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Phosphorus availability influences cricket mate attraction displays

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Adopting a stoichiometric perspective (e.g. the balance of carbon, nitrogen and phosphorus in organisms and their resources) has enhanced our understanding of ecological phenomena at a variety of hierarchical levels of organization. Unfortunately, little is presently known about how stoichiometry directly influences animal behaviour. Here we use a stoichiometric perspective to investigate how phosphorus availability in the environment influences mate attraction behaviour in insects. Using adult male European house crickets (*Acheta domesticus*), we manipulated the availability of dietary phosphorus and we quantified how survival, propensity to signal acoustically or not ('signallers' versus nonsignalling 'silent' males) and lifetime mate attraction signalling were affected. Dietary phosphorus availability did not influence the proportion of signallers versus silent males. However, signallers fed a diet rich in phosphorus had significantly higher signalling efforts than those that consumed a phosphorus-poor diet. Interestingly, signallers also lived longer than silent males, but neither signaller nor silent male survival was influenced by diet. Our findings suggest that the availability of dietary phosphorus has the potential to impact mating system evolution.

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Nutritional deficiencies are a common phenomenon in nature, and organisms are often faced with food that is not optimal for their needs. Suboptimal diets have been shown to strongly influence organismal fitness and its associated traits. Variation in fitness-conferring traits has, for example, been linked to the ability to locate, consume and maintain sufficient amounts of dietary protein. Dietary protein influences growth rate (Raubenheimer & Simpson 2003) and compensatory feeding (Cruz-Rivera & Hay 2000; Behmer et al. 2003; Mayntz et al. 2005). Furthermore, sexually selected traits appear to respond directly to protein deficiencies. For example, Hunt et al. (2004) revealed that male crickets reared on diets rich in protein showed significantly greater nymphal survival and faster development; these crickets were also heavier and larger at eclosion, had higher acoustic signalling efforts early in life and signalled more often throughout their lives than the males that were reared on medium- and low-protein diets (Hunt et al. 2004). Together, these results suggest that nutrition can strongly influence fitness and its associated traits.

Organismal fitness has the potential to also be linked to the availability of dietary nitrogen and phosphorus (Bertram et al. 2006). All organisms require both nitrogen and phosphorus to live

(Sterner & Elser 2002). Nitrogen is required to produce nucleic acids, proteins and hormones, and is vital for insect growth (Kainulainen et al. 1996; Rossi et al. 1996; Kerlake et al. 1998), reproduction (Van Emden 1966; Rossi & Strong 1991; Bentz & Townsend 2001), and survival (Salim & Saxena 1991; Rossi et al. 1996; Ayres et al. 2000; De Bruyn et al. 2002; Huberty & Denno 2006). Likewise, phosphorus is required to produce nucleic acids and proteins (as well as phospholipids and ATP), and is also vital for insect growth (Janssen 1994; Busch & Phelan 1999; Perkins et al. 2004), reproduction (Skinner & Cohen 1994) and survival (Clancy & King 1993; Huberty & Denno 2006). Both nitrogen and phosphorus must be obtained in sufficient quantities from food because they cannot be synthesized. Unfortunately, nitrogen and phosphorus are both extremely limited in the environment. Plants, for example, typically have substantially lower concentrations of nitrogen and phosphorus (10–20 times lower) than the insects that consume them (Mattson 1980; Elser et al. 2000). This stoichiometric mismatch between consumers and their food suggests that the availability of nitrogen and phosphorus could critically influence insect fitness (Sterner & Elser 2002; Jeyansingh & Weider 2007). Therefore, the time is ripe to examine how diet stoichiometry affects insect fitness (Jeyansingh & Weider 2007).

