

Individual specialization in diet by a generalist marine predator reflects specialization in foraging behaviour

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Summary

1. We studied chick diet in a known-age, sexed population of a long-lived seabird, the Brünnich's guillemot (*Uria lomvia*), over 15 years ($N = 136$; 1993–2007) and attached time–depth–temperature recorders to examine foraging behaviour in multiple years ($N = 36$; 2004–07).
2. Adults showed specialization in prey fed to offspring, described by multiple indices calculated over 15 years: 27% of diet diversity was attributable to among-individual variation (within-individual component of total niche width = 0.73); average similarity of an individual's diet to the overall diet was 65% (mean proportional similarity between individuals and population = 0.65); diet was significantly more specialized than expected for 70% of individuals (mean likelihood = 0.53). These indices suggest higher specialization than the average for an across-taxa comparison of 49 taxa.
3. Foraging behaviour varied along three axes: flight time, dive depth and dive shape. Individuals showed specialized individual foraging behaviour along each axis. These foraging strategies were reflected in the prey type delivered to their offspring and were maintained over scales of hours to years.
4. Specialization in foraging behaviour and diet was greater over short time spans (hours, days) than over long time spans (years). Regardless of sex or age, the main component of variation in foraging behaviour and chick diet was between individuals.
5. Plasma stable isotope values were similar across years, within a given individual, and variance was low relative to that expected from prey isotope values, suggesting adult diet specialized across years. Stable isotope values were similar among individuals that fed their nestlings similar prey items and there was no difference in trophic level between adults and chicks. We suggest that guillemots specialize on a single foraging strategy regardless of whether chick-provisioning and self-feeding. With little individual difference in body mass and physiology, specialization likely represents learning and memorizing optimal feeding locations and behaviours.
6. There was no difference in survival or reproductive success between specialists and generalists, suggesting these are largely equivalent strategies in terms of evolutionary fitness, presumably because different strategies were advantageous at different levels of prey abundance or predictability. The development of individual specialization may be an important precursor to diversification among seabirds.

Key-words: behavioural strategy, Brünnich's guillemot, foraging behaviour, specialization, stable isotopes, thick-billed murre, *Uria lomvia*

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Introduction

Individual specialization in diet is widespread among generalist predators, and many generalist populations are actually made up of individual specialists (Bolnick *et al.* 2003; Poore & Hill 2006; Martins *et al.* 2008). In some cases, apparent individual specialization is largely a result of sexual or age-related differences in size, experience or dominance (Lewis *et al.* 2002; Elliott *et al.* 2006; Field *et al.* 2007). For example, there are often size differences between sexes leading to different preferred prey sizes (Marquiss & Newton 1982; Jung 1992) or foraging behaviour (Ishikawa & Watanuki 2002; Lewis *et al.* 2005). Similarly, older animals are more experienced, sometimes leading to greater foraging efficiency (Stalmaster & Gessaman 1984; Goss-Custard & Durell 1987; Restani, Harmata & Madden 2000).

Nonetheless, in many cases individual specialization occurs even once sex- or age-related differences are accounted for (Stillman *et al.* 2002; Bolnick *et al.* 2003; Ropert-Coudert *et al.* 2003). Such specialization can occur through variation in internal physiology (Afik & Karasov 1995) or morphology (Grant & Grant 1996; Robinson, Wilson & Shea 1996; Smith & Skúlason 1996). For example, seals with more lipids have higher buoyancy and, therefore, may not be able to access deep water prey items (Beck, Bowen & Iverson 2000; Watanabe *et al.* 2006). Alternatively, specialization can occur through individual variation in dominance (Stillman *et al.* 2002) or through limited memory capacity (Lewis 1986; Nemirosso & Despland 2007). Prey items often require highly stereotyped capture techniques or often only occur in a few patchily distributed locations, and a given individual may only be able to learn a limited number of techniques or locations (Davoren, Montevecchi & Anderson 2003; Estes *et al.* 2003; Cook, Chérel & Tremblay 2006). Time spent learning new capture techniques or finding new locations will inevitably take away from time available to capture prey items using known capture techniques or locations. Few studies have connected long-term dietary specialization with temporal persistence of capture techniques or foraging locations (Cook *et al.* 2006).

Although specialization is known to be widespread, the implications of specialization are poorly known. For example, it is unknown if individual specialists usually have higher foraging success, or fitness, compared to nonspecialists (Araújo & Gonzaga 2007; Bolnick *et al.* 2007; Darimont, Paquet & Reimchen 2007). Exceptions include studies where specialists had higher foraging efficiency and reproductive success than nonspecialists (Watanuki 1992; Voslamber, Platteeuw & Van Eerden 1995; Annett & Pierotti 1999; Golet *et al.* 2000). These improvements may have been partially a result of increased specialization in older animals, as age was not measured in some of these studies. Indeed, few studies examine the temporal scale at which specialization occurs (but see Schindler, Hodgson & Kitchell 1997; Votier *et al.* 2004; Bearhop *et al.* 2006), so it is usually unknown whether specializations are maintained over time.

Here, we examine dietary specialization in a wild population of known-age, sexed seabirds, where adult prey deliveries to

their chicks were followed for 15 years. In the last four years (2004–07), electronic recorders were attached to adults so that specialization in foraging behaviour could be observed. We addressed the following questions: (i) Do individuals specialize in diet? (ii) Do individuals specialize in foraging behaviour or location? (iii) How long are specializations maintained? (iv) Do specialists have higher food delivery rates, reproductive success or survivorship than nonspecialists?

