



Evaluating the effects of water and food limitation on the life history of an insect using a multiple-stressor framework

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Abstract

Many environmental stressors naturally covary, and the frequency and duration of stressors such as heat waves and droughts are increasing globally with climate change. Multiple stressors may have additive or non-additive effects on fitness-related traits, such as locomotion, reproduction, and somatic growth. Despite its importance to terrestrial animals, water availability is rarely incorporated into multiple-stressor frameworks. Water limitation often occurs concurrently with food limitation (e.g., droughts can trigger famines), and the acquisition of water and food can be linked because water is necessary for digestion and metabolism. Thus, we investigated the independent and interactive effects of water and food limitation on life-history traits using female crickets (*Gryllus firmus*), which exhibit a wing dimorphism mediating a life-history trade-off between flight and fecundity. Our results indicate that traits vary in their sensitivities to environmental factors and factor–factor interactions. For example, neither environmental factor affected flight musculature, only water limitation affected survival, and food and water availability non-additively (i.e., interactively) influenced body and ovary mass. Water availability had a larger effect on traits than food availability, affected more traits than food availability, and mediated the effects of food availability. Further, life-history strategy influenced the costs of multiple stressors because females investing in flight capacity exhibited greater reductions in body and ovary mass during stress relative to females lacking flight capacity. Therefore, water is important in the multiple-stressor framework, and understanding the dynamics of covarying environmental factors and life history may be critical in the context of climate change characterized by concurrent environmental stressors.

Keywords Climate change · Cricket · Flight · Food stress · Life-history · Water stress

Introduction

Animals rely on key resources to express fitness-related traits, such as growth, fecundity, and locomotor capacity (van Noordwijk and de Jong 1986; Stearns 1989; Reznick and Yang 1993; Raubenheimer et al. 2005). Therefore, resource limitation may cause stress wherein animals struggle to adequately invest resources into multiple traits

simultaneously (Zera and Harshman 2001; Chown and Nicolson 2004). For example, food provides nutrients needed for somatic growth and reproduction (Wootton 1977; Raubenheimer and Gade 1996; Boggs 2009), and food limitation produces costs for animals—from increased mortality to reduced investment into reproductive and somatic tissue (Wootton 1977; Boggs and Freeman 2005; Boggs 2009). Thus, food limitation can be a stressor (i.e., a factor that disrupts homeostasis, performance, or fitness: Schulte 2014; Kaunisto et al. 2016) for animals. Periods of food limitation are expected to change in frequency and duration with global climate change (Ciais et al. 2005; Currano et al. 2008), and the effects of some aspects of climate change (i.e., warming) on population dynamics may be food dependent in major animal taxa (e.g., temperate insects: Adamo et al. 2012).

Although important, food limitation is only one possible stressor experienced by animals in nature. Other stressors may include temperature extremes, water limitation, and anthropogenic stressors, such as chemical, noise, and light

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pollution (Crain et al. 2008; Benoit et al. 2010; Holmstrup et al. 2010). Often, environmental conditions produce multiple stressors concurrently (Ciais et al. 2005; Holmstrup et al. 2010; McBryan et al. 2013; Sarhadi et al. 2018). For example, water and food availability may be linked in the environment because prolonged drought (water limitation) can reduce the availability of primary-produced food (Ciais et al. 2005; Zhao and Running 2010; Zhang et al. 2012). Animals' use of water and food can also be interdependent. For example, food consumption is linked to water availability because water is needed for digestion and is lost through excretion (Lepkovsky et al. 1957; Raubenheimer and Gade 1994, 1996). In turn, feeding can facilitate water intake. For example, locusts can maintain water balance by preferentially feeding on foods with higher water content in response to increased hemolymph osmolality (Lewis and Bernays 1985; Simpson and Raubenheimer 2008). Some animals can uncouple water availability and food consumption by relying heavily on metabolic water production (e.g., desert rodents: Frank 1988; tenebrionid beetles: Nicolson 1980). Even so, closer examination has revealed that desert rodents will, on occasion, supplement their seed diets with insects (70% water) and green plants (90% water) to maintain water balance (Reichman 1975; Walsberg 2000). The effects of food or water stress are often examined using a single-stressor experimental approach (e.g., manipulating only food while controlling for all other variables, including water availability; Nelson 1993; Boggs and Freeman 2005; O'Brien et al. 2019; Seress et al. 2020). However, the biological and environmental links between food and water indicate that factorial, multiple-stressor studies would be beneficial for understanding the role of complex environmental stressors in animal life history and physiology (Crain et al. 2008; Boggs 2009; Holmstrup et al. 2010; Kaunisto et al. 2016).