To date, there has been only one study that has examined the relationship between stoichiometry and behaviour. Bertram et al. (2006) revealed that there is a correlation between acoustic mate attraction signalling and body phosphorus content in crickets. Crickets produce acoustic mate attraction displays (signals) by

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rubbing their forewings together (Alexander 1961). Each closing stroke of the forewings produces a pulse of sound. Crickets concatenate these pulses together into chirps or trills (species dependent). Acoustic signals function to attract conspecific female crickets and repel conspecific male crickets (Alexander 1961). Male mating success is dependent on the quality and quantity of the acoustic signals (Alexander 1961; Hedrick 1986; Zuk 1987; Cade & Cade 1992; Wagner et al. 1995; Gray 1997; Nelson & Nolen 1997; Hedrick & Weber 1998; Gray & Cade 1999a, b; Wiegmann 1999). Bertram et al. (2006) revealed that male Texas field crickets, *Gryllus texensis*, that showed 'signaller' behaviour (produced acoustic mate attraction signals) had significantly more phosphorus in their bodies than males that showed nonsignalling 'silent' behaviour. Bertram et al.'s (2006) study also revealed that the acoustic displays of the signallers were significantly and positively correlated with the total amount of phosphorus in each cricket's body: males that signalled more on average throughout a 24-h day had significantly higher total body phosphorus content than males that rarely signalled. Bertram et al. (2006) found no relationship between signalling time and total body nitrogen content. Overall, these results suggest that cricket signalling effort may be influenced by the availability of dietary phosphorus (Bertram et al. 2006).

Although Bertram et al.'s (2006) findings are intriguing, they were necessarily correlative in nature; cause and effect have yet to be determined. Our goal here was, therefore, to quantify whether dietary phosphorus availability directly influences cricket signalling effort. We manipulated phosphorus availability in diets, fed these diets to commercially supplied adult male European house crickets (*Acheta domesticus*), and measured the response by quantifying male cricket acoustic mate attraction signalling throughout their adult lives. Specifically, we examined how propensity to produce acoustic signals (signallers) or not (silent) was influenced by dietary phosphorus availability. For signallers, we also examined how dietary phosphorus availability influenced age at signalling onset, number of days spent signalling, average nightly time spent signalling, average number of signalling bouts per day, average signalling bout duration, amount of time that males spent signalling throughout their lives, age at signalling termination and overall lifetime signalling effort. Additionally, we examined how phosphorus availability influenced adult male survival (for both signallers and silent males) and the relationship between survival and signalling effort (for signallers).

METHODS

European house crickets (*A. domesticus*) were purchased from Port Credit Pet Centre in Port Credit, Ontario as fourth- and fifth-instar juveniles (i.e. one or two moults from adulthood). They were housed together and reared under standardized conditions (temperature: 26 ± 4 °C, 12:12 h light:dark cycle, uncontrolled humidity) in 36-litre plastic containers (36 × 28 × 23 cm) until they moulted into adulthood. All juveniles were provided with unlimited food (Harlan Teklad Rodent diet no. 8604), water and shelter (cardboard egg cartons). Food and water were replenished twice weekly, and containers were cleaned as necessary. Crickets were examined daily to determine whether any had undergone final moult (become adults).

On the first day of adulthood, each male was housed individually in a 500 ml plastic-coated paper bowl (7 × 11 cm, height × diameter) with a shelter, and provided with unlimited access to water. Each newly moulted adult male was then randomly assigned to a high-, medium- or low-phosphorus diet treatment. Each male was provided with an unlimited amount of its diet from the day that it reached adulthood until the day that it died a natural death. Each male also had its long-distance acoustic mate attraction signals monitored electronically throughout its adult life.

Dietary Treatments

We fed adult male *A. domesticus* one of three custom powdered diets that ranged from 0.2 to 1.0% phosphorus. We used this range because it mimics the natural range of field cricket food. Crickets are omnivores, feeding on plants, fungi and insects (including conspecifics); these foods tend to range from 0.2% phosphorus (mean phosphorus content of terrestrial plant leaf matter) to ~0.8% phosphorus (mean phosphorus content of terrestrial insects; Sterner & Elser 2002).

