Sex-specific differences in body condition indices and seasonal mass loss in Tufted Puffins

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ABSTRACT. Reduced prey availability can affect the growth and survival of nestling seabirds. However, few studies have demonstrated similar effects on indices of adult body condition. We examined body condition and seasonal mass loss of breeding adult male and female Tufted Puffins (*Fratercula cirrhata*) at Chiniak Bay, Kodiak Island, Alaska, in 2004–2005. We determined sex using genetic analysis, developed a discriminant function to determine sex using morphometric measurements, and examined the body condition of adult males and females relative to the growth rates of their offspring. We found that morphological measurements were only moderately useful for sexing Tufted Puffins, with 74% of adults ($N = 176$) correctly classified. We also found that the relationship between adult body mass and size differed between sexes and conclude that body condition indices must be calculated separately for each sex to avoid inter- and intrasexual bias. Body condition of male and female Tufted Puffins declined during the chick-rearing period. However, body condition of females did not differ between years, whereas male condition declined to a greater degree during 2004 when the mass of young at fledging was significantly lower. Although these results suggest that adult male Tufted Puffins sacrifice their own body condition in years of diminished nestling growth and females do not, reasons for this apparent intersexual difference in reproductive strategies remain unclear.

SINOPSIS. **Diferencias específicas por sexo en índices de la condición corporal y pérdida estacional de masa en individuos de *Fratercula cirrhata***

Una reducida disponibilidad de presas puede afectar el crecimiento y la sobrevivencia de pichones de aves marinas. Sin embargo, pocos estudios han demostrado efectos similares en índices de la condición corporal de adultos. Durante el 2004–2005, examinanos la condición corporal y la pérdida estacional de masa de adultos reproductivos de ambos sexos de *Fratercula cirrhata*. El estudio se hizo en la Bahía Chiniak, de la isla Kodiak, Alaska. Determinamos el sexo de las aves mediante análisis genético, y luego desarrollamos un modelo de funćion discriminativa pra determinar el sexo utilizando morfometría. En las aves examinamos la condición de adultos de ambos sexos para relacionarlos dicho estado a la tasa de crecimiento de los pichones. Encontramos que la morfometría era moderadamente útil para sexar a las aves, clasificando tan solo un 74% ($N = 176$) de los adultos. También encontramos que la relación entre la masa corporal y el tamaño en los adultos difería entre los sexos y concluimos que los índices de la condición corporal debían calcularse por separado, en cada sexo, para evitar sesgo inter e intrasexual. La condición corporal de los machos y las hembras en la especie, se redujo durante el periodo de cría de los pichones. Sin embargo, no se encontraron diferencias en la condición corporal de las hembras entre años, mientras que la de los machos se redujo en gran medida durante el 2004, cuando la masa corporal de los pichones (al tiempo de volar) se redujo significativamente. Estos resultados sugieren que los machos adultos sacrifican su condición corporal en años donde hay reducción en el crecimiento de los pichones, mientras que las hembras no lo hacen. La razón de esta diferencia en la estrategia reproductiva intersexual permace sin resolverse.

Key words: Alcidae, body condition, cost of reproduction, fledging mass, *Fratercula cirrhata*, parental care, seabird, sexual dimorphism

Marine ecosystems are dynamic environments with oceanographic conditions fluctuating at a variety of temporal and spatial scales. Perturbations in physical state affect marine food webs (McGowan et al. 1998, Anderson and Piatt 1999) and, in turn, affect the reproductive success of seabirds by altering the availability of prey for young (Hedd et al. 2002, Durant et al. 2003) and by limiting the energy reserves of adults (Chastel et al. 1995). The effects of reduced prey availability on nestling growth and fledging success are well documented (Litzow et al. 2002, Suryan et al. 2002), but few studies have demonstrated similar effects on indices of adult body condition (Bolton et al. 1993, Kitaysky et al. 1999).

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Life-history theory stipulates that animals face a trade-off between current reproductive effort and future reproductive output (Lack 1968). Thus, a "cost of reproduction" exists and animals must balance investment in current reproduction with their own probability of survival in a manner that maximizes lifetime fitness (Williams 1966). Seabird life histories are characterized by relatively long lives with low annual fecundity and, therefore, even a small survival cost can have substantial ramifications for lifetime fitness.