Materials and methods

DIET

Observations were made at the Coats Island Brünnich's guillemot [*Uria lomvia* (Linnaeus, 1758)] west colony (62°57'N, 82°00'W), Nunavut, Canada (Gaston, Woo & Hipfner 2003; Gaston, Gilchrist & Hipfner 2005) during the breeding season. At least three continuous (24 or 48 h) observational watches of breeding sites were completed from a blind at the Q study plot, within 5 m of the birds, each year 1993–2007. We did not conduct feeding watches when it was too dark to see deliveries (roughly 01:00–02:00 h in late July; 23:00–04:00 h in mid-August) because chicks are rarely fed at this time (Gaston & Bradstreet 1993; Gaston *et al.* 2003). During these observation sessions, prey items delivered to chicks at the colony were identified whenever possible. Size was estimated assuming that the length of the white streak on the bill is 5 cm (Elliott & Gaston *in press*). Energy content and prey mass were calculated from species-specific mass-length regressions and energy densities developed for fish delivered by guillemots at Coats Island (Elliott & Gaston *in press*). Adults are colour banded, allowing for individual identification.

FORAGING BEHAVIOUR

Guillemots were caught with a noose pole (2004: $N = 23$; 2005: $N = 33$; 2006: $N = 80$; 2007: $N = 37$). We secured LOTEK 1100LTD time–depth–temperature recorders (TDR; Lotek Marine Technology, St. John's, Newfoundland, Canada) with duct tape to plastic bands that were attached to the legs of guillemots (Elliott *et al.* 2008b). The TDRs were cylindrical (mass = 4.5 g; diameter = 1 cm; length = 3.3 cm; sampling interval = 3 s) with absolute error after correcting for drift of about ± 2 m; dives shallower than 3 m were ignored. Whereas back-mounted TDRs are known to impact guillemot provisioning rates, trip duration, mass loss and dive depth (Watanuki, Mehlum & Takahashi 2001; Tremblay *et al.* 2003; Hamel, Parrish & Conquest 2004; Paredes, Jones & Boness 2005; Elliott, Davoren & Gaston 2007) and alter time allocation during the dive cycle (Elliott, Davoren & Gaston 2008a), our smaller, leg-mounted devices had no measurable effect on any of these parameters (Elliott *et al.* 2007). 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.* 2007, 2008b). Because we also knew when the bird arrived at the colony from the continuous watches, we were able to determine flight time between the last dive and delivery.

By assuming that the last dive or dive bout before a prey delivery represented the foraging behaviour associated with that prey item, we were able to determine dive depth, dive shape and flight time associated with each prey item. Foraging behaviour is stereotyped for a given prey item and occurs along three major axes (Elliott *et al.* 2008b) representing 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 that we could monitor variability in foraging behaviour by measuring dive depth, dive shape and flight time. We were able to determine feeding locations for benthic prey items by assuming that maximum dive depth for these deliveries was equal to the ocean depth, that birds returned via the shortest route possible that did not pass over land and that they flew at 75 km hr^{-1} from the west (Elliott & Gaston 2005; Elliott *et al.* 2008b).

STABLE ISOTOPE ANALYSIS

To determine whether specialization occurred in adult diet, we collected plasma samples (half life = about 1 week) from adult guillemots at Q-plot after each feeding watch in 2003 and 2006. All samples were kept frozen until preparation in the laboratory, where they were freeze dried. To estimate the variance in stable isotope values attributable to individual variation in diet, we subtracted 0.09, which is the individual variance in fractionation for guillemot feathers (Becker *et al.* 2007). To examine the prey base, we collected prey items as they were being delivered to chicks. Prey items were frozen until preparation in the laboratory, where they were freeze dried, and selected muscle tissue and lipids were removed.

REPRODUCTIVE SUCCESS AND SURVIVORSHIP

We monitored the breeding plot daily, so hatch date, age at departure and reproductive success were known (Gaston *et al.* 2005). Only birds with hatch dates known within 48 h were used. We assumed all chicks that disappeared after 14 days fledged successfully. We banded a sample of chicks 3–10 days old with a numbered metal band and we were therefore able to determine the age of many individuals. We calculated adult survival directly by assuming that all birds that disappeared had died because breeding plot philopatry is essentially 100% after year 5 (Steiner & Gaston 2005). We sexed one member of all pairs observed in 2005–07 by polymerase chain reaction (PCR) and assumed the sex of its partner. Many of these assignments were confirmed by observations of copulation. By back-casting, we were able to assign sex for most birds observed throughout the study.

STATISTICAL ANALYSIS

All statistics were calculated with R 2.4.1. To determine the degree of individual specialization in diet, we used three indices recommended by Bolnick *et al.* (2002): the Shannon index approximation of the proportion of within-individual component of total niche width (WIC/TNW), the mean proportional similarity between individuals and population (IS) and the mean likelihood (W_i) of individual's diet being drawn from population diet. All three indices are highly correlated (Bolnick *et al.* 2002). Although WIC/TNW has several drawbacks, including being biased by the number of prey items captured by an individual and because it does not consider an animal that captures only rare items to be specialized (Bolnick *et al.* 2002; Sargeant 2007), we include WIC/TNW in our analyses because it is intuitive and has been widely reported facilitating comparisons with other taxa (Bolnick *et al.* 2003). We also include the more statistically rigorous IS and W_i because the former is more easily interpretable and W_i has a parametric hypothesis-testing framework (Bolnick *et al.* 2002; Sargeant 2007). The null value (no specialization) for all of the indices except WIC/TNW is 1.0 and they decrease with increased specialization. The null value for WIC/TNW is determined by bootstrapping (Bolnick *et al.* 2002). The

