

# Body condition indices are better surrogates for lean mass and water content than for body fat content in an insect

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## Keywords

age; cricket; *Gryllus*; lipid; sex; wing dimorphism; body condition indices; body fat content.

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## Abstract

Ecologists and evolutionary biologists often use body condition indices (BCIs) to approximate an animal's energetic state, which is important because energy (typically, lipid) reserves influence an animal's investment into fitness-related traits. A BCI's utility is typically assessed by examining its ability to predict standardized fat content (fat mass in fresh mass after correcting for body size) across a population. Less frequently, a BCI is assessed as a response variable by comparing its sensitivity to a particular treatment or factor (e.g. food availability or age) relative to that of standardized fat content. We assessed five common BCIs (or equivalent) with these two approaches in the wing-dimorphic sand field cricket (*Gryllus firmus* Scudder 1902). All of the BCI methods significantly predicted standardized fat content in both sexes and wing morphs where the scaled mass index and Que'telet's index explained the most and least amount of variation, respectively. The BCIs and fat content were also similarly affected by adult age. However, BCIs were universally better proxies for lean mass and water content than for fat content. The relationships between BCIs and standardized lean mass and water content were stronger than those between BCIs and standardized fat content, and the effect sizes of age on BCIs were closer to that of lean mass relative to that of fat content. Thus, although BCIs reasonably predicted energy (fat) stores in *G. firmus*, they may be more indicative of lean mass or water content in insects. If BCIs are surrogates for protein and water storage, they may still approximate the storage of resources that fuel fitness-related traits. Yet, future work is required to understand which body components (e.g. fat, protein or water) are most tightly linked to fitness, and whether traditional BCIs explain variation in fitness-related body components across animal taxa.

## Introduction

Ecologists and evolutionary biologists regularly measure an animal's condition because it is typically assumed to reflect an animal's energetic state, which is important given energy is a finite resource that constrains investment into fitness-related traits (Zera and Harshman, 2001; Roff, 2002; Peig & Green, 2009, 2010; Wilson & Nussey, 2010; Labocha *et al.*, 2014). Thus, body condition has long been linked to a range of important traits—from immunocompetence to survival (Evans, 1969; Navarro, Marzal, de Lope & Moller, 2003). Stored lipids are the primary energy reserve of animals (Bell & Coleman, 1980; Arrese & Soulages, 2010), and a number of body condition indices (BCIs) have been used to non-destructively estimate an animal's standardized fat content (e.g., mass of fat in animal after correcting for body size) (Peig & Green, 2009, 2010; Kelly *et al.*, 2014; Labocha *et al.*, 2014; Warner, Johnson & Nagy, 2016). Yet, the utility of BCIs has been questioned (Wilder, Raubenheimer & Simpson, 2016) – in part,

due to the somewhat tenuous link between BCIs and the standardized fat content of animals (Peig & Green, 2009; Kelly *et al.*, 2014; Labocha *et al.*, 2014; Warner *et al.*, 2016). Conventional BCIs may only marginally predict standardized fat content if they instead reflect other body components. For example, BCIs may be better surrogates for lean (i.e. non-lipid) mass, which represents body protein content, or water content (Susenbeth & Keitel, 1988; Mitchell, Rosebrough, & Conway, 1997; Quiniou & Noblet, 1997; Schulte-Hostedde, Millar & Hickling, 2001; Mohrmann *et al.*, 2006; reviewed in Wilder *et al.*, 2016; Beauchamp *et al.*, 2021). Therefore, BCIs may reflect a dynamic mixture of lipid and non-lipid components (Wilder *et al.*, 2016).

