



Effects of juvenile and adult condition on long-distance call components in the Jamaican field cricket, *Gryllus assimilis*

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Complex signals may arise through either content- or efficacy-based selection. Content-based signals are thought to evolve because of the information content they provide to the receiver. Such signals may function as multiple messages, each relaying different information or types of information. For example, some signals or signal components may indicate different aspects of condition, or condition at different life stages (quality signals), while others relay information on signaller location, or function in species recognition. Or they may act as redundant signals of overall condition, or as backup signals of the same aspect of condition. Efficacy-based signals are proposed to evolve because of the way in which they influence the production, transmission, reception or processing of the signal. We manipulated juvenile and adult condition in male Jamaican field crickets, *Gryllus assimilis*, to test whether changes in components of the male's long-distance acoustic mate attraction signal were consistent with content- or efficacy-based selection. Several call components exhibited condition-dependence, and may be under content-based selection. Interpulse duration, pulse rate and chirp duration appeared to honestly signal juvenile condition, while dominant frequency appeared to signal adult condition. Thus, these signal components appeared to be acting as multiple messages of quality. Pulse number, interchirp duration and chirp rate were highly stereotyped and probably function in species recognition. Call number increased with decreasing condition and was likely under efficacy-based selection. No call components appeared to have the potential to act as redundant signals.

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Many species possess multiple sexual signals (Møller & Petrie 2002). Despite the prevalence of such signals in nature, the reason for their occurrence remains unclear (reviewed in Candolin 2003). There are several hypotheses regarding the evolution of complex signalling (reviewed in: Candolin 2003; Hebets & Papaj 2005). Some invoke content-based selection, in which signals are proposed to have evolved because of the information content that they provide to the receiver. Others are efficacy-based in that they propose that complex signals have evolved because of the way in which they influence the production, transmission, reception or processing of the signal (Hebets & Papaj 2005).

Two widely investigated, content-based hypotheses for the evolution of complex signals are the multiple messages and redundant signals hypotheses (reviewed in: Candolin 2003; Hebets & Papaj 2005). In a recent review, Hebets & Papaj (2005) expanded

the multiple message hypothesis to include three alternative hypotheses: quality, quality plus and species recognition. The quality model proposes that each signal relays information about a different aspect of signaller condition, or of condition at a different life stage (Møller & Pomiankowski 1993; Johnstone 1996; Hebets & Papaj 2005). For example, in male bowerbirds, feather ultraviolet-violet brightness and bower quality are correlated with endoparasite load and ectoparasite load, respectively (Doucet & Montgomerie 2003). Thus, females can determine the amount of each parasite type a male is carrying by assessing these two traits. The quality plus hypothesis is that one signal, or signal component, gives information on signaller quality, while another signal conveys other information, such as signaller location or territory quality (Hebets & Papaj 2005). Finally, the species recognition hypothesis proposes that one signal conveys information on signaller quality, while another signal functions in species recognition.

The redundant signals hypothesis has been described in two main ways throughout the literature. Møller & Pomiankowski (1993) proposed that redundant signals each provide independent estimates of overall condition and that each signal differs in

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the magnitude and direction of the error associated with signalling overall condition. Thus, a female should assess all signals in order to obtain the most accurate estimate of overall male condition. Alternatively, [Johnstone \(1996\)](#) proposed a ‘backup’ hypothesis in which multiple signals convey information about the same aspect of condition, rather than overall condition. For example, in male curassow, knob weight, wattle height and wattle width are all indicators of male age, a character used by females during mate selection ([Buchholz 1991](#)).