Experimental manipulation of reproductive effort in seabirds has demonstrated a cost of reproduction in terms of survival (Golet et al. 1998) and future reproductive output (Wernham and Bryant 1998). However, it is less clear how costs are adjusted in response to reduced prey availability. Experiments where nestling food demand is manipulated by supplemental feeding have demonstrated that adults will reduce provisioning effort in response to decreased demand (Wernham and Bryant 1998, Harding et al. 2002, Gjerdrum 2004). Cross-fostering experiments have also shown that adults can modulate provisioning in response to chick needs (Bertram et al. 1996, Hamer et al. 1998, Varpe et al. 2004). However, studies seeking to determine if adult seabirds will compromise their own body condition to continue provisioning offspring when prey availability decreases or offspring demand increases have produced conflicting results (Barrett and Rikardsen 1992, Takahashi et al. 1999, Weimerskirch et al. 2001, Gaston and Hipfner 2006). Moreover, sex-specific roles in parental care and differences in capacity to store energy reserves may lead to sex-specific modulation of body condition.

Three general scenarios can be envisioned for the responses of chick-rearing seabirds to limited prey availability (Gaston and Hipfner 2006): (1) adults maintain body condition and modulate rates of chick-provisioning with food availability, (2) rates of nestling provisioning are held constant and adult body condition varies with food availability, and (3) adult body condition and chick-provisioning rates are simultaneously adjusted. It is unlikely that any of these scenarios operates across the entire spectrum of food availability; upper and lower thresholds for adult body condition likely exist and adults may compromise body condition to provision nestlings at some minimum rate. Additionally,

body condition of adults and growth of nestlings are potentially buffered by flexible time budgets (Burger and Piatt 1990). Nevertheless, previous studies have detected correlations between body condition and food abundance (Bolton et al. 1993, Kitaysky et al. 1999), as well as simultaneous adjustment of adult body mass and provisioning effort (Weimerskirch et al. 2001, Gaston and Hipfner 2006). Thus, body condition of some species of seabirds may reflect variation in food availability during the breeding season.

Studies of the seasonal dynamics of body condition generally involve scaling body mass to structural size as an index of body condition because accurate measurement of body stores necessitates sacrificing the bird and requires time-intensive chemical analyses. Alternatively, seasonal dynamics of body condition can be examined using analysis of covariance (ANCOVA), with mass as the dependent variable, season as a factor, and an index of structural size as a covariate (Garcia-Berthou 2001). Both methods assume that mass scaled to structural size provides a useful estimate of body condition (defined as energy stores scaled to body size), but this has not been validated for Tufted Puffins (*Fratercula cirrhata*). However, Niizuma et al. (2002) found that differences in mass between incubating and chick-rearing Rhinoceros Auklets (*Cerorhinca monocerata*; actually a puffin species) were due primarily to loss of lipid reserves. Although indices of body condition are often calculated separately for males and females, sexual dimorphism is subtle in many seabird species and, therefore, sexes are sometimes pooled for analyses (Chastel et al. 1995, Tveraa and Christensen 2002). However, pooling sexes for analysis is valid only when including structural size eliminates the effect of sex on body mass. Pooling sexes is not appropriate if the relationship between mass and structural size is sex specific.

We examined the seasonal dynamics of adult body condition in Tufted Puffins and relate interannual differences in body condition to the growth rate and survival of nestlings. Our primary objective was to determine how adult male and female Tufted Puffins prioritize competing goals of maintaining their own body condition and maximizing the growth rate of their offspring. We developed a body condition index by first determining the sex of adult Tufted Puffins using both molecular techniques

and morphometric measurements, then determined whether the relationship between mass and structural size was sex specific.

METHODS

Study site. Our study was conducted during the breeding seasons of 2004–2005 on Chiniak Island within Chiniak Bay northeast of Kodiak Island, Alaska (57°40′N, 152°20′W). Chiniak Island is approximately circular with a diameter of 0.5 km and has a colony of >5000 breeding pairs of Tufted Puffins (CTW, pers. obs.) nesting in earthen burrows on grassy slopes around the perimeter of the island.