The three custom research diets were designed, manufactured and purchased from Harlan Teklad (Harlan Teklad Inc, P.O. Box 44220, Madison, WI, U.S.A.). The TD.07248–TD.07250 names listed below are Harlan Teklad's identifiers for these custom research diets. The 'high' diet (TD.07250) contained 1.0% phosphorus, the 'medium' diet (TD.07249) contained 0.6% phosphorus, and the 'low' diet (TD.07248) contained 0.2% phosphorus. Most of the dietary phosphorus was delivered using calcium phosphate (high = 35.53 g/kg; medium = 17.98 g/kg; and low = 0.44 g/kg), however, 1.9 g/kg came from the casein used as a protein source. Because we used calcium phosphate to deliver the phosphorus, we balanced the calcium levels across the diets with calcium carbonate (high = 0.0 g/kg; medium = 12.75 g/kg; low = 25.75 g/kg). Each diet also contained 236.6 g/kg of protein (272 g/kg casein), fat (42.7 g/kg; 2.7 g/kg from casein and 40 g/kg from soybean oil), L-cystine (4 g/kg), corn starch (150 g/kg), maltodextrin (50 g/kg), sucrose (377.362 g/kg), cellulose (50 g/kg), minerals (no calcium or phosphorus included in this mix; 13.4 g/kg), vitamins (10 g/kg), choline bitartrate (2.5 g/kg) and antioxidants (8.0 mg/kg).

Acoustic Monitoring

An electronic acoustic recorder (EAR; Bertram & Johnson 1998; Bertram et al. 2004) was used to monitor each male's long-distance acoustic mate attraction signals. A microphone was hung within each cricket's container, approximately 5 cm above the cricket. The acoustic recording system would select a microphone, record the container's noise level (amplitude), amplify the signal, convert it from AC to DC, filter it, and save it to disk. Another container's microphone would then be selected. Only one microphone was turned on at a time, and each microphone was sampled eight times per second. The resultant data were summarized into a second-by-second description of all individuals' long-distance mate attraction signalling behaviour throughout the course of their lives.

Each male's mating signals were monitored for 24 h/day throughout their adult lives (day 1 post final moult until death). The EARs were sometimes turned off for a few minutes around noon so that individuals could be added or removed. On these days, cricket signalling was monitored for 23 h instead of 24 h; it is rare for crickets to signal at this time, so it is unlikely that we missed many signals throughout the entire lives of these crickets. The EAR allowed us to monitor the acoustic signalling behaviour of as many as 128 male crickets simultaneously (Bertram & Johnson 1998; Bertram et al. 2004).

Using a program we wrote for MatLab, we extracted from these data whether or not a male signalled acoustically, then classified him as a signaller or a silent male. Signallers produced acoustic signals at least once during the course of their lives; silent males never signalled acoustically. For signallers, we also extracted the age at which they first started signalling, the proportion of nights they signalled out of the total number of nights they were alive, their average daily total signalling time over all the days they were alive (average number of minutes signalling per day from 0900 hours to 0900 hours the next day), their average daily total signalling time only over the days that they signalled acoustically, their lifetime signalling time (the total number of hours they

signalled through their entire lives), their average daily bout duration (the number of minutes signalling continuously without taking at least a 1 min break), their average daily bout rate (the average number of signalling bouts per day), and the age at which they last signalled. Our MatLab code, along with detailed designs and building specifications of our EARs, can be found in Bertram et al. (2004).

Because crickets were likely to hear their neighbours, we attempted to minimize neighbour effects by inserting 7 cm of acoustic foam between the tops, bottoms and sides of all cricket containers. This acoustic foam reduced the noise levels, making the acoustic signals of nearest neighbours appear more distant (approximately 1–2 m away), and ensured that each individual's microphone only picked up the focal individual's signals, not the nearest neighbour's signals (Bertram et al. 2004). Individuals within each treatment were randomly distributed across the EARs both spatially and temporally to ensure there were no unintended clustering effects.

