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RESEARCH ARTICLE

Intralocus sexual conflict over optimal nutrient intake and the evolution of sex differences in life span and reproduction

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Abstract

1. Despite widespread variation in life span across species, three clear patterns exist: sex differences in life span are ubiquitous, life span is commonly traded against reproduction, and nutrition has a major influence on these traits and how they trade-off. One process that potentially unites these patterns is intralocus sexual conflict over the optimal intake of nutrients for life span and reproduction. If nutrient intake has sex-specific effects on life span and reproduction but nutrient choice is genetically linked across the sexes, intralocus sexual conflict will occur and may prevent one or both sexes from feeding to their nutritional optima.
2. Here we determine the potential for this process to operate in the decorated cricket *Gryllodes sigillatus*. Using the Geometric Framework for Nutrition, we restrict male and female crickets to diets varying in the ratio of protein to carbohydrates and total nutrient content to quantify the effects on life span and daily reproductive effort in the sexes. We then use inbred lines to estimate the quantitative genetic basis of nutrient choice in males and females. We combine the nutrient effects and genetic estimates to predict the magnitude of evolutionary constraint for these traits in each sex. Finally, we present male and female crickets with a much broader range of diet pairs to determine how the sexes actively regulate their intake of nutrients.
3. We show that protein and carbohydrate intake have contrasting effects on life span and reproduction in the sexes and that there are strong positive intersexual genetic correlations for the intake of these nutrients under dietary choice. This is predicted to accelerate the evolutionary response of nutrient intake in males

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but constrain it in females, suggesting they are losing the conflict. Supporting this view, males and females regulate nutrient intake to a common nutrient ratio that was not perfectly optimal for life span or reproduction in either sex, especially in females.

4. Our findings show that intralocus sexual conflict over the optimal intake of nutrients is likely to be an important process generating sex differences in life span and reproduction and may help explain why females age faster and live shorter than males in *G. sigillatus*.

KEYWORDS
carbohydrate, evolutionary constraint, genetic correlation, nutritional geometry, protein, sex-specific nutritional optima

1 | INTRODUCTION

Average life span is known to vary greatly within and between species (e.g. Shilovsky et al., 2017), yet three clear patterns have emerged from decades of empirical research. First, sex differences in life span are ubiquitous across the tree of life (e.g. Austad & Fischer, 2016; Maklakov & Lummaa, 2013). In many species of insects (e.g. Austad & Fischer, 2016; Bonduriansky et al., 2008) and mammals (e.g. Austad, 1997; Clutton-Brock & Isvaran, 2007), females typically live longer than males, whereas the reverse pattern is more common in birds (e.g. Donald, 2007) and nematodes (McCulloch & Gems, 2003). Second, dietary restriction (a reduction in food intake without malnutrition) is known to extend life span in a wide range of species (Mair & Dillin, 2008). On average, dietary restriction reduces the risk of death across species by as much as 60% and this effect is 20% stronger in females than in males (Nakagawa et al., 2012). For decades, the effect of dietary restriction on life span was attributed to the restricted intake of calories (Masoro, 2005). However, studies on insects (Bruce et al., 2013; Fanson et al., 2009; Harrison et al., 2014; Jensen, McClure, et al., 2015; Lee et al., 2008; Maklakov et al., 2008; Rapkin et al., 2017) and mice (Solon-Biet et al., 2014, 2015) have shown that a balanced intake of macronutrients is far more important for extending life span. In each species, life span was extended on medium to high calorie diets containing lower protein (P) to carbohydrate (C) ratios. Indeed, P restriction appears more effective in extending life span than caloric restriction across species (Nakagawa et al., 2012). Third, reproduction is costly and is commonly traded against life span (Reznick, 1985; Williams, 1966). On average, dietary restriction reduces reproduction across species and this reduction is greater in females than males (Moatt et al., 2016). When coupled with the fact that dietary restriction extends life span across species and this effect is also more pronounced in females than males (Nakagawa et al., 2012), this suggests that the trade-off between reproduction and life span is both taxonomically widespread and sex specific (Moatt et al., 2016). There is also growing support from insect studies that the trade-off between reproduction and life span is stronger in females than males, as well as evidence that the intake of key macronutrients is important in regulating this relationship (Harrison et al., 2014; Jensen, McClure, et al., 2015; Maklakov et al., 2008; Rapkin et al., 2017).

Despite the consistency of these three patterns across a diversity of taxonomic groups, a general process linking them is currently lacking. One process that has the potential to unite these patterns is intralocus sexual conflict over the optimal intake of nutrients (Maklakov & Lummaa, 2013). In general, intralocus sexual conflict occurs because many sexually homologous (or shared) traits are subject to contrasting selection but have a common genetic basis in the sexes (Bonduriansky & Chenoweth, 2009). This generates an evolutionary 'tug-of-war' between the sexes that can prevent one or both sexes from evolving to their sex-specific phenotypic optima and hinder the evolution of sexual dimorphism in the shared trait(s) (Bonduriansky & Chenoweth, 2009; Lande, 1980). If different optimal intakes of nutrients are needed to maximise life span and reproduction in the sexes, and if the genes that regulate dietary choice for these nutrients are linked across the sexes, then intralocus sexual conflict over the optimal intake of nutrients may constrain feeding behaviour and prevent the sexes from reaching their specific nutritional optima for these traits. This may promote the evolution of sex differences in life span either directly or indirectly via a trade-off with reproduction (Maklakov & Lummaa, 2013). Formal demonstration that intralocus sexual conflict over the optimal intake of nutrients for life span and reproduction is operating in a population requires showing a sex difference in the effects of nutrient intake on these traits and positive intersexual genetic correlations (r_{MF}) for the intake of nutrients under dietary choice (Bonduriansky & Chenoweth, 2009). While this process will, in theory, be strongest when the effects of nutrient intake on these traits are directly opposing in the sexes and r_{MF} equals 1 (Bonduriansky & Chenoweth, 2009), it is important to note that these parameters do not allow the strength of intralocus sexual conflict to be directly quantified. One approach that has proved useful in this regard is to measure the potential for the between-sex additive genetic covariance matrix (**B**) for nutrient intake to

constrain the predicted evolutionary response of these traits in the sexes using the multivariate breeder's equation (Lande, 1980). The ratio of the predicted evolutionary response of nutrient intake in the sexes when **B** has been measured in the population to the response when **B** has been set to zero (i.e. the case where nutrient intake is assumed to be genetically independent in the sexes) provides a direct measure of the strength of intralocus sexual conflict (Agrawal & Stinchcombe, 2009).

Despite the potential for intralocus sexual conflict over the optimal intake of nutrients to explain the evolution of sex differences in life span and reproduction, very few direct empirical tests of this process actually exist. In the black field cricket *Teleogryllus commodus* and the spring field cricket *Gryllus veletis*, there are sex differences in the effect of P and C on life span and reproductive performance (Harrison et al., 2014; Maklakov et al., 2008) and in *D. melanogaster* there are sex differences in the effects of these nutrients on reproduction but not LS (Jensen, McClure, et al., 2015). When given dietary choice, male and female *G. veletis* regulate to different nutrient ratios that maximise sex-specific life span and reproduction (Harrison et al., 2014), whereas in *T. commodus* and *D. melanogaster* the sexes regulate to the same nutrient ratio that is not optimal for life span nor reproduction in either sex (Jensen, McClure, et al., 2015; Maklakov et al., 2008). While the studies on these latter two species implicate an indirect role for intralocus sexual conflict over the optimal intake of nutrients, neither study estimated the genetics of nutrient intake under dietary choice. Other studies on these species, however, quantified both the effects of nutrient intake in the sexes and the genetics of nutrient intake under dietary choice (Rapkin et al., 2017; Reddiex et al., 2013). Reddiex et al. (2013) used a subset of inbred lines from the *Drosophila* genetic reference panel to show small but significant sex differences in the effects of P and C intake on reproduction and a large and positive r_{MF} for C intake but not for P intake. Importantly, the effects of P and C intake on reproduction were estimated using ridge analysis as a deviance from the population mean nutrient intake under dietary choice, which may explain the smaller sex difference observed in this study (Reddiex et al., 2013). A more recent study using an outbred population of *T. commodus* documented a much larger sex difference in the effects of P and C intake on both LS and reproduction and documented large and positive estimates of r_{MF} for the intake of both nutrients under dietary choice (Rapkin et al., 2017). Despite this, in both species the structure of **B** did little to constrain the predicted evolutionary response of feeding behaviour and the sexes regulated their intake of these nutrients differently under dietary choice (Rapkin et al., 2017; Reddiex et al., 2013). While this suggests that intralocus sexual conflict is likely to be weak in these populations, the fact that nutrient regulation was not optimal for male and female reproduction in *D. melanogaster* (Reddiex et al., 2013) or for life span and reproduction in either sex of *T. commodus* (Rapkin et al., 2017) suggests that this process is unlikely to be completely resolved. At present, we know very little about how widespread or strong intralocus sexual conflict over the optimal intake of nutrients is and even less about the potential consequences it may have for the evolution of sex differences in life span and reproduction. More empirical work on this topic is clearly needed.