Chick growth and fledging mass. We began monitoring burrows on 24 July in 2004 and on 22 July in 2005. Nestlings that could not be reached through the entrance were accessed using holes excavated in previous years and sealed with either plywood or flat rocks. We weighed chicks using spring scales (±2 g) and measured flattened wing length from the wrist to the wingtip (±1 mm) every 4–5 d throughout the nestling period and every 4 d as chicks approached fledging age. When hatch date was unknown, we estimated age using a wing length versus age regression derived from known-age nestlings. We calculated growth rate for each nestling as the slope of the linear regression equation relating mass and age between ages 10 and 30 d, the near-linear portion of the growth curve (Gjerdrum 2001). Nestlings with fewer than three measurements of mass between 10 and 30 d of age were excluded from growth rate analyses. We defined fledging success as the number of chicks reaching a minimum wing length of 130 mm per egg hatched (Gjerdrum et al. 2003) and assumed that chicks that disappeared before attaining this minimum were dead. We defined the peak mass of an individual as the maximum mass measured during the nestling period and fledging mass as the final mass recorded prior to fledging (disappearance of nestlings with a wing length >130 mm). Mass recession was defined as the difference between peak mass and fledging mass. Nestlings that had not fledged (1 of 35 in 2004 and 2 of 44 in 2005) by the day of the final nest check (12 September 2004 and 11 September 2005) were excluded from analysis of fledging mass.

Adult condition. Because reproductive success and growth rates of Tufted Puffin chicks can be influenced by investigator disturbance (Pierce and Simmons 1986, Whidden et al. 2007), we captured all adults from burrows located outside of growth monitoring plots. Adult Tufted Puffins were captured by hand in their burrows or with a 7 × 10 m net draped over a cluster of 20–30 burrow entrances. If an adult was captured more than once, we included only data from the first capture in our analysis to ensure that all observations were independent. We restricted capture efforts to four periods: prior to egg-laying (22 May–2 June), late incubation (1–11 July), early-chick rearing (2005 only; 4–13 August), and late chick-rearing (23 August–4 September). For each adult, we determined wing chord length (WCL; carpal joint to tip of longest primary), bill length (BL), and straight tarsus length (TL). Wing chord was measured using a ruler (±1 mm), whereas bill and tarsus measurements were taken using dial calipers (±0.1 mm). Body mass was determined using a spring scale (±2 g). Blood samples were collected in heparinized 250-µl Natelson tubes after puncturing either the alar or tarsal vein with a 25-gauge needle. Blood was transferred immediately into 1.5 ml microcentrifuge tubes and stored on ice until frozen as either whole blood or blood cells at −20°C until analysis. DNA was extracted using a DNeasy tissue kit (QIAGEN Inc., Valentia, CA) and determination of sex was performed according to the methods of Griffiths et al. (1998).

Statistical analyses. We performed all statistical analyses using the Statistical Analysis System (SAS Institute 2006) with the α-level set at 0.05. With the exception of nestling mass recession and adult female tarsus lengths, all data met assumptions required for parametric statistical tests (Sokal and Rohlf 1981). We used a nonparametric test (Mann-Whitney U test) to compare nestling mass recession between years. Tarsus lengths of females were not normally distributed due to slight negative skew and mild leptokurtosis. A normal distribution of tarsus lengths was obtained using a doubly-reflected square-root transformation (3-sqrt(40.4-tarsus)). However, data transformation had no effect on results, including classification success based on discriminant function analysis. Therefore, we report analyses based on raw values to maximize the utility of the discriminant function in a field setting.

We compared growth rate of nestlings, peak mass, and mass at fledging between years using Student's t-tests with a Bonferroni correction for multiple comparisons. We tested for interannual differences in fledging success using Fisher's Exact Test. Student's t-tests with a Bonferroni correction were used to determine if morphometric parameters differed between the sexes. We assumed that sex determined by genetic analysis was correct and used discriminant function analysis (DFA) and classification using a jack-knifing procedure (cross-validation) to assess the accuracy of sexing via morphometric measurements. The linear discriminant function for each sex was reduced into a single discriminant function by subtracting the "male" function from the "female" function (Jodice et al. 2000). We developed a sexes-pooled body size index (Rising and Somers 1989, Green 2001) by performing a principal component analysis (PCA) on the three structural measurements (WCL, BL, and TL) and extracting the first principal component (PC1).

