Body Girth as an Alternative to Body Mass for Establishing Condition Indexes in Field Studies: A Validation in the King Penguin

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ABSTRACT

Body mass and body condition are often tightly linked to animal health and fitness in the wild and thus are key measures for ecophysiologists and behavioral ecologists. In some animals, such as large seabird species, obtaining indexes of structural size is relatively easy, whereas measuring body mass under specific field circumstances may be more of a challenge. Here, we suggest an alternative, easily measurable, and reliable surrogate of body mass in field studies, that is, body girth. Using 234 free-living king penguins (Aptenodytes patagonicus) at various stages of molt and breeding, we measured body girth under the flippers, body mass, and bill and flipper length. We found that body girth was strongly and positively related to body mass in both molting \((R^2 = 0.91)\) and breeding \((R^2 = 0.73)\) birds, with the mean error around our predictions being 6.4%. Body girth appeared to be a reliable proxy measure of body mass because the relationship did not vary according to year and experimenter, bird sex, or stage within breeding groups. Body girth was, however, a weak proxy of body mass in birds at the end of molt, probably because most of those birds had reached a critical depletion of energy stores. Body condition indexes established from ordinary least squares regressions of either body girth or body mass on structural size were highly correlated \((r = 0.91)\), suggesting that body girth was as good as body mass in establishing body condition indexes in king penguins. Body girth may prove a useful proxy to body mass for estimating body condition in field investigations and could likely provide similar information in other penguins and large animals that may be complicated to weigh in the wild.

Introduction

Because body condition is often related to individual health and fitness in wild animals (Potti 1993; Atkinson and Ramsay 1995; Chastel et al. 1995; Dobson and Michener 1995; Merila and Wiggins 1995; Christe et al. 1998; Dobson et al. 1999; Madsen and Shine 1999; Saraux et al. 2011; Balbontín et al. 2012), measuring individual condition is of central interest for physiologists and ecologists (Schulte-Hostedde et al. 2005). Body condition reflects an animal’s energy reserves, and information on body reserves can yield important insights on foraging behavior (Kato et al. 2008) and on the quantity of resources extracted from the environment (i.e., energy income), as well as on resource allocation to various functions (Boggs 1992; i.e., energy outcome).

In animals, body condition is classically determined by regressing body mass \(M_b\) on some index of structural size using ordinary least squares (OLS) regression (Piersma 1984; see reviews in Brown 1996; Green 2001; Schulte-Hostedde et al. 2005). A high residual \(M_r\) implies that the individual is in good condition or has large body reserves because it is heavy relative to its size (Jakob et al. 1996; Schulte-Hostedde et al. 2001). While noninvasive, this method requires researchers to ob-
tain both the animal’s $M_b$ and an index of structural size. However, in some species, $M_b$ may not always be easy to measure during specific life-history stages and/or under specific field conditions. This is notably the case for large colonial seabirds, particularly heavy species that often incubate their eggs and brood their chicks in windy and rainy locations among numerous and aggressive conspecifics (e.g., Williams 1995; Côté 2000; Kokko et al. 2004). In these colonial species, local conditions may render in situ measurements of $M_b$ (i.e., within the colony) complicated, and displacing individuals from their reproductive site for weighing may result in breeding failure. Researchers would thus benefit from a simple and rapid method for assessing body condition without the need of $M_b$ measurements.

