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SUBCOLONY VARIATION IN BREEDING SUCCESS IN THE TUFTED PUFFIN (*FRATERCULA CIRRHATA*): ASSOCIATION WITH FORAGING ECOLOGY AND IMPLICATIONS

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Abstract.—Large-scale oceanographic processes are the main drivers of seabird breeding success, but small-scale processes, though not as well understood, can also be important. We compared the success of Tufted Puffins (*Fratercula cirrhata*) breeding at two subcolonies only 1.5 km apart on Triangle Island, British Columbia, Canada, 2002–2005. In addition, we used stable-isotope analysis to test the hypothesis that parental foraging strategies differed between the two subcolonies, potentially underlying the variation in breeding success. Success was concordant across years at the two sites but, overall, Tufted Puffins bred more successfully at Strata Rock than at Puffin Rock. They raised chicks in all four years at Strata Rock, but in only three years at Puffin Rock; in two of those three years, Strata Rock chicks were, on average, 60 g and 100 g heavier than Puffin Rock chicks just before fledging. Discriminant analysis of carbon and nitrogen stable-isotope ratios in egg yolk and chick blood in 2004 and 2005 indicated that parental foraging differed between the two subcolonies, with both spatial ($\delta^{13}C$) and trophic-level ($\delta^{15}N$) differences involved. Thus, our study demonstrates the existence of foraging asymmetries in a pelagic seabird at a small spatial scale (between subcolonies), complementing patterns found at larger scales (between colonies). Moreover, the foraging asymmetries were associated with inequalities in fitness measures. We conclude that small-scale processes—in this case, systematic differences in the foraging ecology of local groups—can interact with large-scale oceanographic processes to determine seabird breeding success. *Received 21 February 2006, accepted 28 September 2006.*

Key words: breeding success, *Fratercula cirrhata*, provisioning, stable isotopes, subcolonies, Tufted Puffin.

Variation sous-coloniale du succès de reproduction de *Fratercula cirrhata*: Association avec l'écologie de la quête alimentaire et implications

Résumé.—Les processus océanographiques à grande échelle sont les principaux phénomènes influençant le succès de reproduction des oiseaux de mer mais les processus à petite échelle, même s'ils ne sont pas aussi bien compris, peuvent aussi être importants. Nous avons comparés le succès de *Fratercula cirrhata* se reproduisant à deux sous-colonies distantes de seulement 1,5 km sur l'île Triangle, en Colombie-Britannique (Canada), de 2002 à 2005. De plus, nous avons utilisé

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l'analyse des isotopes stables afin de tester l'hypothèse selon laquelle les stratégies parentales de quête alimentaire diffèrent entre les deux sous-colonies, ce qui peut impliquer une variation du succès de reproduction. Le succès concordait entre les années aux deux sites mais de façon générale les Macareux huppés se reproduisaient avec plus de succès à Strata Rock qu'à Puffin Rock. Ils ont élevé des poussins à Strata Rock au cours des quatre années de l'étude mais seulement pendant trois ans à Puffin Rock. Lors de deux de ces trois années, les poussins de Strata Rock étaient, en moyenne, 60 g et 100 g plus lourd que ceux de Puffin Rock juste avant l'envol. Une analyse discriminante des rapports des isotopes stables de carbone et d'azote dans le vitellus des œufs et le sang des poussins en 2004 et 2005 a indiqué que les stratégies parentales de quête alimentaire étaient différentes entre les deux sous-colonies, avec des différences au niveau spatial ($\delta^{13}C$) et trophique ($\delta^{15}N$). Ainsi, notre étude démontre l'existence d'asymétries dans la quête alimentaire d'un oiseau de mer pélagique à une petite échelle spatiale (entre des sous-colonies), ce qui complémente les patrons trouvés à des échelles plus grandes (entre les colonies). De plus, les asymétries dans la quête alimentaire étaient associées à des inégalités dans les mesures du fitness. Nous concluons que les processus à petite échelle – dans ce cas-ci, les différences systématiques dans l'écologie de la quête alimentaire de groupes locaux – peuvent interagir avec des processus océanographiques à grande échelle pour déterminer le succès de reproduction d'oiseaux de mer.