We examined the seasonal dynamics of body condition index using ANCOVA (in GLM using Type III SS). Adults captured during early chick-rearing in 2005 ($N = 13$ females and 10 males) were excluded from this analysis because we did not capture any birds during this period in 2004. Three females had outlier PC1 scores, with two substantially smaller in all morphometric measures and a third the size of a large male. Inclusion of these three birds had no effect on results of statistical tests, but did influence parameter estimates and, therefore, we excluded them from all analyses. Body mass was the dependent variable in our model, whereas sex, reproductive stage, and year were included as factors along with body size index (PC1); a covariate that controls for structural size (Garcia-Berthou 2001). The initial global model included all two-way interactions. Interaction terms were subsequently dropped when $P > 0.10$. Simple effects tests (LSMEANS/SLICE) were used to examine significant two-way interactions A × B (i.e., year × reproductive stage). This procedure tests for effects of A for each B, which is calculated by extracting the appropriate row from the coefficient matrix for the A × B LSMEANS and using it to form an F-test. When interactions were not significant, we tested for differences between reproductive stages using Tukey's HSD test to control for multiple comparisons. Sex-specific

differences in regulation of body condition in response to experimental manipulation of reproductive effort have previously been reported for seabirds (Velando and Alonso-Alvarez 2003). Therefore, we decided a priori to repeat the analysis separately for male and female puffins. For this analysis, we developed sex-specific body size indices in the same manner as for the sexes-pooled dataset by extracting PC1 from a PCA on the three structural measurements.

Residuals of mass regressed against PC1 from a PCA on morphometric measures are commonly used as an index of body condition (see references in Green 2001 and Schulte-Hostedde et al. 2005). Therefore, we applied this technique to the pooled-sexes dataset. We then regressed the output residuals (sexes-pooled residuals) against the sexes-pooled body size index separately for each sex to determine if the sex-specific relationship between body mass and structural size detected in our original ANCOVA produced intra-sexual bias in indices of body condition. Finally, to determine if residuals were still affected by body size index when controlling for other effects, we ran separate ANCOVAs for each sex with the sexes-pooled residual as the dependent variable and reproductive stage, year, and the year*stage interaction as factors, and with the sexes-pooled body size index as a covariate. Values are provided as mean ± 1 SE unless noted otherwise.

RESULTS

Nestling growth and fledging mass. For both years, the estimated mean hatch date was 20 July and mean fledging date was 3 September. Fledging success did not differ between years (Fisher's Exact Test: $P = 0.40$), with success rates of 87.9% (29 of 33 hatchlings) in 2004 and 95.2% (40 of 42) in 2005. Growth rates of puffin chicks were significantly lower ($t = -2.5$, $P = 0.017$) in 2004 (14.35 ± 0.47 g/day, $N = 28$) than 2005 (16.18 ± 0.57 g/day, $N = 41$). The difference in mean growth rate between years was 1.9 g/day (95% CI: 0.3, 3.3). Peak mass of nestlings was also significantly lower ($t = -4.8$, $P < 0.0001$) in 2004 (526.1 ± 10.0 g, $N = 28$) than in 2005 (583.5 ± 11.9 g, $N = 38$). The difference in mean peak mass between years was 57.4 g (95% CI: 33.7, 81.1). Mass at fledging was significantly lower ($t = -6.9$, $P < 0.0001$) in 2004 (467.3 ± 11.9 g, $N = 28$)
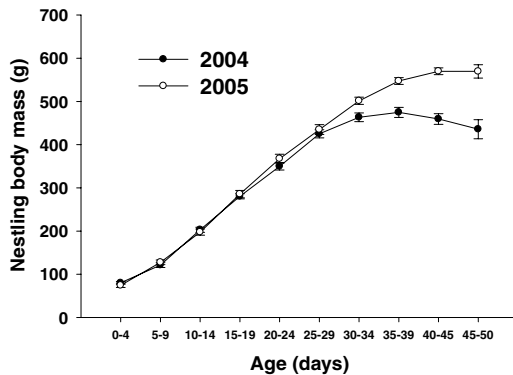
Fig. 1. Mean (± SE) mass of nestlings in 5-d age-bins in 2004 ($N = 34$) and 2005 ($N = 43$). Sample sizes in each age-bin averaged 27 (range 13–34) in 2004 and 34 (12–43) in 2005.