The aim of our study was therefore to determine a reliable general surrogate measure of $M_b$, simple to perform in the field and accurate enough to be substituted for $M_b$ when establishing body condition indexes from OLS regressions with a structural size index. For this purpose, we established a general proxy for body condition indexes from OLS regressions with a structural size index. For this purpose, we established a general proxy for body condition indexes from OLS regressions with a structural size index. Here, we focused on estimates of $M_b$ and body condition above critical $M_b$ for breeding as well as molting penguins. Our proxy to $M_b$ was based on a measure of bird corpulence, that is, body girth ($G_b$), measured under the flippers. The rational for choosing $G_b$ as an index of $M_b$ and body condition was based on the fact that changes in $G_b$ in king penguins may reflect changes in both fat and muscle (thus protein) mass. Indeed, in penguins, fat reserves are mostly subcutaneous, being distributed more or less regularly all over the body, including the thoracic region (Groscolas 1990), so that $G_b$ probably varies with the width of fat layer and thus fat mass. On the other hand, body proteins are stored mainly in pectoralis muscles and also in the integument (Cherel et al. 1994b), suggesting that $G_b$ may also be a good indicator of protein stores. Contingent with the idea that estimating body condition requires obtaining both the animal’s $M_b$ and an index of structural size, our aim was to investigate the relationship between $M_b$ and $G_b$ at different stages of the annual cycle and in both sexes and to test whether $G_b$ could be used as a surrogate measure for $M_b$ for establishing body condition indexes. We first investigated the relationship between $M_b$ and $G_b$ for penguins at different stages of their yearly cycle and made use of the natural changes occurring in $M_b$ and $G_b$ to test whether our predictions showed intraindividual consistency, that is, whether changes in $M_b$ were related to changes in $G_b$. We then tested for potential sex effects and investigated whether $G_b$ yielded similar information to $M_b$ when establishing condition indexes in king penguins. We further validated our equations by testing whether we could confidently predict $M_b$ from $G_b$ by (1) using a jackknife approach as previously described by Halsey et al. (2008) and (2) using a test group, that is, individual birds that were different from those used in the calibration process. Working on those two different data sets thus allowed greater confidence in our prediction equations.

**Methods**

**Data Collection and Data Sets**

Data were collected in the Baie du Marin colony (Possession Island, Crozet Archipelago, 46°25′S, 51°45′E), which is host to ca. 24,000 breeding pairs. Morphometric measurements ($M_b$, $G_b$, and bill and flipper length) were obtained from a total of 234 free-living king penguins during three different field seasons in 2000–2001 (year 1; $N = 123$ birds), 2009–2010 (year 2; $N = 51$), and 2011–2012 (year 3; $N = 60$). In addition, in 2011–2012, we also obtained repeated morphometric measurements on 10 fasting males that were captured at the onset of breeding and kept captive as part of another study; we used these measurements to validate our equations predicting $M_b$ from $G_b$ (see below).

**Morphometric Measurements**

On capture, penguins were transported to a nearby dry shelter (within 10 m of the colony), and $M_b$ was measured to the nearest ± 2 g; $G_b$ was obtained by measuring the circumference of the body to the nearest 1 mm just beneath the flippers, surrounding the bird with a flexible tape measure around the pectoralis. All $G_b$ measurements were standardized, performed with the animal in an upright position, and measures were taken when pectoralis circumference was at its maximum (i.e., stretched out during inspiration); $G_b$ was also initially measured at the abdomen ($G_{abdom}$), but the relationship between $G_{abdom}$ and $M_b$ proved variable between years and experimenters, and thus we dropped $G_{abdom}$ from further analyses. Classic measurements of bill length (using dial caliper from bill tip to the point of the jaw) and flipper length (using a solid metal ruler, flipper fully extended, from the sternum to its tip) were also obtained to the nearest 1 mm (see Fahlman et al. 2006 for details on those measurements).

**Relating Body Mass to Body Girth**

To investigate whether $G_b$ was related to $M_b$ in the king penguin, we used data acquired from the 234 free-living birds. Overall, in these birds, $M_b$ values ranged from 7 to 19 kg, and $G_b$ values ranged from 52 to 78 cm (see table 1). In year 1, $M_b$, $G_b$, and bill and flipper length were measured in a total of 46 molting and 77 breeding birds. In king penguins, the yearly and massive prebreeding molt lasts around 4 wk and is associated with
prolonged onshore fasting, during which birds lose about 40% of their body mass (Cherel et al. 1994a). From their plumage aspect, molting birds (unknown sex) were categorized as individuals in premolt (i.e., new feathers growing beneath the skin but no old feathers shed; \( N = 10 \)), at molt onset (i.e., ruffled plumage, a few breast feathers lost; \( N = 8 \)), midmolt (i.e., breast, back, and hip feathers lost; \( N = 12 \)), or molt end before departure to sea to refeed (i.e., new plumage, a few remnants of old plumage on the head, new tail not completely grown; \( N = 16 \)). Breeding birds were measured as courting birds, that is, after having been fasting ashore for a few days at the onset of breeding (22 males and 17 females, which were sexed according to breeding phenology; Stonehouse 1960), incubating birds (\( N = 17 \), unknown sex), or chick-brooding birds (\( N = 21 \), unknown sex). Incubating birds were measured at partner relief, when leaving the colony after an incubation shift of approximately 15 d. Brooding birds were measured when arriving ashore to resume their parental shift on the chick, after having foraged at sea for 8–15 d. In year 2, the same measurements were obtained on 51 breeding birds (9 incubating and 42 chick-brooding birds). Those birds were sexed from breeding phenology (28 males and 23 females) and DNA analysis (Griffiths et al. 1998) and measured when leaving the colony at the end of a breeding shift (at partner relief). In addition, 40 of the 51 birds were recaptured and measured when returning to the colony to start their subsequent breeding shift, after foraging at sea for \( 14.5 \pm 0.7 \) d (mean \pm SE). Finally, during year 3, we captured and measured a total of 60 unsexed birds at the end of the molt process. Of those, 30 were re-measured \( 24.1 \pm 0.6 \) d later as they returned to the colony to breed (i.e., 14 prebreeding birds that had not yet started courting and 16 birds actively engaged in courtship).