Finally, hypotheses invoking efficacy-based selection propose that complex signals have evolved because of their function in signal production, transmission, reception and/or processing (reviewed in [Hebets & Papaj 2005](#)). Traits under efficacy-based selection are thought to have evolved in response to environmental variability, or sensory constraints in the receiver (reviewed in [Hebets & Papaj 2005](#)). For example, [Maynard Smith & Harper \(2003\)](#) describe a nightingale system in which males spend the majority of the night calling in order to attract females flying overhead to mate with them. However, males can never be sure of the presence of females and must, therefore, signal as much as possible to maximize their likelihood of being heard by a passing female. In doing so, males can lose up to 5–10% of their body mass. Thus, rather than signalling effort being an index of condition, constant signalling is a cost of efficacy. [Ryan & Cummings \(2005\)](#) predict that this is the case for most examples of long-distance signalling. Thus, signals selected for efficacy should also exhibit condition-dependence but function differently in female choice. Alternatively, males in poor current condition may choose to invest even more into signalling because their reduced condition means that they are less likely to survive and reproduce long term. As such, investment in efficacy-based signals may actually increase with decreasing condition, as males attempt to compensate for decreasing future reproduction.

Here we distinguish between the various content- and efficacy-based hypotheses by manipulating male cricket condition at the juvenile and adult stages of life and observing the effects on components of the male’s sexual signal. Male field crickets signal acoustically to attract females by raising their forewings and rubbing them together, producing a pulse of sound with each

closing stroke. These pulses are concatenated into chirps ([Fig. 1](#)). Females are known to approach (e.g. [Wagner et al. 1995](#); [Gray & Cade 1999](#)) and select mates (e.g. [Cade & Cade 1992](#)) based on the acoustic properties of the male’s long-distance call. Once a female makes physical contact with a male, he switches to a short-distance courtship call (E. M. Whattam, personal observation). Long-distance and courtship calls are multicomponent signals, consisting of several call parameters. Some of these call parameters are at least partly uncorrelated and, thus, have the potential to act as separate signals ([Scheuber et al. 2003a](#)). For example, [Scheuber et al. \(2003a, b\)](#) found that in the field cricket *Gryllus campestris*, chirp rate decreases when adult condition is decreased, and carrier frequency increases (due to decreased wing size) when juvenile condition is decreased. In cricket species in general, calling behaviour tends to decrease when different aspects of condition are decreased. This is not surprising, given that calling behaviour is energetically expensive ([Hoback & Wagner 1997](#)). For example, [Hedrick \(2005\)](#) found that when adult male field crickets (*G. integer*) are fasted for 2 days, their mass decreases (indicating a decrease in condition), as does their long-distance calling bout duration (average time for which males call continuously). Moreover, [Hedrick \(2005\)](#) found that the decrease in mass is proportional to the reduction in bout duration. This suggests that bout duration is an accurate signal of current condition in this species.

Female crickets exhibit distinct preferences for many components of the male long-distance mate attraction call, most of which involve an increase in calling ([Wagner & Hoback 1999](#)). For example, female Texas field crickets, *G. texensis*, prefer males that spend the most time calling throughout the night ([Cade & Cade 1992](#)), that produce the largest number of pulses per trill ([Gray & Cade 1999](#)) and that produce short intercall intervals ([Wagner et al. 1995](#)). Similarly, female variable field crickets, *G. lineaticeps*, prefer males with high chirp rates and long chirp durations ([Wagner & Hoback 1999](#)).

Females also receive fitness benefits by mating with males that advertise condition through these call parameters; for example, female variable crickets that are mated to males that produce high chirp rates experience increased lifetime fertility, while females