Fig. 2. Mean body mass (± SE) adjusted for body size of adult (A) male and (B) female Tufted Puffins during different stages of reproduction in 2004 and 2005. Sample size is shown on each bar.

than 2005 (563.6 ± 8.2 g, $N = 38$). The difference in mean fledging mass between years was 96.3 g (95% CI: 66.3, 122.0). Mass recession was significantly greater ($U = 12.3$, $P = 0.001$) in 2004 (58.8 ± 8.8 g, $N = 28$) than 2005 (19.9 ± 5.4 g, $N = 38$). Thus, reduced fledging mass in 2004 was due to a combination of lower peak mass and greater mass recession (Fig. 1).

Sex determination. DNA analysis of 176 adult Tufted Puffins revealed 69 males and 107 females. Males had larger tarsus ($t = -5.7$, $P < 0.0001$), wing chord ($t = -4.0$, $P < 0.0001$), and culmen ($t = -6.1$, $P < 0.0001$) measurements than females. Adult male and female Tufted Puffins had mean tarsus lengths of 36.3 ± 1.2 (SD) mm and 35.3 ± 1.2 mm, mean wing chord lengths of 204.0 ± 4.5 mm and 201.2 ± 5.0 mm, and mean culmen lengths of 60.5 ± 2.4 mm and 58.4 ± 2.1 mm, respectively. The first discriminant function (D1) from a DFA classified 130 of 176 (74%) observations to the correct group: D1 = 57 − (0.53878 × TL) − (0.35291 × BL) − (0.07977 × WCL). Adults with greater discriminant scores than the cutoff (−0.025) were classified as female and those with lower scores as male.

Seasonal and sex-related variation in body mass. For both sexes combined, males only, and females only, the first principal component (PC1; body size index) from a PCA on the three structural measures explained 51.7%, 51.0%, and 40.6% of the variance, respectively. Mass of adult Tufted Puffins was significantly
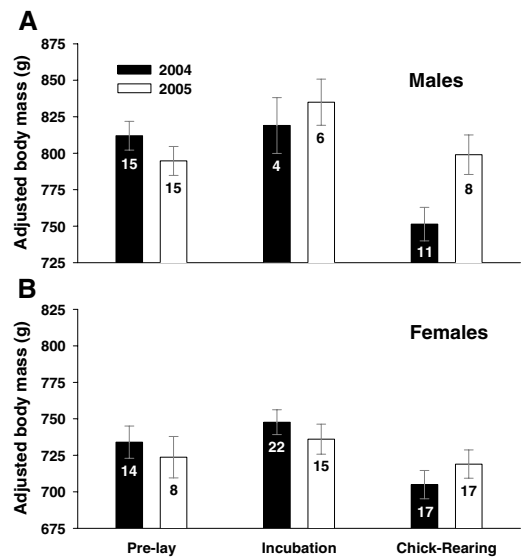
affected by sex ($F_{1,143} = 45.4$, $P < 0.0001$), body size index (PC1; $F_{1,143} = 21.4$, $P < 0.0001$) and reproductive stage ($F_{2,143} = 11.4$, $P < 0.0001$). The effect of year was not significant ($F_{1,143} = 2.2$, $P = 0.14$), but there was a significant year*reproductive stage interaction ($F_{2,143} = 3.8$, $P = 0.025$). The effects of all other two-way interactions were not significant ($P > 0.3$). The parameter estimate for the effect of sex on body mass was −53.37 (95% C.I.: −69.03, −37.71) indicating that, for a given structural body size, females averaged 53 g lighter than males.