Pooling all data, we used a linear mixed model (LMM) analysis to determine whether \( G_b \) accurately related to \( M_b \) and whether this relationship depended on the molting, reproductive, and nutritional (mainly fasting duration) status of the animals. We thus specified \( M_b \) as the dependent variable and \( G_b \) and status as the independent variables and considered the statistical interaction between \( G_b \) and status. Because birds were sampled by different experimenters in different years, year was added as a cofactor in the model to test whether predictions of \( M_b \) from \( G_b \) were consistent between years (and thus experimenters). Bird identity was added as a random factor in order to control for repeated measurements on the 70 birds that had been sampled twice in years 2 and 3. Whenever interactions were significant, we used separate linear regression models (LMs) to analyze how changes in molting or breeding status might affect \( M_b \) predictions from \( G_b \). Estimated slopes were then calculated and compared using 95% confidence intervals (CI95).

### Sex Effects

We used the 90 free-living birds for which sex was determined in years 1 and 2 to investigate whether sex affected the predictions of \( M_b \) from \( G_b \). The relationship between \( M_b \) and \( G_b \) was tested separately in males and females using linear regressions, and the slopes of both regressions were then compared using CI95.
Estimating Changes in Body Mass from Changes in Body Girth

We further investigated whether changes in \( G_b \) reliably reflected changes in \( M_b \) (i.e., whether \( G_b \) variation could be used consistently as a predictor of \( M_b \) variation within individuals), using the free-living individuals that were captured twice in year 2 (\( N = 40 \), measured after a breeding shift and then at return to the colony for the next breeding shift) and year 3 (\( N = 30 \), measured at molt end and then at return to the colony for breeding). We calculated the change in \( M_b \) and \( G_b \) that occurred during a foraging sojourn at sea and regressed changes in \( M_b \) on changes in \( G_b \).

Using Body Girth to Establish Condition Indexes

To test whether \( G_b \) could be used as a reliable surrogate measure for \( M_b \) when establishing condition indexes along with measures of structural size in penguins, we separately regressed \( M_b \) and \( G_b \) on structural size using all data obtained on free-living birds. The residuals obtained from both regressions gave us a classical body condition index (Schulte-Hostedde et al. 2005). We assessed the error associated with our predictions of \( M_b \) from \( G_b \) using two different methods. First, on free-living birds, we used a jackknife approach as presented by Halsey et al. (2008). In this approach, we used the same birds for which the predictive equation was established in order to validate it (see Halsey et al. 2008 for details). Briefly, all data were pooled, and we regressed \( M_b \) on \( G_b \) a total of 305 times (i.e., once per case for which we had both \( M_b \) and \( G_b \)), each time removing a different data point from the analysis. The predicting equation was then used to predict \( M_b \) from \( G_b \) for the data point that had been removed. We then tested how well observed and predicted \( M_b \) were correlated, and the absolute percentage error of our estimates was calculated as \[ \frac{|\text{observed} - \text{predicted}|}{\text{observed}} \times 100. \]