values were calculated using INDSPEC.EXE, using the 'numerical sum' option (Bolnick *et al.* 2002). We used each delivery as a unit, without correcting for mass, because we were interested in connecting foraging behaviour with delivery item, and specific behaviour was associated with each delivery. As all specialization parameters calculated by INDSPEC.EXE are highly correlated (Bolnick *et al.* 2002), we used W_i , because it was easily calculated on an individual basis, to examine whether specialization correlated with sex, age and measures of evolutionary fitness. To determine the degree of individual specialization in foraging behaviour, we correlated dive depth, dive shape and flight time at time 1 with dive depth, dive shape and flight time at time 2, where time 1 and time 2 could be separated by days, weeks or years (see 'Temporal scale' below). We calculated repeatability in foraging tactics using the methods of Lessells & Boag (1987) and report the repeatabilities (R_{LB}) in the accompanying figures. To determine the degree of specialization in adult diet, we correlated carbon and nitrogen isotope values within and across seasons. We used VARISO.EXE (Araújo *et al.* 2007) to compare specialization in adult stable isotope signatures to prey stable isotope signatures. Because carbon and nitrogen values were highly correlated, we only analyzed nitrogen values to compare self-feeding and chick-provisioning values. Data used for specialization analyses and stable isotope analyses are included in Appendix S1 and S2.

TEMPORAL SCALE

The sampling interval for each component of our study set a lower limit on the temporal scale we could investigate. We conducted feeding watches approximately 1 week apart, so we were able to examine specialization during a single watch ('day scale'), across watches in a single season ('season scale') and across multiple years ('year scale'). TDRs were attached for 48 h periods, so we could examine specialization during a single watch ('day scale') for each individual. For a subset of individuals, TDRs were re-attached 10 days later ('season scale') or in another year ('year scale'). Stable isotopes were collected from the same individual during the same year ('season scale') and across both years ('year scale'). The time-scale for chick blood is likely their entire lifetime (about 10 days) while the time-scale for adult plasma is about 1 week. Thus, we repeated statistical analyses over multiple temporal scales and calculated coefficients of variation to determine how degree of specialization changed over time.

Results

DIET

Specialization occurred across a number of temporal scales, with specialization being higher over short time-scales (Table 1). The observed value for WIC/TNW was much less than the bootstrap value ($P < 0.0001$; Table 1). Because one out of 136 individuals had a niche width equal to zero [it brought back only capelin, *Mallotus villosus* (Müller, 1776)] which can deflate WIC/TNW values (Bolnick *et al.* 2002), we re-ran the procedure with this individual removed and WIC/TNW increased by only 0.1%. Consequently, we did not exclude individuals with niche width equal to one for the remaining analyses. Out of 97 individuals, 69 had a proportional similarity index (PS_i) with $P < 0.05$ compared to the bootstrap values. The average likelihood of an individual's

Table 1. Specialization indices for Brünnich's guillemots from Coats Island, Nunavut, Canada, across various temporal scales and for each sex. Expected values given no specialization are shown for comparison; values lower than the expected value represent specialization. Groups that are not significantly different from each other are shown in bold or italics

Index	Expected value	Time-scale			Sex	
		Year	Season	Day	Male	Female
<i>N</i>		136	175	198	34	26
TNW/BIC	0.9381 ± 0.0003	0.73	0.63 ± 0.03	0.39 ± 0.03	0.70	0.79
<i>IS</i>	1.0	0.64	0.61 ± 0.04	0.47 ± 0.02	0.61	0.68
<i>W_i</i>	1.0	0.63 ± 0.01	0.57 ± 0.03	0.43 ± 0.02	0.60 ± 0.03	0.69 ± 0.03

TNW/BIC, within-individual component of total niche width expressed as a proportion; *IS*, average overlap between an individual's diet and the overall population diet expressed as a proportion; *W_i*, mean likelihood of individual's diet drawn from population diet.

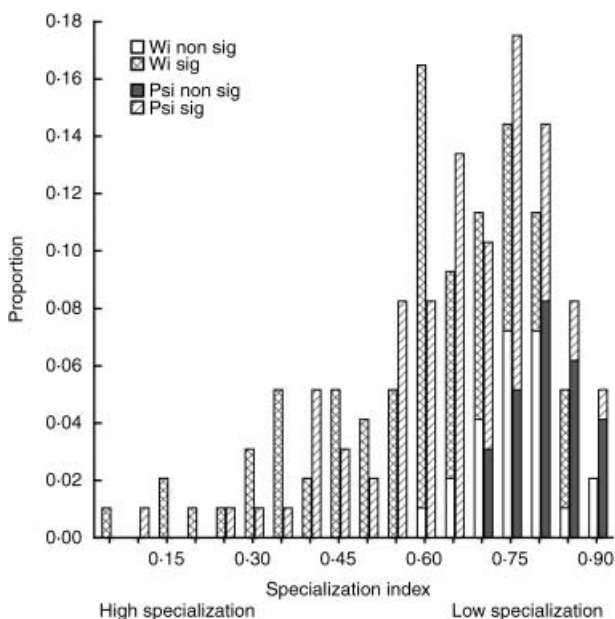


Fig. 1. Proportion of adult Brünnich's guillemots with *W_i* (white) or *PS*, (black) at or within 0.05 of a given value ($n = 136$). Individuals showing significant specialization at the $P = 0.05$ level are shown with hatched/double-hatched barring.