WHILE BREEDING, PELAGIC seabirds typically travel long distances away from colonies in search of prey distributed in patches at sea. This has been a key factor in the evolution of life-history strategies characterized by high adult survival rates, delayed recruitment, and low annual fecundity (Lack 1968, Gaston 2004). Access to adequate food to support successful breeding can vary across a wide range of spatial and temporal scales (Schneider and Duffy 1985). Multi-annual events, such as shifts in the North Atlantic Oscillation (Thompson and Ollason 2001), as well as annual events, such as El Niño–Southern Oscillations (Schreiber and Schreiber 1984), dramatically affect food availability for marine birds over very large areas. Food availability also can vary among breeding colonies, because of factors such as the distance to profitable feeding areas (Davoren and Montevecchi 2003) and colony size, which influences the intensity of intraspecific competition (Forero et al. 2002). In addition, feeding conditions at sea often vary from day to day because of the vagaries of weather (Finney et al. 1999).

However, processes operating at smaller scales also influence seabird breeding success. For example, older, more experienced birds often breed successfully while their inexperienced neighbors do not (Daunt et al. 1999). Experienced birds may be more efficient at obtaining food, may expend more energy raising offspring, or both (Forslund and Pärt 1995). In addition, the success of individuals breeding at the same site could differ if they systematically seek different prey types (Annett and Pierotti 1999) or tend to return repeatedly to distinctive feeding areas (Irons 1998). Whatever its cause and the scale at which it operates, variation in food availability can produce marked differences in the life-history trajectories of individuals (Hennicke and Culik 2005).

Here, we investigate the magnitude and underlying causes of variation in breeding success at a spatial scale that has received little attention: between discrete breeding aggregations (hereafter "subcolonies") at a single breeding colony. At Triangle Island, British Columbia, Canada, Tufted Puffins (*Fratercula cirrhata*; hereafter "puffins") breed in subcolonies that vary in size from tens to thousands of pairs (Rodway et al. 1990). Puffins are the most pelagic of the Alcidae, foraging in oceanic waters ≤100 km from the colony while raising at most a single chick annually in an earthen burrow excavated in deep soil (Piatt and Kitaysky 2002).

During preliminary investigations in 2002, we found that puffins breeding at one subcolony (Strata Rock) were raising large, heavy chicks, whereas puffins at another subcolony (Puffin Rock) only 1.5 km away were failing. We conducted systematic research in three subsequent years (2003–2005) to determine whether the difference in breeding success at the two subcolonies was consistent and, if it was, its possible behavioral basis. In 2002, and again in 2003, we noted that puffins at Strata Rock continued to provision their chicks with large Pacific sandlance (*Ammodytes hexapterus*), believed to be the puffins' preferred prey species (Gjerdrum et al. 2003), long after this became a rare item delivered to chicks at Puffin Rock. This led us to hypothesize that puffins breeding at the two subcolonies employ different foraging strategies to obtain prey with which to provision offspring. Cultural foraging asymmetries have been documented in other seabirds, at larger scales (between breeding colonies up to many kilometers apart; Hamer et al. 2001, Bull et al. 2004, Grémillet et al. 2004), and also in other avian species (e.g., Goss-Custard 1996). In 2004 and 2005, we collected fresh eggs and chick blood from both subcolonies to test that hypothesis, predicting that eggs, chicks, or both at Puffin Rock could be distinguished from those at Strata Rock on the basis of their stable isotopic signatures (δ^{15}N and δ^{13}C). Stable-isotope analysis (SIA) has proven effective at identifying spatial, temporal, and trophic-level differences in foraging between individuals or groups in other species (Hebert et al. 1999), including gender-, age-, and colony-based differences in seabird foraging behavior (Forero et al. 2005).

METHODS

Study site.—The study was conducted at Triangle Island, British Columbia (50°52′N, 129°05′W), during the 2003–2005 breeding seasons. We also include relevant observations from 2002. Triangle Island supports the largest colony of puffins in British Columbia (~25,000 breeding pairs, including ~11,000 on Puffin Rock and 2,000 on Strata Rock). However, Strata Rock is within view of other subcolonies along the east side of Triangle Island that, in aggregate, support ~11,000 pairs (Vermeer 1979, Rodway et al. 1990).