The mass of males was affected by reproductive stage ($F_{2,52} = 6.4$, $P = 0.003$) and body size index ($F_{1,52} = 10.7$, $P = 0.002$). There was no significant year effect ($F_{1,52} = 1.9$ $P = 0.17$), but the interaction between year and reproductive stage was significant ($F_{2,52} = 4.2$, $P = 0.02$). Simple effects tests revealed that the mass of chick-rearing males was lower in 2004 than 2005 (Fig. 2A). Mass of female puffins was significantly affected by reproductive stage ($F_{2,88} = 5.2$, $P = 0.008$) and body size index ($F_{1,88} = 12.1$, $P = 0.0008$). Effects of year and all two-way interactions on body mass of females were not significant ($P > 0.3$ for all). Post hoc analyses revealed that female mass was significantly

lower during chick rearing than late-incubation, whereas mass of pre-laying females did not differ from other reproductive stages (Fig. 2B).

Body condition indices. The regression of mass on body size index (PC1) was significant for the pooled-sexes dataset ($F_{1,149} = 63.5$, $P < 0.0001$, $r^2 = 0.3$), the males-only dataset ($F_{1,57} = 6.5$, $P = 0.01$, $r^2 = 0.1$) and the females-only dataset ($F_{1,90} = 11.8$, $P = 0.0009$, $r^2 = 0.11$, Fig. 3). There was a significant negative linear relationship between residuals output from the pooled-sexes regression and body size index for males ($F_{1,67} = 4.7$, $P = 0.014$) and a negative relationship that approached significance for females ($F_{1,90} = 3.6$, $P = 0.061$; Fig. 4). These negative relationships indicate a bias in body condition index (residuals) is produced when sexes are pooled for analysis. For the more complex ANCOVA within males, residuals from pooled-sexes were significantly affected by body size index ($F_{1,52} = 5.8$, $P = 0.011$) and by reproductive stage ($F_{2,52} = 6.3$, $P = 0.004$). The effect of year was not significant for males ($F_{1,52} = 1.7$, $P = 0.2$), but the year*reproductive stage interaction was ($F_{2,52} = 4.1$, $P = 0.022$). For females, the effect of body size index on sexes-pooled residuals approached significance ($F_{1,85} = 3.7$, $P = 0.058$) and the effect of reproductive stage was significant ($F_{2,85} = 5.0$, $P = 0.009$). For both sexes, the parameter estimate for the effect of body size on sexes-pooled residuals was negative (means [95% CI]; males: $\theta = -10.65$ [-19.5, -1.78]; females: $\theta =$
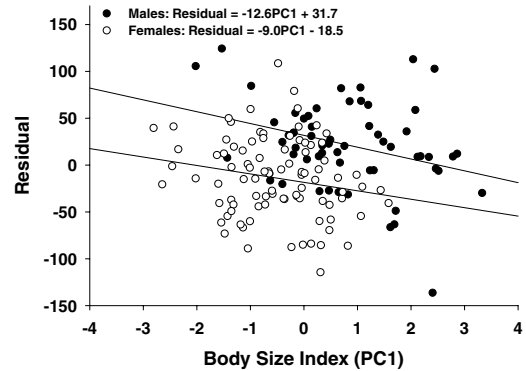

Fig. 4. The relationship between body condition index (residuals) and body size index in adult male and female Tufted Puffins. The residuals were output from a regression between adult body mass and body size index using a sexes-combined dataset. A slope of zero would indicate no relationship between body condition index and body size index and thus no intrasexual bias. The negative slopes indicate pooling sexes produces intra-sexual bias in body condition indices with structurally smaller birds having inflated indices of body condition relative to larger birds within each sex.

-8.94 [-18.33, 0.33]), indicating a bias toward better body condition in structurally smaller birds of each sex. This bias is an artifact of using sexes-pooled residuals.