Multiple stressors may have an additive effect on a given animal trait (e.g., survival or growth) where the stress due to two factors is simply the sum of either factor alone (Todgham and Stillman 2013). However, multiple stressors may result in interactive, non-additive effects, such as synergistic or antagonistic effects (Folt et al. 1999; Todgham and Stillman 2013; Piggott et al. 2015). Synergistic effects occur when the combined cost due to both stressors is greater than expected from additive effects alone. Antagonistic effects of multiple stressors occur if the combined cost due to both stressors is less than either stressor alone. In contrast, the effects of two potential stressors may be neither additive nor non-additive (e.g., when a trait is affected by only one or neither stressor). To date, multiple-stressor studies have focused largely on the costs associated with combinations of food, chemical, pathogen, and thermal stress (reviewed in Crain et al. 2008; Holmstrup et al. 2010; Kaunisto et al. 2016). Yet, water's role in the multiple-stressor framework is less understood, despite the fundamental role of water

in terrestrial life and its increasing scarcity in many global regions (Gray 1928; Graham 1973; Chown et al. 2011; Takei 2015; Kaunisto et al. 2016; Sarhadi et al. 2018).

Hence, we used a factorial design to examine the independent and interactive effects of food and water limitation on several fitness-related traits. In particular, we used female sand field crickets (*Gryllus firmus* Scudder 1902), which exhibit two distinct wing morphs or life-history strategies that vary in investment into reproductive and somatic tissues during early adulthood (i.e., Roff 1984; Walker and Sivinski 1986; Zera 2005). Long-winged (LW) females can invest into flight muscle (dorso-longitudinal muscle, DLM) at a cost of reduced investment into ovary mass while short-winged (SW) females do not invest significantly in DLM but rather exhibit increased investment into ovaries relative to LW females (Roff 1984; Zera et al. 1994; Zera 2005).

We tested several predictions in female *G. firmus* using the multiple-stressor framework. The first set of predictions tested whether the effects of multiple stressors were additive (prediction 1a), non-additive (i.e., interactive: synergistic or antagonistic; prediction 1b), or neither additive nor non-additive (prediction 1c) for each trait. We leveraged the variation in wing morphology in *G. firmus* (see above) to test another set of predictions (predictions 2a and 2b). Here, we tested whether life-history strategy influences environmental sensitivity. For prediction 2a, we predict water and food limitation will result in more costs to LW females because these individuals tend to express the trait of flight capacity by allocating significant resources toward DLM and associated flight fuels, whereas SW females do not (Zera and Mole 1994; Zera et al. 1994; Zera and Denno 1997; Chown and Nicolson 2004; Zera 2005). For example, DLM investment may be prioritized by LW females in stressful environments given the adaptive significance of flight capacity, which is to facilitate dispersal away from low-quality environments (reviewed in Roff 1994a; Guerra 2011). This prioritization of flight capacity may exacerbate the costs of stressors to traits not related to flight (e.g., ovary mass or survival). For prediction 2b, we predict individuals with greater muscle stores will be less sensitive to food and water limitation. Specifically, LW females would incur fewer costs during food and water limitation because these individuals (unlike SW females) can catabolize protein from DLM to intrinsically generate water. Some vertebrates oxidize protein long before their fat stores are depleted and rely on protein oxidation to supplement water during reproduction, potentially because protein oxidation produces five times as much endogenous water as fat oxidation per kJ (sensu 'protein for water' hypothesis: reviewed in McCue et al. 2017; Bruschi et al. 2018). By examining the role of life-history strategy in the costs of multiple stressors, we will improve our understanding of the effects of resource-related stress,

and we encourage further tests using the multiple-stressor framework.

Materials and methods

Study species

The sand field cricket (*Gryllus firmus*) is native to the southeastern United States and found most abundantly in Florida (Scudder 1902; Veazey et al. 1976; Capinera et al. 2004). The animals used in this study were acquired from three nearly true-breeding selected blocks of SW and LW crickets (Zera and Cisper 2001; Zera and Larsen 2001; Zera 2005; Glass and Stahlschmidt 2019; Stahlschmidt et al. 2020). Cricket stock originated from populations near Gainesville, FL that exhibit morph frequencies of approximately 0.4 SW and 0.6 LW (Zera et al. 2007). Crickets were raised in outbred populations (blocks) that were artificially selected for several decades to produce either SW or LW morphs that have been previously described (Zera 2005). Three replicate blocks of crickets were used in this study. Throughout ontogeny, crickets were reared in standard conditions: 16-h photoperiod at 28 ± 1 °C with ad libitum access to water (water-filled shell vials plugged with cotton) and commercial dry cat food.

Experimental design

To examine how water and food limitation independently and interactively affected mortality and investment into body mass, flight muscle, and reproductive tissue in *G. firmus*, a factorial design was used on SW and LW females during early adulthood (i.e., a $2 \times 2 \times 2$ factorial design including water treatment, food treatment, and wing morphology as factors). In *G. firmus* females, the first 5 days of adulthood are characterized by intense energy demands as this is the period during which many LW females invest in flight muscle and females of both wing morphs increase ovary mass by 100-fold or more (Zera and Larsen 2001; Zera 2005). Crickets feed intermittently in nature (Gangwere 1961), meaning they may forego feeding for several days at a time. Therefore, we examined the effects of food presence vs. absence during the first 5 days of adulthood. To compare the effects of water vs. food limitation, we also manipulated water availability in the same presence vs. absence manner. Further, our data indicate that most *G. firmus* survive 5 days without water and/or food (see below), and a related species (*G. lineaticeps*) also exhibits relatively high rates of survival after a similar duration of water and food limitation (Padda et al. 2021).