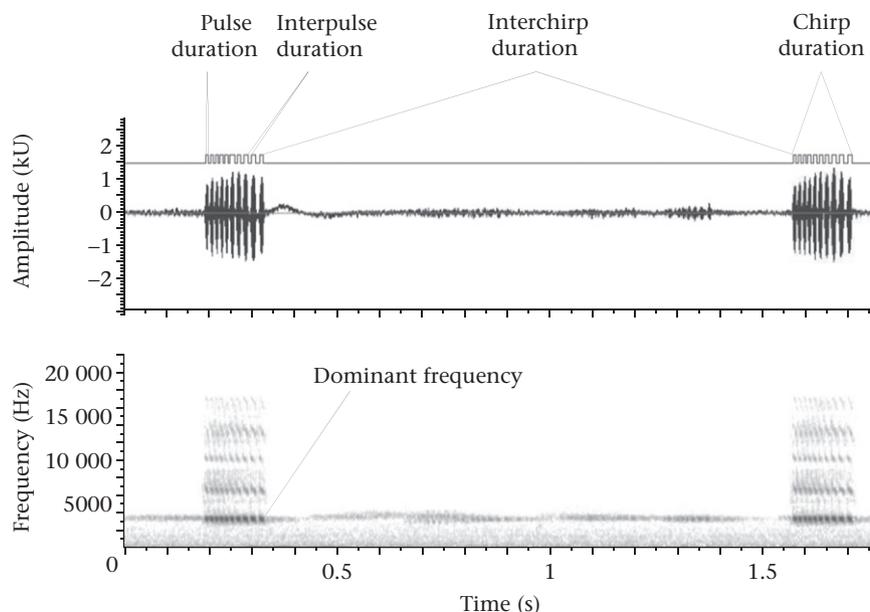


Figure 1. Several parameters of the long-distance mate attraction call of *G. assimilis*.

mated to males that produce long chirp durations experience increased longevity (Wagner & Harper 2003). Female crickets have even been shown to prioritize some male signals (and their associated benefits) over others. Wagner & Basolo (2007) found that when both chirp rate and chirp duration are varied simultaneously, females still prefer higher chirp rates, but show no preference for calls with longer chirp durations (which are usually preferred) when the chirp rate is low. Thus, females appear to prioritize chirp rate, and its associated benefit of greater lifetime fertility, over chirp duration, which is associated with increased female longevity. Similarly, Scheuber et al. (2004) found that female *G. campestris* prefer low carrier frequency and high chirp rates, but they prioritize carrier frequency (the static, long-term signal) over chirp rate (the dynamic, short-term signal). Carrier frequency, as the less variable, long-term signal, may be more indicative of overall male suitability to the environment and thus could indicate indirect genetic benefits to the female (Candolin 2003). Chirp rate, on the other hand, being more indicative of short-term fluctuations in condition may advertise direct benefits, such as higher sperm count (Andersson 1994; Candolin 2003). It is reasonable to assume that male *G. assimilis* also signal condition via the components of their long-distance call, which is similar in structure to that of other cricket species, and that females exhibit preferences for males that advertise their condition in this way because they receive benefits by mating with males that have the preferred call components.

We also examined whether call component expression was affected by an interaction between condition at one life stage and condition at the other life stage. Our study is one of the first to manipulate multiple aspects of condition within the same individuals to examine whether interactions between different aspects of condition affect sexual signal expression. Scheuber et al. (2003a, b) performed a series of studies investigating the effects of current and past condition on calling behaviour in field crickets (*G. campestris*). However, adult (current) condition was manipulated in one study group, while juvenile (past) condition was manipulated in a separate group. Thus, it was not possible to evaluate whether there was an effect of an interaction between condition at the juvenile life stage and condition at the adult life stage. However, it is likely that past condition affects current condition. For example, smaller males (i.e. those that were in poor past condition) should be able to maintain current condition more easily than larger males (i.e. those that were in good past condition), since small males require a smaller absolute amount of food than large males in order to maintain the same mass relative to their body size. As such, signal components that indicate current condition (i.e. those under content-driven selection) may also be affected by past condition, which should be seen as an interaction effect between juvenile and adult condition. Thus, while Scheuber et al. (2003b) only manipulated juvenile diet, it is possible that both juvenile and adult condition were affected as a result. By manipulating juvenile and adult condition within the same individuals, we were able to examine the effect on multiple signal components if condition at one life stage affected condition at another life stage.

We manipulated condition in laboratory-reared offspring of field-caught Jamaican field crickets, *G. assimilis*, via dietary limitation to determine how components of the male's long-distance call responded to changes in condition at the juvenile and adult life stages. Our methodology did not allow us to investigate predictions of the quality plus hypothesis. Thus, we were limited to investigating whether the changes in calling behaviour that resulted from the manipulation of male condition at the two life stages were consistent with predictions from the following nonmutually exclusive hypotheses: multiple messages (quality), multiple messages (species recognition), redundant signals (overall condition), redundant signals (backup signals) and efficacy-based

selection. We predicted that call parameters acting as redundant signals of overall condition should respond similarly to a change in condition at either life stage, since changes at either stage will affect 'overall' condition. If the call components are acting as backup signals of the same aspect of condition, then they should only reflect changes in a single specific aspect of condition. Similarly, if the call components are acting as multiple messages of signaller quality, they should only respond to changes in condition at the specific life stages for which they signal. However, signals that function in species recognition, on the other hand, should be highly stereotyped and, thus, be unaffected by changes in condition (Hebets & Papaj 2005). Finally, if a call component has evolved through efficacy-based selection, it should also exhibit condition-dependence, or may even increase with decreasing condition.