Statistical Analyses

Statistical analyses were conducted using JMP software (SAS Institute Inc., 100 SAS Campus Drive, Cary, U.S.A.). The Shapiro–Wilk goodness-of-fit test was used to ensure data and their errors did not differ significantly from normal distributions. We approximated normal distributions using an arcsine transformation on proportion data and log transformation on all other non-normal data. We used chi-square analysis to determine whether diet influenced the proportion of males showing signalling versus silent behaviour. We used ANOVA to quantify whether diet influenced all aspects of signalling behaviour (age at signalling onset, proportion of nights signalled, average nightly signalling time, average nightly signalling time using only nights that they signalled, average bout duration, average bout rate, age at signalling termination and total time that individuals spent signalling throughout their lives). We also used a principal component analysis to quantify overall signalling effort because signalling effort combines average nightly signalling time, bout duration and bout rate. The first principal component explained 72% of the overall signalling variation and loaded similarly on all parameters (log mean signalling time = 0.666; log mean bout duration = 0.573; mean bout rate = 0.477). We used ANOVA to quantify whether signalling effort (PC1) was influenced by diet. ANOVA was also used to determine whether body weight at death was diet dependent. When ANOVA revealed a significant difference between diet treatments, we used a Tukey–Kramer HSD test to quantify which diets were statistically different from each other. Because of the large number of ANOVAs ($N = 12$) used, we reduced the significance level to $P < 0.0161$ using the 'false discovery rate' method.

We used regression to determine whether measures of signalling behaviour were influenced by either body weight or length of life. Because of the large number of regressions ($N = 15$) used, we reduced the significance level to $P < 0.0151$ using the false discovery rate method. We used survival analyses to determine whether survival was influenced by either dietary phosphorus availability or behaviour (signaller or silent).

RESULTS

Many males were silent, never producing acoustic signals (Table 1). The proportion of signallers versus silent males was not influenced by dietary phosphorus availability. Phosphorus availability did, however, strongly influence the overall amount of effort that signallers invested in acoustic mate attraction. Using the first principal component that combined mean daily signalling time, mean daily bout rate and mean daily bout duration, we found that males fed a phosphorus-rich diet (1.0% P) had significantly higher signalling efforts than males fed

a medium (0.6% P) or poor (0.2% P) diet (ANOVA: $F_{2,104} = 6.33$, $P = 0.0025$; $R^2_{\text{adj}} = 0.09$; Fig. 1). This multivariate finding was strongly supported by the univariate statistics (Table 1). Males that consumed a rich phosphorus diet had significantly higher average nightly signalling times than males that consumed a diet low in phosphorus, regardless of whether we analysed all the data or only the subset of days that they signalled. There was also a nonsignificant tendency for males that consumed a rich phosphorus diet to signal for longer bout durations without taking a break and to produce more signalling bouts through the course of an average 24-h day (Table 1). Although diet did not affect the age of signalling onset or the age of signalling cessation, males that consumed the phosphorus-rich diet signalled on a significantly greater proportion of days than males that consumed the low-phosphorus diet. Furthermore, males that consumed the rich phosphorus diet signalled significantly more often throughout their entire lives (lifetime time spent signalling). These results strongly support the hypothesis that dietary phosphorus availability strongly influences acoustic mate signalling behaviour.

On average, signallers lived significantly longer than silent males (62.68 ± 4.35 days versus 16.74 ± 2.89 days; survival analysis: log-rank chi-square = 39.7201, $P < 0.0001$). This difference in survival could be because males that died prior to the average signalling age (11 days) were classified as silent. Therefore, we reran this analysis after excluding all males that lived fewer than 11 days. Signallers were still found to live longer than silent males, although the survival difference was not nearly as profound (62.68 ± 4.35 days versus 55.45 ± 3.74 days; survival analysis: log-rank chi-square = 4.1731, $P = 0.0411$). Dietary phosphorus availability did not influence the survival of either signallers or silent males (Table 1).

Signallers that lived longer put more effort into signalling (PC1) than males that lived for shorter lengths of time ($t_{105} = 6.75$, $P < 0.0002$, $R^2_{\text{adj}} = 0.0700$). Univariate statistical analyses supported this finding as males that lived longer spent more time signalling each day ($t_{105} = 2.93$, $P = 0.0042$, $R^2_{\text{adj}} = 0.0668$) and produced bouts of longer durations ($t_{105} = 3.15$, $P = 0.0021$, $R^2_{\text{adj}} = 0.0775$), although life span was not influenced by bout rate ($t_{105} = 1.20$, $P = 0.2316$). Males that lived longer also started signalling later in life ($t_{105} = 4.46$, $P < 0.0001$, $R^2_{\text{adj}} = 0.1514$), stopped signalling later in life ($t_{105} = 27.62$, $P < 0.0001$, $R^2_{\text{adj}} = 0.8779$) and spent more total time signalling throughout their lives ($t_{105} = 6.75$, $P < 0.0002$, $R^2_{\text{adj}} = 0.2962$).