Newly molted adults (< 2 days after final ecdysis) were assigned to one of four treatment groups: no stress (ad lib. water and food [dry cat food]), water stress (no water but ad lib. food), food stress (ad lib. water but no food), and water + food stress (neither water nor food) for a 5-day study period. All crickets ($n = 172$ for SW, $n = 257$ for LW) were individually housed in small translucent deli cups (473 ml) containing shelter (overturned 30 ml opaque containers with an access hole) at 28 ± 1 °C. The relative humidity of cups containing crickets in the ‘no water stress’ and ‘water stress’ treatments were $82.5 \pm 3\%$ and $62.5 \pm 4\%$, respectively, as determined by a humidity sensor (U23, Onset Computer Corp., Bourne, MA, USA). At the onset of the experiment, each cricket’s body mass and wing morphology (SW or LW) were recorded. From a subset of the no stress and water stress crickets ($n = 31$ for SW, $n = 27$ for LW), food consumption was measured by recording food mass at the onset and at the end of the study. After 5 days, mortality was recorded. Final body mass of surviving crickets was recorded, and then these individuals were euthanized and stored at -20 °C.

After storage, a subset of crickets that survived treatment ($n = 57$ for SW, $n = 91$ for LW) were dried at 55 °C to a uniform consistency. Crickets were then re-weighed to determine water content (WC; % of final body mass), which allowed for the determination of the effects of treatment (particularly, water availability) on water balance. The remaining surviving crickets ($n = 88$ for SW, $n = 84$ for LW) were dissected. During dissections, flight musculature (DLM) was scored from 0 to 2, where 0 indicated DLM was absent, 1 indicated white, histolyzed (non-functional) DLM, and 2 indicated pink, functional DLM (Crnokrak and Roff 2002; King et al. 2011; Glass and Stahlschmidt 2019). None of the SW crickets in our study exhibited functional DLM, and LW crickets largely exhibited histolyzed DLM (see below). Previous work indicates that LW *G. firmus* exhibiting histolyzed DLM (LW[h]) are more physiologically similar to SW *G. firmus* relative to LW *G. firmus* exhibiting functional DLM (LW[f]) (Zera et al. 1997; Zera and Larsen 2001). Yet, the distinction between LW (i.e., both LW[h] and LW[f]) and SW *G. firmus* is important because LW(h) and LW(f) *G. firmus* can differ from SW *G. firmus* in adult body mass, DLM status, and rates of development and growth (Glass and Stahlschmidt 2019). The behavioral and investment strategies of the wing morphs vary in their sensitivities to oxidative and immune challenges in *G. firmus* (Stahlschmidt et al. 2020; Stahlschmidt and Glass 2020), and to combined water limitation and heat in *G. lineaticeps* (Padda et al. 2021). This design allowed for the examination of the effects of wing morphology—LW or SW—from a large data set ($n = 429$), and of wing morphology and flight muscle status—SW; LW(h), LWs with DLM scores of 0 or

1; and LW(f), LWs with DLM scores of 2—from a smaller subset of data ($n = 172$).

Next, ovaries were removed from dissected crickets ($n = 172$) and dried at 55 °C to a constant mass to estimate investment into reproduction (Roff and Fairbairn 1991; Crnokrak and Roff 2002; Glass and Stahlschmidt 2019). Ovary mass in *G. firmus* is proportional to egg number (Roff 1994b; ZRS unpublished). The legs of all crickets (including those that did not survive treatment) were collected, and femurs were measured. Femur length was used as a proxy for adult body size because crickets cease structural body growth after reaching the adult stage (Simmons 1986; Glass and Stahlschmidt 2019; Nguyen and Stahlschmidt 2019). Femur length positively correlated with absolute water content (i.e., mg per individual; $R = 0.37$; $P < 0.001$).

Statistical analyses

Data were tested for normality using Shapiro–Wilk tests, and natural logarithm-transformations were required for food intake, dry ovary mass, and WC data sets. Data were then analyzed using SPSS (v.25 IBM Corp., Armonk, NY), and two-tailed significance was determined at $\alpha = 0.05$. To examine the independent and interactive effects of treatments (water and food as separate fixed factors) and either wing morphology (herein, “morph”: SW or LW) or (when possible) morph-DLM status (herein, “morph-DLM”: SW, LW[h], or LW[f]), a restricted maximum likelihood method was used for linear mixed model analyses on final body mass, food consumption, dry ovary mass, and WC. For each mixed model, treatments and morph were included as main effects—that is, a total of three treatments (food, water, and morph or morph-DLM; note: food stress and combined food and water stress crickets were excluded from food consumption models). Although individuals were randomly assigned to treatment groups, initial body mass and femur length varied across morph and/or treatment groups. Therefore, initial body mass was included as a covariate for the final body mass, food consumption, and ovary mass models because it was an independent proxy for body size. Final body mass was not included as a covariate because it was not independent of food consumption or ovary mass. All models included selected block as a random effect, and tested for interactions between and among treatments and morph.