A BCI's surrogacy as a reliable estimate of an animal's energetic state can generally be assessed using two approaches. First and most typically, it is determined by testing for a positive correlation between a BCI and animal body fat content across a population (e.g. Peig & Green, 2009; Kelly, Tawes & Worthington, 2014). This approach can also be used to assess

whether non-lipid body components (e.g. dry mass, lean mass or water content) exhibit similar or stronger relationships to a BCI relative to standardized fat content (Schulte-Hostedde *et al.*, 2001; Warner *et al.*, 2016; reviewed in Wilder *et al.*, 2016). Second, it can be determined by comparing the sensitivities of animal fat content and a BCI to a particular treatment or factor (e.g. whether food limitation has a similar effect on standardized fat content as it does on a BCI). This second approach is important because BCIs are often examined as response variables (e.g. examining changes in a BCI due to age or food limitation: Peig & Green, 2010; Kelly *et al.*, 2014). Yet, to our knowledge, both of these approaches have never been fully integrated to assess the accuracy of BCIs.

Therefore, we assessed five commonly used BCIs (or equivalent; see below) with these two approaches using the wing-dimorphic sand field cricket (*Gryllus firmus*). In many insect taxa that disperse through flight, there is a tradeoff between flight capacity and reproduction that is mediated by wing morphology – long-winged (LW) individuals are often flight-capable while short-winged (SW) individuals lack flight capacity but exhibit greater reproductive investment (reviewed in Guerra, 2011). The wing dimorphism in *G. firmus* influences lipid and protein metabolism, stress tolerance, and investment into flight and reproduction in young adult females (Crnokrak & Roff, 1998; Zera, 2005; Zera & Zhao, 2006; Stahlschmidt *et al.*, 2020a). Yet, the effects of age on body condition and composition (e.g. standardized fat content, lean mass and water content) in *G. firmus* are less understood. Therefore, we specifically examined how adult age affected body fat content, lean mass, and BCIs in *G. firmus* of both sexes and wing morphs. Our design allowed us to comprehensively assess the surrogacy of BCIs for body composition.

## Materials and methods

### Study species

*Gryllus firmus* is native to the southeastern U.S. and found most abundantly in Florida (Capinera, Scott & Walker, 2004). Crickets used in this study were acquired from four selected, nearly true-breeding blocks (i.e. two short-winged [SW] blocks and two long-winged [LW] blocks) that have been previously described (Zera, 2005; Glass & Stahlschmidt, 2019). Throughout ontogeny, crickets were reared in standard conditions: 16-h photoperiod at  $28 \pm 1^\circ\text{C}$  with *ad libitum* access to water (water-filled shell vials plugged with cotton), commercial dry cat food (Special Kitty Gourmet, Walmart Stores, Inc.), and shelter (cardboard egg cartons).

### Experimental design

Within 4 days after molting into adults, both sexes of crickets were group-housed in age- and morph-matched cohorts in 15 L translucent plastic containers in standard conditions (see above). Cohorts were comprised of both sexes to facilitate mating, and they were isolated on six occasions for a total of 24 cohorts (i.e. six cohorts from each of the four blocks). *Gryllus*

*firmus* only live up to 25 days post-adult molt in their natural environment (Zera, Zhao, & Kaliseck, 2007) so *G. firmus* in our study were sampled through  $\leq 25$  days of adulthood to reflect an ecologically relevant lifespan. Random sub-samples of crickets were removed from each cohort at the onset of the study (i.e. within 4 days of final ecdysis) and weekly thereafter for a total of four sampling time points ( $n = 361$  total). This approach reduced the density of crickets in each container as crickets aged to approximate field conditions that are characterized by relatively few older adults (Zera *et al.*, 2007). Each sub-sampled cricket was weighed on an analytical balance ( $\pm 0.1$  mg) before being euthanized by freezing at  $-20^\circ\text{C}$ , stored at  $-20^\circ\text{C}$ , and later analyzed for body components (see below).

### Body composition and body size

For each cricket, total water content and dry mass were determined, and then the two components of dry mass (fat content and lean mass) were determined. After storage at  $-20^\circ\text{C}$ , crickets were dried at  $55^\circ\text{C}$  to a constant mass. Crickets were then re-weighed to determine dry mass and total water content. Next, each cricket was ground using a mortar and pestle. Ground dry tissue from each cricket (approx. 100 mg) was weighed, its exact amount was recorded, and it was added to a filter paper disk (55 mm diameter; Grade 1 Whatman, GE Healthcare UK Limited, Buckinghamshire, UK). Disks were rolled to enclose the ground tissue, and they were then each placed into a 15 mL glass vial. Previous work in insects demonstrates that a diethyl ether method for fat extraction produces results that are quantitatively similar to analytical chromatography (Williams, Thomas, MacMillan, Marshall & Sinclair, 2011). Therefore, each glass vial was filled with diethyl ether (#296082, Sigma Aldrich, St. Louis, MO, USA) and sealed. Ether was removed and replaced daily for a total of three washes. Filter paper rolls were then dried at  $55^\circ\text{C}$  to a constant mass, re-weighed to determine lean mass and, by subtraction, fat content.