A key finding of the meta-analytical work of Nakagawa et al. (2012) and Moatt et al. (2016) is that the effects of dietary restriction on life span and reproduction are markedly stronger in the five most commonly studied laboratory model species (*Saccharomyces cerevisiae*, *Caenorhabditis elegans*, *D. melanogaster*, *Mus musculus* and *Rattus norvegicus*). Moatt et al. (2016) also noted a general shortage of studies examining the effects of dietary restriction on reproduction, especially in males. Consequently, there is a need for more empirical studies on a broader range of species, as well as studies with direct side-by-side comparisons of the effect of dietary restriction on males and females. Field crickets provide a powerful, alternate system for investigating the evolution of sex differences in the effects of nutrition on life span and reproduction because reproductive effort can be easily quantified in both sexes (Archer & Hunt, 2015). As is the case for many insect species, reproductive effort in female crickets can be measured as the number of eggs produced (e.g. Head et al., 2005; Hunt et al., 2004). Male field crickets produce an advertisement call to attract a mate and the amount of time spent calling each night can be used as a good measure of male reproductive effort because calling is a metabolically expensive activity (e.g. Kavanaugh, 1987) and females show a strong preference for males that call more each night (e.g. Bentsen et al., 2006). In the decorated cricket *Gryllodes sigillatus*, we have shown that males age more slowly and live longer than females and that this pattern can be explained by sex differences in age-dependent reproductive effort: male calling effort increases with age but female egg production decreases with age (Archer et al., 2012). These divergent life-history strategies are underpinned by a positive genetic correlation between early life reproductive effort and the rate of ageing in both sexes, although this relationship is more than twice as strong in females than in males (Archer et al., 2012). Moreover, age-dependent reproductive effort, life span and ageing all exhibit a strong positive r_{MF}, suggesting that these traits are not free to evolve independently in the sexes (Archer et al., 2012). We do not currently know, however, the effect that nutrition has on life span and reproduction in *G. sigillatus* and whether intralocus sexual conflict over the optimal intake of nutrients contributes to the observed sex differences in these traits.

Here, we formally document the existence and directly quantify the strength of intralocus sexual conflict over the optimal intake of nutrients for reproduction and life span in *G. sigillatus*. We start by restricting male and female crickets to a geometric array of 24 holidic diets that vary in the ratio of P to C and total nutrient content to quantify the linear and nonlinear effects of these nutrients on daily reproductive effort, lifetime reproductive effort and life span in the sexes. Next, we use inbred lines to estimate the genetic basis of nutrient choice in males and females when given a pair of diets that differ in P:C ratio but have the same total nutritional content. We combine these genetic estimates with the linear effects of P and C intake on life span and daily reproductive effort to predict the magnitude of evolutionary constraint for these traits in each sex. Finally,

we present male and female crickets with a much broader range of diet pairs that differ in both the P:C ratio and total nutrient content to determine how the sexes actively regulate their intake of nutrients. We calculated the regulated intake point for each sex, defined as the point in nutrient space that individuals actively defend when given dietary choice (Simpson & Raubenheimer, 2012), and mapped this onto the nutritional landscapes for life span and daily reproductive effort to determine if nutrient regulation is optimal for these traits.

2 | MATERIALS AND METHODS

2.1 | Experimental animals

The *G. sigillatus* used in this study were descended from 500 adult crickets collected in Las Cruces, New Mexico, in 2001 and used to initiate a large, outbred laboratory culture maintained at a population size of approximately 5,000 crickets breeding panmictically (Ivy & Sakaluk, 2005). Cricket cultures were housed in ten 15 L plastic containers and provided with a mixture of cat food (Go-Cat Senior®; Purina) and rat food (SDS Diets), water provided in 60 ml glass tubes plugged with cotton wool and an abundance of cardboard egg cartons for shelter. Food, water and egg cartons were replaced and containers cleaned weekly. Moistened cotton wool in a 12 cm (diameter) petri dish was provided to each culture when adults were detected for oviposition. Each generation, nymphs were collected at hatching and randomly transferred between culture containers to enforce gene flow. In total, we established nine inbred lines from this outbred culture by enforcing 23 generations of full-sib mating, followed by 26 generations of panmixis within each line (Ivy et al., 2005). Each inbred line was housed in two 15 L plastic containers and maintained under the same conditions as outlined above for our outbred culture.

All experimental crickets were collected as newly hatched nymphs from the oviposition pads, housed individually in a plastic container (5 cm × 5 cm × 5 cm) and provided with a piece of egg carton for shelter and water in a 2.5 ml plastic vial plugged with cotton wool. Crickets were fed dry cat pellets (Go-Cat Senior; Purina), their enclosure cleaned, and food and water replaced each week. When crickets reached final instar, they were checked daily for eclosion (day 0) whereby they were allocated at random to an experiment and diet treatment (see below). All experimental crickets were mated to a virgin cricket of the opposite sex that was allocated at random from the outbred culture. In each experiment, mating occurred on the evening of day 7 and was repeated weekly thereafter for the duration of the experiment. On the evening of mating, the mating partner was introduced into the container of the experimental cricket at 18:00 and removed the following morning at 9:00. During this period, the artificial diet(s) was removed to prevent any consumption by the mating partner. All mating partners were between 10 and 12 days of age post-eclosion and were maintained in a series of 15 L plastic containers according to sex and age and only used once.

All crickets were maintained in a constant temperature room set to 32 ± 1°C and a 14-hr:10-hr light/dark cycle.

2.2 | Artificial diets and measuring dietary consumption

We made 24 holidic, dry diets that varied in the ratio of P to C, as well as overall nutrient concentration, based on the protocol of Simpson and Abisgold (1985). This represents the same array of diets used in a number of our previous studies (e.g. Bunning et al., 2016; Rapkin et al., 2017, 2018; South et al., 2011). The composition of diets is provided in Table S1 and can be visualised in Figure S1.

Each cricket was given either one or two dishes of diet of measured dry weight on the day they eclosed, being replaced every 2 days for the duration of the experiment (until death in Experiment 1 and 20 days in Experiments 2 and 3). Diet and water were provided in platforms constructed by gluing a vial lid (1.6 cm diameter, 1.6 cm deep) upside down into a Petri dish (5.5 cm diameter) allowing any diet spilt during feeding to be collected. Diet was kept in a drying oven (model FD 115; Binder) at 30°C for 48 hr to remove any moisture prior to weighing. Feeding platforms containing diet were weighed before and after each feeding period using an electronic balance (model EP214C, Ohaus Explorer Professional; Ohaus). Prior to final weighing, faeces were removed from the feeding platform using forceps. Diet consumption was calculated as the difference in dry weight of diet before and after feeding and converted to a P and C intake by multiplying by the proportional representation of each nutrient in the diet (South et al., 2011).

2.3 | Experiment 1: Quantifying sex differences in the effects of P and C intake on life span and daily reproductive effort

To characterise and compare the effects of P and C on life span and daily reproductive effort in the sexes, 10 outbred crickets of each sex were allocated at random to each of the 24 diets on their day of eclosion. However, some crickets escaped (especially males during transfer to the electronic call monitoring device, see below) or died prematurely (before mating at 8 days) and were excluded from the final analysis (males: total $n = 211$; females: total $n = 231$). The exclusion of these crickets was unrelated to diet (males: $\chi^2 = 26.08$, $df = 23$, $p = 0.30$; females: $\chi^2 = 26.66$, $df = 23$, $p = 0.27$) and did not qualitatively alter the outcomes of our analysis of life span. All experimental crickets were fed and mated following the protocols outlined above until death. Each cricket was checked daily for mortality.

The reproductive effort of males and females was measured every 8 days until death. To measure female reproductive effort, each female was provided with a small Petri dish (5 cm diameter) filled with moist sand for oviposition for a 7-day period, after which it was removed and frozen at −20°C for storage and replaced with a fresh dish of moist sand. To count eggs, the contents of each Petri

dish was emptied into a round container (10 cm diameter, 5 cm height) of water, swirled for 30 s and the eggs removed from the surface of the sand with forceps and counted. Male reproductive effort was measured as the total amount of time spent calling between 18:00 and 9:00 each night sampled, using a custom-built electronic monitoring device (Archer et al., 2012). Lifetime reproductive effort was calculated as the total number of eggs produced or seconds spent calling over the lifetime of the female and male respectively. Daily reproductive effort was calculated by dividing this measure by life span for each individual.

We used a multivariate response surface approach (Lande & Arnold, 1983) to quantify the linear and nonlinear (i.e. quadratic and correlational) effects of P and C intake on our response variables for each sex. The intake of P and C and our response variables were standardised to a mean of zero and standard deviation of one using a *Z* transformation prior to analysis. Nonparametric thin-plate splines were used to visualise the nutritional landscapes for each response variable and were constructed using the '*Tps*' function in the 'FIELDS' package of R (R Core Team, version 3.1.2, Vienna, Austria). It is important to note that while nonparametric thin-plate splines are excellent for visualising nutritional landscapes, they will not always perfectly mirror the outcomes of the response surface analysis that examines the best linear and quadratic relationships between nutrient intake and our response variables. For each nutritional landscape, we estimated the location of the global maximum (i.e. nutritional optima) and its 95% confidence region using nonparametric bootstrapping implemented with the '*OptRegionTps*' function in the 'OPTIMAREGION' package of R (del Castillo et al., 2016).

