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Sex-specific nutritional requirements of mating in insects with contrasting mating systems

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Fitness of most animals is affected by the amount and ratio of nutrients they consume. Therefore, maximizing fitness relies on consumers fine-tuning their intake towards a specific nutritional target. However, mating might alter this target because the nutrient ratio that maximizes reproductive investment often differs from ratios that elevate the expression of other fitness traits, e.g. survival and immunity. Therefore, consumers may be under selection to shift their intake towards nutrient ratios that promote reproductive success only when the likelihood of mating is high or after mating activity. Here, we tested how mating affects total macronutrient intake and the protein-to-carbohydrate ratio consumed by males and females given a dietary choice. Three insect species, namely Australian field crickets, *Teleogryllus commodus*, decorated crickets, *Gryllodes sigillatus*, and cockroaches, *Nauphoeta cinerea*, were studied. Males in these species differ in the traits they use to attract females and in postcopulatory sexual selection, while females differ in the timing and magnitude of offspring investment. Despite these differences, mating triggered increased macronutrient intake in females across all species, while male intake remained unchanged. This elevated consumption indicates that mating increases the energetic demands of females more than males. Neither sex altered the nutrient ratio consumed after mating, despite nutrient ratios mediating trade-offs between aspects of reproduction, e.g. sexual display versus sperm production, and other life-history traits, e.g. survival, in these species. We speculate that this is because selection skews nutrient regulation strategies towards ratios that promote reproductive success, and mating does not trigger deviation from these relatively fixed courses. In addition, the magnitude and direction of sex differences in protein and carbohydrate intake as well as how tightly each sex regulates their macronutrient intake, differed between species. We discuss what this suggests about species-specific physiology and the costs of reproduction.

Optimal foraging theory predicts that animals regulate their food intake to maximize their fitness (Pyke, 2019). The solution to this regulatory challenge was initially assumed to be simple: maximize net energy intake (MacArthur & Pianka, 1966). In fact, consumers often improve their fitness by regulating the energy they consume and the balance of macronutrients that provide this energy (Simpson & Raubenheimer, 2012). For example, in many insects, lifespan or reproduction depend on the relative intake of protein, P, carbohydrate, C, (Dussutour & Simpson, 2012; Jensen et al., 2015; Maklakov et al., 2008; Malod et al., 2017) or lipid, L, (Vaudo et al., 2016; Zanco et al., 2021). Similar patterns are observed in diverse species such as slime moulds (Dussutour et al., 2010), mice (Solon-Biet et al., 2015) and stickleback fish (Moatt et al., 2019). Optimal foraging is clearly a complicated balancing act.

Multiple insects (Al Shareefi & Cotter, 2019; Sun et al., 2022; Talal et al., 2024), mammals (Sørensen et al., 2008; Uwimbabazi et al., 2021), fish (Filho et al., 2018) and slime moulds (Dussutour

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et al., 2010) meet this regulatory challenge and eat nonrandomly from different, unbalanced foods to broadly defend a specific regulated intake point, RIP (Simpson et al.; 2004). In theory, RIPs should overlap with individual intake targets; that is, the nutrient ratios that maximize fitness (Simpson et al., 2004). In practice, this is not always the case. Mismatches between intake targets and RIPs indicate that nutrient regulation is challenging, not least because nutritional needs can change over the life-course (Treidel et al., 2021), in response to an altered state e.g. following immune challenge, (Cotter et al., 2019) or environmental conditions e.g. predation risk (Hawlena & Schmitz, 2010). Mating is one activity that can influence individual nutritional requirements.

Reproduction is costly; searching for, or avoiding, potential mates (Rowe, 1994), displaying secondary sexual traits (Kotiaho et al., 1998) or producing offspring (Martin, 2007) require resources. Energy is central to meeting these demands, as reflected by the elevated metabolic rate in breastfeeding women (Motil et al., 1990) and in crickets calling to attract mates (Kavanagh, 1987). Specific nutrients also play important roles in reproduction. For example, female insects require protein to produce eggs (Harrison et al., 2014; Rapkin et al., 2018; Reddiex et al., 2013), while growing large sexually selected weapons (mandibles) in male broad-horned beetles, *Gnatocerus cornutus*, necessitates increased protein and carbohydrate intake (House et al., 2016). Accordingly, eating large amounts of specific nutrient ratios often promotes reproductive trait expression.

However, nutrient ratios that increase reproductive success can reduce the expression of other traits. Such obligate dietary trade-offs are clear in many female insects, where high-protein intake maximizes fecundity but reduces lifespan (Fanson et al., 2009; Harrison et al., 2014; Lee et al., 2008; Maklakov et al., 2008). Male decorated crickets, *Gryllodes sigillatus*, face a similar trade-off; males maximize their calling effort by eating high-carbohydrate, low-protein diets, which are associated with poor encapsulation, an immune parameter (Rapkin et al., 2018). Perhaps then, rather than consuming a nutrient ratio that maximizes reproductive traits at the expense of other fitness traits, it pays to shift nutrient intake towards ratios that promote reproductive success when the likelihood of mating is high (e.g. in the presence of mates) or in response to mating? In this case, we suggest that whether consumers adjust their intake following mating depends on how much dietary optima for reproduction and other traits diverge. Where dietary optima overlap, we would not expect to see any adjustments to nutrient intake after mating. Where there is divergence, we would expect that whether individuals adjust their intake or not depends on how those individuals resolve trade-offs between reproductive investment and other fitness traits, e.g. lifespan and immunity. This may depend on the life history of a species and the intensity of sexual selection.

Data provide mixed support for consumers adjusting nutrient intake after mating. In two-spot ladybirds, *Adalia bipunctata*, spermatophore consumption prompts females to eat more after mating (Perry, 2011). In *Drosophila melanogaster*, male sex peptide transfer increases female feeding rates (Barnes et al., 2008) and mating promotes protein consumption (Camus et al., 2018; Lee et al., 2013). Female two-spotted crickets, *Gryllus bimaculatus*, show a similar move towards higher protein intake after mating (Tsukamoto et al., 2014), whereas mated female house crickets, *Acheta domesticus*, display a stronger preference for sucrose than virgins (Tierney et al., 2023). In males, whether mating affects nutrient intake remains unclear. In *D. melanogaster*, males that mated at least once did not consistently alter the amount or ratio of protein and carbohydrate they consumed (Camus et al., 2018). This pattern did not change when males mated multiply (Sydney et al., 2024), a scenario that more accurately reflects natural *D. melanogaster* male mating costs. In general, when and how much males shift their nutrient intake after mating remains unclear.

Here, we tested how male and female insects regulate their intake of protein and carbohydrate when offered one of four diet pairs and whether these strategies change after mating. We studied three species whose nutritional ecology is well understood: the decorated house cricket, *Gryllodes sigillatus*; Australian field cricket, *Teleogryllus commodus* and speckled cockroach, *Nauphoeta cinerea*. Males from each species face a dietary trade-off involving different aspects of reproduction; carbohydrate-biased diets typically promote success in precopulatory sexual selection, i.e. increased sexual signalling (South et al., 2011) but reduce success in postcopulatory sexual selection, i.e. fewer sperm (Bunning et al., 2015). In female crickets, high-protein diets that promote fecundity are associated with reduced lifespan (Hawkes et al., 2022; Rapkin, Archer, et al., 2017). Individuals faced with these trade-offs appear to compromise and select intermediate protein:carbohydrate, P:C, ratios that enable moderate expression of each trait.

Differences in reproductive physiology and behaviour are also observed among our focal species. In cricket species, mating triggers increased egg laying (Itgi et al., 1982; Loher & Edson, 1973) and females mate several times (Jennions et al., 2007; Sakaluk et al., 2002). In speckled cockroaches, mating promotes rapid oocyte growth and fertilized ova develop inside a brood pouch, emerging as first-instar nymphs. Parturition initiates the development of the next oocyte batch meaning that females reproduce in discrete cycles, each lasting around 50 days, which is ~25% of adult female maximum lifespan (A. J. Moore et al., 2003). Moreover, the receipt of a spermatophore inhibits female receptivity (Roth, 1962). Some females are monogamous during their lifetime, while others are briefly receptive to remating after giving birth to their first clutch (Roth, 1964). Given these differences, we predicted that females of all three species would eat more after mating, but that these effects would be least pronounced in cockroaches, which will not reproduce again until their current brood emerge, indicating that there may be stronger selection on feeding to optimize lifespan in this species than in crickets. Moreover, considering that crickets require high-protein intake to reproduce while female cockroaches have a low demand for protein for egg laying relative to other insects (Archer et al., 2022), we expected that mating would trigger elevated protein consumption in crickets but not cockroaches.