Second, we tested whether our equations yielded reasonable estimates of \( M_b \) when used in a test group, that is, in birds different from those used for the calibration. For this, we used the data obtained from the 10 males that had been caught at the onset of breeding in year 3 and kept fasting in a pen for

| Table 2: Estimates of linear mixed model specifying king penguin body mass (\( M_b \)) as dependent variable; body girth (\( G_b \)), bird status (i.e., breeding or molting stages), and interaction between \( G_b \) and bird status as independent variables; year as cofactor; and individual identity as random factor |
|---------------------------------|----------------|--------|--------|--------|
|                                 | Estimate ± SE | df     | \( t \) | \( P \) |
| Intercept                       | -13,613.8 ± 1,882.5 | 224 | -7.23 | <.001 |
| Year \(_{2010-2011}\)           | -424.3 ± 304.0 | 224 | -1.40 | .16   |
| Year \(_{2011-2012}\)           | -224.9 ± 164.5 | 224 | -1.37 | .17   |
| \( G_b \)                       | 411.8 ± 29.5  | 63   | 13.97 | <.001 |
| Fremolt                         | 4,575.1 ± 7,537.8 | 224 | .61   | .54   |
| Molt onset \(_{216.0} \)        | 14,548.0 ± 6,848.1 | 224 | 2.12  | .03   |
| Midmolt                         | 741.7 ± 6,991.6 | 224 | .11   | .91   |
| Molt end                        | 4,985.5 ± 2,855.5 | 63   | 1.71  | .09   |
| Prebreeding \(_{216.0} \)       | -11,057.3 ± 3,811.7 | 63 | -2.90 | .005  |
| Courtship                       | -2,542.1 ± 2,935.9 | 63 | -.87  | .39   |
| Incubation                      | -4,519.7 ± 3,192.4 | 224 | -1.42 | .16   |
| \( G_b \) × old plumage         | -50.9 ± 104.6 | 224 | -.49  | .63   |
| \( G_b \) × molt onset          | -215.9 ± 102.8 | 224 | -2.11 | .04   |
| \( G_b \) × midmolt             | -1.5 ± 108.8  | 224 | -0.01 | .99   |
| \( G_b \) × molt end            | -92.6 ± 47.2  | 63   | -1.96 | .054  |
| \( G_b \) × prebreeding         | 189.1 ± 59.4  | 63   | 3.18  | .002  |
| \( G_b \) × courtship           | 37.6 ± 46.4   | 63   | .81   | .42   |
| \( G_b \) × incubation          | 69.0 ± 51.1   | 63   | 1.35  | .18   |

Note. The \( R^2 \) of the model, calculated as the squared correlation between the fitted and observed values, was 0.89. Number of observations, \( n = 305 \); number of birds, \( N = 234 \). Significant values are given in bold.
Figure 1. Relationship between body mass ($M_b$) and body girth ($G_b$) in king penguins. Data are for birds measured at various stages of molt (premolt, molt onset, midmolt, and molt end) and various stages of reproduction (prebreeding, courting, incubating, and brooding).
Table 3: Slope estimates and 95% confidence intervals (CI₉₅) for linear regressions of body mass on body girth in king penguins at different stages of molt and breeding (see also fig. 1).

<table>
<thead>
<tr>
<th>Stage</th>
<th>Intercept</th>
<th>Slope</th>
<th>Slope CI₉₅</th>
<th>P</th>
<th>R²</th>
</tr>
</thead>
<tbody>
<tr>
<td>Premolt</td>
<td>−9,038.7</td>
<td>360.9</td>
<td>209.4–512.3</td>
<td>.002</td>
<td>.73</td>
</tr>
<tr>
<td>Molt onset</td>
<td>934.2</td>
<td>194.9</td>
<td>−48.2–438.0</td>
<td>.17</td>
<td>.29</td>
</tr>
<tr>
<td>Midmolt</td>
<td>410.3</td>
<td>148.9</td>
<td>118.5–702.0</td>
<td>.02</td>
<td>.43</td>
</tr>
<tr>
<td>Molt end</td>
<td>336.6</td>
<td>28.6</td>
<td>280.5–392.7</td>
<td>&lt;.001</td>
<td>.65</td>
</tr>
<tr>
<td>Prebreeding</td>
<td>−24,691.6</td>
<td>591.5</td>
<td>408.3–774.8</td>
<td>&lt;.001</td>
<td>.77</td>
</tr>
<tr>
<td>Courtship</td>
<td>−15,938.1</td>
<td>444.9</td>
<td>390.8–499.1</td>
<td>&lt;.001</td>
<td>.83</td>
</tr>
<tr>
<td>Incubation</td>
<td>−17,256.6</td>
<td>463.0</td>
<td>389.8–536.3</td>
<td>&lt;.001</td>
<td>.83</td>
</tr>
<tr>
<td>Brooding</td>
<td>−18,609.5</td>
<td>490.6</td>
<td>414.4–566.8</td>
<td>&lt;.001</td>
<td>.64</td>
</tr>
</tbody>
</table>