We used a sequential model building approach (South et al., 2011) to determine whether the linear and nonlinear effects of P and C intake differed for the same response variables across the sexes and across different response variables within the sexes. We also quantified the degree of divergence in the nutritional optima of our response variables by calculating the angle ($\boldsymbol{\theta}$) between the linear nutritional vectors and the Euclidean distance (d) between the global maxima for the two response variables being compared. Smaller values of $\boldsymbol{\theta}$ and d mean that the two response variables are maximised in similar regions of nutrient space, whereas larger values mean they are maximised in different regions of nutrient space (Rapkin et al., 2018). Full details of these calculations are provided in Text S1.

2.4 | Experiment 2: The quantitative genetics of nutrient choice

To estimate the quantitative genetic basis of nutrient choice within and between the sexes, we measured the nutrient choice of males and females using our nine inbred lines. At eclosion, 20 crickets of each sex from each inbred line (total $n = 180$ males and 180 females) were given a choice between two diets that differed in the P:C ratio but with the same nutrient concentration [P:C ratio, total nutritional content]: diet 4 [5:1, 84%] and diet 24 [1:8, 84%] (Figure S1). All experimental crickets were fed and mated following the protocols outlined above for 20 days.

We estimated the (broad-sense) genetic variance–covariance matrix (**G**) and corresponding estimates of heritability (h^2) and genetic correlations for the intake of P and C within (r_M and r_F) and between the sexes (r_{MF}) using a multivariate animal model (Wilson et al., 2010). We quantified the extent of intralocus sexual conflict over the intake of P and C using a modified version of the rate of adaptation metric (***R***, Agrawal & Stinchcombe, 2009) that directly measures the effect that **B** has on the predicted evolutionary response of nutrient intake in the sexes. When $\boldsymbol{R} = 0.5$, **B** reduces the predicted evolutionary response of nutrient intake so that it only increases half as much as expected if P and C intake were genetically independent in the sexes. When $\boldsymbol{R} = 2.0$, **B** accelerates the predicted evolutionary response of nutrient intake in the sexes twice as much as expected under genetic independence. When $\boldsymbol{R} = 1.0$, **B** has little effect on the predicted evolutionary response of nutrient intake in the sexes. Full details of these calculations are provided in Text S2.

2.5 | Experiment 3: Sex differences in nutrient regulation under dietary choice

To determine whether the sexes differentially regulate their intake of P and C under dietary choice, we conducted a second dietary choice experiment using outbred crickets taken at random from our culture. At eclosion, 80 crickets of each sex were allocated at random to one of four possible diet pairs ($n = 20$ crickets per diet pair for each sex). The four diet pairs varied in both the P:C ratio and total nutrient concentration [P:C ratio, total nutritional content]: diet pair 1: diet 2 [5:1, 36%] versus diet 22 [1:8, 36%]; diet pair 2: diet 2 [5:1, 36%] versus diet 24 [1:8, 84%]; diet pair 3: diet 4 [5:1, 84%] versus diet 22 [1:8, 36%]; diet pair 4: diet 4 [5:1, 84%] versus 24 [1:8, 84%] (Table S1). All experimental crickets were fed and mated following the protocols outlined above for 20 days.

To determine if male and female crickets showed a dietary preference when provided within each diet pair, we used a paired *t* test comparing the total consumption of each diet in the pair. To examine sex differences in the regulated intake of P and C, we used a multivariate analysis of variance (MANOVA) that included sex, diet pair and their interaction as fixed effects in the model and the intake of P and C as the response variables. We used univariate ANOVAs to determine which nutrient(s) contributed to any overall multivariate effect. As there were four diet pairs per sex, we used Fisher's least significant difference post hoc analysis to determine which were significant at $p < 0.05$.

We calculated the regulated intake point as the mean intake of P and C across diet pairs. To test for a difference in the regulated intake point across the sexes, we used an analysis of covariance (ANCOVA) that included sex as a fixed effect, P intake and the interaction between sex and P intake as random effects and C intake as the response variable. Significance of the interaction term indicates that the regulated intake point differs significantly across the

sexes. We mapped the RIP onto the nutritional landscapes for life span, daily and lifetime reproductive effort in each sex to determine if males or females are optimally regulating their intake of nutrients to maximise these traits. We consider nutrient regulation as optimal for a given trait if the regulated intake point overlaps the 95% confidence region of the global maximum on the nutritional landscape (Rapkin et al., 2018). However, given that the 95% confidence region of the global maxima is known to be large when sample sizes are modest (Rapkin et al., 2018), we also estimated the Euclidean distance (d_*) between the global maxima for each response variable and the regulated intake point in the sexes. Full details of this calculation are provided in Text S3.

None of the experiments conducted for our study required animal ethics approval.

3 | RESULTS

3.1 | P and C intake have divergent effects on life span and daily reproductive effort in the sexes

The intake of P and C had clear linear and nonlinear effects on life span in *G. sigillatus* (Table 1). In females, there was a linear increase in LS with the intake of C but not the intake of P (Table 1). There was also a significant negative quadratic effect of C intake but not P intake on life span, and inspection of the nutritional landscape reveals a peak at a high intake of C and low intake of P centred around a P:C ratio of 1_P:5.21_C (global maximum: P = 1.27 mg, C = 6.62 mg, Table 1, Figures 1a and 2a). The significant negative correlational effect of nutrient intake further demonstrates that life span in females is maximised at a low intake of P and a high intake of C (Table 1; Figure 1a). In contrast, male life span increased linearly with the intake of both nutrients, although this trait was more than twice as responsive to the intake of C as P (Table 1). There were also significant negative quadratic effects of both nutrients on male life span, and inspection of the nutritional landscape shows a peak at a high intake of nutrients centred around a P:C ratio of 1_P:3.37_C (global maximum: P = 1.39 mg, C = 4.68 mg, Table 1, Figures 1b and 2b). The correlational effect of nutrients on male life span was negative but not statistically significant (Table 1). Formal comparison of the nutritional landscapes showed significant sex differences in the linear and quadratic effects but not the correlational effect of nutrient intake on life span (Table 2). The sex difference in linear effects resulted from the fact that life span increased with P intake in males but not in females and because female life span is more responsive (i.e. steeper gradient) to the intake of C than male life span (Table 2). However, this sex difference was minimal, as indicated by the small angle between the linear nutritional vectors and the reduced distance between the global maxima for life span in the sexes (Table 2). The sex difference in quadratic effects occurred because the peak in

TABLE 1 The linear and nonlinear effects of daily protein (P) and carbohydrate (C) intake on life span, daily reproductive effort and lifetime reproductive effort in male and female *Gryllodes sigillatus*

	Linear effects		Nonlinear effects		
	P	C	P × P	C × C	P × C
Females					
Life span					
Gradient ± *SE*	−0.01 ± 0.05	0.62 ± 0.05	−0.08 ± 0.06	−0.29 ± 0.05	−0.25 ± 0.11
t_{230}	0.19	11.88	1.28	5.94	2.34
p	0.85	0.0001	0.20	0.0001	0.021
Daily reproductive effort					
Gradient ± *SE*	0.43 ± 0.05	0.57 ± 0.05	−0.43 ± 0.05	0.03 ± 0.05	0.45 ± 0.09
t_{230}	8.94	11.92	9.07	0.63	5.21
p	0.0001	0.0001	0.0001	0.53	0.0001
Males					
Life span					
Gradient ± *SE*	0.17 ± 0.06	0.46 ± 0.06	−0.26 ± 0.08	−0.13 ± 0.06	−0.22 ± 0.12
t_{211}	2.62	7.26	3.28	2.27	1.80
p	0.01	0.0001	0.001	0.024	0.074
Daily reproductive effort					
Gradient ± *SE*	−0.03 ± 0.06	0.44 ± 0.06	0.06 ± 0.08	−0.22 ± 0.07	−0.18 ± 0.12
t_{211}	0.52	6.90	0.72	3.11	1.44
p	0.61	0.0001	0.47	0.002	0.15

Note: The sign of the linear gradient describes the direction of the relationship between P and C and the response variable (life span or reproductive effort), the nonlinear gradients describe the curvature of this relationship, with a negative gradient indicating a peak on the landscape and a positive gradient indicating a trough of the landscape.