Field protocols and sampling.—We used binoculars and spotting scopes to observe puffins daily from a viewing blind. We recorded the date when the first adult puffin was seen delivering food to its offspring in a burrow and used that to gauge the start of hatching. We then waited 15 days before beginning to weigh and measure puffin chicks at 10-day intervals in an area of Puffin Rock (hereafter "Old Plot") separate from our two main study sites (hereafter "Puffin Rock" and "Strata Rock"). The 15-day delay allowed most adult puffins to hatch their chicks and to cease constant chick brooding (Piatt and Kitaysky 2002). In this way, we measured the progression of breeding with minimum disturbance to this highly sensitive species (Pierce and Simons 1986).

As the earliest-hatched chicks on Old Plot approached fledging (typically at about 40–45 days of age), we excavated large numbers of burrows on a single day at Puffin Rock and Strata Rock. All chicks found were weighed (±2 g with a 300-g or 1-kg Pesola spring balance) and measured (maximum flattened wing chord, ±1 mm with a rule). These data enabled us to compare burrow occupancy and chick growth among undisturbed puffins at the two subcolonies. In 2002, individual chicks were weighed and measured at five-day intervals beginning in the middle of the chick-rearing period at both Puffin Rock and Strata Rock; we report observations collected late in the chick period, 17–21 August.

In 2004 and 2005, we collected 10 fresh eggs from early-laying puffins on Puffin Rock and Strata Rock, under permit from the Canadian Wildlife Service. Each egg was weighed on an electronic balance (±0.1 g), and its length and maximum breadth were measured with Vernier calipers (±0.1 mm). Eggs were then frozen (in 2004) or stored in ethanol (in 2005). In 2004, when we later visited Puffin Rock and Strata Rock just before the start of fledging, we also bled 10 chicks at each site (0.2 mL drawn from the brachial vein). In 2005, only six and seven chicks were bled at Puffin Rock and Strata Rock, respectively—a year of poor breeding success for all seabirds at Triangle Island. Blood samples were immediately frozen (in 2004) or placed in ethanol (in 2005). The eggs and chick blood samples were used to compare foraging ecology of adult puffins at the two subcolonies using stable-isotope analysis.

Stable-isotope analyses.—Nitrogen stable-isotope ratios can be used to assess the trophic level at which a consumer has fed, because ^{15}N becomes systematically enriched at successive trophic levels (Peterson and Fry 1987). Carbon stable-isotope ratios can be used to infer the type of marine habitat in which a consumer has fed, because ^{13}C is enriched in benthic or inshore environments compared with pelagic or offshore environments (DeNiro and Epstein 1978).

We removed lipids from egg yolks (Blight and Dyer 1959), so that δ^{15}N and δ^{13}C signatures were derived solely from yolk protein. Chick blood samples were freeze-dried for 12 h. Lipid-free yolk samples and freeze-dried blood samples were then ground to a powder using a mortar and pestle and stored in glass vials.

Samples were analyzed at the Stable Isotopes in Nature Laboratory at the University of New Brunswick. Approximately 0.2 mg of dried, powdered sample was loaded into a tin capsule and combusted in a Carlo Erba NC2500 elemental analyzer (Thermo Fisher Scientific, Milan, Italy); resultant gases were delivered via continuous flow to a Finnigan Mat Delta XP mass spectrometer (Thermo Scientific, Waltham, Massachusetts). Ratios of ^{12}C/^{13}C or ^{14}N/^{15}N are expressed in delta (δ) notation, measured in parts per thousand (‰), and reported relative to international standards for carbon (Peedee Belemnite Carbonate, PDB) and nitrogen (atmospheric N_2, air). Isotope values were corrected using International Atomic Energy Agency (IAEA) standards for all runs: sucrose (CH6): $\bar{x} = 10.43 \pm 0.05$‰ SD; polyethylene (CH7): $\bar{x} = -31.81 \pm 0.03$‰ SD; N1: $\bar{x} = 0.26 \pm 0.24$‰ SD; and N2: $\bar{x} = 20.32 \pm 0.12$‰ SD. In assessing the accuracy of the mass spectrometers, one standard deviation of sample repeats within runs were δ^{13}C < 0.10‰ and δ^{15}N < 0.14‰.