diet given the overall diet = 0.0382 ± 0.0006 and for 68 out of 97 individuals, the likelihood had a P -value of < 0.05 ; for 43 the likelihood had a P -value of < 0.0005 (the Bonferroni-corrected value). The distribution of specialization values was skewed (Fig. 1), with only 14% of individuals with $PS_i < 0.5$ and 20% with $W_i < 0.5$. Although females had lower specialization than males across all four indices, the differences were relatively small and neither sex was significantly different from the overall average, with the exception of *W_i* (Table 1). There was no relationship between age and *W_i* ($t_{112} = 0.39$, $P = 0.69$, $R^2 = 0.00$).

The degree of specialization is most easily illustrated by the individuals specializing on rare items. For example, Arctic shanny [*Stichaeus punctatus*, (Fabricius, 1780) 1.5%], snakeblenny [*Eumesogrammus praecius* (Krøyer, 1836), 2.1%], fish doctor (*Gymnelus* Reinhardt, 1834 sp., 2.1%) and amphipods [*Parathemisto libellula* (Lichtenstein, 1822), 6%] all constitute

less than 10% of the overall diet across all years. Out of the 136 individuals observed in the study, 59% of Arctic shanny deliveries were made by a single male, 76% of amphipod deliveries were made by four individuals, 53% of fish doctor deliveries were made by five individuals and 44% of snakeblenny deliveries were made by four individuals. The temporal persistence of these patterns is shown by the example of bird 02029, the Arctic shanny specialist, which in 1997 brought in nine (60% of its diet and 81% of all shannies brought in that year) Arctic shannies and, 10 years later (2007) brought in seven (37% of its diet and 80% of all shannies brought in that year). Arctic shanny appeared in its diet in all but one of the intervening years.

FORAGING BEHAVIOUR

Dive depth, dive shape and flight time persisted for each individual over scales of a single day to multiple years (Fig. 2). Despite smaller time-scales being averaged over fewer data points and therefore tending towards lower R^2 values, the smaller time-scales consistently had higher R^2 values, suggesting that specialization in foraging behaviour was highest over short time-scales. Furthermore, there was higher variability over long time-scales for dive shape ($F_{3,138} = 11.66$, $P < 0.001$), flight time ($F_{2,138} = 5.81$, $P = 0.004$) and dive depth ($F_{3,138} = 4.03$, $P = 0.02$) (Fig 2). The within-individual component (W/T) of dive depth was 0.44, dive shape was 0.35 and flight time was 0.34. There was no difference between sexes in dive shape (males: $28 \pm 5\%$ V-shaped; females: $35 \pm 9\%$ V-shaped; $P = 0.67$) and flight time (males: 20.8 ± 2.7 min; females: 21.2 ± 3.3 min; $P = 0.92$) between sexes, but dive depth was deeper for females (70 ± 5 m vs. 29 ± 2 m for males; $P < 0.0001$). Nonetheless, the correlation between dive depth at time 1 and dive depth at time 2 was present within each sex (e.g. year-scale: $R^2 = 0.72$, $t_{21} = 7.32$, $P < 0.00001$, males; $R^2 = 0.81$, $t_{25} = 10.03$, $P < 0.00001$, females). For the subset of known-age birds, there was no relationship between age and dive depth ($P = 0.52$), dive shape ($P = 0.64$) or flight time ($P = 0.53$).

The degree of specialization was well-exemplified by the most 'extreme' cases. The longest dive we recorded was 278 s. This dive was the final dive in a 13-dive bout where the final five dives to 120–126 m all exceeded 250 s, averaging 267 s in