An ordinal logistic generalized linear mixed model was performed on the categorical DLM scores (scored from 0 to 2, see above) and treatments and morph were included as main effects. Similarly, a binary logistic generalized linear model was used on data from each cricket to determine the main and interactive effects of treatments and morph on survivorship (0: did not survive treatment; 1: survived treatment). For both generalized linear models, femur length

was included as a covariate to account for variation in body size. Non-significant interactive effects were removed from the final (reported) generalized linear models because doing so did not increase the Akaike information criterion, and we report the most parsimonious models below.

For all models, values are presented as estimated marginal means ($\pm 95\%$ confidence intervals) because covariates were included in analyses—that is, reported values account for variation in body size (femur length) or body mass depending on the analysis (see above). When significant interactive effects were detected (e.g., the interaction of food and water treatments on WC; see below), post hoc analyses on pairwise comparisons were used to determine differences between treatment group combinations. Post hoc tests used the sequential Bonferroni method to control for Type I error rate due to multiple comparisons.

Results

There was a positive effect of water availability on dry food consumption where individuals with access to water had higher food consumption than those without water access (Table S1; Fig. 1). Food consumption also positively covaried with starting body mass, but it was not influenced by morph-DLM or the interaction between water treatment and morph (Table S1; Fig. 1).

Crickets with access to water had higher water content than water-limited individuals, and food availability also affected water content (Table S2; Fig. 2A). Short-winged crickets also had greater water content than LWs (Table S2; Fig. 2A). There was a significant interactive effect of food and water treatments on water content where individuals given ad lib. access to water but not food had the highest

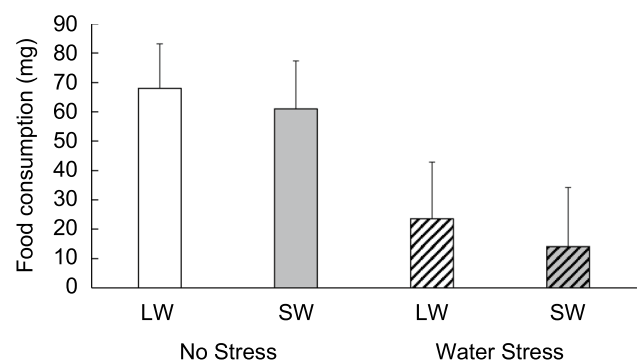


Fig. 1 Effects of water stress on food consumption during early adulthood in female *G. firmus* during early adulthood. Short-winged (SW) morphs are depicted by gray bars, and long-winged (LW) morphs are depicted by white bars. Diagonally striped bars designate water stress. Values are displayed as estimated marginal means (\pm s.e.m.) because initial body mass was included as a covariate

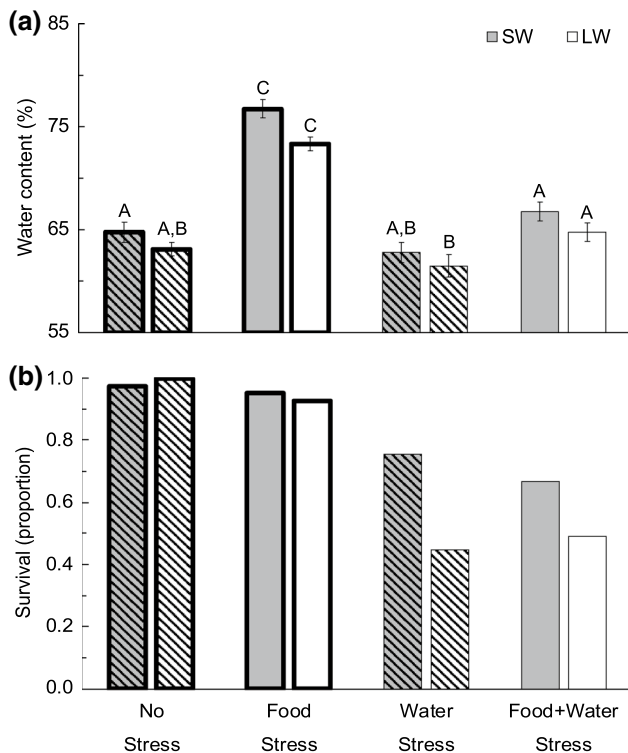


Fig. 2 Effects of no stress, food stress, water stress, and combined food and water stress during early adulthood on **a** water content (% of fresh mass), and **b** survival in female *G. firmus*. Short-winged (SW) morphs are depicted by gray bars, and long-winged (LW) morphs are depicted by white bars. Diagonally striped bars designate individuals with access to food, and bolded bars designate those with access to water. Values are displayed as estimated marginal means (\pm s.e.m.) because either body mass or size was included as a covariate (see text for details). Letters above each column denote differences among treatment group combinations for traits influenced by interactive effects (see text for details)

water content (Table S2; Fig. 2A). Water content was not affected by other interactive effects (Table S2; Fig. 2A).