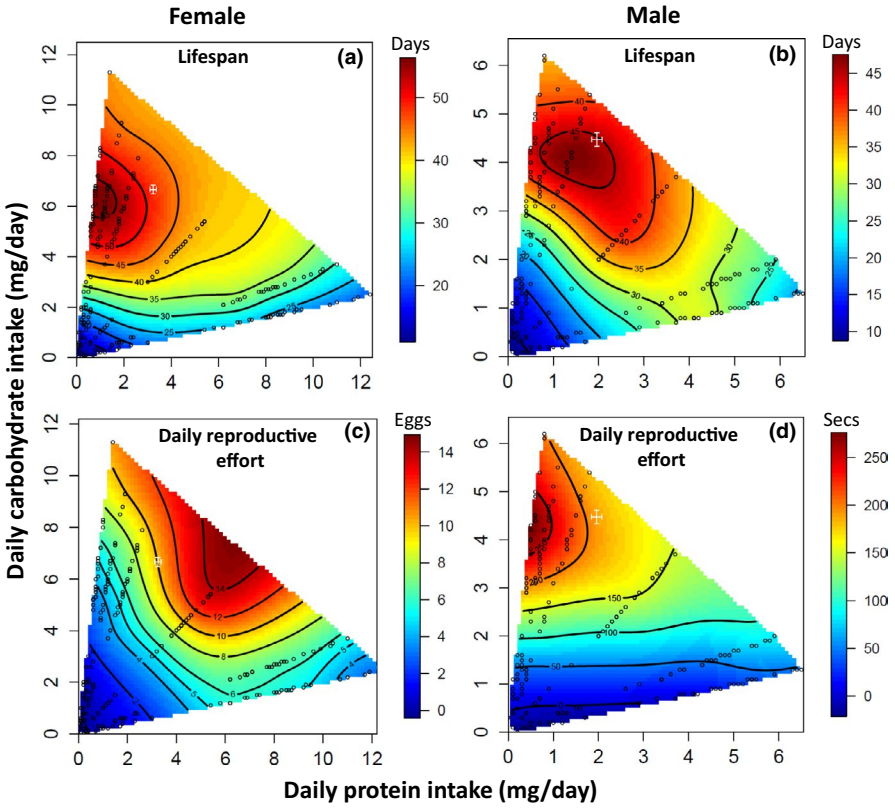

FIGURE 1 The nutritional landscapes characterising the linear and nonlinear effects of protein and carbohydrate intake on (a, b) female and male life span and (c, d) female and male daily reproductive effort. In each landscape, the red regions represent higher values of the trait, whereas blue regions represent lower values of the trait. The open black symbols represent the intake of nutrients for individual flies along each of the six nutritional rails. The white crosses represent the regulated intake point (and 95% credible intervals) calculated in Experiment 3

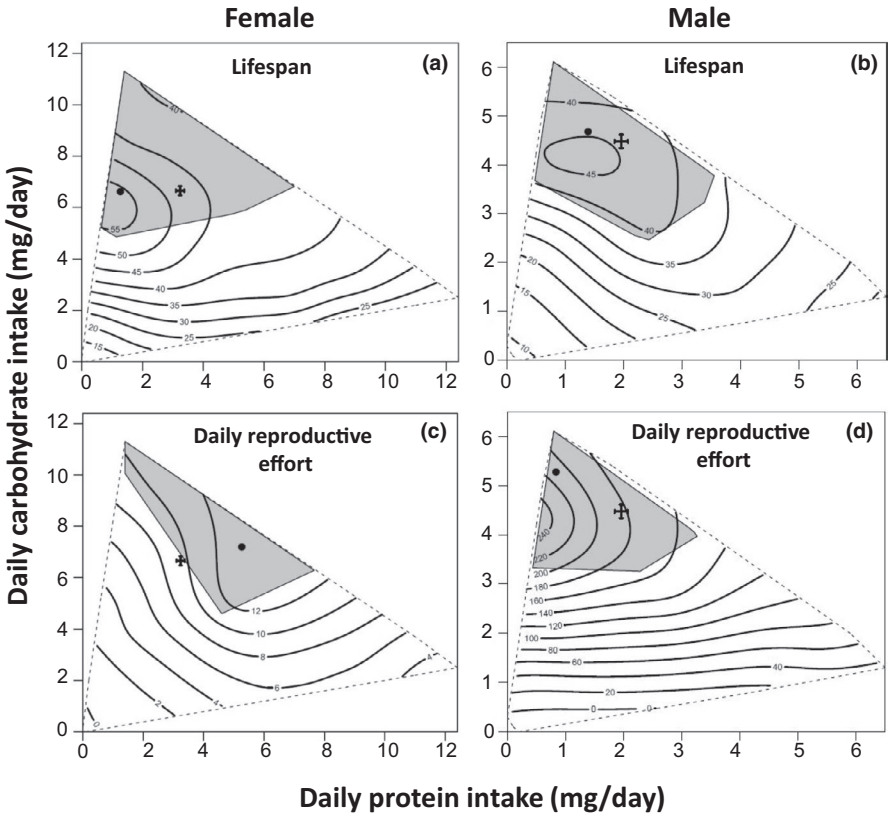

FIGURE 2 The 95% confidence region (solid grey fill) for the global maximum (closed black circle) on each nutritional landscape for (a, b) female and male life span and (c, d) female and male daily reproductive effort. On each landscape, the regulated intake point (and 95% credible intervals) is provided as a black cross and the dashed black line represents the boundary of the data

life span with C intake in females was more pronounced (i.e. stronger curvature) than the peak in male life span with the intake of this nutrient (Table 2).

The intake of P and C also had clear linear and nonlinear effects on daily reproductive effort in *G. sigillatus* (Table 1). In females, there was a linear increase in daily reproductive effort with the intake of

TABLE 2 Sequential *F*-tests comparing the effects of protein (P) and carbohydrate (C) intake on life span and daily reproductive effort between and within the sexes of *Gryllodes sigillatus*. For each comparison, we also estimate the angle (θ) between the linear nutritional vectors and the median Euclidean distance (d) between the two global maxima (measured in milligrams). The 95% confidence intervals (CIs) for θ and d are provided beneath these estimates in brackets

	SS_R	SS_C	df_1	df_2	F	p	θ (95% CIs)	d (95% CIs)
Females versus Males								
Life span								
Linear	315.67	308.64	2	436	4.97	0.007[A]	20.61°	2.38
Quadratic	284.90	278.38	2	432	5.06	0.007[B]	(3.63°, 36.43°)	(2.22, 2.51)
Correlational	275.05	275.03	1	430	0.03	0.86		
Daily reproductive effort								
Linear	311.13	288.01	2	436	17.50	0.0001 [C]	41.14°	5.72
Quadratic	271.08	248.58	2	432	19.55	0.0001[D]	(23.49°, 59.70°)	(5.66, 5.74)
Correlational	247.09	237.52	1	430	17.32	0.0001		
Females								
Life span versus Daily reproductive effort								
Linear	284.44	261.76	2	456	19.75	0.0001[E]	37.81°	5.21
Quadratic	229.47	210.37	2	452	20.52	0.0001[F]	(25.43°, 49.49°)	(5.10, 5.30)
Correlational	209.44	198.02	1	450	25.94	0.0001		
Males								
Life span versus Daily reproductive effort								
Linear	338.88	333.43	2	416	3.40	0.03[G]	24.46°	1.18
Quadratic	325.25	318.59	2	412	4.30	0.01[H]	(2.28°, 43.73°)	(1.13, 1.24)
Correlational	314.57	314.53	1	410	0.06	0.82		

Note: Univariate tests: [A]P: $F_{1,436} = 4.66$, $p = 0.031$, C: $F_{1,436} = 3.85$, $p = 0.05$; [B]P × P: $F_{1,432} = 3.13$, $p = 0.077$, C × C: $F_{1,432} = 4.34$, $p = 0.038$; [C]P: $F_{1,436} = 34.34$, $p = 0.0001$, C: $F_{1,436} = 2.85$, $p = 0.09$; [D]P × P: $F_{1,432} = 34.08$, $p = 0.0001$, C × C: $F_{1,432} = 7.11$, $p = 0.008$; [E]P: $F_{1,456} = 38.35$, $p = 0.0001$, C: $F_{1,456} = 0.44$, $p = 0.51$; [F]P × P: $F_{1,452} = 25.47$, $p = 0.0001$, C × C: $F_{1,452} = 19.89$, $p = 0.0001$; [G]P: $F_{1,416} = 4.90$, $p = 0.027$, C: $F_{1,416} = 0.06$, $p = 0.81$; [H]P × P: $F_{1,412} = 7.93$, $p = 0.005$, C × C: $F_{1,412} = 0.92$, $p = 0.34$.

P and C, although this trait was more responsive to the intake of the former than the latter macronutrient (Table 1). There was also a significant negative quadratic effect of P intake but not C intake on daily reproductive effort, and inspection of the nutritional landscape reveals that this trait peaks at a high intake of nutrients centred around a P:C ratio of 1_P:1.37_C (global maximum: P = 5.26 mg, C = 7.19 mg, Table 1, Figures 1c and 2c). The significant positive correlational effect of nutrient intake further demonstrates this increase in daily reproductive effort with the intake of both nutrients (Table 1). In contrast, daily reproductive effort in males only increased linearly with the intake of C and there was a significant negative quadratic effect for the intake of this nutrient (Table 1). Inspection of the nutritional landscape showed that daily reproductive effort in males was maximised at a high intake of nutrients centred around a P:C ratio of 1_P:6.19_C (global maxima: P = 0.85 mg, C = 5.26 mg, Table 1, Figures 1d and 2d). The correlational effect of nutrients on nightly calling effort was negative but not statistically significant (Table 1). Formal comparison of the nutritional landscapes showed significant sex differences in the linear, quadratic and correlational effects of nutrient intake on daily reproductive effort (Table 2). The sex difference in linear effects occurred because female daily reproductive effort increased with P intake but male daily reproductive effort did not, resulting in a much larger angle between the linear nutritional vectors and distance between the global maxima in the sexes than was the case for life span (Table 2). The sex difference in quadratic effects occurred because female daily reproductive effort but not male daily reproductive effort peaked with P intake, whereas the opposite pattern occurred with C intake (Table 2). The sex difference in the correlational effect occurred because female daily reproductive effort increased with the covariance between the intakes of these nutrients whereas male daily reproductive effort did not (Table 2). Qualitatively similar nutrient effects were found for female and male lifetime reproductive success (Table S2, Figure S2a,b), although the peak of this trait is slightly more C biased in both females (1_P:1.80_C, global maximum: P = 4.42 mg, C = 7.94 mg, Figure S3a) and males (1_P:6.50_C, global maximum: P = 0.82 mg, C = 5.33 mg, Figure S3b) than daily reproductive effort. Similarly, there were significant sex differences in the linear, quadratic and correlational effects of nutrient intake on lifetime reproductive effort and this was driven by the same nutrient effects as shown for daily reproductive effort