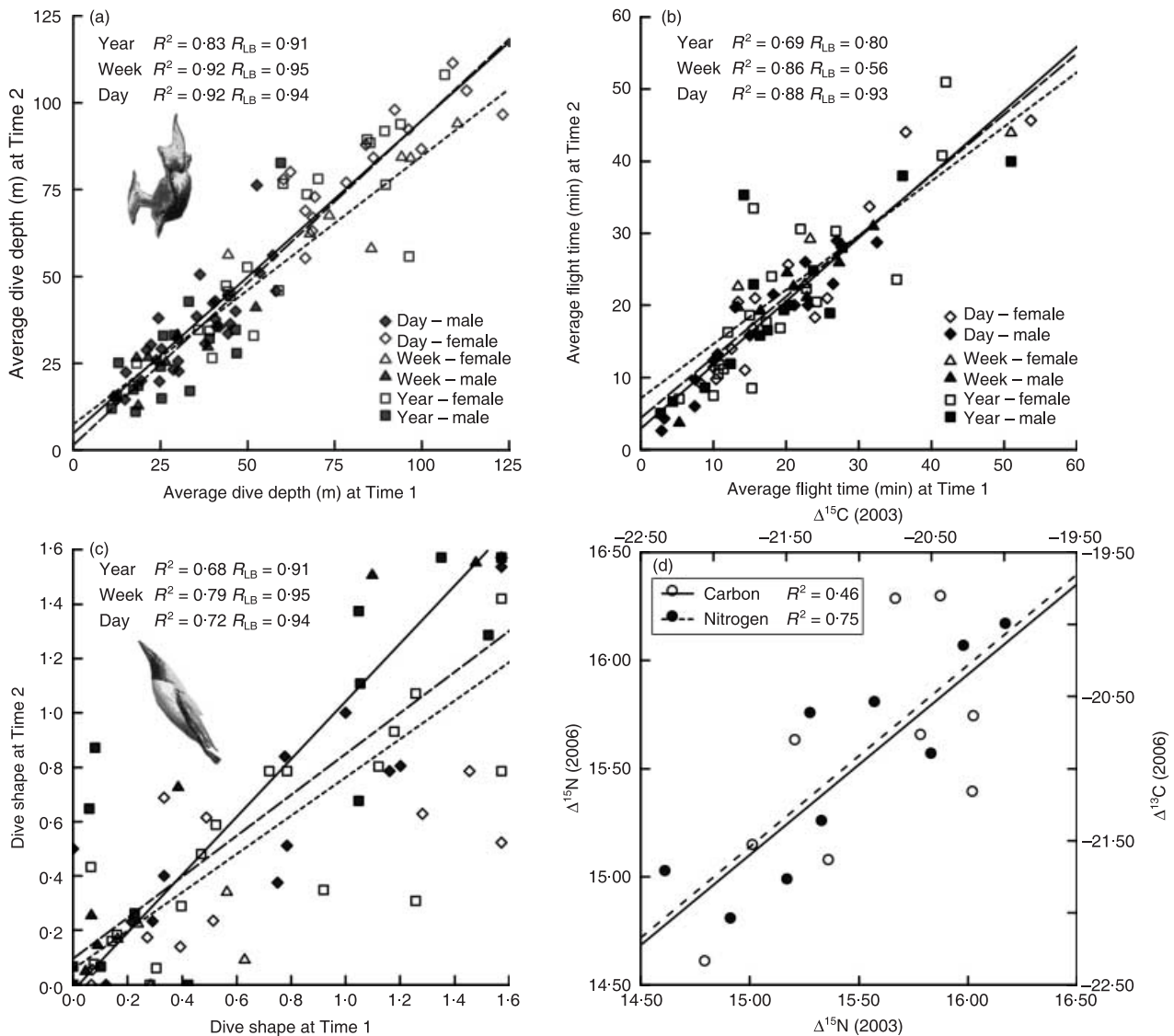


Fig. 2. Temporal persistence across individual Brännich's guillemots of average (a) dive depth, (b) flight time, (c) dive shape (proportion of V-shaped dives, arcsin-transformed) and (d) stable isotope values (‰). For (a)–(c), closed symbols represent males, open symbols represent females, squares, separated by >1 year; triangles, within a season separated by >1 week; diamonds, within 1 day; R_{LB} , Lessels and Boag repeatability (1987). For (d), closed symbols represent $\Delta^{15}\text{N}$ and open symbols represent $\Delta^{13}\text{C}$.

dive duration and 267 s in surface pause duration. The individual later returned with a sculpin. Of the 22 out of 40 045 dives that exceeded 250 s, 15 were by this individual and five more were by another individual. The maximum dive depth was 148 m, which occurred on the final dive in a four-dive bout to 143–148 m averaging 223 s in dive duration and 234 s in surface pause duration. Of 13 dives that exceeded 140 m, 11 were by the same individual.

STABLE ISOTOPES

Stable isotope values for adult plasma varied among prey items once adults were grouped according to the prey type that they fed to their chicks ($\delta^{13}\text{C}$: $F_{4,24} = 3.10$, $P = 0.04$; $\delta^{15}\text{N}$: $F_{4,24} = 7.45$, $P = 0.001$; Fig. 4). Adults feeding their chicks

small pelagic items (amphipods, small capelin and sandlance, *Ammodytes* Linnaeus, 1758 sp.) had similar stable isotope signatures (Fig. 4). Adults feeding their chicks large items [sculpin, benthics, large capelin and Arctic cod, *Boreogadus saida* (Lepechin, 1774)] had similar signatures (Fig. 4). Stable isotope signatures persisted within individuals across years (Fig. 2). The estimated WIC/TNW from chick blood was 0.53 ± 0.19 (^{13}C), 0.39 ± 0.10 (^{15}N), from adult plasma was 0.01 ± 0.21 (^{13}C) and 0.74 ± 0.09 (^{15}N) and from adult red blood cells was 0.03 ± 0.18 (^{13}C) and 0.60 ± 0.10 (^{15}N) (Fig. 3). Stable isotope values for ^{13}C and ^{15}N were correlated for both adult plasma ($r^2 = 0.10$) and chicks ($r^2 = 0.23$). There was no difference in trophic level between adults ($\delta^{15}\text{N} = 15.51 \pm 0.04$) and chicks ($\delta^{15}\text{N} = 15.41 \pm 0.23$, $t_{10} = 0.48$, $P = 0.64$).