Dry mass of male crickets, which was measured following their natural death, was not influenced by diet (Table 1). Signallers tended to weigh more than silent males, but this difference was not significant: on average, signallers weighed 65.70 ± 2.60 mg whereas silent males weighed 58.78 ± 1.84 mg (ANOVA: $F_{1, 100} = 4.72$, $P = 0.0322$, $R^2_{\text{adj}} = 0.0355$). There was no relationship between any signalling parameter and dry mass. Likewise, survival was not influenced by dry mass ($t_{100} = 0.73$, $P = 0.4690$).

DISCUSSION

Our findings reveal that dietary phosphorus availability influences the amount of effort that *Acheta domesticus* signallers spend on acoustic mate attraction. Male crickets that consumed a diet rich in phosphorus had higher overall signalling efforts (PC1 incorporating average daily signalling time, bout duration and bout rate) than males that were fed medium- or low-phosphorus diets. Males that had more access to phosphorus also signalled more throughout the day and signalled on proportionately more days. Additionally, there was a tendency for these males to signal for longer bout durations and produce more bouts per day than males that were fed a diet low in phosphorus. To our knowledge, this is the first experimental study to show that dietary phosphorus availability influences insect acoustic mate signalling behaviours.

Table 1
Body mass, longevity and acoustic signalling parameter descriptive statistics for house crickets, subdivided by behavioural type (signaller and silent) and dietary treatment (low-phosphorus = 0.2% P; medium phosphorus = 0.6% P; high phosphorus = 1.0% P)

Parameter	Low (0.2% P)	Medium (0.6% P)	High (1.0% P)	Test statistic	P	df
All: number of males	90	91	93			
All: dry mass (mg)	60.48±2.91 (26–103)	60.33±2.33 (31–86)	62.50±2.75 (41–121)	F=0.2037	0.8160	2, 99
Silent: number of males	48	59	60			
Signaller: number of males	42	32	33			
Proportion of silent males	0.53	0.65	0.65	$\chi^2=2.6432$	0.2667	2, 271
All: adult survival (days)	26.31±3.23 (1–119)	23.70±2.81 (1–107)	28.32±3.10 (1–110)	$\chi^2=1.4892$	0.4749	2, 271
Silent: adult survival (days)	12.23±5.57 (1–108)	16.83±4.66 (1–107)	20.27±5.00 (1–98)	$\chi^2=2.0484$	0.3591	2, 164
Signaller: adult survival (days)	45.86±4.78 (7–119)	40.78±5.01 (5–101)	45.91±5.38 (7–110)	$\chi^2=3.1473$	0.2073	2, 104
Signaller: age at signalling onset (days)	11.60±1.00 (2–30)	11.41±1.52 (3–37)	9.67±1.12 (3–36)	F=0.7594	0.4705	2, 104
Signaller: number of days signalling (days)	22.76±3.56 (1–70)	18.09±2.74 (1–63)	30.06±4.25 (1–90)	F=2.7529	0.0684†	2, 104
Signaller: proportion of days signalling	0.45±0.04 (0–0.9)	0.45±0.04 (0–0.9)	0.62±0.04 (0–0.9)	F=4.9153	0.0091*	2, 104
Signaller: mean signalling time overall days (min)	19.34±4.31 (1–111)	23.25±5.98 (1–148)	36.55±5.56 (1–123)	F=5.8886	0.0038*	2, 104
Signaller: mean signalling time over signalling days (min)	31.40±5.47 (1–122)	43.74±10.47 (1–268)	54.70±6.92 (1–153)	F=5.2770	0.0066*	2, 104
Signaller: lifetime signalling (h)	18.53±5.06 (0–142)	18.53±6.12 (0–173)	28.60±5.35 (0–147)	F=4.8013	0.0101*	2, 104
Signaller: mean bout rate (signalling bouts/day)	23.73±1.86 (3–51)	27.36±2.17 (6–53)	30.29±2.36 (7–66)	F=2.5400	0.0838†	2, 104
Signaller: mean bout duration (min)	1.55±0.28 (0–8)	1.40±0.26 (0–6)	2.39±0.33 (0–8)	F=3.5873	0.0311†	2, 104
Signaller: age stopped signalling (days)	39.02±4.05 (6–97)	33.72±4.80 (12–101)	43.81±5.56 (7–110)	F=1.1849	0.3099	2, 104

