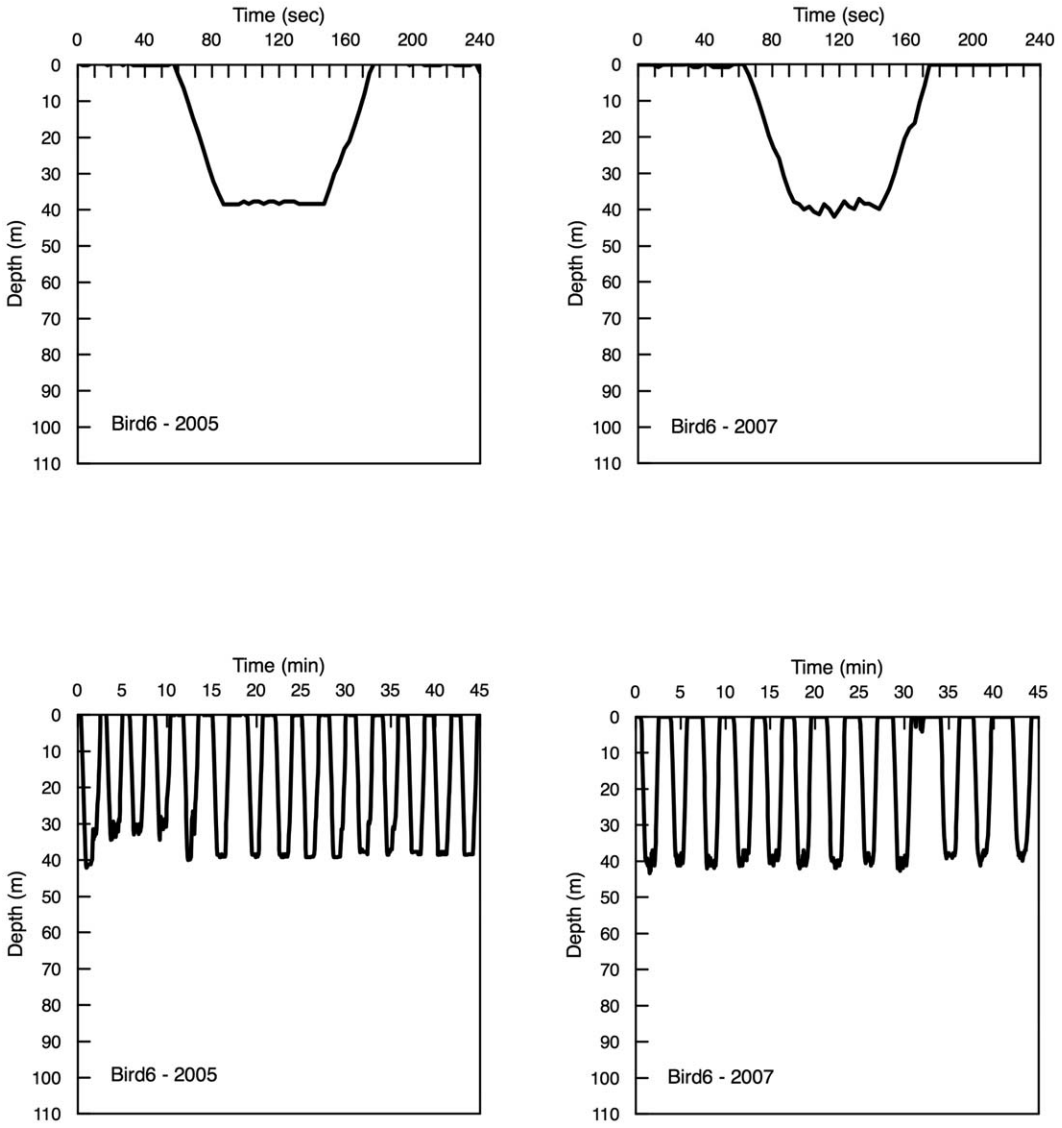

Figure 6. Shallow, flat-bottomed dives of Bird 6, a male specializing almost exclusively on cod.