Survival was greater in SW individuals, larger individuals, and those with access to water (Table S3; Fig. 2B). There was not a significant effect of food treatment on survival (Table S3; Fig. 2B), and all treatment–morph interactions were also non-significant (all $P > 0.40$).

Final body mass was greater in individuals with access to food and to water, and it was influenced by initial body mass (Table S4; Fig. 3A). An interactive effect of food and water influenced final body mass where the positive effect of food on body mass was greater when water was available (Table S4; Fig. 3A). Final body mass was influenced by a morph-DLM (dorso-longitudinal muscle) and food interaction (Table S4) where body mass in LW(h) crickets incurred fewer costs due to food limitation (Fig. 3A). Morph-DLM did not influence final body mass, and there were no interactive effects of morph-DLM and water treatment or

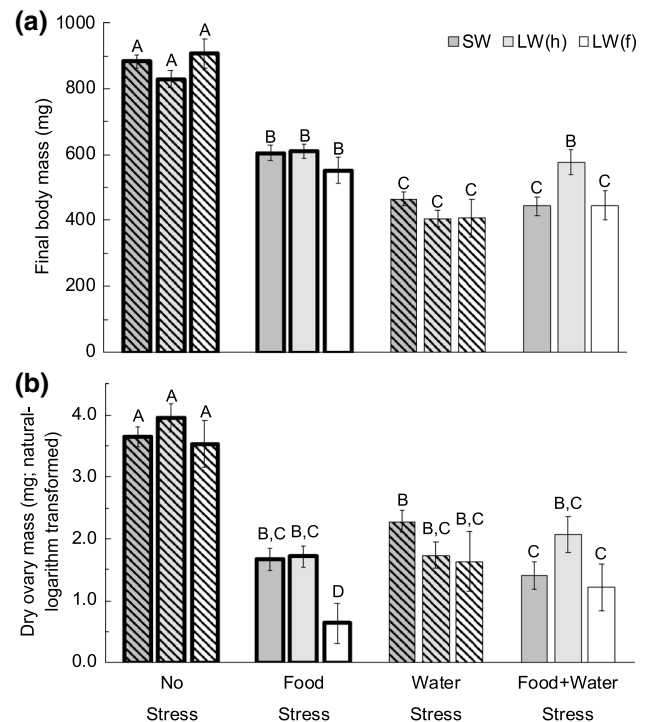
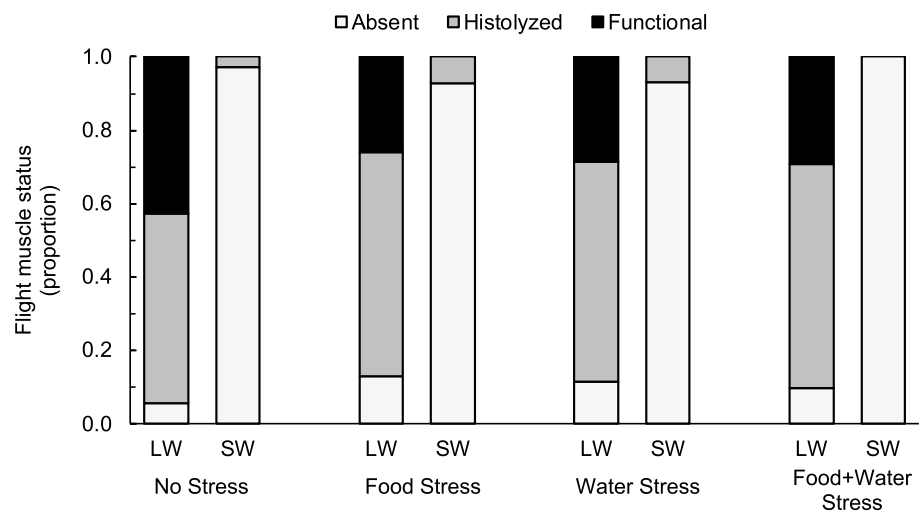


Fig. 3 Effects of no stress, food stress, water stress, and combined food and water stress during early adulthood on **a** final body mass and **b** ovary mass in female *G. firmus*. Short-winged (SW) morphs are depicted by dark gray bars, long-winged morphs with histolyzed flight muscle (LW(h)) are depicted by light gray bars, and long-winged morphs with functional flight muscle (LW(f)) are depicted by white bars. Diagonally striped bars designate individuals with access to food, and bolded bars designate those with access to water. Values are displayed as estimated marginal means (\pm s.e.m.) because initial body mass was included as a covariate (see text for details). Letters above each column denote differences among treatment group combinations for traits influenced by interactive effects (see text for details)

morph-DLM, water, and food on final body mass (Table S4; Fig. 3A).