Femur length is a reliable indicator of body size in other crickets (Simmons, 1986; Kelly *et al.*, 2014), and it strongly correlates with body mass, head width and gonad mass in *G. firmus* (Glass & Stahlschmidt, 2019; Nguyen & Stahlschmidt, 2019; Stahlschmidt *et al.*, 2020b; Table 1). Therefore, the legs of all crickets were collected, and femur lengths were measured using digital calipers ( $\pm 0.01$  mm) to estimate body size.

### Body condition indices

Because they were correlated with other body components (Table 1), femur length ( $L$ ) and fresh body mass ( $M$ ) were used to determine four BCIs (*sensu* Peig & Green, 2010): (1) Fulton's index 'K' ( $K = M/L^3$ ), (2) Que'telet's index or the body mass index ('BMI' =  $M/L^2$ ), (3) residual index ' $R_i$ ' (residuals from an ordinary least squares regression of ln-transformed  $M$  against ln-transformed  $L$  for the study population) and (4) scaled mass index ( $\hat{M}_i$ , standardization of body

**Table 1** Pearson product-moment correlations between body components and both fresh body mass and body size (femur length) of *Gryllus firmus* used in the study ( $n = 361$ )

	Fresh body mass (mg)		Femur length (mm)	
	$r$	$P$	$r$	$P$
Dry mass (mg)	0.96	<0.001	0.76	<0.001
Water mass (mg)	0.98	<0.001	0.80	<0.001
Water mass (%)	-0.47	<0.001	-0.40	<0.001
Lean mass (mg)	0.945	<0.001	0.75	<0.001
Fat mass (mg)	0.83	<0.001	0.65	<0.001
Fat mass (%)	0.39	<0.001	0.31	<0.001

mass at a fixed value of a linear body size based on the scaling relationship between  $M$  and  $L$  for a reference population; equation 1).

$$\hat{M}_i = M_i (L_o/L_i)^{b_{SMA}} \quad (1)$$

Here,  $M_i$  and  $L_i$  are the body mass and  $L$  of individual  $i$ , respectively;  $b_{SMA}$  is the scaling exponent determined by the regression of  $\ln M$  on  $\ln L$ . Further,  $L_o$  is the mean value of  $L$  (for the reference population; see Fig. S1), and  $\hat{M}_i$  is the predicted body mass for individual  $i$  when its  $L$  is standardized to  $L_o$ . Equation 1 was modified to determine standardized fat content, lean mass, and water content (*sensu* Peig & Green, 2009; Kelly *et al.*, 2014) using data from the experimental population (i.e.  $L_o$ , and the regression of  $\ln$  fat,  $\ln$  lean, and  $\ln$  water on  $\ln L$ ) because these data for a reference population were not available.

A BCI should be insensitive to changes in body size (e.g. it should not vary among age classes because it must remove the effects of ontogenetic growth; Peig & Green, 2010). Related, in species exhibiting sexual size dimorphism, there should be no difference in BCI between the sexes (Peig & Green, 2010). Body size (femur length) did not change with age in our study (all study animals were adults), but it was different between the sexes (females > males) and wing morphs (LW > SW; Appendix S1). Allometric relationships between body size (log-transformed  $L$ ) and body mass (log-transformed  $M$ ), as well as fat content, lean mass, and water content, varied due to sex and wing morphology in our study (Appendix S1). Body mass, fat content, lean mass and water content were all influenced by interactions between sex and body size and between morph and body (Appendix S1). Thus, data were separated by sex and morph to determine  $R_i$ ,  $\hat{M}_i$ , and standardized fat content, lean mass and water content. Datasets (i.e. data from males, females, SWs, and LWs) for standardized fat content, lean mass and water content, as well as all BCIs, were also analyzed separately (see below).