TABLE 3 Broad-sense genetic variance–covariance (**G**) matrix for protein (P) and carbohydrate (C) intake in male and female *Gryllodes sigillatus*. The subscripts m and f refer to males and females respectively. h^2 refers to heritability estimates with standard error (*SE*) in brackets. The genetic (co) variance within males and females is along the diagonal and the additive genetic covariance between the sexes is on the lower off-diagonal. Genetic correlations (r_M, r_F and r_{MF}) are provided in bold above off-diagonal, with 95% confidence intervals provided in brackets beneath these estimates. Estimates in italics are significant at $p < 0.05$

	h^2	P_m	C_m	P_f	C_f
P_m	*0.84* *(0.61, 0.96)*	0.46 (0.18, 1.98)	**0.61** **(−0.06, 0.91)**	**0.78** **(−0.08, 0.96)**	**0.65** **(−0.34, 0.94)**
C_m	*0.56* *(0.26, 0.82)*	0.31 (−0.33, 1.94)	0.75 (0.29, 4.02)	**0.59** **(−0.33, 0.89)**	**0.64** **(−0.01, 0.94)**
P_f	*0.85* *(0.53, 0.96)*	0.52 (−0.45, 2.37)	0.49 (−0.75, 3.41)	1.33 (0.44, 6.26)	**0.79** **(−0.07, 0.97)**
C_f	*0.55* *(0.29, 0.84)*	0.23 (−0.98, 2.12)	0.59 (−0.87, 4.65)	0.56 (−0.97, 4.70)	1.44 (0.37, 6.35)

(Table S3). However, the angle between the linear nutritional vectors and distance between the global maxima in the sexes were both slightly smaller than shown for daily reproductive effort (Table S3).

The observed divergence in the nutritional requirements of the sexes also influenced the magnitude of the trade-off between life span and reproduction. In females, there was a significant difference in the linear, quadratic and correlational effects of nutrient intake on life span and daily reproductive effort (Table 2). The difference in linear effects occurred because daily reproductive effort increased with P intake but life span did not, and the difference in quadratic effects occurred because daily reproductive effort peaked with P intake whereas life span peaked with C intake (Table 2). The difference in correlational effects occurred because daily reproductive effort increased but life span decreased with the covariance between nutrient intakes (Table 2). This results in nutritional optima for life span and daily reproductive effort that are located in different regions of nutrient space for females (Figure 1a,c), as evidenced by the large angle between the linear nutritional vectors and distance between the global maxima (Table 2). In contrast, only the linear and quadratic effects of nutrient intake on life span and daily reproductive effort differed in males (Table 2). The difference in linear effects was the result of life span but not daily reproductive effort increasing with P intake and the difference in quadratic effects was due to a peak in life span but not in daily reproductive effort with the intake of P (Table 2). Compared to females, this divergence in nutritional effects is relatively minor resulting in nutritional optima for life span and daily reproductive effort that are located in similar regions of nutrient space in males (Figure 1b,d), as well as a smaller angle between the linear nutritional vectors and the distance between the global maxima (Table 2). Collectively, this indicates a stronger nutrient space-based trade-off between daily reproductive effort and life span in females than males.

We observed qualitatively similar differences in the effects of nutrient intake on life span and lifetime reproductive effort in the sexes, although the degree of divergence was not as large as for life span and daily reproductive effort (Table S3). This resulted in smaller angles between the linear nutritional vectors and distances between the global maxima for life span and lifetime reproductive effort compared to life span and daily reproductive effort, especially in females (Table S3). These similarities in the differential effects of nutrient intake on life span and lifetime reproductive effort to those observed for life span and daily reproductive effort are not altogether surprising given the similar effects that nutrient intake has on daily and lifetime reproductive effort in the sexes (Table S3). In females, only the linear effects of nutrient intake on daily and lifetime reproductive effort differed and results from the former being more responsive to P intake than the latter, resulting in a small angle between the linear nutritional vectors and distance between the global maxima for these traits (Table S3). In contrast, the linear, quadratic and correlational effects of nutrient intake on daily and lifetime reproductive effort in males did not differ significantly and the angle between the linear nutritional vectors and distance between the global maxima were considerably smaller than observed in females (Table S3).

3.2 | Nutrient intake is heritable and positively genetically correlated across the sexes

The genetic variance–covariance matrix (**G**) for the intake of P and C under dietary choice is provided in Table 3. The intake of P and C was highly heritable and estimates were of similar magnitude in both males and females. These estimates were, however, larger for the intake of P than the intake of C in both sexes (Table 3). There were strong positive genetic correlations between the intake of P and C within each sex (r_M and r_F), although this estimate was higher for females than males (Table 3). Importantly, we show strong positive genetic correlations for the intake of P and C between the sexes (r_{MF}, Table 3) indicating the potential for intralocus sexual conflict to constrain the evolution of nutrient intake in male and female *G. sigillatus*.

3.3 | The predicted evolutionary response of nutrient intake differs in males and females

Our estimates of $\Delta\bar{\boldsymbol{z}}$, $\Delta\bar{\boldsymbol{z}}_{\mathbf{B}=0}$ and $\boldsymbol{R}$ for life span and daily reproductive effort in the sexes, as well 95% credible intervals for these estimates,

are presented in Table 4. There is a clear difference in the magnitude of these parameter estimates across the sexes. For each trait examined, estimates of $\Delta\bar{z}$ exceeded those for $\Delta\bar{z}_{\mathbf{B}=0}$ in males, whereas the reverse pattern was true for females (Table 4). Consequently, estimates of ***R*** were consistently greater than 1.0 (ranging from 1.62 to 2.41) in males but consistently lower than 1.0 (ranging from 0.39 to 0.56) in females (Table 4). The same pattern was observed for estimates of ***R*** for lifetime reproductive effort (Table S4). Collectively, this suggests that the structure of **B** accelerates the predicted evolutionary response of P and C intake in males, whereas it appears to constrain the predicted evolutionary response of these nutrients in females.

3.4 | The sexes regulate to the same suboptimal nutrient ratio

When given the choice between two diets, both sexes showed a clear preference for the diet containing the highest concentration of C (Figure 3a,b). MANOVA revealed a significant multivariate effect of sex and diet pair, but not the interaction between these terms, on the intake of nutrients under dietary choice (Table 5). Univariate ANOVAs showed that both P and C intake contributed to the observed differences between the sexes (Table 5), with females having a significantly higher intake of both nutrients (Figure 4). Likewise, univariate ANOVAs showed that both P and C intake contributed to the observed differences across diet pairs (Table 5). In females, post hoc analysis showed that the pattern of P intake was diet pair 1 = 2 < 4 < 3 and C intake was diet pair 3 = 1 < 4 = 2, whereas in males the pattern of P intake was 1 = 2 < 4 < 3 and C intake was 3 < 1 < 2 = 4 (Figure 4).

The regulated intake point was estimated at a mean total P intake of 71.22 ± 3.06 mg and C intake of 146.40 ± 3.97 mg for females (1_P:2.06_C) and a mean total P intake of 43.14 ± 2.49 mg and C intake of 98.45 ± 3.04 mg for males (1_P:2.28_C) (Figure 4). ANCOVA revealed that the regulated intake point did not differ significantly between the sexes (sex: $F_{1,156} = 7.09$, $p = 0.009$; P intake: $F_{1,156} = 0.96$, $p = 0.33$; sex by P intake: $F_{1,156} = 2.20$, $p = 0.14$) indicating that males and females regulate their intake of nutrients to a common P:C ratio.

Mapping the regulated intake point for females and males onto the nutritional landscapes presented in Figure 1 shows that it did not coincide perfectly with the estimated maxima for life span and daily reproductive effort for either sex (Figure 2). The same was true for lifetime reproductive effort (Figures S2 and S3). For life span, the regulated intake point overlapped the 95% confidence region of the global maxima in both females (Figure 2a) and males (Figure 2b), but the regulated intake point was located further from the estimated maxima in females (d_* = 2.59 mg; 95% credible intervals = 2.56 mg, 2.61 mg) than in males (d_* = 1.52 mg; 95% credible intervals = 1.51 mg, 1.54 mg). For daily reproductive effort, the regulated intake point overlapped the 95% confidence region of the global maxima in males (Figure 2c) but not in females (Figure 2d) and the regulated intake point was located further from the estimated maxima in females (d_* = 2.69 mg; 95% credible intervals = 2.67 mg, 2.71 mg) than in males (d_* = 1.90 mg; 95% credible intervals = 1.89 mg, 1.92 mg). Likewise, the regulated intake point overlapped the 95% confidence region of the global maxima for lifetime reproductive effort in males (Figure S3b) but not in females (Figure S3a) and again the regulated intake point was located further from the estimated maxima in females (d_* = 2.41 mg; 95% credible intervals = 2.39 mg, 2.43 mg) than in males (d_* = 1.93 mg; 95% credible intervals = 1.91 mg, 1.94 mg). Collectively, this suggests that males are better than females at optimally regulating their intake of nutrients for reproductive effort, but this sex difference appears less pronounced for life span.