METHODS

Crickets were third- and fourth-generation offspring of field-caught individuals collected during 12–24 September 2008, in and around Austin, TX, U.S.A. Prior to the start of the experiment, crickets were reared in communal 68-litre plastic containers. A 10 × 15 cm hole was cut in each lid, with wire mesh glued to it, to provide the crickets with light and air. Crickets were housed in a greenhouse bay in the Nesbitt Building at Carleton University, Ottawa, Ontario, Canada. They were kept on a 12:12 h light:dark cycle with lights on at 0700 hours, at a temperature of $26 \pm 4^\circ\text{C}$. They were fed powdered rat chow (Harlan Teklad Rodent diet no. 8604) and water ad libitum, and were provided with egg cartons for shelter.

Upon reaching the fourth to sixth instar, juvenile males were removed from the communal bins and placed individually into 500 ml plastic containers containing a 30 ml plastic cup filled with gravel and water, a crumpled piece of paper towel for shelter and a 2.54 × 2.54 cm plastic food dish ($N = 166$). They were then randomly assigned to one of four dietary treatments. Each treatment consisted of either a high (H) or a low (L) juvenile diet, followed by a high (H) or a low (L) adult treatment (resulting in a full factorial design of juvenile diet–adult diet: HH, HL, LH, LL). The low dietary treatments (both juvenile and adult) consisted of a continuous cycle of ad libitum food for 2 days, followed by 2 days of fasting. The high dietary treatments consisted of ad libitum food at all times. Crickets were examined every 2 days to ensure they were still alive, to replenish their food and water, and, if they were juveniles, to determine whether they had reached adulthood. On fasting days, males on the low diet were given empty dishes, while males on the high diet were given fresh food. On feeding days, all males were given fresh food. Males were kept on the juvenile diets until reaching adulthood. They were then placed on their adult diet until they were removed from the experiment. If we discovered a male's moulted exoskeleton in his container, we left it undisturbed, regardless of the dietary treatment (to allow each male the opportunity to consume the exoskeleton).

Upon reaching adulthood, males were placed, still in their individual containers, into the New Electronic Acoustic Recorders (NEARs). The system consisted of 96 individually recording microphones. Each microphone was coupled with a single LED light that provided the males with the same LD 12:12 h cycle as the rearing room. Each microphone was housed in an acoustically isolated enclosure (a cooler box made of 2-inch (5.08 cm) thick Styrofoam that was internally lined with 1-inch (2.54 cm) thick acoustic foam) to minimize sound contamination from neighbouring males. The microphones were continuously monitored by CricketSong software (Cambridge Electronic Design Ltd, Cambridge, U.K.). Male calls consist of individual pulses of sound that are grouped into chirps (Fig. 1). The CricketSong software

automatically analyses the sound wave recorded by the microphone and calculates, in real time, the mean pulse duration, mean interpulse duration (time between pulses), mean number of pulses per chirp, mean chirp duration, mean interchirp duration (time between chirps), mean amplitude and mean dominant frequency of the call (Fig. 1). From these data we were then able to calculate mean pulse rate and chirp rate (number of pulses and chirps, respectively, per minute). During recording, pulse onset is determined when the amplitude recorded by the microphone passes a species-specific threshold (40.0 dB for *G. assimilis*). However, this threshold is also adjusted dynamically by CricketSong to account for individuals that call at higher-than-average amplitudes. For these individuals, the threshold is raised to a level proportional to the amplitude of the pulse and decays back to the original value within 1–8000 ms (the exact rate of decay is proportional to the size of the pulse, allowing the system to be self-scaling). For very quiet individuals, the minimum threshold was manually reset to values below the species-specific value. CricketSong also measures call output, and we were thus able to obtain measures of the mean number of calling bouts per night (periods of continuous calling with no more than a 1 min pause), mean calling bout duration, mean time spent calling per night and total time spent calling during days 7–28 of adulthood.