Although not a BCI *per se*, the analysis of covariance (ANCOVA) method (reviewed in Kelly *et al.*, 2014) was also used as a fifth method to account for  $L$  when examining the effects of age on  $M$  in each sex and morph. The advantages and limitations of all five of these methods have been

discussed by others in several excellent reviews (e.g. Peig & Green, 2009, 2010; Labocha *et al.*, 2014).

## Statistical analysis

Data were tested for normally distributed residuals and analyzed using SPSS (v.26 IBM Corp., Armonk, NY, USA). Two-tailed significance was determined at  $\alpha = 0.05$ . To examine how well BCIs predicted both standardized fat content and standardized lean mass, linear regression analyses were performed for each sex and morph. Here, standardized fat content, lean mass and water content were each regressed on each BCI (see above), and coefficients of determination ( $R^2$ ) were calculated as estimates of effect size. To examine the effects of age on body composition and BCIs, linear mixed model analyses were performed on each BCI, as well as standardized fat content, lean mass and water content, for each sex and morph. Mixed models were also performed on fresh body mass of each sex and morph where femur length was included as a covariate to control for body size (i.e. the ANCOVA method to infer effects on body condition). All linear models included selected block as a random effect, and eta-squared ( $\eta^2$ ) was determined as an estimate of effect size.

## Results

All BCIs strongly predicted standardized fat content and lean mass (Table 2). Across the four datasets (i.e. data from males, females, SWs, and LWs), BCIs explained 8–47% of the variation in fat content, 28–75% of the variation in lean mass, and 42–87% of the variation in water content (Table 2). The  $\hat{M}_i$  explained the most variation in fat content (mean  $\pm$  SEM:  $44 \pm 2\%$ ), lean mass ( $69 \pm 3\%$ ), and water content ( $74 \pm 5\%$ ) while Que'telet's index (BMI) was the least predictive of body composition (fat:  $11 \pm 2\%$ ; lean:  $32 \pm 2\%$ ; water:  $54 \pm 7\%$ ; Table 2).

Age strongly affected standardized fat content, lean mass, and water content, as well as all BCIs, with the exceptions of water content in SW crickets and  $R_i$  in LW crickets (Fig. 1; Table 3). The effect size ( $\eta^2$ ) of age tended to be lower for fat content (mean  $\pm$  SEM:  $0.13 \pm 0.1$ ) and water content ( $0.15 \pm 0.1$ ) relative to lean mass ( $0.29 \pm 0.3$ ) and the BCIs ( $0.25 \pm 0.02$ ; Table 3).

## Discussion

We used several datasets to examine the reliability of five common BCIs to estimate animals' energetic states with two approaches. First, the value of a given BCI is typically assessed by its relationship to animal fat content, and all of the five BCI methods (including the ANCOVA method) we examined significantly predicted standardized fat content in both sexes and morphs of *G. firmus* (Table 2). Second, a BCI can be evaluated by comparing whether it responds similarly to a treatment or factor as fat content (e.g. whether food limitation has a similar effect on standardized fat content as it does on a BCI). We demonstrate that BCIs and fat content were similarly

**Table 2** Relationships between body condition indices and aspects of body composition (standardized fat content, lean mass and water content) in both sexes and wing morphs of adult *Gryllus firmus* ( $n = 361$ )