Male crickets of both species call to attract females, promoted by high-carbohydrate intake, which also favours a long life. In *G. sigillatus*, but not in *T. commodus*, the spermatophore transferred at mating contains a spermatophylax, which is a nuptial gift that females feed on during mating (Alexander & Otte, 1967). The larger these gifts, the more sperm is transferred at mating and the greater male fertilization success (Sakaluk et al., 2019). Investing in spermatophylax production requires eating diets rich in protein and carbohydrate (Rapkin et al., 2016). In cockroaches, although relatively high-protein diets promote sperm production (Bunning et al., 2015), high-carbohydrate intake helps males produce pheromones that elevate their attractiveness (South et al., 2011). The extra costs of mating in decorated crickets associated with nuptial gift transfer, likely promote an increase in nutrient intake and a shift towards higher protein ratios relative to the other cricket species or cockroaches. We predicted the least pronounced shifts in intake in male cockroaches, whose sexual attractiveness depends on their pheromone profiles (presumably less labile and metabolically expensive than acoustic sexual display). While studying three species does not enable us to make robust comparisons or control for phylogeny, by studying species that differ so much in their reproduction we can begin to explore how much

reproductive strategies and mating systems might alter mating effects on nutrient regulation in either sex.

METHODS

Experimental Animals and Husbandry

Australian black field cricket, Teleogryllus commodus

The *T. commodus* used in this study originated from 700 adult females collected from Smith's Lake, New South Wales, Australia, in March 2009. The offspring of these crickets were used to establish a large panmictic laboratory colony. This laboratory colony consisted of 12 large containers, 90 × 60 × 50 cm, with ~500 crickets per container. Each container was provided with cardboard egg cartons for shelter, water in 60 mL test tubes plugged with cotton wool and a 50% mixture of cat food (Purina Go Cat Senior, St Louis, MO, U.S.A., protein 31%, fat 9%) and rat food (CRME food, SDS Diets, Essex, U.K., protein 18.4%, fat 3.4%). The containers were cleaned, and fresh food and water were provided weekly. When adults were detected in these containers, moistened cotton wool was provided inside a Petri dish, which was 12 cm in diameter, as an oviposition substrate. At each generation, nymphs were collected en masse at hatching and randomly transferred between containers to enforce gene flow. When sufficient nymphs were collected to establish 12 new containers, at 500 nymphs per container, the parental generation was euthanized by freezing at −20 °C. During the experiment, our laboratory colony had been maintained in accordance with the abovementioned protocol for 10 nonoverlapping generations. Our colony was maintained in a constant-temperature room set to 28 °C ± 1 °C and a 14:10 h light:dark (LD) cycle.

At generation 11, newly hatched nymphs were collected to serve as experimental animals or mating partners. Each nymph was housed in an individual plastic container, 5 × 5 × 5 cm, and provided with a single segment of cardboard egg carton for shelter, water in a 2.5 mL test tube plugged with cotton wool and a 50% mixture of cat and rat food. For the first 2 weeks, this food was provided as a ground powder in the lid of a 1.5 mL Eppendorf tube and as whole pellets thereafter. The containers were cleaned, and fresh food and water were provided weekly. At the final instar stage, the crickets were checked daily for newly eclosed adults. Male and female adult crickets were randomly allocated to experimental treatments (see below) or to serve as mating partners for experimental animals. Each cricket was established in a larger, individual container, 20 × 10 × 10 cm, and provided with water in a 10 mL test tube plugged with cotton wool and a single segment of cardboard egg carton for shelter. Experimental crickets were provided with their respective diets (see below), whereas mating partners were provided with cat food and rat food in pellet form. Experimental animals and their mating partners were housed in a constant-temperature room set to 28 °C ± 1 °C and a 14:10 h LD cycle.

Decorated cricket, Gryllodes sigillatus

The *G. sigillatus* used in these experiments originated from 500 adult females collected from Las Cruces, NM, U.S.A., in June 2001. The offspring of these crickets were used to establish a large panmictic laboratory colony. This colony consisted of 12 large containers, 40 × 40 × 200 cm, with ~500 crickets per container. Each container was provided with cardboard egg cartons for shelter, water in 60 mL test tubes plugged with cotton wool and a 50% mixture of cat food, Purina Go Cat Senior, St. Louis, MO, U.S.A., and rat food, SDS Diets, Essex, U.K. These populations were maintained, and nymphs were collected to establish the next generation following the procedure outlined for *T. commodus*. During the experiment, our laboratory colony had been maintained in accordance with this protocol for 38 nonoverlapping generations. Our colony was maintained in an incubator, Percival, I-66VL, Perry, U.S.A. set to 28 °C ± 1 °C, and a 14:10 h LD cycle.

At generation 39, newly hatched nymphs were collected and reared to adulthood in individual 5 × 5 × 5 cm containers, following the procedure outlined for *T. commodus*. At adulthood, we randomly allocated male and female crickets to experimental treatments (see below) or to serve as mating partners for these experimental animals. Each cricket was established in a larger, individual container, 20 × 10 × 10 cm, and provided with their respective diet following the procedure outlined for *T. commodus*. The experimental animals and their mating partners were housed in a constant-temperature room set to 28 °C ± 1 °C and a 14:10 h LD cycle.

Speckled cockroach, Naupheota cinerea

Cockroaches were collected from a laboratory colony with over 200 000 individuals housed in 10 large plastic containers of 80 × 50 × 30 cm, in an incubator, Percival, I-66VL, Perry, U.S.A., which was set to 28 °C ± 1 °C and a 14:10 h LD cycle. The colonies were fed dry rat food, SDS diets, Essex, U.K., and provided with water in eight 60 mL test tubes plugged with cotton wool weekly. Every 3 months, the containers were cleaned and several thousand individuals were transferred randomly between containers to maintain gene flow and genetic variation (Corley et al., 2001).

Final instar nymphs were collected from each large culture container and sorted into smaller, single-sex containers of 17 × 12 × 6 cm. These single-sex cultures were checked daily for newly eclosed adults, which were removed and established in individual containers, 20 × 10 × 10 cm, and provided with water in a 10 mL test tube plugged with cotton wool. Male and female cockroaches were either randomly allocated to experimental treatments, or to act as mating partners for these experimental animals. Experimental cockroaches were provided with their respective diet pairs, whereas mating partners were provided with two rat food pellets. All cockroaches were housed in a constant-temperature room, maintained at 28 °C ± 1 °C and a 14:10 h LD cycle.

Artificial Diets and Measuring Dietary Intake

Four dry, meridic, powdered diets that varied in P:C ratio, as well as overall nutrient concentration, %P + %C, were made in accordance with the protocol of Simpson and Abisgold (1985). Proteins consisted of a 3:1:1 mixture of casein, albumen and peptone, and digestible carbohydrates comprised a 1:1 mixture of sucrose and dextrin. All diets contained the same proportion of Wesson's salts (2.5%), ascorbic acid (0.28%), cholesterol (0.55%) and vitamin mix (0.18%). After adding the appropriate dry weight of protein and carbohydrate to the diet mixture, the remainder of the mixture was made up to the appropriate dilution with crystalline cellulose. The composition of these diets is provided in Table S1 and Fig. S1.