Ovaries were heavier in crickets with access to food, in those with access to water, and in SW or LW(h) crickets (Table S5; Fig. 3B). An interactive effect of food and water influenced ovary mass where the positive effect of food on ovary mass tended to be stronger when water was available (Table S5; Fig. 3B). Ovary mass was also affected by an interaction among morph-DLM, water, and food, and by initial body mass (Table S5; Fig. 3B). However, it was not affected by interactions between morph-DLM and food or morph and water (Table S5; Fig. 3B). Food and water treatments did not influence DLM status, but LW females had more functional flight muscle than SWs (Table S6; Fig. 4). Larger females also had higher flight muscle scores (Table S6).

Fig. 4 Effects of no stress, food stress, water stress, and combined food and water stress during early adulthood on flight muscle in female *G. firmus*. Flight muscle data are displayed in frequencies. White bars indicate an absence of flight muscle (dorso-longitudinal muscle, DLM), gray bars indicate histolyzed DLM, and black bars indicate functional DLM



Discussion

Single-stressor studies are commonly used to investigate the effects of environmental stress on life-history traits (Wall 1970; Weaver and Pratt 1981; Stillman 2003; Deutsch et al. 2008; Colinet et al. 2018). These studies are important for understanding the effects of stress on life history because they are direct and convey the importance of a given stressor while controlling for or eliminating confounding factors. Yet, due to the complexity of natural environments where concurrent stressors are common, multiple-stressor studies likely better reflect conditions in nature (Arnell 1999; O'Brien et al. 2004; Crain et al. 2008; Boggs 2009; Holmstrup et al. 2010; Kaunisto et al. 2016; Sarhadi et al. 2018). Using a multiple-stressor framework, we determined that water and food stress independently and interactively influenced body water content, body mass, and reproductive investment in a wing-dimorphic insect (Figs. 2 and 3). Further, body size influenced absolute water content, flight capacity, and survival; and wing morphology influenced flight capacity and survival (Figs. 2 and 3). Together, these results demonstrate the value of accounting for biotic variation and multiple stressors when investigating the effects of environmental stress on life history. We encourage future investigations into additional biotic factors (e.g., sex and life-history stage) and stressors associated with climate change (e.g., temperature extremes).

Support was not found for prediction 1a (additive effects of multiple stressors). The traits examined in our study sustained no costs, costs from only a single (not both) stressor, or non-additive costs related to food and water limitation. For example, survival did not experience additive or non-additive effects because it incurred costs from water (but not food) limitation (Fig. 2B), in support of prediction 1c. This result demonstrates the value of integrating water availability into the multiple-stressor framework (Arnell 1999;

Mueller and Seneviratne 2012). Terrestrial ecosystem productivity is limited by water availability, and climate models predict an increase in the frequency and duration of droughts globally (O'Brien et al. 2004; Ciais et al. 2005; Mueller and Seneviratne 2012; Sarhadi et al. 2018). Although there was no effect of food availability on survival in our study, reduced survival as a result of food limitation has been documented across a range of taxa, including other insects, mammals, and birds (Juliano 1986; Williams et al. 1993; Huitu et al. 2003; Davis et al. 2005). Previous work in *G. firmus* has shown that food limitation reduced survival when crickets were reared (i.e., developed) under food stress (Glass and Stahlschmidt 2019). In contrast, food limitation in our study was relatively brief (5 days) and occurred only during the adult stage. Further, crickets likely feed intermittently in nature (Gangwere 1961). Thus, a 5-day food limitation period may be insufficient to impact survival, and prolonging our food stress treatment would undoubtedly increase its effect on survival. Therefore, discrepancies between our results and those of other food stress experiments may be the result of variation in the timing of food stress and/or taxonomic differences.

Prediction 1b (non-additive effects of multiple stressors) was supported by some of our results because combined food and water stressors had non-additive effects on somatic and reproductive tissues. Specifically, there was no additional cost to final body mass or ovary mass when animals encountered both stressors compared to when they encountered only one stressor—that is, food stress alone and water stress alone had relatively similar effects as combined food and water stress (Fig. 3). There was an interactive effect of food and water limitation on final body mass and ovary mass where the benefits of food availability were only observed when water was available (Fig. 3), and this was likely because water limitation resulted in a > fivefold reduction in food intake on average in our study. This food–water

interaction may be due to water's role in digestion because water is needed as a solvent to transport and digest food in the alimentary canal and for excretion (Raubenheimer and Gade 1994; Woods and Bernays 2000; Gibbs et al. 2003; Hinsberger and Sandhu 2004). Our results support this argument as individuals without access to water ate less and had a lower water content (Figs. 1 and 2A). Thus, water limitation reduces the consumption and digestion of food (but not vice versa; food limitation increased water content: Fig. 2A), and eating food in the absence of water may even be costly (Gillespie and McGregor 2000; Sinia et al. 2004; Clissold et al. 2014). For instance, feeding during water limitation can disrupt gastrointestinal regulation and dehydrate non-gastrointestinal tissues (Strominger 1947; Lepkovsky et al. 1957; Cizek 1959). Together, our results signify the importance of water availability to life history because water limitation affected more fitness-related traits than food limitation, and water availability mediated the benefits of food availability (Figs. 2 and 3).