focused on temporal trends in diet and contaminants, deriving a regression between mean population values and date (Braune *et al.* 2001; Gaston *et al.* 2003), yet changes in population means actually represent changes in the proportion of specialists and generalists or tactics within individuals. Could changes in diet or contamination merely reflect changes in the proportion of specialists on the study plot? We suggest above that this is not the case, but a stronger argument for temporal changes in diet and contamination would be provided by repeated sampling of the same individuals. In a similar way, measuring age-related trends for survival and reproductive success within individuals (longitudinal sampling) is a much more powerful test of senescence than monitoring life tables (population-wide mean reproductive success or survival at a given age; cross-sectional sampling) because poor breeders may disappear from later age classes, reducing the probability of detecting senescence (Reid *et al.* 2003).

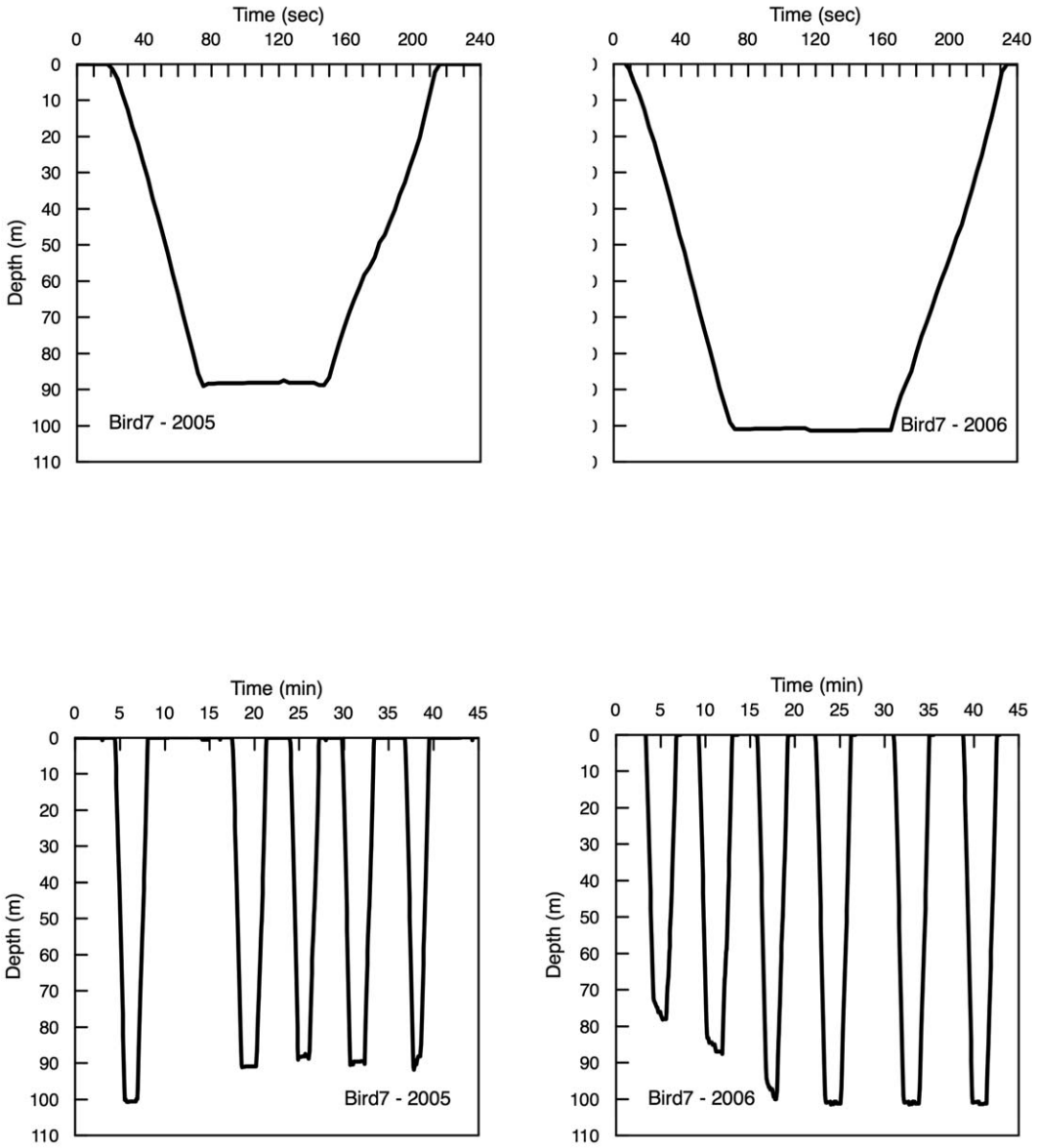

Figure 7. Dive pattern of Bird 7, a female specializing on benthic sculpins resulting in deep, long duration, flat-bottomed dives.

Although ecologists are taught to avoid anthropomorphisms and to view their work objectively, we suggest that some emphasis on the subjective, individual nature of their study animals may be beneficial. Ecologists need to recognize that case-histories of individual birds built up over many years will provide valuable insight into ecological processes complementary to generalizations across populations from single-year studies. For example, applying a theoretical-deductive approach to a small number of well-known individuals may increase knowledge for small populations of conservation interest to a greater degree than hypothesis-testing approaches (Parra *et al.* 2001; see Armstrong and McCarthy 2007). We suggest more studies using longitudinal sampling are needed (Tremblay *et al.* 2005).