To determine how individuals regulate their protein and carbohydrate intake under a dietary choice, individuals were provided with one of four diet pairs created from the four abovementioned artificial diets. Each diet pair contained one diet with a P:C ratio of 1_P:8_C and one diet with a P:C ratio of 5_P:1_C, and these diets were provided in one of two concentrations (%P + %C content), 36% or 84%. This method produced four pairs of diets: diet pair 1, 1_P:8_C (36%) versus 5_P:1_C (36%); diet pair 2, 1_P:8_C (84%) versus 5_P:1_C (36%); diet pair 3, 1_P:8_C (36%) versus 5_P:1_C (84%); diet pair 4, 1_P:8_C (84%) versus 5_P:1_C (84%). These same diet pairs were

used for each species, and they covered a wide nutritional range to ensure that they encompassed the RIP.

In each species, experimental animals were randomly assigned to one of the four diet pairs. As outlined above, all experimental animals were established in individual containers at eclosion and provided with water and their diet pair. Protein and carbohydrate intake was measured for each animal for 21 days, with new diets being provided every 7 days. For each feeding period, a known amount of each diet in the pair was measured and placed in an individual feeding platform, which was created by gluing the upturned plastic lid of a vial, 1.6 cm diameter, 1.6 cm deep, in the centre of a plastic Petri dish. Diets were dried in an oven at 30 °C for 48 h before being weighed and supplied to experimental animals, and remaining diet was weighed once more following the feeding period. Faeces were removed from the remaining diet before weighing using fine forceps. Diet consumption was calculated as the difference in the dry weight of each diet before and after feeding, and converted into protein and carbohydrate intake by multiplying by the proportion of these macronutrients in the diet. The total intake of protein and carbohydrate was determined by adding the protein and carbohydrate intake from each diet in the pair.

Experimental Design

In each species, half of the experimental males and females fed each diet pair were randomly allocated to be mated, whereas the other half remained virgins. This allocation and the subsequent mating of experimental animals were undertaken at 7 days after eclosion for each species. Consequently, the following four treatment groups were produced for each diet pair and species: (1) virgin males, (2) mated males, (3) virgin females and (4) mated females. In the treatment groups where mating occurred, experimental animals were randomly assigned a mating partner of the same age. All matings were conducted in a constant-temperature room set to 28 °C ± 1 °C under red lighting in the original container of experimental animals.

For *T. commodus* and *G. sigillatus*, mating was considered successful if the male transferred an ampulla to the female that remained attached for at least 45 min, which is the average time taken for complete sperm transfer in these species (Bussière et al., 2006; Sakaluk, 1984). For *N. cinerea*, mating was considered successful if the male and female remained in copula for at least 15 min, which is the average time taken to successfully transfer a spermatophore in this species (Bouchebti et al., 2016). For all species, if mating did not occur within an hour, then another partner was provided until successful mating was observed. Diets were removed from the container during mating and returned immediately after mating. For *T. commodus* and *G. sigillatus*, the feeding behaviour of 30 crickets of each sex per diet pair and mating status were examined, yielding a total sample size of 480 for each species. For *N. cinerea*, the feeding behaviour of 25 cockroaches of each sex per diet pair and mating status were examined, yielding a total sample size of 400.

Statistical Analyses

Trigonometry was used to separate the total amount and ratio of macronutrients consumed by individuals when given a dietary choice (Camus et al., 2018; Sydney et al., 2024). In quantifying the total amount of macronutrients consumed by each individual, the length of the vector starting at the origin (0,0) to the point in nutrient space representing the total consumption of protein and carbohydrate was calculated. The length of this vector, $\overrightarrow{\| v \|}$, was calculated as $\overrightarrow{\| v \|} = \sqrt{a^2 + b^2}$, where a is the total consumption of protein and b is the total consumption of carbohydrate for each individual. Therefore, larger $\overrightarrow{\| v \|}$ values represent greater total diet and macronutrient consumption.

To quantify the ratio of macronutrients consumed by each individual, the angle, α, between $\overrightarrow{\| v \|}$ and the protein axis, a, was calculated as $\alpha = cos^{-1}(\overrightarrow{\| v \|} \cdot a / \overrightarrow{\| v \|} \| a \|)$. a starts at the origin (0,0) and terminates at the point where a parallel line (to the carbohydrate axis) extending from the total consumption of protein and carbohydrate intersects the protein axis. α varies between 0 and 90°, with angles over 45° indicating that an individual consumes more carbohydrate than protein and angles less than 45° signifying that an individual consumes more protein than carbohydrate.

Multivariate analysis of variance (MANOVA) in SPSS was used to determine whether $\overrightarrow{\| v \|}$ and α varied across species, sexes and mating status treatments. In our initial MANOVA model, species, sex and mating status as well as their interactions were included as fixed effects and $\overrightarrow{\| v \|}$ and α were response variables. Univariate ANOVAs were used to determine how $\overrightarrow{\| v \|}$ and α contributed to any significant overall multivariate effects. By excluding diet pairs in these models, the effects of our model terms on $\overrightarrow{\| v \|}$ and α when averaged across diet pairs were examined, which corresponds to the RIP. As the main effect of species and all interactions involving species were significant in our multivariate model (Table 1), separate analyses were conducted for each species. For each species, the same MANOVA model that included sex, mating status and their interaction as fixed effects and $\overrightarrow{\| v \|}$ and α as response variables was run. Univariate ANOVAs were used to determine whether $\overrightarrow{\| v \|}$ and α contributed to any significant overall multivariate effects for each species.

Median protein intake and median carbohydrate intake were used as the most robust point estimate of the RIP. The median rather than the mean intake of protein and carbohydrate was used as our estimate of the RIP, as the median provides a better measure

Table 1
Overall MANOVA model examining the effects of species, sex and mating status as well as their potential interactions, on vector length ($\overrightarrow{\| v \|}$) and vector angle (α)

Model terms	Pillai's trace	*F*	*df*	*P*
MANOVA				
A	1.18	974.47	4,2696	0.0001
B	0.35	360.89	2,1347	0.0001
C	0.07	49.88	2,1347	0.0001
A × B	0.13	47.96	4,2696	0.0001
A × C	0.03	11.33	4,2696	0.0001
B × C	0.05	33.46	2,1347	0.0001
A × B × C	0.03	8.16	4,2696	0.0001
Univariate ANOVA	Nutrient regulation			
A	$\overrightarrow{\| v \|}$	4297.54	2,1348	0.0001
	α	304.96	2,1348	0.0001
B	$\overrightarrow{\| v \|}$	582.86	1,1348	0.0001
	α	32.27	1,1348	0.0001
C	$\overrightarrow{\| v \|}$	93.24	1,1348	0.0001
	α	0.03	1,1348	0.86
A × B	$\overrightarrow{\| v \|}$	34.85	2,1348	0.0001
	α	59.09	2,1348	0.0001
A × C	$\overrightarrow{\| v \|}$	22.79	2,1348	0.0001
	α	0.77	2,1348	0.46
B × C	$\overrightarrow{\| v \|}$	63.88	1,1348	0.0001
	α	0.04	1,1348	0.84
A × B × C	$\overrightarrow{\| v \|}$	15.39	2,1348	0.0001
	α	0.10	2,1348	0.90

Univariate ANOVA was used to determine the mechanism by which $\overrightarrow{\| v \|}$ and α contributed to the overall significant multivariate effects. A: species; B: sex; C: mating status.

of central tendency when data are skewed, which is often the case with the intake of macronutrients. The feeding data were bootstrapped, and the median protein and median carbohydrate of each bootstrapped resample were recomputed, $B = 1000$ resamples were used. In calculating the 95% distribution-free confidence region (CR) on the location of the median RIP, the algorithm developed by Hu and Yang (2013) was used and implemented in the R (R Core Development Team, 2020) package distfree.cr, function 'distrfree.cr', (Hu & Yang, 2013), which was applied to all bootstrapped bivariate medians. This method accounts for the actual shape of the distribution inherent in the two-dimensional data, and it has been shown to provide better coverage than other existing methods aimed at finding distribution-free CRs for normal and non-normal data, variable sample sizes and different degrees of correlation between the two variables being examined (Hu & Yang, 2013). We provide an R code function (named 'CRIntakeTarget') that performs the bootstrapping and calls the distribution free CR computation (Text S1). It returns the median point estimate, the area of the CR (computed using the convex hull of the points on the border of the region) the border of the region and the plot of the median protein and carbohydrate intake with the superimposed CR. As macronutrient intake is constrained to non-negative values (individuals cannot eat a negative amount of diet), it is likely that there is a positive correlation between the mean and variance of these values. Consequently, the area of the 95% CR for the RIP was divided by the median total macronutrient intake, i.e. mean protein intake + mean carbohydrate intake. Therefore, the resulting 95% CRs represent the variation around the median RIP for each sex and mating status treatment, with larger values representing more variation in nutrient regulation around this estimate and smaller values representing less variation.