In addition, and due mostly to birds at the end of molt, an apparent break point in the data could be seen around a Gb of approximately 60 cm (fig. 1). For molting birds, break point analysis revealed a change in slope when Gb was 56.8 ± 0.7 cm (fig. 2), corresponding to the average Gb of birds at the end of molt (see table 1). The pre–break point regression equation (corresponding to birds with a Gb lower than 57 cm) was eq_molt: Mb = −17,256 ± 875 + 468.9 ± 14.5 × Gb (LM; R² = 0.91; F₁₀₄ = 1,039, P < 0.001) and one for breeding birds (eq_breed): Mb = −18,226 ± 1,329 + 482.9 ± 21.1 × Gb (LM; R² = 0.73; F₁₁ overtime = 521.1, P < 0.001).

Using Body Girth to Estimate Body Condition in King Penguins

Regressions of Mb or Gb on the SSI were both significant (LMs; F₁₉₃ = 12.2 and 5.7, P < 0.001 and 0.01, for regressions with Mb or Gb respectively). The residuals of both regressions were highly correlated (Spearman’s rank correlation, r = 0.92; P < 0.001; fig. 4), suggesting that Mb and Gb could be used interchangeably to establish body condition indexes in concert with structural size measures in king penguins. Removing birds at the end of molt (birds below the 57-cm break point in Gb) from the analyses did not substantially change the results (r = 0.85; P < 0.001).

Predicting Changes in Body Mass from Changes in Body Girth

In the 70 birds that were measured twice in years 2 and 3, that is, before leaving for foraging at sea and at their subsequent return to the colony some 2–3 wk later, we found that changes in Mb could be predicted by changes in Gb (LMs; R² = 0.32; F₁₆₅ = 31.8, P < 0.001; fig. 3), suggesting that the estimation of Mb from Gb was consistent within individuals. The associated equation was δMb (g) = −1,923 ± 236 + 206.7 ± 36.7 × δGb (cm). Thus, a change in Gb of 1 cm was associated with a change in Mb of approximately 207 g.

Testing Our Predictions

Using a jackknife approach (Halsey et al. 2008) on the 305 cases for which we had both Mb and Gb and using eq_molt and eq_breed to predict the body mass of molting and breeding birds, respectively, we found that predicted Mb was highly correlated with observed Mb (Spearman’s rank correlation, r = 0.92; P < 0.001; fig. 5A). The mean absolute percentage error of our predictions was 6.4% ± 0.3% (range: 0.04%–24.5%), and the percentage error distribution for our estimates was normal (P = 0.27), suggesting that our predicted Mb did not systematically underestimate or overestimate measured Mb. Again, removing birds at the end of molt from the analysis did not substantially change the results (r = 0.87; mean absolute percentage error = 6.3% ± 0.3%).

In the 10 captive males caught at the onset of reproduction, we found a strong relationship between measured Mb and Gb as estimated from Gb using the eq_breed equation (LMM; R² = 0.71; t = 12.50, P < 0.001; fig. 5B). The mean absolute percentage error was remarkably close to that reported using the jackknife approach, that is, 6.3% ± 0.5% (range: 0.1%–22.0%), and the percentage error for our estimates was normally distributed as well (P = 0.41).