We did not detect an effect of food or water limitation on flight muscle (DLM; Fig. 4). Thus, it is possible that the maintenance of flight muscle is not plastic in response to environmental stress. However, previous work has demonstrated that *G. firmus* experiencing food limitation during the adult stage (King et al. 2011) and during development (Glass and Stahlschmidt 2019) prioritize flight muscle investment, possibly as an adaptive mechanism to leave poor conditions. Further, flight muscle capacity in *G. firmus* can also be reduced during stress related to oxidative damage and to immune challenge (Stahlschmidt et al. 2020; unpublished). Other insect studies have demonstrated bidirectional plasticity in flight muscle status in response to stressors, supporting both flight muscle maintenance and loss due to stress (Stegwee et al. 1963; Edwards 1969; Sniegula et al. 2017). Non-insect taxa also exhibit phenotypic plasticity in flight muscle physiology. Although the basal metabolism of birds varies dramatically to that of insects, flight muscle in birds is analogous to that of insects because the flight muscles of birds and insects are similar in composition, use of flight fuels, and flight muscle metabolism (Suarez et al. 1991; Jenni-Eiermann and Jenni 1992; Zera and Mole 1994; Zera et al. 1994; Jenni and Jenni-Eiermann 1998; Klaassen et al. 2000; Marden 2000). The flight muscles of migratory birds atrophy during overwintering, and some birds may also catabolize flight muscle when they are water stressed or breeding (e.g., to reallocate water and nutrients to egg production) (Veasey et al. 2000; Weber and Hedenström 2001; Gerson and Guglielmo 2011a, b). Furthermore, seasonal plasticity of flight muscle is documented for some shorebirds (Swanson and Merkord 2013). Although the metabolic physiology of insect and non-insect taxa (i.e., birds) flight muscle is different, their observed responses to environmental stressors are consistently similar within both taxonomic groups.

Considering the variable responses to the environment (e.g., some stressors promote flight capacity while others reduce flight capacity), future studies should continue to examine the independent and interactive effects of multiple stressors on flight muscle plasticity in crickets given its link to lifetime reproduction (Roff 1984) and dispersal ability (Sun et al. 2020).

Across taxa, investment into flight muscle often trades off with investment into other traits (Roff 1977; Zera et al. 1994; Zera and Mole 1994; Veasey et al. 2001; Kullberg et al. 2005; Zera 2005; Nespolo et al. 2008; Owen and Moore 2008). For example, our results indicate that LW(f) *G. firmus* had reduced investment into reproduction when stressed (Fig. 3B). Similarly, flight capacity is associated with reduced reproductive investment in other wing-dimorphic insects (Guerra 2011). In insects, flight capacity can also trade-off with development rates and other physiological traits (Chown and Nicolson 2004). Migrating birds exhibit reduced immune function and increased oxidative damage (Schwilch et al. 1996; Costantini et al. 2008; Owen and Moore 2008; Jenni-Eiermann et al. 2014), and flying reduces immune function in other *Gryllus* species (Adamo et al. 2008). Recent work expands the costs of macroptery in *G. firmus* to other non-reproductive traits because environmental variability during development can influence flight-related trade-offs with body size and with rates of growth and development (Glass and Stahlschmidt 2019). In agreement with previous literature evaluating the costs of flight muscle, our results indicate that flight muscle maintenance may produce yet another cost: increased mortality (LW *G. firmus* had lower survival than SW individuals: Fig. 2B; Chown and Nicolson 2004). Future work should clarify this potential cost by comparing the flight muscle status of surviving and dead LW crickets to formally test the prediction that flight muscle investment is directly associated with stress-induced death. We encourage the continued examination of the dynamic interplay between flight capacity and other traits, in the context of environmental variability and/or stress.