Ethical Note

The species used in this study are not covered by the directive 2010/63/EU on the protection of animals used for scientific purposes or by the Animals Scientific Procedures Act, U.K. legislation. However, experiments were conducted in accordance with the ASAB/ABS guidelines for the ethical treatment of nonhuman animals in behavioural research and we adhered to all directions in relevant EU legislation, 2010/63/EU, that is, we used the minimum number of animals necessary and caused the minimum degree of harm via appropriate husbandry throughout the experiment. Animals were euthanized by freezing at the end of the experiment.

RESULTS

Our overall MANOVA model showed significant effects of species, sex and mating status on the length of the vector, $\|\overrightarrow{v}\|$, describing macronutrient consumption and the vector angle, α, describing macronutrient preference (Table 1). Univariate ANOVAs showed that $\|\overrightarrow{v}\|$ and α differed significantly across species and sexes, but only $\|\overrightarrow{v}\|$ differed significantly with mating status (Table 1). All two-way interactions and the three-way interaction between these terms were significant (Table 1), indicating that macronutrient regulation varied across species and sexes, as well as in response to mating. Univariate ANOVAs showed that for all interaction terms involving mating status, this overall multivariate effect was driven by changes in $\|\overrightarrow{v}\|$ but not α, i.e. mating shifted how much food was consumed but not the nutrient ratio consumed (Table 1). However, the significant multivariate interaction between species and sex was driven by changes in $\|\overrightarrow{v}\|$ and α (Table 1; i.e. species and sexes differ in the amount and ratio of nutrients consumed). The significant main effect of species, as well as all interactions including this term, justifies examining the effects of sex and mating status on $\|\overrightarrow{v}\|$ and α separately in each species.

In *T. commodus*, there were significant multivariate effects of sex and mating status on $\|\overrightarrow{v}\|$ and α, and a significant interaction between these terms (Table 2). The effect of sex was driven by females having, on average, a higher $\|\overrightarrow{v}\|$ (Fig. 1a) but a lower α than males (Fig. 1b; i.e. eating more food overall and selecting a more protein-rich food). The effect of mating status was driven by mated crickets having, on average, a higher $\|\overrightarrow{v}\|$ than virgin crickets (Table 2, Fig. 1a), whereas α did not differ with mating status (Table 2, Fig. 1b). The significant interaction between sex and mating status was exclusively driven by changes in $\|\overrightarrow{v}\|$, and it occurred because the increase in $\|\overrightarrow{v}\|$ with mating was restricted to females but not to males (Table 2, Fig. 1a). However, this interaction did not occur for α (Table 2, Fig. 1b). The RIP and 95% CRs for mated and virgin crickets of each sex are presented in Fig. 2a. Mated females regulated their intake of macronutrients to a higher median intake of protein, 346.68 mg, and carbohydrate, 731.55 mg, than virgin females, whose median protein intake was 276.90 mg, and median carbohydrate intake was 573.01 mg, but this pattern yielded similar P:C intake ratios of $1_P{:}2.11_C$ and $1_P{:}2.07_C$, respectively (Fig. 2a). In contrast, virgin and mated males had similar median intakes of protein (virgin: 164.22 mg; mated: 169.14 mg) and carbohydrate (virgin: 554.41 mg; mated: 564.26 mg) and P:C ratios (virgin: $1_P{:}3.38_C$; mated: $1_P{:}3.34_C$), although this ratio was more carbohydrate-biased than in females. In both sexes, the area of the 95% CR was consistently smaller for virgin (females: 2.47 mg^2; males: 1.96 mg^2) than mated (females: 3.07 mg^2; males: 3.35 mg^2) crickets (Fig. 2a). Within each mating status treatment, the sex difference in the 95% CR was less consistent: in virgins, the 95% CR was larger in females than in males, whereas the opposite pattern occurred in mated *T. commodus* (Fig. 2a).

The pattern of macronutrient regulation observed in male and female *G. sigillatus* with mating status was remarkably similar to that documented for *T. commodus*. That is, there were significant multivariate effects of sex and mating status on $\|\overrightarrow{v}\|$ and α, and a significant interaction between these terms (Table 3). The effect of sex was also driven by females having, on average, a higher $\|\overrightarrow{v}\|$ (Fig. 1c) but a lower α (Fig. 1d) than males. The effect of mating status was driven by mated crickets tending to have a higher $\|\overrightarrow{v}\|$ than virgins (Table 3, Fig. 1c), but no significant change in α with mating status was observed (Table 3, Fig. 1d). The significant interaction between sex and mating status was also driven by changes in $\|\overrightarrow{v}\|$ because the increase in $\|\overrightarrow{v}\|$ with mating occurred in females but not in males (Table 3, Fig. 1c). No interaction was

Table 2
MANOVA examining the effects of sex and mating status, as well as their interaction, on $\|\overrightarrow{v}\|$ and α in *Teleogryllus commodus*

Model terms	Pillai's trace	$F_{2,475}$	P
MANOVA			
Sex	0.52	258.78	0.0001
Mating status	0.12	31.34	0.0001
Sex × mating status	0.09	23.00	0.0001
Univariate ANOVA			
Model terms	**Nutrient regulation**	**$F_{1,476}$**	**P**
Sex	$\|\overrightarrow{v}\|$	133.04	0.0001
	α	195.53	0.0001
Mating status	$\|\overrightarrow{v}\|$	58.71	0.0001
	α	0.90	0.34
Sex × mating status	$\|\overrightarrow{v}\|$	40.36	0.0001
	α	0.01	0.91

Univariate ANOVAs were used to determine the mechanism by which $\|\overrightarrow{v}\|$ and α contributed to the overall significant multivariate effects in each species.