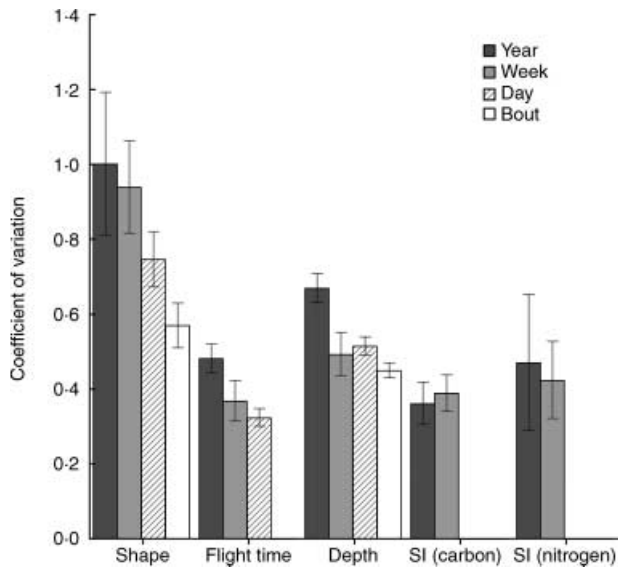


Fig. 3. Coefficient of variation for dive parameters and stable isotope values averaged across individual Brünnich's guillemots over >1 year, >1 week, within a day and within a single bout.

REPRODUCTIVE SUCCESS AND SURVIVAL

There was no relationship between W_i and departure age ($t_{129} = -1.03$, $P = 0.31$), hatch date corrected by year ($t_{202} = -0.99$, $P = 0.32$), fledging success ($t_{15} = 0.10$, $P = 0.94$), year ($t_{13} = -1.73$, $P = 0.32$), survival ($t_{96} = -0.45$, $P = 0.66$), return rate in the following year ($t_{13} = -0.21$, $P = 0.84$) or coefficient of variation of energy intake ($t_{96} = 0.96$, $P = 0.34$). Average energy intake ($t_{326} = 3.92$, $P = 0.0001$, $R^2 = 0.05$) increased with W_i .

Discussion

Although the number of individuals showing extreme specialization amounted to only the minority of the population (Fig. 1), certain individuals specialized on the same prey item over time-scales from days to years (Figs 2, 5). Specialization was highest on the scale of a single day, but some individuals maintained specialization over the entire 15-year period (cf. Svanbäck & Persson 2004). Specialization was slightly higher for males than for females, presumably because males tended to feed at dawn and dusk when rare prey items (Arctic shanny, snakeblenny, amphipods) were usually captured. Nonetheless, the difference in specialization between sexes or age groups was small (Table 1), so there remained considerable unexplained between-individual variation in diet. Individuals were more specialized over the scale of a single day compared to over the scale of several years; 27% of diversity in prey use over the scale of years was attributable to among-individual differences (i.e. $WIC/TNW = 0.73$; Table 1) while 61% of diversity over the scale of a single day was attributable to among-individual differences. Likewise, the average similarity of an individual's diet to the overall diet (IS) increased from 47% over one day to 64% over several years (Table 1). For

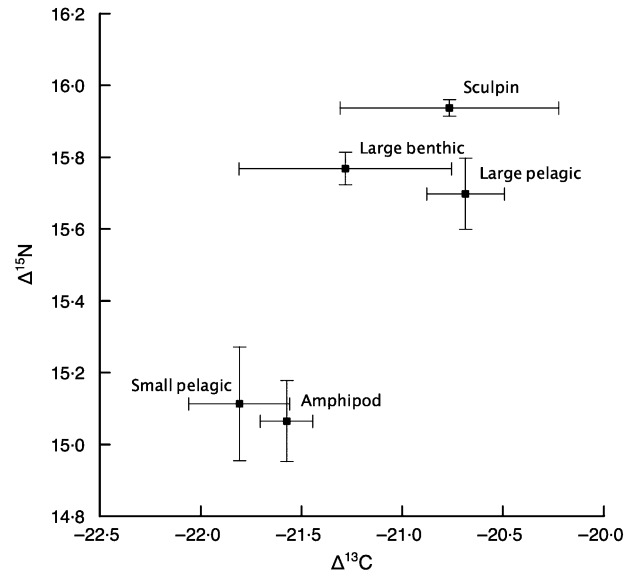


Fig. 4. Stable isotope values from adult plasma for Brünnich's guillemots that specialize (>75% of feeds) when feeding their chicks with a given prey group. 'Small' prey items were <10 cm.

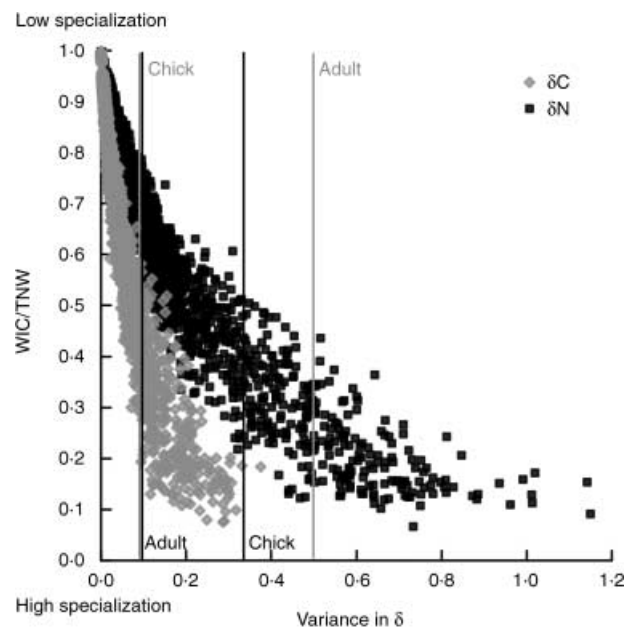


Fig. 5. Monte Carlo simulations of WIC/TNW as a function of variance in δC (grey) and δN (black) with actual values for chick blood, adult plasma shown by vertical lines. Monte Carlo simulations varied relative contributions of different prey items, with known stable isotope values, and estimated variance in adult stable isotope values for the various prey combinations.

comparison, the average value for WIC/TNW from 49 studies of specialization in a wide variety of taxa was 0.79 and varied from 0.38 to 1.0 (Bolnick *et al.* 2003). The level of specialization we observed was therefore higher than that of the average value reported in other studies, especially since most studies cited by Bolnick *et al.* (2003) measured specialization over the

time-scale of days to weeks, and the comparable value from our study is therefore 0.39 or 0.63.