Prediction 2a (flight capacity influences environmental sensitivity) was partially supported because the body and ovary mass in flight-capable (i.e., LW[f]) *G. firmus* tended to be particularly sensitive to food and/or water availability (Fig. 3). Prediction 2b was not supported. As in other studies, LW *G. firmus* did allocate significantly more resources toward DLM relative to SW females (Fig. 4; Roff 1977; Roff 1984; Roff and Fairbairn 1991; Zera and Mole 1994; Zera et al. 1994; Zera and Denno 1997; Zera 2005; Nespolo et al. 2008). Yet, despite likely containing more fat body than SWs (Zera 2005), LW females in our study exhibited increased mortality when stressed, potentially due to reduced water content (Fig. 2). Long-winged female *Gryllus* tend to exhibit greater metabolic rates than SW females

(Zera and Mole 1994; Zera et al. 1997; Nespolo et al. 2008; but see Clark et al. 2016; Stahlschmidt and Glass 2020), and higher mortality in LW females may be associated with their greater metabolic rates relative to SW females. Investment into flight muscle in *Gryllus* likely incurred a survival cost in our study (LWs in Fig. 2B), but some birds use flight muscle to their advantage because they catabolize muscle tissue to promote fitness. For example, survival and reproductive investment in birds can increase when protein is catabolized to liberate protein-bound water (Veasey et al. 2000, 2001; Kullberg et al. 2005; Gerson and Guglielmo 2011a, b). This taxon-specific difference in the sensitivity of muscle tissue to environmental stress (i.e., whether to catabolize or maintain muscle during stress) may be linked to the functional or adaptive significance of a given muscle tissue. Flight muscle in *Gryllus* and other insects allows for dispersal when environmental conditions are poor (Edwards 1969; Davis 1975; Roff 1994a; Guerra 2011), which likely creates strong selection on flight muscle maintenance in stressful environments. However, muscle tissue used for locomotion and prey capture is catabolized during reproduction in female pythons, and protein and water are allocated into eggs when breeding-related foraging and feeding ceases (Stahlschmidt et al. 2011; Brusch et al. 2018). A “protein for water” strategy is also used by passerine birds during migration, which catabolize protein to maintain water balance during long flights (Gerson and Guglielmo 2011a, b), and by water-stressed rodents (Bintz and Mackin 1980; McCue et al. 2017). Although this strategy is used by animals with high- and low-energy demands (i.e., birds and mammals, and pythons, respectively), its ubiquity across animal taxa is unknown and may be absent in protein-limited animals. Thus, subsequent work must continue to consider the functional or adaptive significance of a given muscle tissue in the context of the studied animal’s life history when making predictions about the effects of multiple stressors (particularly, those related to water stress) on muscle tissue.

Experimental and biogeographical evidence indicates strong selection for smaller body size due to warming (e.g., temperature-size rule, and Bergmann’s rule: Bergmann 1847; reviewed in Angilletta 2009; Gardner et al. 2011). However, smaller individuals are particularly susceptible to non-thermal stressors associated with warming events (water and food limitation: Arnell 1999; O’Brien et al. 2004; Ciais et al. 2005; Sarhadi et al. 2018). As examples, smaller *G. firmus* had reduced water stores, survival, and dispersal capacity in our study, and smaller desert songbirds are more vulnerable to water loss and dehydration than larger birds (Albright et al. 2017). Thus, a smaller body size may increase fitness when considering only warming, but a small body size could increase fitness costs when considering multiple concurrent stressors (e.g., thermal and non-thermal stressors). A smaller body size also constitutes fitness costs

because smaller animals have fewer mating opportunities, produce fewer and smaller offspring, and are less likely to hold territory (Peters and Peters 1986; Mathis 1991; Tejedo 1992; Kolm 2001; Dubey et al. 2009). Recent work indicates that both large and small body sizes are likely susceptible to multiple environmental stressors (Gibb et al. 2018). Therefore, understanding how animal body size responds to environmental stressors exacerbated by climate change (e.g., drought frequency and duration) is crucial to predicting ecological change, such as changes in phenology and population dynamics (Sillett et al. 2000; Walther et al. 2002).

In summary, our study illustrates the importance of incorporating water into the multiple-stressor framework by demonstrating that water availability has a larger effect on traits than food availability, affects more traits than food availability, and mediates the effects of food availability in *G. firmus* (Figs. 2 and 3). The multiple-stressor framework has a rich history in ecotoxicology where it has been applied to systems in which water is freely available (i.e., aquatic ecosystems: Cada et al. 1987; Johnsen and Jakobsen 1987; reviewed in Kaunisto et al. 2016). Thus, the role of water has been underemphasized in the multiple-stressor framework despite the importance of water to terrestrial animals (e.g., MacMillen 1990). Understanding water limitation, including its interactive effects with other covarying environmental factors, is increasingly important as the frequency and duration of droughts increase with climate change (Arnell 1999; Ciais et al. 2005; o’Brien et al. 2004; Mueller and Seneviratne 2012). Three major components of climate change (i.e., water and food variability, and warming) naturally covary. Hence, future multiple-stressor work should continue to explore the effects of all three factors on life-history traits, as well as on trait–trait interactions (e.g., shifts in trade-offs or allocation strategies) (Killen et al. 2013; Glass and Stahlschmidt 2019; Kellermann and Heerwaarden 2019; Padda et al. 2021).

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Declarations

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