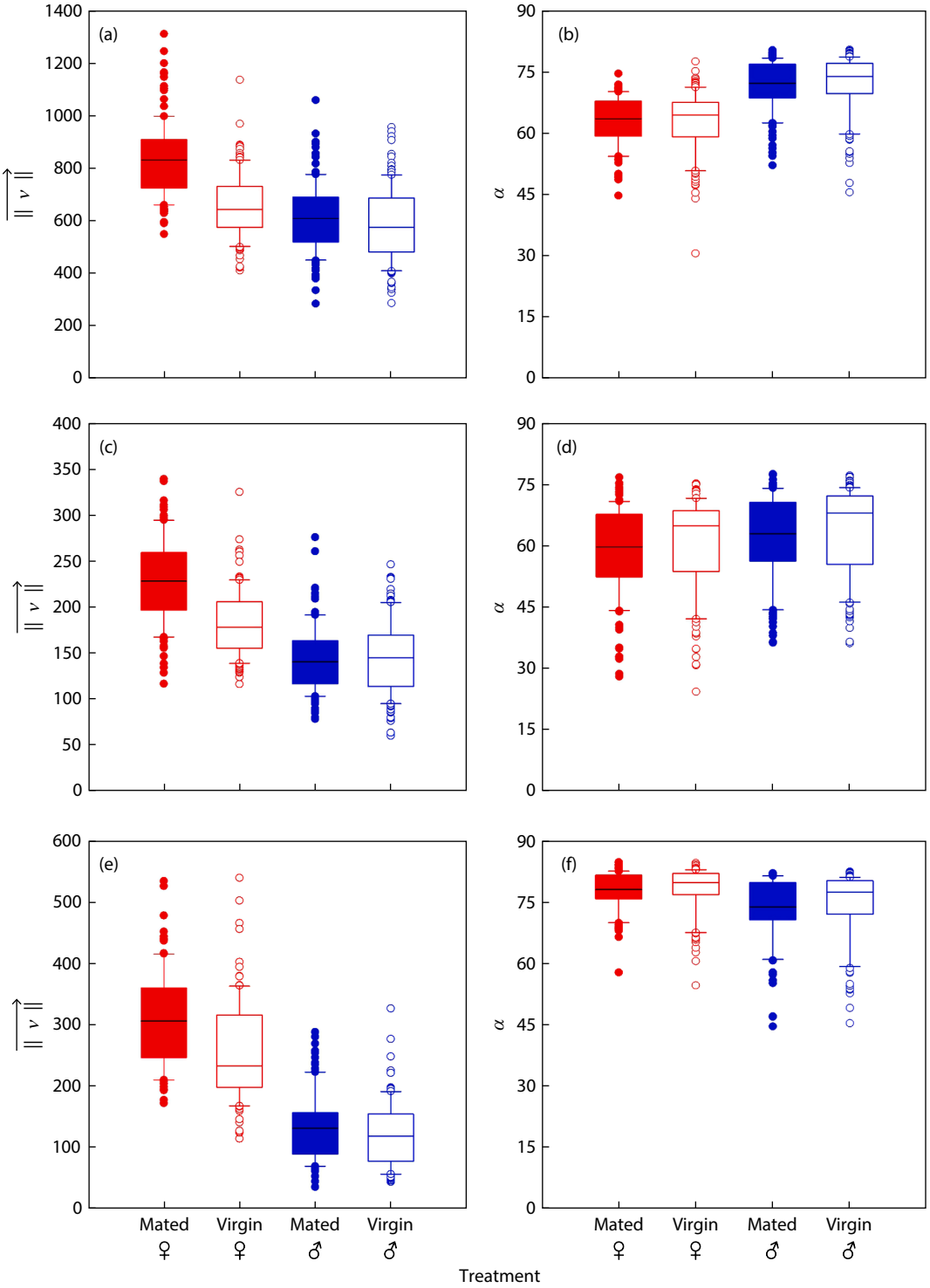

Figure 1. Box plots showing the effects of sex and mating status on nutrient regulation, given by the total consumption of diets ($\overrightarrow{\| v \|}$) and macronutrient preference (α): (a, b) *Teleogryllus commodus*, (c, d) *Gryllodes sigillatus* and (e, f) *Nauphoeta cinerea*. Females are shown by red bars and symbols, and males are shown by blue bars and symbols. In each sex, open bars and points represent virgin individuals, whereas closed bars and points represent mated individuals. The boxes show the median values for each species, sex, treatment; associated quartiles and the minima and maxima, excluding any outliers.

found for α (Table 3, Fig. 1d). As observed in *T. commodus*, mated female *G. sigillatus* regulated their intake towards a higher median intake of protein (102.11 mg) and carbohydrate (193.53 mg) than virgin females (median P intake = 78.13 mg, median C intake = 152.46 mg) but the regulated P:C ratios of mated (1_P:1.90_C) and virgin (1_P:1.95_C) females were similar (Fig. 2b). Virgin and mated males, however, had similar median intakes of protein (virgin: 54.96 mg; mated: 55.83 mg) and carbohydrate (virgin: 122.18 mg; mated: 114.65 mg) and P:C ratios (virgin: 1_P:2.22_C; mated: 1_P:2.05_C), and this ratio was more carbohydrate-biased in males

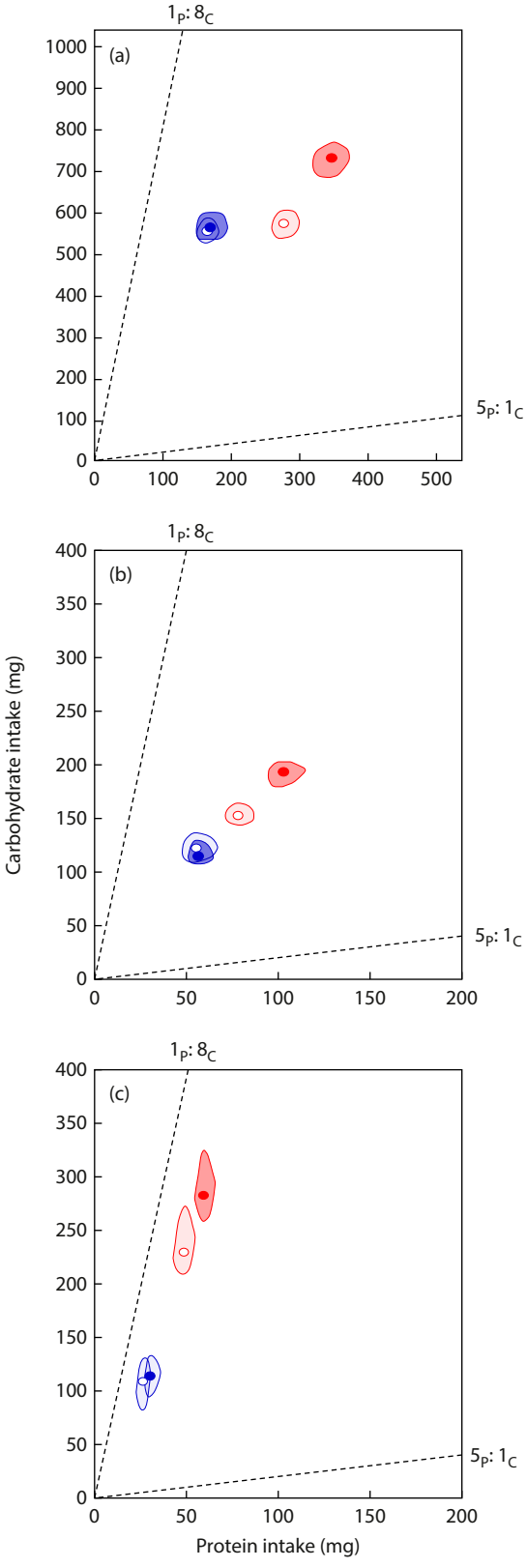

Figure 2. Median intake of protein and carbohydrates (known as the regulated intake point) by male and female: (a) *Teleogryllus commodus*, (b) *Gryllodes sigillatus* and (c) *Nauphoeta cinerea*. Blue symbols and shading for the 95% confidence regions represent males of each species, whereas red symbols and shading represent females of each species. Open symbols and light shading represent virgin individuals, whereas closed symbols and dark shading represent mated individuals.

Table 3
MANOVA examining the effects of sex and mating status, as well as their interaction, on $\overrightarrow{\| v \|}$ and α in *Gryllodes sigillatus*

Model terms	Pillai's trace	$F_{2,475}$	P
MANOVA			
Sex	0.40	160.01	0.0001
Mating status	0.07	17.48	0.0001
Sex × mating status	0.09	22.91	0.0001
Univariate ANOVA			
Model terms	Nutrient regulation	$F_{1,476}$	P
Sex	$\overrightarrow{\| v \|}$	305.24	0.0001
	α	9.37	0.002
Mating status	$\overrightarrow{\| v \|}$	33.90	0.0001
	α	0.60	0.44
Sex × mating status	$\overrightarrow{\| v \|}$	45.68	0.0001
	α	0.02	0.88

Univariate ANOVAs were used to determine the mechanism by which $\overrightarrow{\| v \|}$ and α contributed to the overall significant multivariate effects in each species.

than females (Fig. 2b). In females, the area of the 95% CR was smaller for virgin (1.04 mg^2) than mated (1.12 mg^2) crickets, but larger for virgin (2.06 mg^2) than mated (1.21 mg^2) males (Fig. 2b). Irrespective of mating status, the 95% CR was consistently smaller for female *G. sigillatus* than males (Fig. 2b).