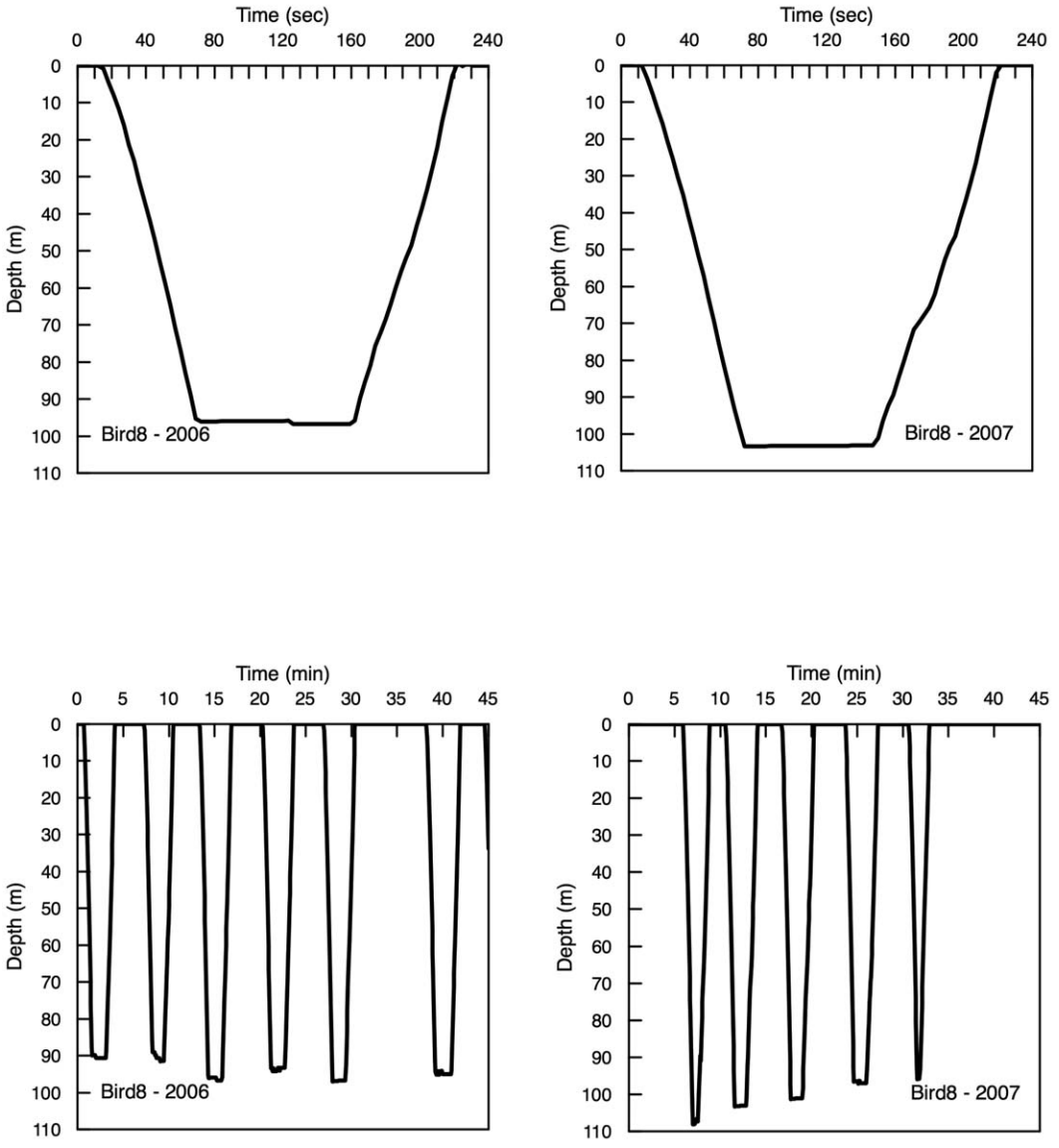

Figure 8. Dive pattern of Bird 8, a female specializing on benthic sculpin—exemplified by deep, long duration, flat-bottomed dives.

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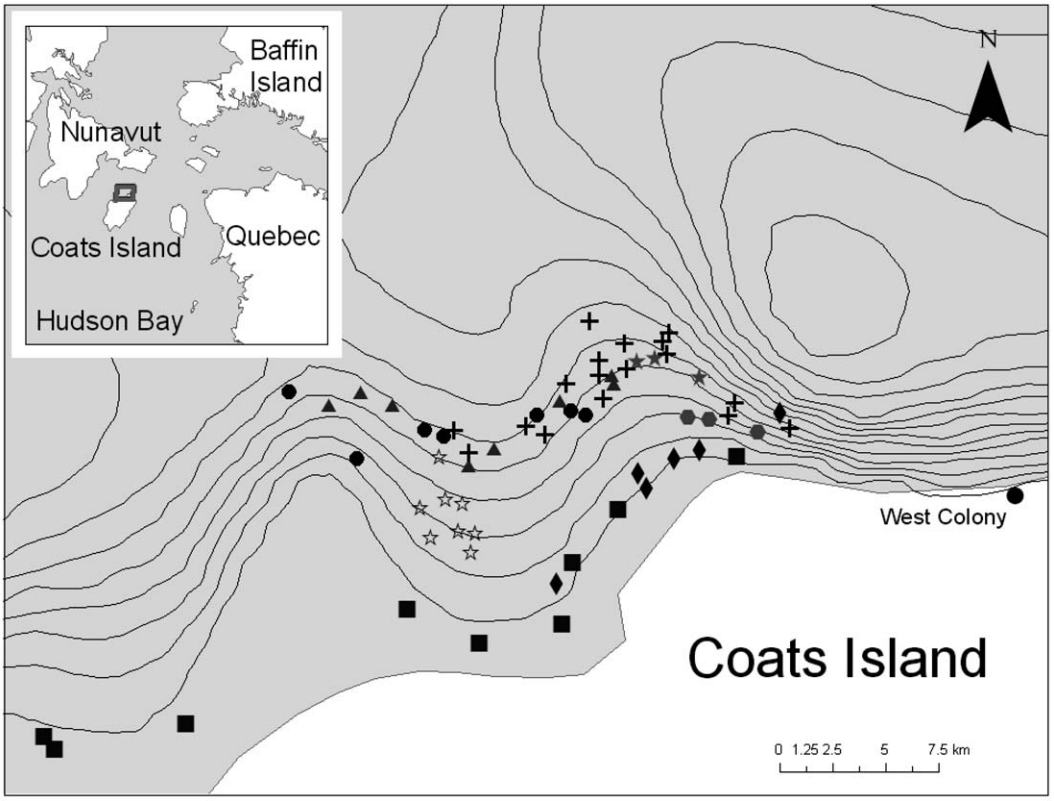

Figure 9. Locations where benthic prey were collected by nine individual murres at Coasts Island, including the four benthic specialists presented in Table 1. Each symbol represents a different individual. The lines represent 20 m isobaths.

da. All handling and equipping followed the guidelines of the Canadian Committee for Animal Care under the University of Manitoba Protocol Number F04-030.