Statistical analyses.—We used *t*-tests to compare egg size measurements between the two subcolonies. To assess differences in chick growth rates between subcolonies, we used analysis of covariance (ANCOVA), with mass as a dependent variable, wing length (a rough surrogate for age) as a continuous independent variable, and subcolony as a grouping variable. Analyses were run for each year separately, because chicks were not produced at both subcolonies in all four years. Those analyses were first run including both main effects plus the subcolony * wing length interaction term; however, if the interaction term was not significant ($P > 0.05$), the analysis was rerun including only main effects.

Finally, in 2004 and 2005, we used discriminant analysis to test whether eggs, chicks, or both at Puffin Rock could be distinguished from those at Strata Rock on the basis of their δ^{15}N and δ^{13}C signatures. In these analyses, Wilks' lambda tests for the equality of the centroids in bivariate plots (i.e., δ^{15}N and δ^{13}C). As noted, we used different preservation techniques in the two years because of field constraints; that may preclude reliable inference about interannual differences in isotopic signatures (Feuchtmayr and Grey 2003). In addition, we have no information on the isotopic fractionations involved in synthesizing egg and blood proteins from diet, because we did not collect prey samples used throughout breeding; that precludes reliable inference about isotopic differences between the two sample types. Consequently, we took a conservative approach, restricting our analyses to pairwise (Puffin Rock or Strata Rock) comparisons of the same sample type (yolk or blood) within each year.

Results

Egg size and timing of laying.—Egg size differed little between the two subcolonies in either 2004 or 2005 (*t*-tests, all $P > 0.1$; Table 1). Eggs were ~2% less dense when measured at Strata Rock than at Puffin Rock in 2004 ($t = 3.90$, df = 18, $P < 0.01$), which suggests that laying began earlier at Strata Rock, but there was no such difference

Table 1. Measurements of Tufted Puffin eggs at Puffin Rock and Strata Rock, 2004–2005. Among egg measurements, only egg density in 2004 differed significantly between the two subcolonies.

	2004		2005	
	Puffin Rock	Strata Rock	Puffin Rock	Strata Rock
Date eggs measured	26 May	27 May	24 May	26 May
Number of eggs measured	10	10	10	10
Length (mm)	70.4 ± 1.4	72.1 ± 2.7	71.0 ± 1.5	71.5 ± 1.7
Breadth (mm)	48.4 ± 1.0	49.0 ± 1.2	48.9 ± 1.3	48.6 ± 1.7
Volume index (cm^3)	168.0 ± 8.0	173.0 ± 8.9	169.6 ± 9.0	169.0 ± 14.7
Mass (g)	89.9 ± 4.0	90.2 ± 4.9	90.9 ± 4.5	90.3 ± 6.6
Density index (g cm^{-3})	0.53 ± 0.01	0.52 ± 0.01	0.54 ± 0.01	0.54 ± 0.01

in 2005 ($t = 0.20$, df = 18, $P > 0.8$; Table 1). If we assume that the Puffin Rock eggs were fresh in 2004, and that eggs lose 18% of their initial mass (Rahn and Ar 1974) over 44 days of incubation (Piatt and Kitaysky 2002), the 2% difference in density amounts to ~5 days. On the basis of dates when we first observed puffins delivering food to offspring at Puffin Rock, laying was earliest in 2004, one week later in 2005, and two additional weeks later in 2003 (Table 2).

Burrow occupancy.—We found fewer puffin chicks at Puffin Rock (range: 0–30% occupancy) than at Strata Rock (range: 11–66% occupancy) in all three years, though the difference was very small in 2005 (Table 2). Although we do not know how occupancy varied at laying between the two sites, chicks hatched in 12 of the 30 burrows (40%) monitored from 15 days after the start of hatching on Old Plot in 2003, yet none survived to fledge. Thus, total breeding failure at Puffin Rock in that year was attributable to a high rate of chick mortality, not to low burrow occupancy.