Values are means ± SE (with ranges in parentheses). Statistical tests: ANOVA (F), survival analysis (χ^2) or chi-square analysis (χ^2). Significant outcomes are shown in bold. †P < 0.1; *P < 0.05.

It is presently unknown whether signalling effort influences mating success in *A. domesticus*. *Acheta domesticus* females prefer (1) males that are more dominant over those that are submissive (Crankshaw 1979; Nelson & Nolen 1997), (2) males that produce three-pulse chirps over those that produce two-pulse chirps (Stout et al. 1983; Stout & McGhee 1988) and (3) larger males over smaller ones (Gray 1997). While the relationship between signalling effort and mating success has never been formally examined in this species, we hypothesize that mating success is positively influenced by signalling effort because the number of females that are attracted to a given male usually depends on that male's level of advertisement. For example, in a natural population of Texas field crickets, *G. texensis*, males that signalled most often mated most often (Cade & Cade 1992). Likewise, under field conditions, female

G. campestris are more attracted to males that signal more often (Holzer et al. 2003). Together these results suggest that males that signal with high effort have higher mating success. Thus, we feel comfortable suggesting that because dietary phosphorus availability influences signalling effort, it also may influence male mating success.

What might drive our observed relationship between phosphorus and male acoustic mate signalling behaviour? Bertram et al. (2006) hypothesized that RNA drives the relationship between signalling and phosphorus. Extensive protein synthesis is required for high metabolic activity (Welle & Nair 1990; Quigg & Beardall 2003), possibly because high metabolic rates generate excess free radicals, increasing protein damage and necessitating its repair or replacement (Welle & Nair 1990; Quigg & Beardall 2003). Given that acoustic signalling is a highly energetically demanding activity (Prestwich & Walker 1981; Prestwich 1994; Hoback & Wagner 1997; Reinhold 1999; Wagner & Hoback 1999), the muscle and glandular tissue involved should have high metabolic activity, and therefore, could require high allocation to RNA. This RNA hypothesis has yet to be tested in crickets.

Another possible explanation for the relationship between dietary phosphorus availability and signalling effort is gene regulation. Phosphorus availability is thought to influence gene regulation, especially the regulation of phosphorus transporter genes (summarized in Jeyansingh & Weider 2007). Because phosphorus transporters influence phenotypic expression, their regulation could have significant fitness consequences (Jeyansingh & Weider 2007). The genetic implications of phosphorus availability could, therefore, also drive our observed relationship between phosphorus and male signalling behaviour. Jeyansingh & Weider's (2007) recent paper describes the fundamental links between genes and elements and emphasizes the role of P transporter genes in a variety of organisms and discusses their fitness consequences.

Some invertebrates compensate behaviourally for poor-phosphorus diets either by adjusting their ingestion rate and thus changing the balance of elements available to them (Plath & Boersma 2001; Raubenheimer & Simpson 2003; Frost et al. 2005; but see Perkins et al. 2004), or by increasing the variety of foods that they consume (Denno & Fagan 2003; Raubenheimer & Simpson 2003; Frost et al. 2005). Both of these compensatory behaviours require that the individuals self-assess their nutritional state as well as the nutritional state of their food (Simpson & Raubenheimer 1993; Simpson et al. 1995; Frost et al. 2005). Although it is unknown whether crickets can assess these states, even if they do