Discussion

Our study aimed at validating the use of a surrogate measure for body mass when estimating body condition in species for which an accurate measure of Mb may be difficult to obtain under field conditions. Our results suggest that the simple measure of Gb may provide an accurate and reliable candidate. In king penguins, Gb can be measured without having to move the animal from its breeding territory and with minimal disturbance, provided care is taken to measure the animal in a

Sex Effect

From the 90 birds that were sexed in years 1 and 2, we found no significant differences for the relationship between Mb and Gb according to sex; Gb strongly predicted Mb in males (LM; R² = 0.71; F₁₄₉ = 116.9, P < 0.001) and females (LM; R² = 0.70; F₁₄₉ = 88.6, P < 0.001), and the slopes of the relationships were not significantly different. Indeed, CI₉₅ overlapped substantially, that is, 431.3 ± 39.9, CI₉₅ = 353.2–509.7, for males and 378.6 ± 40.2, CI₉₅ = 299.8–475.5, for females.
Figure 2. Segmented regression analyses between body mass ($M_b$) and body girth ($G_b$) for molting and breeding king penguins. The top panel shows a two-step (segmented) linear relationship between $M_b$ and $G_b$ for molting birds, with estimated break point (±SE) reported along the X-axis. The bottom panel shows a single linear relationship between $M_b$ and $G_b$ for breeding birds. Data are for birds measured at various stages of molt (premolt, molt onset, midmolt, and molt end) and various stages of reproduction (prebreeding, courting, incubating, and brooding).

standardized position (e.g., upright king penguin sitting on its egg). Conversely, this may be one of the drawbacks when measuring $G_b$ in situations where animals are crouched, lying flat on eggs, or highly nervous and agitated. Nonetheless, our results show that $G_b$ strongly predicted $M_b$ in king penguins, regardless of year (i.e., different experimenters and different years), sex, and stage within molting or breeding groups (though the relationship was not as good for birds at the end of molt, as discussed below). These findings suggest that $G_b$ is a relatively robust estimator of $M_b$ in different situations. As stated in the “Introduction,” this strong correlation between $M_b$ and $G_b$ is likely due to the fact that $G_b$ changes mostly in relation to the width of the subcutaneous fat layer and also to the mass of the pectoralis muscles and the integument. These two traits are indeed the two major protein stores in king penguins and thereby the two main contributors to the changes in $M_b$ during foraging or fasting (Cherel et al. 1994b). Importantly, we found some significant effects of specific physiological states on the relationship between $G_b$ and $M_b$ with molting and breeding birds appearing to differ slightly. In this context, we derived two different equations for predicting $M_b$ from $G_b$. The slightly lower slope coefficient obtained for molting birds suggests that a similar $G_b$ is associated with slightly lower $M_b$ in molting than in breeding birds. Such a difference might be explained by the fact that changes in $G_b$ in molting birds may be in part a reflection of the molt process, including a more or less ruffled plumage. Indeed, in molting penguins, feather synthesis first occurs under the skin and contributes to increasing the thickness of the skin/subcutaneous fat/feather layer and consequently $G_b$ (Groscolas 1978; Groscolas and Cherel 1991; Cherel et al. 1994a). Thus, before the emergence of the new feathers from under the skin, variations in $G_b$ are likely not only linked to variations in energy reserves but partly linked to the molt process itself. In other words, at the beginning of the molt, $G_b$ likely overestimates $M_b$ and actual energy reserves.

Also in molting birds, we noted a break point in the data set at a $G_b$ of 57 cm, which corresponded to an $M_b$ of approximately 9.3 kg. Below this break point, $G_b$ poorly predicted $M_b$. Interestingly, this 9.3-kg $M_b$ is similar to the critical $M_b$ (c$M_b$) determined in breeding king penguins at a critical energy
Figure 3. Changes in body mass ($\delta M_b$) versus changes in body girth ($\delta G_b$) during a foraging sojourn at sea in king penguins. Data were obtained from 70 birds that were first measured when leaving the colony for refeeding at sea (either at the end of molt or at the end of a breeding shift) and then remeasured when subsequently returning ashore. The regression line for predicting $\delta M_b$ from $\delta G_b$ is shown ($R^2 = 0.32; F_{1,68} = 31.8, P < 0.001$).