DISCUSSION

Sexual dimorphism and body condition indices. Morphometric measurements of male and female Tufted Puffins in our study were similar to those reported by Piatt and Kitaysky (2002) in the Gulf of Alaska. Although males were larger than females for all three structural features, determining the sex of Tufted Puffins based on morphometrics was only moderately accurate (74%). Because Piatt and Kitaysky (2002) reported significant regional variation in the size of both sexes, our discriminant function may not be applicable outside of our study area. Therefore, we strongly advocate use of genetic sexing techniques, whenever possible.

Our results demonstrate that body condition indices must be calculated separately for male and female Tufted Puffins because pooling the sexes produced significant intra- and intersexual bias. This is not surprising given that Shiomi and Ogi (1991) determined male Tufted Puffins are
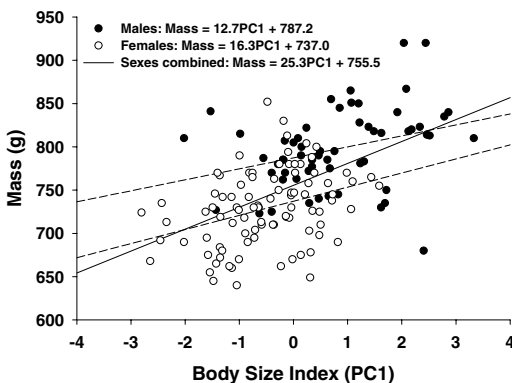

Fig. 3. The relationship between adult body mass and body size index in male ($r^2 = 0.1$) and female ($r^2 = 0.11$) Tufted Puffins. The solid line depicts the relationship when both sexes are combined ($r^2 = 0.3$).

larger and shaped differently than females, with smaller gravimetric proportion of wing muscles to leg muscles. The body condition index we calculated using data for both sexes was biased with structurally smaller birds having inflated indices of body condition (Fig. 4). This issue is particularly concerning because it may lead to spurious correlations between body condition index and other factors that vary with body size. Although some investigators separate the sexes prior to analysis (Erikstad et al. 1997) or test for sex-specific relationships between body mass and structural size prior to pooling data (Moe et al. 2002), others assume that scaling mass to structural size accounts for sex-specific differences (Chastel et al. 1995, Tveraa and Christensen 2002). Our results indicate that when using an index of body condition, it is imperative to either analyze sexes separately or to test for sex-specific differences prior to pooling data. If structural size is to be used in ANCOVA (Garcia-Berthou 2001), then sex should be included as a factor to avoid bias.

It is often of interest to correlate energy reserves with physiological parameters such as stress hormones (Kitaysky et al. 1999, Lormee et al. 2003) and plasma metabolites (Alonso-Alvarez et al. 2002). This is generally done by scaling body mass to structural size to generate a body condition index. Although indices of body condition based on ratios and residuals are easily calculated and may provide a useful nondestructive tool for estimating energy reserves, studies have revealed that ratio-based indices may produce spurious effects and should be avoided (Jakob et al. 1996, Garcia-Berthou 2001, Green 2001) and that residual based indices should be used with caution (Green 2001).

That said, residuals from ordinary least squares regression of mass versus structural size may provide an accurate measure of body condition (Golet and Irons 1999, Schulte-Hostedde et al. 2005). Indeed, residuals produced from a regression of body mass on the first principal component extracted from a PCA on a suite of structural features have been employed by many investigators (Rising and Somers 1989, Chastel et al. 1995, Erikstad et al. 1997, Moe et al. 2002, Tveraa and Christensen 2002). Despite their widespread use, validation of body condition indices in studies of seabirds is rare (Golet and Irons 1999) and we encourage future investigators to evaluate the efficacy of their methods.

Seasonal mass loss. Growth rates of nestlings in our study were among the highest recorded for this species (reviewed by Piatt and Kitaysky 2002), and were significantly lower in 2004 than 2005. Fledging success was also high in both years. The high rates of nestling growth and fledging success suggest that foraging conditions were generally good for Tufted Puffins during the chick-rearing period. However, the lower fledging mass of nestlings in 2004 suggests that prey availability differed between years. In fact, nestlings diets were of lower quality (lower lipid content) in 2004 than in 2005 (CTW, unpubl. data), suggesting that high quality prey was not as available in 2004. Although the mass of chick-rearing males and females, corrected for body size, was also lower in 2004, the difference was only significant for males. In addition, adult males lost a greater percentage of their body mass between late incubation and late chick-rearing than females in both years (Fig. 2). Thus, our results are consistent with sex-specific body mass regulation.

