



## 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

While breeding, pelagic seabirds typically travel long distances

difference in breeding success at the two sub-colonies was consistent and, if it was, its possible behaviour

We removed lipids from egg yolks (Blight and Dyer 1959), so that  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  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 mo

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 (Pia 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

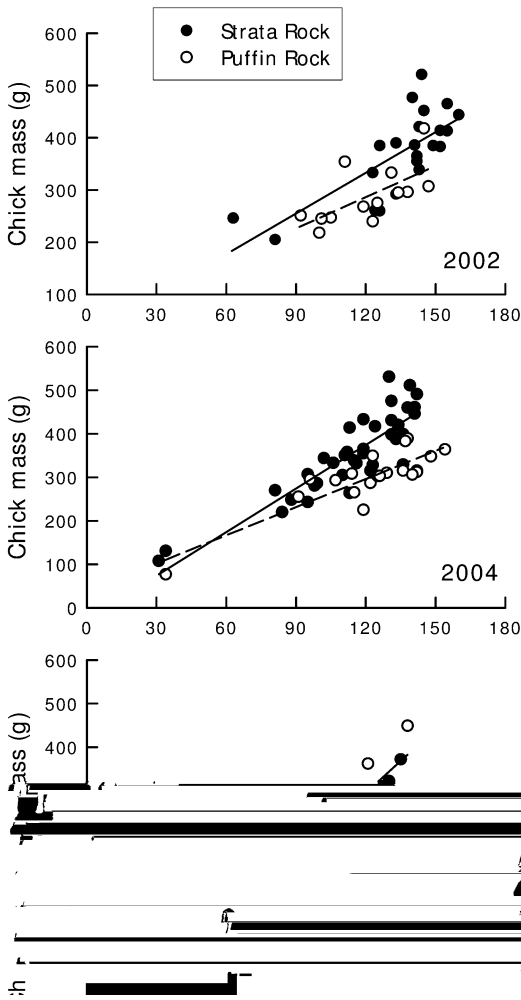


Fig. 1. Mass in relation to wing length for Tufted Puffin chicks weighed and measured at Puffin Rock (open symbols) and Strata Rock (closed symbols), Triangle Island, 2002–2005. Relationships differed significantly between subcolonies in 2002 (in elevation) and 2004 (in slope).

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).

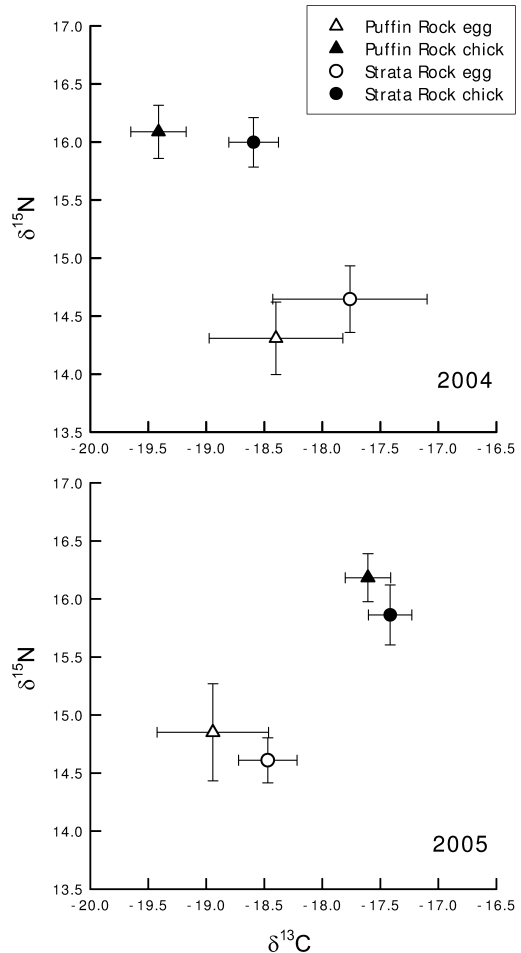


Fig. 2. Mean  $\delta^{13}C$  and  $\delta^{15}N$  ( $\pm 95\%$  confidence intervals) values for Tufted Puffin egg yolks (open symbols) and chick blood (closed symbols) at Puffin Rock (triangles) and Strata Rock (circles), 2004–2005. All  $n = 10$ , except for 2005 chick blood samples, for which  $n = 6$  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 Pu n Rock in 2003, a year of moderate El Niño conditions. In both 2002 and 2004, Tuffed Pu n chicks were substantially heavier (by about 60 g and 100 g) as they approached fledging at Strata Rock than at Pu n 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 pu ns that bred at Strata Rock and Pu n 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 sand-lance delivered to chicks until late in the season at Strata Rock but not at Pu n 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, pu ns laid ~5 days earlier at Strata Rock than at Pu n 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, pu ns 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 pu n nestling periods are >40 days (Pia 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 Pu n (*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 pu n breeding areas on Pu n Rock than on Strata Rock, and they occasionally kleptoparasitize pu ns returning with food. (Harris 1980, p. 116)

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 of marine reserves and other



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