Chick size and mass.—In 2002, puffin chicks on Puffin Rock were lighter in mass at a given wing length than chicks on Strata Rock (ANCOVA, model $R^2 = 0.63$, wing length $F = 33.32$, df = 1 and 32, $P < 0.001$; subcolony $F = 6.74$, df = 1 and 32, $P < 0.05$). As they approached fledging, Strata Rock chicks were, on average, ~60 g heavier than Puffin Rock chicks (Fig. 1). We found no live puffin chicks on Puffin Rock in 2003 (Table 2), but we found seven apparently healthy chicks on Strata Rock (mean ± SD, 318.1 ± 34.1 g in mass, and 109.0 ± 7.5 mm in wing length). In 2004, the ANCOVA (model $R^2 = 0.79$) included a significant wing length * subcolony interaction ($F = 6.09$, df = 1 and 53, $P < 0.05$). Thus, the slope of the line relating chick mass to wing length was steeper at Strata Rock than at Puffin Rock, so that Strata chicks were, on average, ~100 g heavier as they approached fledging (Fig. 1). Data were too few in 2005 for meaningful statistical tests. However, visual inspection indicated that, for the few chicks that survived, the mass-to-wing-length relationship was similar at the two subcolonies (Fig. 1).

Stable-isotope signatures.—Using discriminant analysis, we found significant differences between Puffin Rock and Strata Rock egg yolk isotopic signatures in 2005 ($R^2 = 0.32$, Wilks' lambda = 0.68, $F = 4.03$, df = 2 and 17, $P < 0.01$), and chick blood isotopic signatures in 2004 ($R^2 =$

Table 2. Tufted Puffin burrow occupancy rates at Puffin Rock and Strata Rock, 2003–2005.

	2003		2004		2005	
	Puffin Rock	Strata Rock	Puffin Rock	Strata Rock	Puffin Rock	Strata Rock
First feeding observed	14 July	–	23 June	–	1 July	–
Burrow check date	26 August	26 August	6 August	5 August	23 August	22 August
Number of burrows checked	43	46	67	53	53	56
Number of burrows with chicks (%)	0 (0%)	7 (15%)	20 (30%)	35 (66%)	4 (8%)	6 (11%)

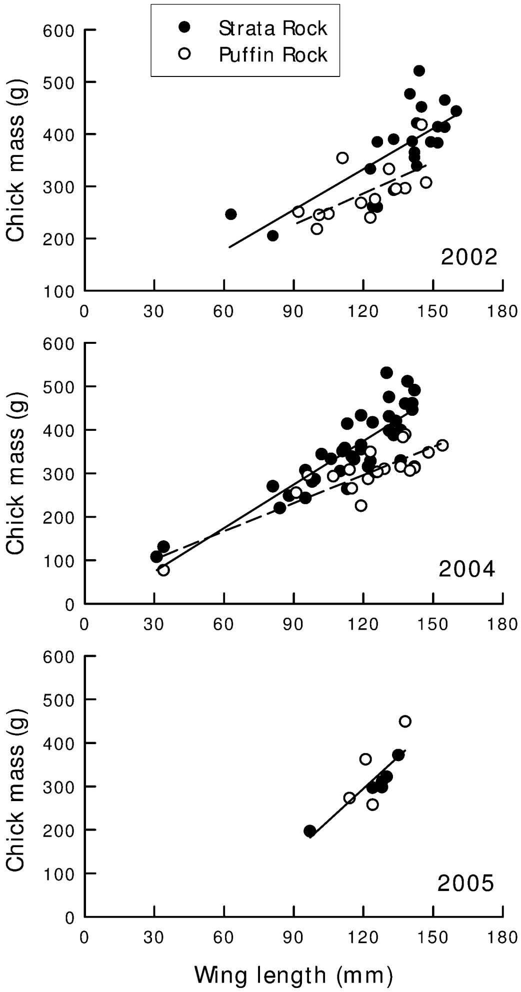

FIG. 1. Mass in relation to wing length for Tufted Puffin chicks weighed and measured at Puffin Rock (open symbols) and Strata Rock (closed symbols), Triangle Island, 2002–2005. Relationships differed significantly between subcolonies in 2002 (in elevation) and 2004 (in slope).