	Fulton's index	Que' telet's index or body mass index	Residual index	Scaled mass index
Std. fat content (mg)				
Males	89 (0.33)	16 (0.08)	45 (0.20)	118 (0.40)
Females	89 (0.35)	25 (0.13)	42 (0.20)	151 (0.47)
Short-winged	85 (0.34)	14 (0.08)	28 (0.15)	121 (0.42)
Long-winged	105 (0.36)	34 (0.16)	73 (0.28)	166 (0.47)
Std. lean mass (mg)				
Males	244 (0.57)	71 (0.28)	142 (0.44)	282 (0.61)
Females	297 (0.64)	100 (0.37)	142 (0.46)	507 (0.75)
Short-winged	279 (0.63)	65 (0.28)	102 (0.38)	372 (0.69)
Long-winged	281 (0.60)	96 (0.34)	201 (0.52)	459 (0.71)
Std. water content (mg)				
Males	512 (0.74)	135 (0.42)	309 (0.63)	551 (0.75)
Females	866 (0.84)	285 (0.63)	505 (0.75)	1158 (0.87)
Short-winged	262 (0.61)	121 (0.42)	165 (0.50)	249 (0.60)
Long-winged	605 (0.76)	393 (0.68)	535 (0.74)	505 (0.73)

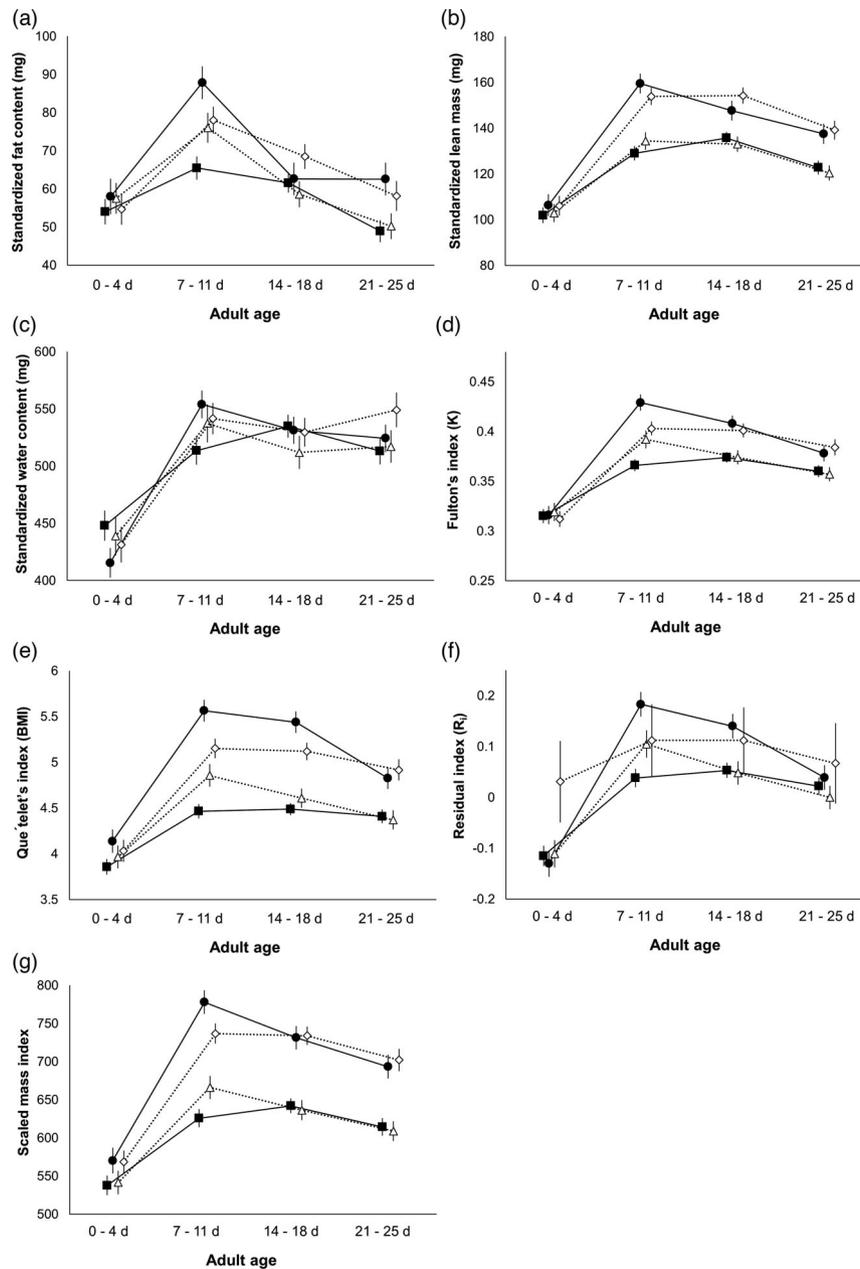
$F$  values are displayed for each result, all of which were highly significant ( $P < 0.001$ ), and parenthetical values indicate effect sizes ( $R^2$ ).