4 | DISCUSSION

In most species, males and females share a genome and express many shared phenotypic traits, yet these traits are commonly

TABLE 4 The predicted response of protein (P) and carbohydrate (C) intake in the sexes when the additive genetic covariance matrix between the sexes (**B**) is estimated directly from our breeding design ($\Delta\bar{z}$) versus when it is set to zero ($\Delta\bar{z}_{\mathbf{B}=0}$), and the corresponding ***R*** constraint metric of Agrawal and Stinchcombe (2009). The 95% CIs for $\Delta\bar{z}$, $\Delta\bar{z}_{\mathbf{B}=0}$ and ***R*** are provided in brackets beneath the estimates. We estimate these parameters for both life span and daily reproductive effort

	Males			Females		
	$\Delta\bar{z}$	$\Delta\bar{z}_{\mathbf{B}=0}$	***R***	$\Delta\bar{z}$	$\Delta\bar{z}_{\mathbf{B}=0}$	***R***
Life span						
P	0.24 (−0.28, 1.20)	0.12 (−0.05, 1.17)	1.62 (−3.91, 26.40)	0.46 (−0.30, 2.57)	1.15 (0.10, 3.41)	0.41 (−0.45, 3.37)
C	0.57 (−0.11, 2.33)	0.30 (0.06, 1.91)	1.88 (−0.07, 10.71)	0.85 (0.14, 3.07)	1.72 (0.29, 5.04)	0.56 (0.05, 3.18)
Daily reproductive effort						
P	0.31 (−0.20, 1.63)	0.08 (−0.12, 0.83)	2.41 (−39.99, 51.27)	0.78 (−0.13, 3.57)	1.84 (0.27, 5.30)	0.39 (−0.10, 2.80)
C	0.61 (−0.11, 2.66)	0.24 (0.03, 1.41)	2.34 (−0.76, 16.11)	0.93 (0.17, 3.77)	2.28 (0.36, 6.69)	0.44 (0.02, 2.56)

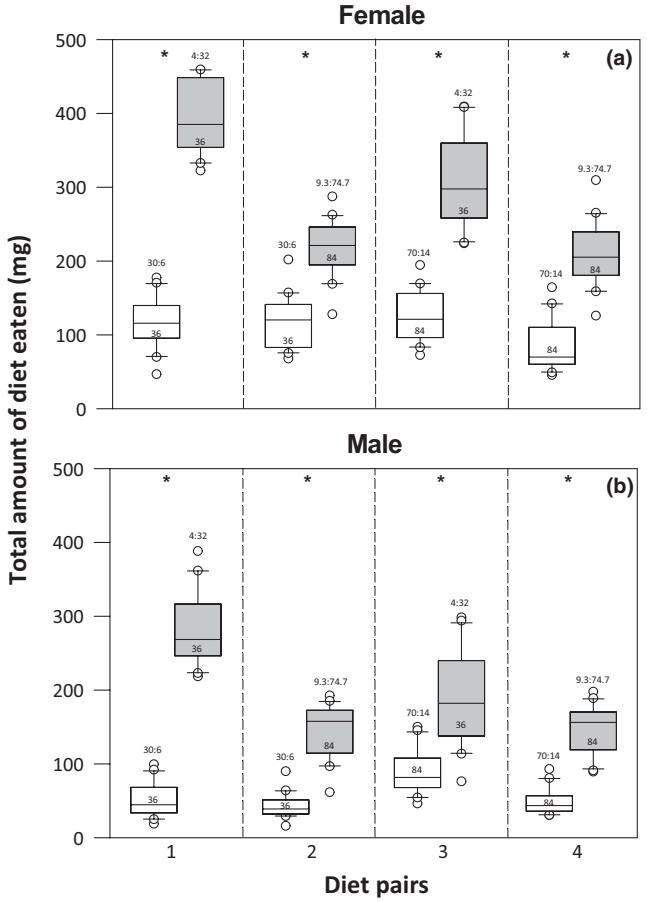

FIGURE 3 The mean (± *SE*) absolute consumption of each diet in the four diet pairs by (a) female and (b) male *Gryllodes sigillatus*. For each diet pair, the grey bars represent the consumption of the high carbohydrate diet in the pair and the white bars represent the consumption of the high protein diet in the pair. The actual P:C ratio of diets in each pair is provided above each bar and the total nutrient content of each diet is provided at the base of the bar (as a per cent). The asterisks above each diet pair represent a significant difference in the consumption of diets at $p < 0.05$ determined using a paired *t* test

selected in different directions. This generates intralocus sexual conflict that can constrain the independent evolution of these shared traits and prevent the sexes from reaching their phenotypic optima (Bonduriansky & Chenoweth, 2009). Intralocus sexual conflict is widely accepted as a potent evolutionary force with several important implications, including the maintenance of genetic variation (e.g. Foerster et al., 2007; Prasad et al., 2007), increasing the risk of extinction (e.g. Kokko & Brooks, 2003) and driving speciation (e.g. Parker & Partridge, 1998; Rice, 1996). Despite this, few concrete empirical examples of this process exist, especially where the specific trait(s) mediating the conflict have been identified (Bonduriansky & Chenoweth, 2009). This is particularly true for intralocus sexual conflict over the optimal intake of nutrients for LS and/or reproduction where only two empirical tests currently exist (Rapkin et al., 2017; Reddiex et al., 2013). This lack of attention is surprising given that sex-specific effects of nutrient intake on life span and reproduction are well-documented (Harrison et al., 2014; Jensen, McClure, et al., 2015; Maklakov et al., 2008; Rapkin et al., 2017) and the genes regulating nutrient choice are likely to be linked in the sexes (Rapkin et al., 2017; Reddiex et al., 2013). If operating, this process has the potential to prevent the sexes from independently evolving to their nutritional optima for these traits and may drive the sex differences in life span commonly observed across animal species (Austad & Fischer, 2016; Maklakov & Lummaa, 2013).

Here, we show in the decorated cricket *G. sigillatus* that P and C intake has contrasting effects on life span and reproduction in the sexes and that there are positive genetic correlations across the sexes for the intake of these nutrients when given dietary choice. This provides the necessary conditions for intralocus sexual conflict over the optimal intake of these nutrients to operate (Bonduriansky & Chenoweth, 2009). Indeed, we show that the sex-specific effects of P and C intake on life span and reproduction combined with the genetic architecture of nutrient intake under choice accelerates the predicted evolutionary response of nutrient intake in males but constrains it in females, suggesting that females are losing this ongoing conflict. In support of this view, males and females were shown to regulate to the same nutrient ratio when given choice and this shared regulation was not perfectly optimal for life span or reproduction in either sex, although considerably more pronounced in females than males. Collectively, this provides compelling evidence that intralocus sexual conflict over the optimal intake of these nutrients for life span and reproduction is currently operating in this population and is likely to be an important process generating sex differences in life span and reproduction. This process may also help explain why females age faster and live shorter than males in *G. sigillatus*, as well as the fact that reproductive effort decreases with age in females but increases with age in males (Archer et al., 2012).

We found that life span in both sexes of *G. sigillatus* was maximised at a high intake of diets containing a low P:C ratio, although females (1_P:5.21_C) did require a slightly higher intake of C than males (1_P:3.37_C) to extend their life span. Inspection of the nutritional landscapes (Figure 1a,b) reveals a sharp decrease in life span for both sexes as the nutrient ratio of the diets became more P biased and as the total intake of nutrients (and calories) was reduced. Consequently, these findings directly contradict the long-held view that caloric restriction extends life span (e.g. Masoro, 2005) and demonstrate that a balanced intake of P and C is more important (Simpson & Raubenheimer, 2012). This outcome is consistent with most nutritional geometry studies documenting an increase in life span on low P:C diets (Bruce et al., 2013; Fanson et al., 2009; Harrison et al., 2014; Jensen, McClure, et al., 2015; Lee et al., 2008; Maklakov et al., 2008; Rapkin et al., 2017; Solon-Biet et al., 2014, 2015) and suggests that the positive effects of P restriction on life span may be a conserved pattern across the animal kingdom (Nakagawa et al., 2012). Sex differences in the effects of P and C on life span have not been as thoroughly examined, with formal statistical comparisons currently existing for only three insect species (Harrison et al., 2014; Jensen, McClure, et al., 2015; Maklakov et al., 2008; Rapkin et al., 2017). These studies have, however,

TABLE 5 Multivariate analysis of variance (MANOVA) examining sex differences in the intake of protein (P) and carbohydrates (C) across diet pairs in *Gryllodes sigillatus*

	MANOVA			
Model terms	**Pillai's trace**	***df***	***F***	***p***
Sex (A)	0.57	2,151	97.88	0.0001
Diet pair (B)	0.96	6,304	46.47	0.0001
A × B	0.03	6,304	0.76	0.61
	Univariate ANOVAs			
Model terms	**Nutrient**	***df***	***F***	***p***
Sex (A)	P	1,152	117.34	0.0001
	C	1,152	149.26	0.0001
Diet pair (B)	P	3,152	71.17	0.0001
	C	3,152	33.44	0.0001
A × B	P	3,152	0.31	0.82
	C	3,152	1.28	0.28