In *N. cinerea*, there were significant multivariate effects of sex and mating status on $\overrightarrow{\| v \|}$ and α, as well as a significant interaction between these terms (Table 4). The effect of sex was driven by females having, on average, a higher $\overrightarrow{\| v \|}$ (Fig. 1e) and α than males (Fig. 1f; i.e. female cockroaches ate more food but, in contrast to crickets, selected a more carbohydrate-biased intake target than males). The effect of mating status was driven by mated cockroaches having a higher $\overrightarrow{\| v \|}$ than virgin cockroaches (Table 4, Fig. 1e). However, α did not differ with mating status (Table 4, Fig. 1f). The significant interaction between sex and mating status occurred because the increase in $\overrightarrow{\| v \|}$ with mating was restricted to females, although the magnitude of this increase in females was not as large as that observed in both cricket species (Table 4, Fig. 1e). The interaction term for α was not significant (Table 4, Fig. 1f). Mated females regulated their intake of macronutrients to a higher median intake of protein (58.78 mg) and carbohydrate (282.90 mg) than virgin females (median P intake = 47.93 mg, median C intake = 229.91 mg) but the regulated P:C ratio of mated (1_P:4.81_C) and virgin (1_P:4.80_C) females was similar (Fig. 2c). In contrast, virgin and mated males had similar median intakes of

Table 4
MANOVA examining the effects of sex and mating status, as well as their interaction, on $\overrightarrow{\| v \|}$ and α in *Nauphoeta cinerea*

Model terms	Pillai's trace	$F_{2,395}$	P
MANOVA			
Sex	0.57	263.85	0.0001
Mating status	0.05	10.90	0.0001
Sex × mating status	0.02	3.17	0.043
Univariate ANOVA			
Model terms	Nutrient regulation	$F_{1,396}$	P
Sex	$\overrightarrow{\| v \|}$	510.21	0.0001
	α	30.10	0.0001
Mating status	$\overrightarrow{\| v \|}$	17.69	0.0001
	α	0.01	0.92
Sex × mating status	$\overrightarrow{\| v \|}$	6.04	0.014
	α	0.28	0.60

Univariate ANOVAs were used to determine the mechanism by which $\overrightarrow{\| v \|}$ and α contributed to the overall significant multivariate effects in each species.

protein (virgin: 25.97 mg; mated: 29.31 mg) and carbohydrate (virgin: 109.34 mg; mated: 114.37 mg) and P:C ratios (virgin: 1_P:4.21_C; mated: 1_P:3.90_C), and this ratio was less carbohydrate-biased than males than females (Fig. 2c). In both sexes, the area of the 95% CR was consistently smaller for mated (females: 1.32 mg^2; males: 1.47 mg^2) than virgin (females: 1.68 mg^2; males: 1.94 mg^2) cockroaches (Fig. 2c). Irrespective of mating status, female *N. cinerea* had consistently smaller 95% CRs than males (Fig. 2c).

DISCUSSION

Where the nutritional needs of specific traits do not overlap, individuals cannot eat a single nutrient ratio to invest maximally in these traits at the same time. That is, diet mediates obligate trade-offs between traits. Understanding how individuals regulate their nutritional intake can shed light on how organisms resolve these trade-offs, and how these strategies are affected by individual demography (e.g. age, sex), condition and the environment. Here, in three different insect species with contrasting mating systems, mating affected total macronutrient intake in females but not in males. Mating only increased how much diet females consumed, without shifting the nutrient ratio that females selected. We reflect on what these results reveal about sex-specific costs of reproduction and how males and females resolve dietary mediated trade-offs between traits that have competing nutritional demands.

Mating increased food, and therefore macronutrient, intake in females from all species, whereas male intake was independent of mating. This increased total consumption in females may indicate that females often invest more resources in producing offspring than males. This sex difference in offspring investment begins at anisogamy; females make few large, expensive gametes, whereas males make many smaller, cheap gametes. Investment in comparatively costly ova rises in all focal species after mating. Mated *T. commodus* females lay 4–6 times more eggs than virgins (Loher & Edson, 1973), and mated *G. sigillatus* produce 5–6 times more eggs than virgins (Itgi et al., 1982). In speckled cockroaches, mating triggers rapid oocyte growth and fertilized ova develop inside a brood pouch, emerging as first-instar nymphs. The high costs of egg production are clear in cockroaches. In unmated females held without food (Barrett et al., 2008) or with nutritionally imbalanced food (Archer et al., 2022), eggs show high levels of programmed cell death. This pattern is a step towards ovarian resorption, whereby females absorb eggs to recoup the resources that they have already invested in ova that will not result in viable offspring (Barrett et al., 2009). Overall, in females from all three insect species, mating triggers increases in the production, growth or maturation of eggs and the energetic demands of these processes trigger an increased intake of macronutrients.

Any resources males save in investing in individual offspring relative to females tend to be allocated towards improving mating and fertilization success (Williams, 1966). This again is a difference rooted in anisogamy: males have many small sperm, and thus their reproductive success is typically limited by how many ova they can access (i.e. how many mates they can secure) and fertilize (Bateman, 1948). Therefore, male crickets invest heavily in reproduction before mating in the form of energetically expensive acoustic sexual displays to attract females. This calling behaviour is associated with a fourfold increase in metabolic rate (Kavanagh, 1987). Similarly, male cockroaches invest in producing sex pheromone profiles that help them outcompete their rivals, i.e. secure dominance, and increase their attractiveness (Moore et al., 1997, 2003). Thus, male food intake may already be high prior to mating to allow investment in these sexually selected traits. The lack of an increase in total macronutrient intake in mated males compared with females indicates that any additional reproductive costs triggered by mating, e.g. replenishing stored sperm, are modest compared with the costs of increasing egg production or egg maturation in females. This result is consistent with the findings of previous studies on *D. melanogaster* showing that males did not consistently adjust their total macronutrient intake following mating (Sydney et al., 2024), while females did (Camus et al., 2018). Similarly, Treidel et al. (2021) showed that the high costs of synthesizing ovaries elevated the demands for energy and protein in female *Gryllus lineaticeps*, whereas males did not face similar costs driven by the biosynthetic costs of reproduction.

When compared with the total intake of macronutrients, neither sex shifted the macronutrient ratio of their RIP after mating. This phenomenon could be due to the following reasons. (1) Individuals are not foraging optimally, so intake does not reflect individual nutritional needs. (2) Intake strategies reflect dietary requirements, but they are constrained and inflexible. (3) Neither sex improves their reproductive output by altering their macronutrient intake. (4) Any benefits of switching with regard to elevated reproductive effort are offset by reductions in the expression of other fitness traits. Therefore, individuals cannot (1 and 2), need not (3) or should not (4) switch their macronutrient ratios following mating.

The first explanation, that is, individuals are not regulating their intake towards an optimal ratio of macronutrients that improves their fitness, seems unlikely. In cockroaches, individuals clearly regulate their intake, and doing so improves their fitness. This is evident because, first the RIPs observed in this study are consistent with those observed in previous works (Fig. 3). South et al. (2011) found that male cockroaches self-select a 1_P:3.2_C ratio; Bunning et al. (2015) found that males consume a 1_P:4.95_C ratio, whereas we identify an intake target of 1_P:4.21_C in virgins (Fig. 3). This consistency in studies conducted across more than a decade and using different diet choice pairs demonstrates that individuals are actively and consistently regulating their nutrition. Second, Bunning et al. (2016) found that when individual cockroaches were given a choice of diets, they had greater fitness than when they were constrained to eat a single diet, irrespective of the composition of that diet. That is, the freedom to regulate nutrient intake elevated individual fitness.

In crickets, we lack data demonstrating that being able to regulate individual intake improves fitness but nutrient landscapes, which map the relationship between macronutrient intake and fitness, show clear peaks in reproductive success associated with protein and carbohydrate intake (Hawkes et al., 2022; Rapkin et al., 2018; Rapkin, Jensen, et al., 2017). This pattern shows selection; individuals whose nutrient regulation strategies fall in a trough, i.e. low point, on these landscapes will be under selection to feed towards the peak. In addition, in both cricket species, quantitative genetic analyses have shown that protein and carbohydrate regulation are heritable (Hawkes et al., 2022; Rapkin, Archer, et al., 2017). Heritability coupled with selection indicates that cricket nutrient regulation could evolve, thereby making it hard to imagine how nutrient regulation strategies do not confer even modest fitness benefits.