Although sex-specific roles in parental care are common among seabirds (Creelman and Storey 1991, Fraser et al. 2002, Paredes et al. 2006), few investigators have determined whether there are commensurate sex-specific differences in loss of body mass. Velando and Alonso-Alvarez (2003) found that female Blue-footed Boobies (*Sula nebouxii*), a species with reverse sexual dimorphism, adjusted body condition in response to experimentally increased nestling demands for food whereas males did not. Conversely, Lormee et al. (2003) found that only male Red-footed Boobies (*Sula sula*), another species with reverse sexual dimorphism, showed a decline in body condition during chick rearing. Although we did not detect a significant difference between years in seasonal mass loss in female puffins, rates of nestling growth and fledging success were high in both years and additional study is needed to determine if adult females simultaneously adjust their own body condition with rates of nestling provisioning when foraging conditions deteriorate further. Future studies examining provisioning behavior in Tufted Puffin pairs of known-sex would be useful to establish whether sex-specific differences in mass loss are due to greater provisioning effort by males in late chick rearing. Studies measuring body condition directly via proximate composition analysis would be helpful to determine if males and females

differ in their capacity to store lipid reserves, as well as to validate the body condition index used in our study.

In addition to sex-specific differences in adjustment of body mass, species-specific differences have also been reported. Adult Leach's Storm Petrels (*Oceanodroma leucorhoa*) increased provisioning effort when mates were removed, but not enough to compensate for loss of their mate and they did not compromise their own body condition to do so (Takahashi et al. 1999). In contrast, adult Thick-billed Murres (*Uria lomvia*) balance their own body condition with that of their nestlings (Gaston and Hipfner 2006). Differences between species may be attributed, in part, to life-history strategy (Takahashi et al. 1999). Leach's Storm Petrel chicks accumulate large lipid reserves during the nestling period (~60 d) that may provide insurance against stochastic provisioning (Ricklefs and Schew 1994). Murres, however, have a short nestling period (<24 d) and selection apparently favors a strategy of synchronous fledging within subcolonies (Benowitz-Fredericks and Kitaysky 2005). When food is scarce, selection may favor adult murres that deplete endogenous energy reserves during the relatively short nestling stage relative to those that prolong the nestling period and negatively affect chick survival. Tufted Puffin nestlings have highly variable rates of growth in the wild (Piatt and Kitaysky 2002) and are physiologically adapted to modulate metabolic rates in response to nutritional limitation (Kitaysky et al. 1999). Nevertheless, our results suggest that adults, or at least adult males, sacrifice their own body condition in years of diminished nestling growth. Furthermore, Weimerskirch et al. (2001) found that adult Yellow-nosed Albatrosses (*Diomedea chlororhynchos*), another species where chicks accumulate large lipid reserves, adjust both body condition and chick provisioning rates during years with anomalously high water temperatures. Thus, the amount of endogenous energy reserves nestlings are capable of storing may not be a useful predictor of whether parents adjust body condition when food availability decreases.

Loss of body mass during reproduction can be viewed as the outcome of adaptive compromises between different selective factors (Moreno 1989, Witter and Cuthill 1993). Multi-year studies of seasonal mass loss (Weimerskirch et al. 2001, Gaston and Hipfner 2006, this study),

together with experimental manipulations of nestling demands (Erikstad et al. 1997, Takahashi et al. 1999), have revealed sex- and species-specific regulation of energy stores. However, the ultimate cause of interspecific and intersexual variation in regulation remains unclear. Thus, prior to using adult body condition as an indicator of prey availability in any species, it is critical to determine if costs of low food availability are borne by the parent, the offspring, or both. Our results suggest that under conditions of relatively high reproductive success and chick growth rates, adult male Tufted Puffins simultaneously adjust body condition and chick growth rates, whereas females do not. Additional insight into sex-specific regulation of seasonal mass loss in Tufted Puffins may be gained from future studies over a broader range of foraging conditions.

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