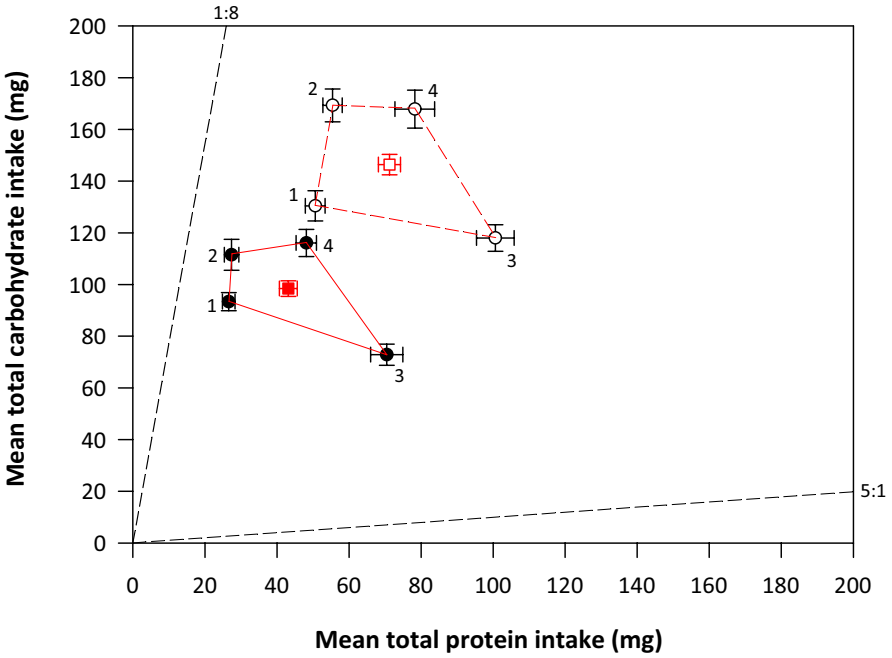

FIGURE 4 The mean (± *SE*) total protein and carbohydrate intake of female (black open circles) and male (black closed circles) *Gryllodes sigillatus* for each of the four diet pairs (labelled by number). The regulated intake point, calculated as the mean intake of nutrients across the diet pairs, is also presented for females (red open square) and males (red closed square) at a P:C ratio of 1_P:2.06_C and 1_P:2.28_C respectively. The red dashed lines and red solid lines represent the span of mean protein and carbohydrate intake between the four diet pairs for females and males respectively. The dashed black lines represent the expected intake of nutrients at a P:C ratio of 1_P:8_C and 5_P:1_C

yielded mixed results with male and female life span being maximised at the same P:C ratio in *D. melanogaster* (Jensen, McClure, et al., 2015), but at different ratios in the field crickets *T. commodus* (Maklakov et al., 2008; Rapkin et al., 2017) and *G. veletis* (Harrison et al., 2014). Interestingly, in both field cricket species, females also required a relatively higher intake of C than males to maximise LS (Harrison et al., 2014; Maklakov et al., 2008; Rapkin et al., 2017). While the proximate reason(s) for this pattern are currently unknown, sex differences in the functioning or sensitivity of nutrient signalling pathways known to regulate life span (such as TOR or AMPK; Tower, 2017) may be responsible. Clearly more work is needed to determine how common sex differences are in the effects of nutrient intake on life span and the mechanism(s) that are responsible for maintaining them.

In comparison to life span, we found much stronger sexual divergence in the effects of P and C intake on reproductive effort in *G. sigillatus*. Although daily reproductive effort was maximised at a high intake of nutrients in both sexes, male daily reproductive effort was maximised at a P:C ratio of 1_P:6.19_C (Figure 1d), whereas female daily reproductive effort was maximised at a P:C ratio of 1_P:1.37_C (Figure 1c). A similar difference was also found for male (1_P:6.50_C, Figure S2b) and female (1_P:1.80_C, Figure S2a) lifetime reproductive effort. It is likely that this difference in the nutritional requirements for reproduction reflects the divergence in the reproductive strategies of the sexes. In most animal species, males invest far less in each offspring than females, resulting in a greater intensity of sexual selection acting on males (Bonduriansky et al., 2008). Males must compete for access to females, the outcome of which is

frequently enhanced by producing the most elaborate sexual traits or behaviours (Bonduriansky et al., 2008). These sexual traits and behaviours are costly to produce and require a high intake of C to provide an abundant source of energy that can be rapidly accessed after digestion (Maklakov et al., 2008; South et al., 2011). This is particularly true for male crickets for whom the production of an advertisement call is metabolically demanding (White et al., 2008) and a major determinant of male mating success (e.g. Bentsen et al., 2006). Our finding that calling effort is maximised at a P:C ratio of 1_P:6.19_C supports this view and is also largely consistent with the nutrient ratio shown to maximise calling effort in *T. commodus* (1_P:8_C, Maklakov et al., 2008; Rapkin et al., 2017) and *G. veletis* (1_P:3_C, Harrison et al., 2014). It is also consistent with the nutrient ratio needed to maximise competitive fitness in male *D. melanogaster* (1_P:2.5_C, Reddiex et al., 2013; 1_P:16_C, Jensen, McClure, et al., 2015). In contrast to males, females do not typically need to compete for matings and their reproductive success is largely determined by the number of eggs they produce (Bonduriansky et al., 2008). In many insect species, P intake is known to regulate vitellogenesis and stimulate oogenesis (Wheeler, 1996), and this likely explains why female *G. sigillatus* require a relatively higher intake of P than males to maximise reproduction (1_P:1_C in *T. commodus*, Maklakov et al., 2008; Rapkin et al., 2017; 3_P:1_C in *G. veletis*, Harrison et al., 2014; 1_P:2_C in *D. melanogaster*, Reddiex et al., 2013; Jensen, McClure, et al., 2015).

Whenever the optimal expression of two traits measured on the same group of individuals occurs in different regions of the nutritional landscape, a nutrient space-based trade-off will exist because both traits cannot be optimised through the same intake of nutrients (Rapkin et al., 2018). Recently, we formally demonstrated that nutrient space-based trade-offs will increase in strength when the degree of overlap of the 95% confidence regions of the global maximum for each trait decreases and when the angle (θ) between the linear nutritional vectors and the Euclidean distance (d) between the global maxima increase (Rapkin et al., 2018). Using this approach, we show that the magnitude of the nutrient space-based trade-off between LS and reproduction is sex specific in our study population of *G. sigillatus*. In males, life span and daily reproductive effort were maximised in similar regions in nutritional space (Figure 1b,d), whereas these traits were maximised in very different regions in females (Figure 1a,c). Accordingly, there was less overlap in the 95% confidence regions of the global maxima for life span and daily reproductive effort in females (Figure 2a,c) than in males (Figure 2b,d), and θ was 1.5 times and d was 4.4 times larger, indicating that this nutrient space-based trade-off is stronger in females than in males. This finding is consistent with all existing insect studies that have used nutritional geometry to examine life span and reproduction in the sexes (Harrison et al., 2014; Jensen, McClure, et al., 2015; Maklakov et al., 2008; Rapkin et al., 2017) and supports the general view that reproduction is costlier in females than in males (Bonduriansky et al., 2008; Hayward & Gillooly, 2011). Moreover, our work shows that the trade-off between life span and reproduction that is core to many evolutionary theories of ageing (e.g. Barnes & Partridge, 2003; Williams, 1966), and often assumed to be dependent on the intake of calories (e.g. Gadgil & Bossert, 1970), is actually regulated by the balanced intake of specific nutrients.

Determining the importance of genes to dietary choice continues to be a central focus in the fields of nutrigenetics and nutrigenomics and there is compelling evidence that preference for the intake of macronutrients has a genetic basis in humans and rodents (e.g. Liu et al., 2013; Reed, 2008). Considerably less is known about the genetics of macronutrient intake in insects, however, with our knowledge being restricted to two species (Rapkin et al., 2017; Reddiex et al., 2013). In *D. melanogaster*, heritability estimates for the intake of P and C were higher for males than females and lower for P intake than C intake in each sex (males: $h^2_P = 0.025$, $h^2_C = 0.191$; females: $h^2_P = 0.185$, $h^2_C = 0.30$; Reddiex et al., 2013). Furthermore, while the genetic correlation between P and C intake was positive and of similar magnitude in the sexes ($r_F = 0.40$ and $r_M = 0.59$), the intersexual genetic correlation was strong and positive for C intake ($r_{MF} = 0.95$) but was significantly weaker for P intake ($r_{MF} = 0.28$). In contrast, heritability estimates for the intake of P and C in *T. commodus* were of similar magnitude in both sexes but were higher for the intake of P than C in each sex (males: $h^2_P = 0.34$, $h^2_C = 0.20$; females: $h^2_P = 0.31$, $h^2_C = 0.15$; Rapkin et al., 2017). Moreover, the genetic correlations between P and C intake were positive in both sexes but stronger in males ($r_M = 0.79$) than females ($r_F = 0.60$) and the intersexual genetic correlations were stronger for P intake ($r_{MF} = 0.79$) than C intake ($r_{MF} = 0.55$). The genetic parameters we estimate for *G. sigillatus* are largely consistent with those reported for *T. commodus*, although a number of subtle differences do exist. For example, although the heritability estimates of P and C intake were similar for the sexes and higher for the intake of P than C (males: $h^2_P = 0.84$, $h^2_C = 0.56$; females: $h^2_P = 0.85$, $h^2_C = 0.55$), these estimates were over twice as large as shown for *T. commodus*. In addition, while our estimates of r_M, r_F and r_{MF} were all positive and similar in magnitude to those reported for *T. commodus*, the sex difference in the strength of r_F and r_M was reversed ($r_F = 0.79$, $r_M = 0.61$) and the asymmetry in the strength of r_{MF} for P ($r_{MF} = 0.78$) and C intake ($r_{MF} = 0.64$) was reduced. Despite these subtle differences in genetic architecture, these studies collectively illustrate both the potential for the dietary choice of macronutrients to evolve, and that this is unlikely to occur independently in the sexes (Lande, 1980).