Foraging behaviour was also maintained over time (Fig. 2). The degree of specialization (0.3–0.4) was somewhat greater than that for dive duration in a benthic seabird (0.51; Wanless, Harris & Morris 1992; Bolnick *et al.* 2003). As guillemots use specific foraging strategies for a given prey type (Elliott *et al.* 2008b), it appeared that a major cause of dietary specialization was the use of consistent behaviours by individuals over time. Males tended to dive shallower than females, presumably because they foraged primarily at dusk and dawn and were therefore limited by light levels (cf. Jones *et al.* 2002; Paredes, Jones & Boness 2006). Nonetheless, dive depth was maintained among individuals of both sexes over time. Otherwise, dive behaviour was independent of sex or age (Table 1) and most of the variation in average dive behaviour over time was attributable to individual differences. Other researchers have reported short-term specialization in foraging locations for guillemots based on water temperature profiles (Mehlum, Watanuki & Takahashi 2001) and routes recorded by bird-borne compasses (Benvenuti *et al.* 1998; Falk *et al.* 2000; Falk *et al.* 2002). Many other marine animals specialize on foraging tactics (Wanless *et al.* 1992; Ropert-Coudert *et al.* 2003) or locations (Irons 1998; Hamer *et al.* 2001; Davoren *et al.* 2003; Weimerskirch, Gault & Chérel 2005; Andrews *et al.* 2007; Mattern *et al.* 2007) over time. For example, individual sea otters [*Enhydra lutris* (Linnaeus, 1758)] specialize over many years on specific feeding strategies, and because foraging strategies are tailored for specific prey items, this results in a high degree of individual specialization in sea otter diet (Estes *et al.* 2003; Laidre & Jameson 2006; Tinker *et al.* 2007).

Stable isotope values from adult plasma, which presumably reflected adult diet over the scale of about 1 week, also persisted across years (Fig. 2). Furthermore, adult and chick trophic levels were similar and adults that fed their chicks amphipods or small pelagic fish tended to have similar $\delta^{15}\text{N}$ values while adults that fed their chicks larger items also tended to have similar $\delta^{15}\text{N}$ values (Fig. 5). This suggests that specialization in foraging tactics during chick-provisioning carried over to self-feeding and contrasts with other studies where adults used different foraging tactics when self-feeding and when chick-provisioning resulting in adults feeding themselves at a lower trophic level than they fed their chicks (Hobson 1993; Davoren & Burger 1999; Benvenuti, Dall'Antonia & Falk 2002). Variance in chick red blood cell $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, which averaged diet over the entire season, predicted WIC/TNW of about 0.39–0.53 (Fig. 3). These values are consistent with that recorded by direct observation over that time-scale ('week scale'; Table 1), and suggest that parents do not tend to 'cancel' each other out from the chicks' perspective (i.e. specialists do not tend to mate with generalists). The variance in adult plasma $\delta^{15}\text{N}$ values predicted WIC/TNW of 0.74, which was within the uncertainty observed by direct observation for chick feeds over a 1–2 week time-scale, and agrees with the idea that individuals feed themselves largely on the same items they feed their chicks (Fig. 3). The variance in $\delta^{13}\text{C}$ was much higher (Fig. 3), suggesting either

that we incompletely sampled the prey base or, as some plasma samples were cloudy, recent food consumption resulted in elevated lipid concentrations in the blood increasing the variance of the δC values as nutrient lipid concentrations can affect δC values (Thompson *et al.* 2000; Lesage, Hammill & Kovacs 2002; Becker *et al.* 2007; Podlesak & McWilliams 2007). Our results add to a growing body of literature showing that variance in stable isotope signature can be a useful tool for assessing specialization (Urton & Hobson 2005; Bearhop *et al.* 2006; Inger *et al.* 2006), although our small variances (0.1–0.6) despite high specialization illustrate the importance of quantitative comparison to prey variances (Araújo *et al.* 2007). Stable isotope values suggested considerable specialization in adult diet and we concluded that individuals had a small repertoire of foraging tactics that they applied repeatedly with little distinction between chick- and self-feeding.

As we found no change in specialization with age, learning presumably happens during the first few years, when the birds return to the colony but do not breed (Steiner & Gaston 2005). Over short time-scales, there is a penalty for deviating away from a successful strategy, as time and energy needs to be spent learning each new strategy (Lewis 1986; Werner & Sherry 1987; Nemiroff & Despland 2007). Over longer time-scales, prey populations are less predictable. For example, capelin has recently replaced Arctic cod as the dominant prey item in our population (Gaston *et al.* 2003). Birds unable to change their foraging strategies to accommodate this shift would pay a large penalty in terms of increased time and energy devoted to a diminishing resource.