affected by adult age in *G. firmus* (Fig. 1; Table 3). However, BCIs were universally better proxies for lean mass and water content than for fat content. The relationships between BCIs and standardized lean mass and water content were stronger than those between BCIs and standardized fat content, and the effect sizes ( $\eta^2$ ) of age on BCIs were closer to that of lean mass relative to that of fat content (Tables 2 and 3). Thus, although BCIs reasonably predicted energy (fat) stores in *G. firmus*, they may better approximate lean mass or water content in insects.

The BCIs' accuracy in predicting body composition in our study was variable, but generally greater than in other studies on crickets that found BCIs poorly reflect fat content (Kelly *et al.*, 2014). We found that BCIs explained 8–47% of the variation in fat content, 28–75% of the variation in lean mass, and 42–87% of the variation in water content (Table 2), which correspond to medium or large effect sizes (Cohen, 1988). The  $\hat{M}_i$  is considered an ideal BCI because it leverages principles of allometric scaling (Peig & Green, 2009, 2010), and  $\hat{M}_i$  was a better predictor of standardized fat content than any other BCI in our study (Table 2). However,  $\hat{M}_i$  more strongly predicted standardized lean mass and water content than standardized fat content (mean  $\pm$  s.e.m.:  $69 \pm 3\%$  and  $74 \pm 5\%$  vs.  $44 \pm 2\%$  of variation explained, respectively; Table 2). Therefore, our results do not indicate that  $\hat{M}_i$  is better at discriminating energy (primarily, lipid) stores from other body components relative to other BCIs. The advantage of  $\hat{M}_i$  lies in its ability to account for the dynamic relationship between  $M$  and  $L$  as body size changes due to growth (Peig & Green, 2009, 2010). However, this advantage may be reduced when examining variation within an age class exhibiting a relatively fixed  $L$  (e.g. in adult insects: Kelly *et al.*, 2014; our study), and we therefore encourage researchers to carefully consider their study taxon when using a BCI to infer energetic state.

Although body size (femur length) did not change with age in our study, we demonstrate strong effects of adult age in both sexes and wing morphs (Fig. 1; Table 3; but see lack of age effect on  $R_i$  in LWs and fat content in SWs). Notably, BCIs and body composition exhibited similar age-related patterns where values increased dramatically after 1 week before generally plateauing or decreasing slightly thereafter (Fig. 1). During early adulthood (i.e. <1 week post-adult molt), wing morphology in female *G. firmus* influences lipid and protein metabolism (Zera, 2005; Zera & Zhao, 2006), and we show that similar morph-related effects on BCIs and lean mass may persist into later adulthood (Fig. 1; Table 3). Further understanding of how wing morphology influences body components throughout adulthood in both sexes of *Gryllus* may provide key insight into the morphological or physiological feature(s) that BCIs represent in insects. For example, nuclear magnetic resonance (NMR) microscopy has been used to non-invasively determine lipid stores in insects and small vertebrates (Schilling *et al.*, 2012; Warner *et al.*, 2016), and NMR could be used to serially measure energetic state throughout the life cycle of wing-dimorphic insects.

In our study, BCIs reliably predicted fat content and responded similarly to age as fat content, but BCIs were also generally better surrogates for non-lipid body components (Fig. 1; Tables 2 and 3). These results question the use of BCIs to approximate energy (fat) storage, in particular, which is presumably important given energy is a finite resource that constrains investment into fitness-related traits (Zera and Harshman, 2001; Roff, 2002; Peig & Green, 2009, 2010). Yet, it is possible that stores of other nutrients, including water and protein, may be similarly important to fitness (reviewed in Wilder *et al.*, 2016). Most of insects' reserves are in the forms of lipids and carbohydrates, but protein is often required for egg production (Beenackers, Van der Horst & Van Marrewijk, 1985; Wall, Wearmouth & Smith, 2002;



**Figure 1** Effects of adult age on (a.) standardized fat content (i.e. standardized to femur length), (b.) standardized lean mass, (c.) standardized water content, and (d. – g.) body condition indices in adult *G. firmus* ( $n = 361$ ; mean  $\pm$  s.e.m.). Data were separated by sex (black symbols; males: squares, females: circles) and wing morphology (white symbols; short-winged: triangles; long-winged: diamonds).