Intralocus sexual conflict over the optimal intake of nutrients for life span and reproduction will occur whenever there are sex differences in the effects of nutrient intake on these traits and a positive r_{MF} for the intake of nutrients under dietary choice (Bonduriansky & Chenoweth, 2009). However, while confirming that these conditions are met in our study demonstrates that intralocus sexual conflict is operating in this population of *G. sigillatus*, it does not characterise the strength or likely outcome of this conflict for the sexes. To address these questions, we predicted the degree of evolutionary constraint (given by the ratio ($\boldsymbol{R}$) of $\Delta \ddot{\bar{\boldsymbol{z}}}$ to $\Delta \ddot{\bar{\boldsymbol{z}}}_{\mathbf{B}=0}$) to the independent evolution of nutrient regulation in the sexes (Lande, 1980). Our estimates of $\boldsymbol{R}$ were consistently above 1.0 in males and below 1.0 in females meaning that the predicted response of nutrient intake is accelerated in males but constrained in females. This asymmetry in

the magnitude of our estimates suggests that females are losing the conflict, with nutrient intake predicted to evolve only half as much as expected under genetic independence compared to males for whom this trait is predicted to evolve twice as much as expected. The magnitude of this asymmetry in ***R*** was also trait specific, being larger for daily and lifetime reproductive effort than for life span, suggesting that females are not losing the conflict to such an extent for this specific trait. Our findings contrast with the patterns shown in *T. commodus* (Rapkin et al., 2017) and *D. melanogaster* (Reddiex et al., 2013) where measures of genetic constraint provided little evidence for intralocus sexual conflict over the optimal intake of nutrients. In *T. commodus*, estimates of ***R*** were consistently greater than 1.0 for life span, daily and lifetime reproductive effort in both sexes, although the magnitude of sex differences in ***R*** were not as consistent, being larger in males than females for daily and lifetime reproductive effort but the reverse pattern existing for life span (Rapkin et al., 2017). In *D. melanogaster*, the evolvability of nutrient preference was nearly twice the average for the population because the direction of the linear effects of P and C intake on reproduction was well aligned with the major axis of **G** for nutrient preference in the sexes (Reddiex et al., 2013). Therefore, our study not only represents the first to demonstrate the potential for intralocus sexual conflict to constrain the evolution of nutrient intake, but also to show that it may have very different outcomes for the sexes. It is important to recognise, however, that our estimates of both **G** and **R** have large credible intervals due to the small number of cricket lines used in our analysis. Consequently, as our arguments on the strength and nature of intralocus sexual conflict over the optimal intake of nutrients are based on point estimates of these measures, they should be interpreted with a degree of caution. Optimal foraging theory predicts that individuals will evolve foraging strategies to maximise their fitness (Stephens & Krebs, 1986). Despite showing a clear advantage to male and female *G. sigillatus* differentially regulating their intake of P and C, we found that the sexes regulated their intake of nutrients to a common P:C ratio. While this finding is consistent with our previous work on this species (Rapkin et al., 2018), there appears to be little consensus on how the sexes regulate the intake of P and C across insect species. For example, studies on the cockroach *Naupheota cinerea* (Bunning et al., 2016), *T. commodus* (Maklakov et al., 2008) and *D. melanogaster* (Jensen, McClure, et al., 2015) have also shown that the sexes regulate their intake to the same P:C ratio. However, other studies on populations of the latter two species (Rapkin et al., 2017; Reddiex et al., 2013), as well as on the field cricket *T. oceanicus* (Ng et al., 2019), the caterpillar *Spodoptera litura* (Lee, 2010) and the cockroach *Blattella germanica* (Jensen, Schal, et al., 2015; Jensen & Silverman, 2018), have shown that females regulate to a higher intake of P than males. This lack of consensus, especially within studies on the same species, highlights the dynamic nature of nutrient regulation in insects and the need for further studies directly comparing the sexes.

More importantly, our work shows that this common pattern of nutrient regulation in *G. sigillatus* is not perfectly optimal for life span nor reproduction in either sex. However, the extent of this mismatch varied across the sexes and for the different traits. In males, the regulated intake point overlapped the 95% confidence region of the estimated maxima for life span, daily and lifetime reproductive effort (Figure 2b,d; Figure S2b), whereas in females this overlap occurred for life span (Figure 2a) but not daily (Figure 2c) or lifetime reproductive effort (Figure S2a). Furthermore, the Euclidean distance (d_*) between the regulated intake point and the estimated maxima for life span, daily and lifetime reproductive effort were consistently larger for females than males, although the difference between the sexes was much smaller for life span than for daily and lifetime reproductive effort. The finding that female *G. sigillatus* are further from their optimal level of nutrient regulation for life span and reproduction than males is therefore consistent with our measures of genetic constraint and the view that females are losing this conflict, albeit to a smaller degree for life span. It also shows that intralocus sexual conflict over the optimal intake of nutrients is likely to be an important process generating sex differences in life span and reproduction and may help explain why females age faster and live shorter than males in *G. sigillatus*, and show contrasting patterns of age-dependent reproductive effort (Archer et al., 2012).

More generally, the suboptimal regulation of P and C intake for life span and reproduction appears a common feature of insect studies where both sexes have been examined (Harrison et al., 2014; Jensen, McClure, et al., 2015; Maklakov et al., 2008; Rapkin et al., 2018; Reddiex et al., 2013). While this suggests that intralocus sexual conflict over the optimal intake of nutrients for these traits may be widespread, an alternate explanation is that other important fitness components have been overlooked. This may include the costs associated with searching for food or mates, which are extremely difficult to measure in the laboratory environment, or other forms of reproductive investment. In our current study, we only measured a single form of reproductive effort in males: the amount of time spent calling to attract a mate. While calling is likely the most energetically expensive form of reproductive effort in crickets (e.g. Kavanaugh, 1987; White et al., 2008) and is known to be a key component of mating success (e.g. Bentsen et al., 2006), male *G. sigillatus* also produce an externally attached spermatophore that consists of two discrete components: the sperm containing ampulla and the much larger gelatinous spermatophylax (Sakaluk, 1984). Immediately after transfer of the spermatophore, the female detaches the spermatophylax from the ampulla with her mandibles and commences feeding on it as sperm is evacuated into her reproductive tract from the ampulla. After consuming the spermatophylax, the female immediately removes and consumes the ampulla, thereby terminating sperm transfer. Therefore the longer the female feeds on the spermatophylax, the more sperm are transferred and larger spermatophylaces are known to take longer to consume (Sakaluk, 1984). The spermatophylax is approximately 85% water (Warwick et al., 2009), with the remainder consisting of free amino acids that serve as powerful phagostimulants where specific combinations increase the likelihood the female will feed on the spermatophylax for longer (Gershman et al., 2012). We have shown that both the weight and

free amino acid composition that increases the amount of time the female feeds on the spermatophylax are maximised on diets with a P:C ratio of 1_P:1.3_C (Rapkin et al., 2016). It is also likely a more protein biased diet (compared to calling effort) increases sperm number, as has been shown in male cockroaches (Bunning et al., 2015) and ants (Dávila & Aron, 2017), although this has yet to be shown in *G. sigillatus*. It is therefore possible that if spermatophore production was included in our measure of male reproductive effort that the nutritional optima for this trait would be shifted towards a higher relative intake of P. This would reduce the magnitude of sex differences in the effects of nutrients on reproduction and bring the regulated intake point into closer alignment with the nutritional optima for reproduction, ultimately weakening the strength of intralocus sexual conflict that we report in this population of *G. sigillatus*. While it was not feasible to collect and analyse spermatophores from each mating in Experiment 1, it is reassuring that Jensen, McClure, et al. (2015) found surprisingly similar nutritional effects to our study when male reproduction was measured as the number of offspring sired in competition and therefore takes both pre- and post-copulatory reproductive processes into account. Clearly, there is the need for more nutritional studies that include the full range of reproductive process, preferable measured side-by-side in males and females (as advocated by Moatt et al., 2016).

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CONFLICT OF INTEREST

None of the authors have a conflict of interest.

AUTHORS' CONTRIBUTIONS

J.H., C.M.H. and S.K.S. designed the experiment; M.H., S.M.L., J.R. and K.J. conducted experimental work; J.H. and J.R. analysed the data; and J.H., J.R. and C.M.H. prepared first draft of the manuscript. All authors contributed to the writing of the final manuscript.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Dryad Digital Repository at https://datadryad.org/stash/share/d2GP5xLTH52jxePsZrnKWz7dc-gDVxGEqkCY8XOg6bA (Hawkes et al., 2022).

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