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Appendix 1. Feeding data for eight Thick-billed Murre at Coats Island 1993-2007. Our study included benthic fish such as snakeblenny, *Eumesogrammus* (abbreviated as EUM); fishdoctor, *Gymnelus* (GYM); daubed shanny, *Leptoclinus* (LEP); sculpin, Cottidae (SCU); Arctic shanny, *Stichaeus* (STI); pelagic prey such as sand eel, *Ammodytes* (AMM); capelin (× 2 refers to two fish per trip), *Mallotus* (CAP); cod, *Boreogadus* (COD); and invertebrates such as squid (SQU), shrimp (SHR) and amphipods (AMP). We report individual totals and 1993-2007 population totals (POP). To simplify presentation, we sometimes group prey into larger classifications (e.g. benthics). Data for a given year were only included if at least five feeds were observed (including unidentified feeds, which are not shown in the tables). Percentages are calculated relative to number of feeds, rather than by mass.

		PELAGICS				BENTHICS					INVERTEBRATES		
BIRD	YEAR	CAP	CAP × 2	COD	AMM	EUM	GYM	STI	LEP	SCU	SQU	AMP	SHR
Bird #1													
85520	2005			0				0			0	**27**	0
	2006			1				0			0	**33**	0
				1.6%				0.0%			0.0%	**98.4%**	0.0%
Bird #2													
67193	2003	8	0	1	0			0			0	**6**	0
	2004	3	0	0	0			0			0	**13**	0
	2006	6	0	0	0			0			0	**52**	2
	2007	6	0	0	0			3			4	**14**	0
		19.5%	0.0%	0.8%	0.0%			2.5%			3.4%	**72.0%**	1.7%
Bird #3													
69944	2005	**20**	**3**	2	0			1				1	
	2006	**28**	**7**	0	0			1				0	
	2007	**10**	**9**	3	2			2				0	
		61.3%	**25.2%**	5.6%	2.2%			4.4%				1.1%	
Bird #4													
60228	2005	**14**						0					
	2006	**6**						0					
		100%						0.00%					
Bird #5													
02029	1993	0	0	1	0	**1**	**0**	**0**	0	0		0	
	1994	0	0	3	0	**1**	**1**	**0**	0	0		0	
	1995	0	0	1	0	**1**	**0**	**0**	0	0		0	
	1996	0	0	5	1	**2**	**0**	**0**	0	0		0	
	1997	0	0	4	1	**0**	**0**	**9**	1	0		0	
	1998	2	0	6	0	**1**	**0**	**5**	0	0		0	

Appendix 1. (Continued) Feeding data for eight Thick-billed Murre at Coats Island 1993-2007. Our study included benthic fish such as snakeblenny, *Eumesogrammus* (abbreviated as EUM); fishdoctor, *Gymnelus* (GYM); daubed shanny, *Leptoclinus* (LEP); sculpin, Cottidae (SCU); Arctic shanny, *Stichaeus* (STI); pelagic prey such as sand eel, *Ammodytes* (AMM); capelin (× 2 refers to two fish per trip), *Mallotus* (CAP); cod, *Boreogadus* (COD); and invertebrates such as squid (SQU), shrimp (SHR) and amphipods (AMP). We report individual totals and 1993-2007 population totals (POP). To simplify presentation, we sometimes group prey into larger classifications (e.g. benthics). Data for a given year were only included if at least five feeds were observed (including unidentified feeds, which are not shown in the tables). Percentages are calculated relative to number of feeds, rather than by mass.