Specialization did not have an effect on measures of evolutionary fitness although generalists tended to deliver slightly more energy per day. Specialists and generalists appeared to be different, but largely equivalent, strategies. Our results contrast with other studies of specialization in seabirds where specialists had higher reproductive success, food delivery rates, chick condition or adult survival (Pierotti & Annett 1990; Watanuki 1992; Voslamber *et al.* 1995; Annett & Pierotti 1999; Golet *et al.* 2000; Votier *et al.* 2004), although Katzner *et al.* (2005) and Votier *et al.* (2004) also found no relationship between specialization and reproductive success. The absence of a difference in the fitness of specialists and generalists begs the question 'Why specialize?' We suggest that the answer may be related to temporal changes in the predictability of resources. When resources are predictable or homogenous, specialization may result in higher fitness, whereas when resource abundance or heterogeneity is less predictable, generalists may have higher fitness (Schindler *et al.* 1997; Svanbäck & Persson 2004; Panzacchi *et al.* 2008; Tinker, Bentall & Estes 2008). As prey abundance at our study site fluctuates over a decadal scale (Gaston *et al.* 2003), there may be a dynamic evolutionary equilibrium between generalists and specialists leading to trophic polymorphism derived from the fact that generalists and specialists may each have higher fitness at various levels of prey abundance or heterogeneity (Svanbäck & Persson 2004; Panzacchi *et al.* 2008; Tinker *et al.* 2008). Indeed, the short-term studies (<10 years) that have previously shown an adaptive advantage to specialization

(Watanuki 1992; Voslamber *et al.* 1995; Golet *et al.* 2000; Votier *et al.* 2004) may have resulted from an adaptive advantage of specialization over the short-term; over the longer periods, with fluctuating prey levels, strategies may balance out.

Both diet and foraging behaviour were more specialized over short periods of time than over long periods of time (Table 1, Fig. 5). Our results fit with the suggestion of Weimerskirch (2007) that birds feeding over small spatial and temporal scales have a higher degree of specialization in foraging location. This was presumably because prey distributions were more predictable over short time-scales. Over short time-scales, repeated use of the same foraging strategies and locations may result in high prey delivery rates (e.g. Lewis 1986; Lowry & Motta 2007). In contrast to other seabirds where individual variation in foraging behaviour correlates with body mass (e.g. body oxygen stores, Watanuki, Kato & Naito 1996; Kato *et al.* 2000; Weimerskirch *et al.* 2006), variance in blood volume, hematocrit, mass and activity-specific metabolic rate was low during the chick-rearing period and there was little scope for variance in oxygen stores or buoyancy (Elliott *et al.* in press; Croll *et al.* 1992). As there was little variation in internal physiology within the chick-rearing period (as opposed to between incubation and chick rearing), specialization was likely a result of learning successful strategies and locations rather than an expression of differences in foraging capabilities resulting from variation in internal physiology (e.g. Lewis 1986; Lowry & Motta 2007; Tucker, Bowen & Iverson 2007). Thus, our results emphasize the growing consensus that many seabirds concentrate their efforts on persistent, predictable food sources by memorizing successful prey capture strategies and locations, particularly over small temporal and spatial scales (Weimerskirch *et al.* 2005; Weimerskirch 2007). Indeed, the need to learn complex foraging strategies may explain why many seabirds have delayed maturity; guillemots at our site spend 2 to 3 years as non-breeders before attempting to breed (Steiner & Gaston 2005).

Although the main cue for specialization may be cognitive, there is some evidence for a connection between internal physiology and specialization. Birds that increased time spent diving between incubation and chick rearing lost more mass than those that did not, with a decrease in metabolically active tissues resulting in improved dive performance (Elliott *et al.* in press). It is possible that individuals that specialize on deep-water or schooling prey lose mass as an adaptation to decrease diving metabolic rate (Fig. 2), thereby mitigating the effect of a dietary switch from prey items that require short dives (e.g. slow invertebrates) during incubation to those that require long dives (e.g. mobile, schooling or deep water fish) during chick rearing. In contrast, individuals that specialize on non-schooling or shallow-water prey may maintain or even gain mass.

The niche variation hypothesis states that animals with broader ecological niches should show greater variation in traits (Galeotti & Rubolini 2004; Bolnick *et al.* 2007). The higher within-population variation at our study site, where niche breadth is high, compared to sites where niche breadth is low (high Arctic, >90% Arctic cod: Falk *et al.* 2000;

Benvenuti *et al.* 2002; Falk *et al.* 2002; low Arctic, >90% daubed shanny: Birkhead & Nettleship 1987a,b; Jones *et al.* 2002) supports the niche variation hypothesis (Bolnick *et al.* 2007). Furthermore, we observe that (i) in the high Arctic there is a single species of guillemot that preys on a small diversity of prey items (Falk *et al.* 2000; Benvenuti *et al.* 2002; Falk *et al.* 2002); (ii) at our study site, there is a single species of guillemot with many trophic polymorphisms, each specializing on one or several of a variety of prey items; and (iii) in the low Arctic where marine communities are even more diverse, there are two species of guillemot that are morphologically almost identical but differ in diet (Birkhead & Nettleship 1987a,b). We therefore suggest that individual dietary and foraging specialization may have been an important precursor to the evolutionary radiation of seabirds, which often include several closely related sympatric taxa that differ largely in diet and foraging tactics (Dieckmann & Doebeli 1999; Friesen, Burg & McCoy 2007a; Friesen *et al.* 2007b).

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Supplementary material

The following supplementary material is available for this article online:

Appendix S1. Data used for specialization analyses – prey deliveries made by individually identified birds over a 15-year period

Appendix S2. Stable isotope values for adult plasma and chick whole blood – data used in Figs 2d, 3 and 5

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