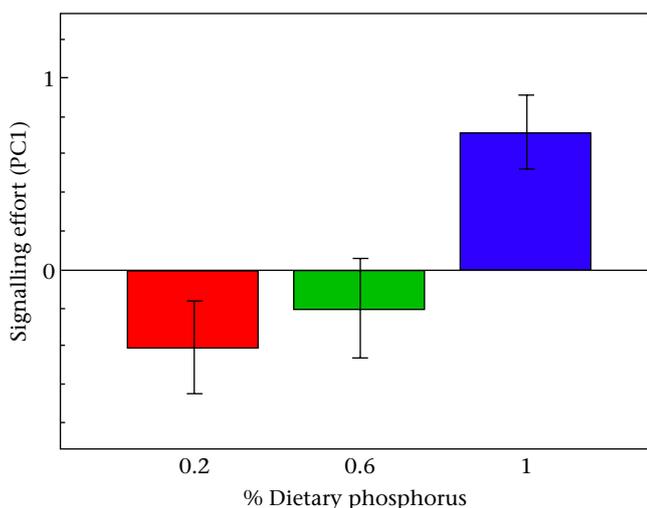


Figure 1. The influence of diet on overall signalling effort in house crickets (PC1). PC1 is the first principal component resulting from a vector space transform that reduced the multidimensional data set combining mean nightly signalling time, bout duration and bout rate to one dimension. PC1 explained 71% of the variance in the multidimensional data set. Because principal component analysis calculates the eigenvalue decomposition of a data covariance matrix following mean centering of the data for each attribute, PC1 values range from negative to positive values. Crickets with positive PC1 scores tended to have high average nightly signalling times, higher average bout rates and bouts of longer average duration. Crickets with negative PC1 scores tended to have lower average nightly signalling times, lower average bout rates and bouts of shorter average duration.

adjust their ingestion rates, their behavioural compensation is not enough to combat the effects of a poor-phosphorus diet, because crickets in our experiment were fed unlimited amounts of food and still showed behavioural and survival effects.

Several cricket species are known to become cannibalistic (Alexander & Otte 1967; Kieruzel & Chmurzynski 1987), especially when faced with other nutrient limitations (Simpson et al. 2006). Given that herbivores contain substantially more phosphorus in their bodies than do plants (Mattson 1980; Sterner & Elser 2002), cannibalism should greatly increase the availability of limited essential elements, resulting in enhanced mate signalling behaviour and possibly increased lifetime fitness.

Because we monitored average nightly signalling time throughout the natural life of *A. domesticus*, our data allowed us to examine survival effects. Dietary phosphorus availability did not influence survival. However, signallers lived longer than nonsignalling silent males. This finding leads to the hypothesis that 'silent' behaviour may be somewhat condition dependent in this species.

Life history theory suggests that a trade-off should exist between signalling and survival. While this has not been tested often in crickets, Hunt et al. (2004) recently revealed that male *Teleogryllus commodus* crickets that signal often in early adulthood die at a younger age than those that spend less time signalling. Contrary to this theory and Hunt et al.'s (2004) finding, we found that silent males did not live as long as signalling males, and that males that signalled most often lived longer than males that rarely signalled.

The European house crickets that we used in our experiment were obtained from a commercial supplier. As such, they were bred in captivity for several generations, fed ad libitum and exposed to a virtually predator-free environment, and thus were likely to have experienced different inbreeding and selection pressures than those of their wild-cricket counterparts (Gray 1997, 1999). Therefore, care must be taken when extending our results to other insect species, as colony artefacts may potentially exist.

Future research should quantify whether more natural cricket species show the same responses to dietary phosphorus availability and whether they can compensate for low-phosphorus availability by altering their foraging behaviours. In addition, it would be helpful to quantify the relationship between male signalling effort, phosphorus availability, protein synthesis and muscle RNA content. Ascertaining how signalling quality (pulse duration, interpulse interval, pulse rate, number of pulses per chirp and chirp amplitude) are influenced by dietary phosphorus availability would also be important, given that many of these quality parameters are also likely to be used by female *A. domesticus* when selecting a mate. Lastly, given the present study focused only on phosphorus availability to adults, future research should also quantify how phosphorus availability during development influences growth, maturity, reproduction, survival and overall fitness.

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