0.66; Wilks' lambda = 0.34, F = 16.28, df = 2 and 17, $P < 0.001$; Fig. 2). There was a difference of similar magnitude in chick blood in 2005 (R^2 = 0.38), which with smaller sample size was marginally nonsignificant (Wilks' lambda = 0.62, F = 3.08, df = 2 and 10, $P < 0.1$). Yolk signatures differed little between subcolonies in 2004 (R^2 = 0.17, Wilks' lambda = 0.83, F = 1.74, df = 2 and 17, $P > 0.2$). Of note, both spatial (i.e., $\delta^{13}C$) and trophic-level (i.e., $\delta^{15}N$) effects contributed to the differences, but to varying degrees (Fig. 2).

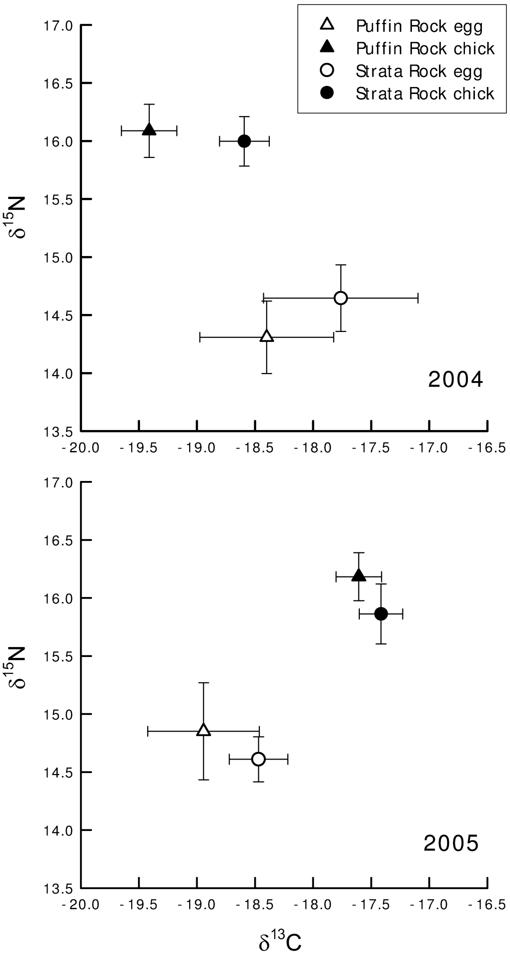

FIG. 2. Mean $\delta^{13}C$ and $\delta^{15}N$ (±95% confidence intervals) values for Tufted Puffin egg yolks (open symbols) and chick blood (closed symbols) at Puffin Rock (triangles) and Strata Rock (circles), 2004–2005. All n = 10, except for 2005 chick blood samples, for which n = 6 at Puffin Rock and n = 7 at Strata Rock. On the basis of discriminant analysis, isotopic signatures differed significantly between subcolonies in chick blood in 2004 and in egg yolks in 2005, and marginally in chick blood in 2005.

DISCUSSION

Puffins bred more successfully at Strata Rock than at Puffin Rock, two subcolonies separated by only ~1.5 km, in three out of four years on Triangle Island. At least a few viable puffin chicks were produced at Strata Rock in all years, whereas none survived on Puffin Rock in 2003, a year of moderate El Niño conditions. In both 2002 and 2004, Tufted Puffin chicks were substantially heavier (by about 60 g and 100 g) as they approached fledging at Strata Rock than at Puffin Rock, respectively. Only in 2005, a very poor year, were occupancy rates and chick masses similar at the two subcolonies. Overall, annual success tended to be concordant at the two sites.