Some previous studies support the second explanation, that is that nutrient regulation strategies are constrained. In *T. commodus* and *G. sigillatus*, the genetic correlations between protein and carbohydrate intake indicate that these heritable traits cannot evolve independent of each another (Hawkes et al., 2022; Rapkin, Archer, et al., 2017). Such correlations could constrain each trait from reaching its specific optimum and cause misalignment between optimal foraging decisions, i.e. intake targets, and realized foraging decisions, i.e. RIPs. Intralocus sexual conflict may provide a

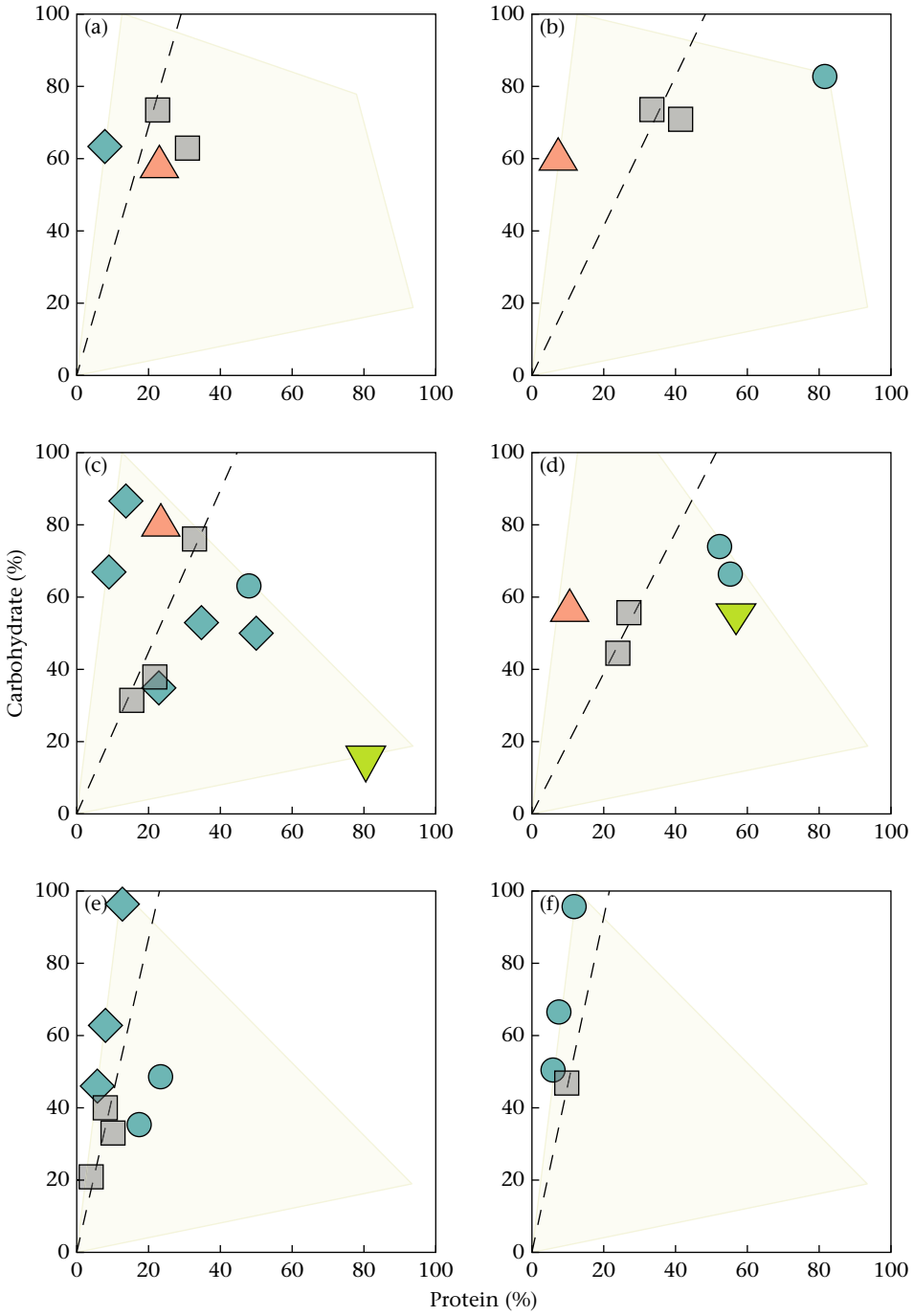

Figure 3. Schematic demonstrating approximate nutritional peak locations in (a, b) *T. commodus*, (c, d) *G. sigillatus* and (e, f) *N. cinerea* males (a, c, e) and females (b, d, f). Beige polygons show the shape of a published nutritional landscape for each species. Peaks have been scaled to a percentage to account for deviation between studies in, for example, how landscapes are mapped (in relation to lifetime/daily intake) and mean consumption between studies. Encapsulation (an aspect of immunity) is shown as a yellow/green inverted triangle, and lifespan is shown as an upright red triangle. Regulated intake points are shown as grey squares apart from the intake estimates from this study, which are instead shown as a line. This is because we did not create a landscape to scale regulated intake points against. These lines show virgin data for each sex and species. Reproductive traits are shown in blue with measures of offspring production/traits that promote fertilization success, which are shown as circles (e.g. sperm counts) and sexual display traits, which are shown as diamonds (e.g. pheromones and acoustic display). Blue diamonds represent the traits that promote success in precopulatory sexual selection, whereas blue circles represent the traits demonstrating realised reproductive success (e.g. offspring production/counts) or the traits that promote success in postcopulatory sexual selection. Where studies report daily and lifetime measures of reproduction, daily values are shown here. The references from which these estimates derive are cited within the main manuscript and in Supplementary Text S2.

second constraint on nutrient regulation. Shared genomic architecture coupled with sex-specific optima can set the stage for intralocus sexual conflict (Hosken et al., 2019), where alleles expressed in one sex are pulled towards the optimal trait value for that sex, and then those same alleles expressed in the other sex are dragged in a different direction (Rice & Chippindale, 2001). This conflict prevents one or both sexes from reaching their optimal trait values. If there is conflict over genes governing nutrient regulation,

then the foraging decisions of females may be influenced by the nutritional needs of males and vice versa. Data on whether sexual conflict constrains sex-specific nutrient intake in cockroaches are lacking. However, evidence of sexual conflict over nutrient regulation in decorated (Hawkes et al., 2022) but not field crickets (Rapkin, Archer, et al., 2017) has been found. Collectively, genetic correlations within or across the sexes may cause some deviation between what crickets should eat and what they actually eat.

The third explanation, that is, switching nutrient intake does not increase reproductive success, may apply to males. In ensuring reproductive success, males must outcompete any rival males, attract mates and then transfer large numbers of sperm and any seminal fluids that promote fertilization success. Each of these different traits may have distinct dietary optima. This is certainly true in *G. sigillatus*, where we have the most complete understanding of dietary impacts on male reproduction. In this species, calling to attract females is maximized on a high-carbohydrate diet (Rapkin et al., 2018). In addition, mating success and the production of attractive pheromone profiles are all maximized on a P:C ratio of 1_P:1.5 $_C$ (Rapkin, Jensen, et al., 2017), while the size of the nuptial gift, and, in turn, sperm transfer, is greatest on a 1_P:1.3_C ratio (Rapkin et al., 2016; Fig. 3). Thus, the 1_P:2.22_C ratio that virgin male *G. sigillatus* select in our experiment may reflect a compromise between eating sufficient carbohydrate to fuel acoustic signals and enough protein to produce high-quality nuptial gifts and increase fertilization success. Similar patterns may explain the 1_P:3.38_C ratio that virgin *T. commodus* males self-select, assuming that producing sperm in this species also requires consuming moderate-to-high amounts of protein. Male cockroaches may also be feeding to navigate a trade-off between different reproductive traits with competing nutritional needs. In this species, sperm production is greatest in males that consume a 1_P:2_C ratio (Bunning et al., 2015), whereas attractiveness to females, via sex pheromone production, is greatest in individuals that consume more carbohydrate (~1_P:8_C) (South et al., 2011). The nutrient ratio that males select (1_P:4.21_C) falls between these divergent targets. Testing the idea that males should not shift their intake to improve their reproductive investment requires capturing how diet affects all aspects of male reproductive success in these species by measuring offspring production against a backdrop of female choice and male–male competition. This is not easy to achieve, but it offers a robust estimate of male reproductive costs.