Lorenz & Anand, 2004; Alqurashi, English & Wall., 2020). Because the ingestion of food is linked to an insect's hemolymph osmolality (reviewed in Clissold *et al.*, 2014), water reserves may constrain the acquisition of macronutrients. Thus, even if BCIs are surrogates for protein and water storage, they may still approximate the storage of resources that fuel fitness-related traits. Further, variation in absolute body mass (rather than size-standardized body mass characterized

by BCIs) may have a greater influence on fitness-related traits than BCIs in some taxa (mammals and birds: reviewed in Rode *et al.*, 2020). Therefore, we advocate for future work to understand which body component(s) are reflected by traditional BCIs in other taxa, and to move toward better proxies for body components linked to fitness (e.g. Schilling *et al.*, 2012; Labocha *et al.*, 2014; Warner *et al.*, 2016; Wilder *et al.*, 2016).

**Table 3** Effects of age on body composition (standardized fat content, lean mass and water content) and body condition indices in both sexes and wing morphs of adult *G. firmus* ( $n = 361$ )

	Males	Females	Short-winged	Long-winged
Std. fat content (mg)	<b>6.5 (0.10)</b>	<b>9.7 (0.15)</b>	<b>8.6 (0.14)</b>	<b>8.0 (0.12)</b>
Std. lean mass (mg)	<b>22 (0.27)</b>	<b>25 (0.31)</b>	<b>15 (0.22)</b>	<b>31 (0.34)</b>
Std. water content (mg)	<b>9.6 (0.14)</b>	<b>24 (0.30)</b>	6.6	<b>13 (0.17)</b>
Fulton's index	<b>16 (0.21)</b>	<b>32 (0.36)</b>	<b>13 (0.19)</b>	<b>30 (0.33)</b>
Que' telet's index or body mass index	<b>14 (0.18)</b>	<b>28 (0.33)</b>	<b>9.6 (0.15)</b>	<b>22 (0.26)</b>
Residual index	<b>17 (0.22)</b>	<b>30 (0.35)</b>	<b>12 (0.18)</b>	0.27
Scaled mass index	<b>15 (0.20)</b>	<b>30 (0.35)</b>	<b>12 (0.18)</b>	<b>31 (0.34)</b>
ANCOVA method	<b>17 (0.22)</b>	<b>37 (0.40)</b>	<b>14 (0.21)</b>	<b>31 (0.34)</b>

*F* values are displayed for each result, bolded values were highly significant ( $P < 0.001$ ), and parenthetical values indicate effect sizes (eta-squared) for significant effects.

Note: ANCOVA method examined effects on body mass and included the covariate of femur length, which was highly significant ( $P < 0.001$ ).

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## Author contributions

ZRS designed the project, analyzed the data and led the writing of the paper. EC collected the data and helped to write the paper.

## Data availability statement

The data that support the findings of this study will be archived in Figshare and publicly available upon acceptance.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Appendix S1.** Figure S1. Relationship between body size (femur length) and body mass for a reference population of adult *G. firmus* ( $n = 2947$ ). Data for the reference population came from both sexes of adult short-winged (SW) and long-winged *G. firmus* from several published papers (Nguyen & Stahlschmidt, 2019; Glass & Stahlschmidt, 2019; Stahlschmidt *et al.*, 2020a, 2020a; Padda, Glass, & Stahlschmidt, 2021), as well as from unpublished data. However, subsets of data (e.g., male-only or SW-only data) were used to determine  $R_i$  and  $\bar{M}_i$  for each sex and wing morph because sexes and wing morphs exhibited different allometric relationships between body size and body mass.