In addition, there was strong evidence that puffins that bred at Strata Rock and Puffin Rock differed in the manner in which they foraged to form eggs and provision chicks. On the basis of discriminant analysis of carbon and nitrogen stable-isotopic ratios, foraging ecology differed between subcolonies during egg production in 2005, though egg size and timing of breeding were similar. Foraging also differed during chick rearing in 2004, when chick growth differed strongly between subcolonies, and to a lesser extent in 2005, when growth was similar in the few chicks that survived. To varying degrees, both spatial ($\delta^{13}C$) and trophic-level ($\delta^{15}N$) differences were involved. Observations in 2002 and 2003, when we saw Pacific sandlance delivered to chicks until late in the season at Strata Rock but not at Puffin Rock, were consistent with results of stable-isotope analysis in subsequent years. Thus, our study demonstrates the existence of foraging asymmetries in a pelagic seabird even at a relatively small spatial scale, complementing patterns found at large scales (Hamer et al. 2001, Bull et al. 2004, Grémillet et al. 2004, Forero et al. 2005).

Unlike in 2005, puffins laid ~5 days earlier at Strata Rock than at Puffin Rock in 2004; but as in 2005, egg size was similar. Although the difference in timing may have contributed to differences in chick growth rates and isotopic signatures in 2004, we suspect that any effect was likely to be small. First, we found marked differences in chick masses at the two subcolonies, even for chicks of a given wing length, thus presumably similar in age. Second, puffins form egg yolk over ≥10 days (Roudybush et al. 1979), and isotopic signatures in blood reflect diet over ≥20 days (Bearhop et al. 2002), whereas puffin nestling periods are >40 days (Piatt and Kitaysky 2002). Thus, the isotopic signatures reflected diet over periods that largely (eggs) or entirely (blood) overlapped at the two subcolonies.

Probably the most significant question arising from our study is whether the foraging asymmetries were directly responsible for the inequalities in fitness parameters. We suggest that there was a causal link, judging from observations in 2002 and 2003. However, Harris (1980) attributed subcolony variation in Atlantic Puffin (*F. arctica*) breeding success to differences in nesting habitats and the associated risks posed by Great Black-backed Gulls (*Larus marinus*). At Triangle Island, more Glaucous-winged Gulls (*L. glaucescens*) nest near puffin breeding areas on Puffin Rock than on Strata Rock, and they occasionally kleptoparasitize puffins returning with food for offspring (St. Clair et al. 2001). Puffins breeding at Puffin Rock may lose food to gulls more often. In addition, some puffins expend considerable energy engaging in evasive behaviors (Blackburn 2004), and those expenditures could influence other facets of foraging and provisioning and, thus, breeding success. However, puffins that breed in steeply sloping habitat are hardly susceptible at all to gulls (St. Clair et. al. 2001) and behave accordingly (Blackburn 2004). Our comparisons of growth rates at Strata Rock and Puffin Rock involved almost exclusively birds in sloping habitats, because they form the vast majority and because we found almost no chicks in any year in burrows on level habitat. We conclude that differences in kleptoparasitism risk are very unlikely to account for the differences in breeding success between the two sites.

We can only speculate on what behavioral mechanisms might underlie the subcolony differences in isotopic signatures. Perhaps puffins departing from distinctive subcolonies tend to start out in the same general direction, cueing in on other departing or returning birds (information transfer; Ward and Zahavi 1973) or birds encountered feeding at sea (local enhancement; Buckley 1997). As a result, individuals might simply be more likely to overlap in foraging areas, profitable or unprofitable, with other individuals from their own subcolony. There could also be systematic differences in important attributes of birds breeding at the different subcolonies (e.g., their age, body condition, or individual life-history tactics), but we have no information with which to assess that possibility.

Finally, there was concordance in annual breeding success at the two subcolonies, which suggests that large-scale oceanographic influences were the primary drivers of puffin breeding success at Triangle Island during our study. Recent research has greatly advanced our understanding of the mechanisms linking large-scale oceanographic conditions and seabird demography (Thompson and Ollason 2001, Gaston et al. 2005). However, our results show that, even on a very small spatial scale within a very large seascape, differences in the foraging behavior of local groups of individuals can link strongly with fitness measures. We believe that this finding has important implications for the design, execution, and interpretation of long-term marine research and monitoring programs. In particular, we suggest that detailed investigation of the extent and magnitude of such small-scale effects in other oceanic regions and in other species of highly mobile marine organisms would be enlightening.

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