Female crickets might not need to adjust their food intake to improve their reproduction. Egg production peaks at a 1_P:1.37_C nutrient ratio for female *G. sigillatus* (Hawkes et al., 2022) and at 1_p:1_c for *T. commodus* (Rapkin, Archer et al., 2017); these ratios are similar to those self-selected by females in our study (i.e. *G. sigillatus* 1_P:1.95_C; *T. commodus* 1_P:2.07_C). Thus, any fitness benefits of switching their nutrient ratios after mating would be modest. However, in female *N. cinerea*, the nutrient ratio that individuals self-select does not maximize reproduction. Fecundity is greatest in females that consume a P:C ratio of approximately 1_P:8_C (Archer et al., 2022; Bunning et al., 2016), but females chose a macronutrient ratio of 1_P:4.80_C (Bunning et al., 2016). In this species, females would clearly increase their egg laying by eating more carbohydrate and less protein. This raises the obvious question of why females do not actively regulate towards a higher intake of carbohydrate when given a diet choice.

The benefits of switching nutrient regulation strategies to elevate reproductive effort may be offset by reductions in the expression of other fitness-related traits, e.g. lifespan and immunity. Many traits typically enhance fitness, such as growing quickly into large adults, resisting infection and producing large numbers of high-quality offspring. Each of these traits may have distinct and nonoverlapping dietary optima; this means that dietary trade-offs may connect fitness-related traits like a spider's web and consumers must weigh their intake choices to balance their investment in each of these traits. Without a more complete understanding of cockroach nutritional needs, we cannot identify which traits may be important in influencing foraging decisions. However, in other cockroach species, high-protein intake reduces lifespan and only has a modest influence on immune responses (Sieksmeyer et al., 2022). Therefore, these traits seem unlikely to explain why *N. cinerea* under consume carbohydrate.

Although the effects of mating on nutrient intake were remarkably consistent, the direction and magnitude of sex differences in the RIPs differed between species. In the two cricket species, females regulated their intake of macronutrients towards more protein than males, but the magnitude of these effects was greater in *T. commodus* than in *G. sigillatus*. This result was driven by male *G. silligatus* choosing to consume relatively more protein than *T. commodus*. This pattern likely reflects that male *G. silligatus*, but not *T. commodus*, produce a gelatinous spermatophylax that the female feeds on during mating (Sakaluk et al., 2019). Larger and amino acid–rich gifts extend the attachment time of the ampulla, which increases sperm transfer and paternity share (Sakaluk et al., 2019). Moreover, the size, free amino acid composition and ampulla attachment time are all maximized on a high intake of macronutrients with a P:C ratio of 1_P:1.3_C (Rapkin et al., 2016). Consequently, it is possible that male *T. commodus* are regulating more towards investment in calling that promotes success in precopulatory sexual selection, whereas male *G. sigillatus* are regulating to improve spermatophylax production and promote success in postcopulatory sexual selection. However, confirming whether this is indeed the case needs phylogenetically controlled analyses of a broader range of species. In *N. cinerea*, the sex difference in the RIP was slight. Compared with the cricket species we examined, females consumed more carbohydrate than males. This result is probably because investing heavily in producing sperm requires more protein than investing in egg production in this species (Bunning et al., 2015, 2016). The fact that females do not need more protein to maximize egg production is surprising though, and contrasts with findings in other insect species (Fanson et al., 2009; Harrison et al., 2014; Lee et al., 2008). This pattern may reflect that most cockroaches, including *N. cinerea*, host endosymbiotic bacteria, *Blattabacterium*, which recycle nitrogen from stored waste and provision hosts with amino acids (Kambhampati et al., 2013; Patiño-Navarrete et al., 2014). As cockroaches in our experiments consumed high-protein rat chow during development, this may provide a ready store of protein during juvenile stages that can be utilized as adults, reducing the protein needs of both sexes. If these endosymbionts are more abundant or active in females than in males, as has been shown in other insect species (Li et al., 2022), this could explain why cockroach RIPs are more carbohydrate-biased in females than in males. Alternatively, this pattern could be explained if female cockroaches can allocate some protein resources to ova production as juvenile so that some of the protein requirements of reproduction have been paid prior to adult emergence. More work is needed to test these ideas.

Finally, the 95% CRs around the median RIPs for males and females were calculated in each mating status treatment. No consistent differences in these estimates were found between virgin and mated individuals. The 95% CR was higher for mated than for virgin crickets of each sex for *T. commodus* but lower for mated than for virgin crickets of each sex for *N. cinerea*. For *G. sigillatus*, the 95% CR was higher for virgin than mated males but lower for virgin than mated females. However, more consistent patterns were observed between the two sexes for each species. Except for virgin *T. commodus*, the 95% CR was consistently higher in males than in females, irrespective of mating status. This result

could reflect that males are striving to feed towards the same intake target, but they are less good at reaching it, or that males are not all aiming towards the same nutritional target. In theory, males may make more mistakes in nutrient regulation if the neurological, physiological or behavioural tools used to assess macronutrient concentration in the diet are less sensitive or precise in males than in females. Although a direct comparison of the sensitivity and precision of these mechanisms between the two sexes is lacking, there is some indirect support for this argument. A recent study showed a dominant pattern of female-biased gene expression for nutrient-sensing pathways in *D. melanogaster* (Bennett-Keki et al., 2023). Furthermore, meta-analysis has shown that female insects are more sensitive to nutritional stress than male insects, when these stressful nutritional conditions are experienced during larval development (Teder & Kaasik, 2023). Therefore, the costs of getting nutrient regulation wrong are greater in females than in males, potentially underpinning stronger selection on female nutrient regulation mechanisms. Alternatively, this difference in 95% CRs could reflect the greater variation in male than in female nutritional targets. In some species, males can adopt alternative mating strategies to secure reproductive success, for example fighting versus sneaking (Andersson, 1994). Males in our focal species may do this too; for example, crickets could invest more, or less, in pheromone production versus acoustic display. In this case, given that dietary optima for different male reproductive traits diverge (Fig. 3), greater variation in 95% CRs could indicate that males may not be feeding towards the same nutritional target at all, while females are all feeding towards a diet that maximizes egg production. Comparing nutrient regulation in species with different male morphs or in different social contexts, e.g. where sexual selection intensity varies, may shed light on these possibilities.

Conclusions

Mating increases female macronutrient intake in all three insect species, but it does not alter male intake or the P:C ratio of the RIP for either sex in any of the species we examined. Although studying three species does not enable us to make robust comparisons about the mechanism by which phylogeny and mating ecology influence nutrient regulation strategies, it provides insights into how conserved these patterns are given species-specific variation in mating strategies. However, the variation between the species that we observed indicates how selection and physiology might shape differences in nutrient regulation strategies and highlights the potential application of large-scale comparative analyses to elucidate these processes. Interspecific variation aside, nutrient regulation strategies seem to be unresponsive to mating activity, and while increasing consumption after mating has fitness benefits for females, the overall benefits of fine-tuning macronutrient intake after mating appears to be much lower in males.

Author Contributions

C. Ruth Archer: Writing – original draft, Visualization, Formal analysis. **Matthew R. Carey:** Writing – review & editing, Investigation. **Charles E. Grant:** Investigation. **Clarissa House:** Writing – review & editing, Investigation. **Amy Molotoks:** Writing – review & editing, Investigation. **Enrique del Castillo:** Writing – review & editing, Methodology, Formal analysis. **Zeya Wagner:** Writing – review & editing, Investigation. **John Hunt:** Writing – original draft, Visualization, Supervision, Methodology, Investigation, Formal analysis, Conceptualization.

Data Availability

All data are available at Figshare: https://doi.org/10.6084/m9.figshare.29654879.v1 (Archer et al., 2025).

Declaration of Interest

The authors declare no conflicts of interest.

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Supplementary Material

Supplementary material associated with this article is available at https://doi.org/10.1016/j.anbehav.2025.123423.

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