		PELAGICS				BENTHICS					INVERTEBRATES		
BIRD	YEAR	CAP	CAP × 2	COD	AMM	EUM	GYM	STI	LEP	SCU	SQU	AMP	SHR
	1999	0	0	8	0	**1**	**1**	**0**	0	0		0	
	2001	2	0	4	0	**2**	**1**	**3**	1	0		0	
	2002	1	0	0	0	**0**	**1**	**3**	0	1		5	
	2004	2	0	1	0	**0**	**0**	**2**	0	0		0	
	2005	3	0	1	0	**1**	**13**	**1**	0	0		0	
	2006	0	0	2	0	**1**	**2**	**12**	0	1		0	
	2007	2	0	4	2	**0**	**3**	**7**	0	0		1	
		8.5%	0.0%	28.4%	2.8%	**7.8%**	**15.6%**	**29.8%**	1.4%	1.4%		4.3%	
Bird #6													
67160	1996	1	0	**10**	0			0				0	
	1997	0	0	**1**	0			4				0	
	1999	3	0	**6**	0			1				0	
	2000	5	0	**5**	1			3				0	
	2004	1	0	**2**	0			1				0	
	2005	2	0	**2**	0			4				0	
	2006	4	0	**2**	0			4				1	
	2007	1	0	**5**	0			0				0	
		24.6%	0.0%	**47.8%**	1.4%			24.6%				1.4%	
Bird #7													
08482	1996	0	0	7	1			0		**0**		0	
	1999	3	0	2	0			1		**6**		0	
	2000	3	0	0	3			1		**0**		1	
	2001	1	0	0	1			2		**4**		0	
	2002	2	0	0	1			0		**3**		0	
	2005	0	0	1	0			7		**5**		0	
	2006	4	0	1	0			0		**10**		0	
	2007	1	0	2	0			4		**4**		1	
		17.1%	0.0%	15.9%	7.3%			18.3%		**39.0%**		2.4%	

Appendix 1. (Continued) Feeding data for eight Thick-billed Murre at Coats Island 1993-2007. Our study included benthic fish such as snakeblenny, *Eumesogrammus* (abbreviated as EUM); fishdoctor, *Gymnelus* (GYM); daubed shanny, *Leptoclinus* (LEP); sculpin, Cottidae (SCU); Arctic shanny, *Stichaeus* (STI); pelagic prey such as sand eel, *Ammodytes* (AMM); capelin (× 2 refers to two fish per trip), *Mallotus* (CAP); cod, *Boreogadus* (COD); and invertebrates such as squid (SQU), shrimp (SHR) and amphipods (AMP). We report individual totals and 1993-2007 population totals (POP). To simplify presentation, we sometimes group prey into larger classifications (e.g. benthics). Data for a given year were only included if at least five feeds were observed (including unidentified feeds, which are not shown in the tables). Percentages are calculated relative to number of feeds, rather than by mass.

		PELAGICS				BENTHICS					INVERTEBRATES		
BIRD	YEAR	CAP	CAP × 2	COD	AMM	EUM	GYM	STI	LEP	SCU	SQU	AMP	SHR
Bird #8													
09445	1995	0	0	2	0			0		**1**		0	
	1996	1	0	4	0			0		**0**		0	
	1997	5	0	1	1			1		**7**		0	
	1998	0	0	0	0			0		**4**		0	
	1999	4	0	0	1			2		**4**		0	
	2000	0	0	1	1			0		**1**		0	
	2001	5	0	1	0			0		**2**		0	
	2002	1	0	0	1			0		**1**		0	
	2003	5	0	0	1			1		**0**		0	
	2004	0	0	1	0			0		**5**		1	
	2005	3	0	1	0			0		**9**		0	
	2006	1	0	0	0			1		**17**		0	
	2007	3	0	1	1			0		**6**		0	
		25.7%	0.0%	11.0%	5.5%			4.6%		**52.3%**		0.9%	
POP		41.2%	0.6%	19.3%	8.1%	2.0%	2.1%	1.4%	6.4%	11.2%	1.5%	6.0%	0.8%