Figure 4. Relationship between the residuals of a regression of body mass ($M_b$) or body girth ($G_b$) on an index of structural size (SSI) in king penguins. The SSI was the first component of a principal component analysis (see “Methods”).

store depletion stage (Cherel et al. 1994b; Gauthier-Clerc et al. 2001; Halsey et al. 2008). Thus, a possible explanation for the poor prediction of $M_b$ from $G_b$ at the end of molt may be that below the $cM_b$, changes in $G_b$ are no longer (or only slightly) associated with changes in $M_b$ and by extension energy stores, because the animal has virtually depleted its energy stores at that advanced stage of fasting. Below the $cM_b$, an animal’s $M_b$ would then essentially reflect the mass of its lean tissues, and variation in $M_b$ would be linked to variations in structural size other than $G_b$ and not to changes in energy reserves and body condition. We did not observe a clear break point in the $M_b$ versus $G_b$ relationship for breeding birds. However, this is probably explained by the small number of breeding birds ($N = 10$) sampled at an $M_b$ below the $cM_b$, and the existence of a similar break point is likely. Thus, predicting $M_b$ from $G_b$ should be avoided for long-term fasting birds that are close to or below the critical body mass (e.g., in birds at the end of molt or after an especially long breeding shift).

Nonetheless, both our prediction equations yielded reasonable estimates of $M_b$, as suggested by the low error (ca. 6%) on body mass we obtained when predicting it from $G_b$ regardless of the method used; that is, using a jackknife approach in the same individuals (whether or not we excluded birds at the end of molt) or predicting $M_b$ from $G_b$ in a test group. This error is actually lower than that reported by Halsey et al. (2008), some 9%, who used a combination of structural size measurements (bill, flipper, and tarsus) to predict the critical $M_b$ of king penguins, although the authors had a lower sample size at hand. Body girth thus provided a dynamic surrogate measure of $M_b$ over an extensive range of situations (interquartile values of body mass ranging from 8.6 to 13.4 kg in molting and breeding birds) and could be used instead of $M_b$ and in combination with structural size to establish a condition index in penguins. This was confirmed by the fact that we found very good correlations ($r = 0.92$) when establishing condition indexes from either $M_b$ or $G_b$ that is, residuals from OLS regressions of either $M_b$ or $G_b$ on structural size (Schulte-Hostede et al. 2005). Further, our results show that $G_b$ was a consistent predictor of $M_b$ within individuals, as suggested by the significant relationship we obtained between changes in $M_b$ and changes in $G_b$ within the same birds. Indeed, $\delta G_b$ was significantly associated with $\delta M_b$, although the mean percentage error of $\delta M_b$ predictions from $\delta G_b$ using a jackknife approach was much higher (i.e., 36.3% ± 8.9%). We found that a 1-cm change in body girth corresponded to a change in body mass of approximately 207 g. Given that, while on land, king penguins are for the most part in phase 2 of fasting and lose approximately 160–190 g/d (e.g., Cherel et al. 1988; Groscolas et al. 2010), it follows that estimates of $M_b$ based on $G_b$ should be made at least 2–3 d apart so that $G_b$ differs by at least 1 cm between two successive measurements.
Figure 5. Observed body mass ($M_b$) versus predicted $M_b$ from body girth ($G_b$) in king penguins. A, Predicted values ($n = 305$) were obtained from the 234 free-living birds from which the predicting equation ($eq_{breed}$ or $eq_{molt}$, used as appropriate) was derived, using a jackknife approach (see Halsey et al. 2008 and “Methods”). B, Predicted values ($n = 79$) were obtained from 10 captive individuals measured several times (six to nine measurements per bird) during prolonged fasting and using $eq_{breed}$.

In conclusion, the method reported in this study provides researchers with an easily measurable surrogate of $M_b$, and our results suggest that $G_b$ may be used instead of $M_b$ along with structural size measurements to derive robust body condition indexes over a range of situations in king penguins. We suggest two different equations for estimating $M_b$ from $G_b$ in molting and breeding king penguins, which should not be sensitive to experimenters, provided that $G_b$ measurements are taken at the armpit, beneath the flippers, and with birds in a standardized upright position. Changes in $G_b$ may also be a useful and dynamic measure for studying changes in $M_b$, although care should be taken as to the time needed between two consecutive measures of $G_b$ to detect relevant changes in $M_b$ and one should be cautious about the errors associated with such predictions. Using body girth to establish body condition is likely to be of interest in other penguins and large seabird species as well and remains to be tested.

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