Males were weighed to the nearest 0.1 mg at 1–2 weeks post-eclosion ($N = 141$). Males were removed from the experiment at 28 days of adulthood. They were euthanized by freezing at -20°C for at least 30 min. All bodies were preserved in a -20°C freezer. We obtained postmortem measures of pronotum area and wet mass (i.e. mass at 4 weeks posteclosion) for each male. Pronotum area was measured from highly magnified photographs taken with a Zeiss Axio Observer inverted microscope of the frozen bodies using AxioVision LE software (Carl Zeiss Imaging Solutions GmbH, Germany).

Statistical Analyses

Raw data from the NEARs were processed and summarized using Spike2 audio software (Cambridge Electronic Design Ltd). We calculated the means for all call parameters during days 7–28 of adulthood ($N = 141$), excluding individuals that did not survive until 28 days posteclosion. The call components were measured for every pulse of sound (or chirp, in the case of chirp-related components, such as chirp length) recorded. Means were then calculated based on the total number of pulses (or chirps). Thus, measurements taken when a male is calling continuously are weighed more heavily than when he is calling sporadically. For this reason, we believe that averaging these measurements over a 24 h period, rather than during a 'peak' calling period, more accurately reflects the true values of these call components.

All data were then analysed using JMP 8 statistical software (SAS Institute, Inc., Cary, NC, U.S.A.). The difference between initial and final sample sizes was due to escapees ($N_{\text{HH}} = 4$, $N_{\text{HL}} = 5$, $N_{\text{LH}} = 1$, $N_{\text{LL}} = 4$) and mortality ($N_{\text{HH}} = 2$, $N_{\text{HL}} = 4$, $N_{\text{LH}} = 1$, $N_{\text{LL}} = 4$). Escape rate and mortality were independent of dietary treatment (chi-square test: escape: $\chi^2_3 = 4.332$, $P = 0.228$; mortality: $\chi^2_3 = 3.250$, $P = 0.355$). Pronotum area was used as an index of structural body size (Scheuber et al. 2003b). Condition was calculated as the residuals of a regression of mass (at 28 days of adulthood) on pronotum area (Gray & Eckhardt 2001).

While there are no one-to-one correlations between any of the call components measured, most of the call components are intercorrelated because of the structural nature of the acoustic signal. For example, chirps are composed of a string of approximately 8–11 pulses (Fig. 1). Thus, chirp duration can be affected by pulse duration and interpulse duration, as well as pulse number.

Altering any one of these components, while holding the other two constant, will affect chirp duration. Furthermore, simultaneous changes in two or more components can cancel each other out when it comes to chirp duration. For example, increased pulse duration, coupled with decreased interpulse duration or a decreased number of pulses can lead to no overall change in chirp duration. To address the intercorrelative nature of these acoustic components, we performed a principal components analysis to reduce the number of variables. We did not include measures of call output (i.e. calling bout number, calling bout duration, time spent calling), but included only the more temporally fine components of calling: pulse duration, interpulse duration, pulse rate, pulses per chirp, chirp duration, interchirp duration, chirp rate, amplitude and dominant frequency.

The effects of juvenile and adult diet on body size, condition and calling behaviour were assessed using two-way ANOVAs. We assessed the effects of diet on calling behaviour using both the principal components and selected individual call parameters that were not highly intercorrelated. We also tested for correlations between call parameters and body size and condition. We corrected for multiple testing by adjusting the significance level using the false discovery rate method defined by Benjamini & Yekutieli (2001) (FDR_{BY}) whenever we examined principal components ($\alpha = 0.020$) or individual call parameters ($\alpha = 0.022$). We opted to use the FDR_{BY} adjusted alpha rather than the Bonferroni adjustment because the Bonferroni adjustment has been shown repeatedly to be overly conservative (e.g. Benjamini et al. 2001; Nakagawa 2004; Narum 2006).

There were significant differences in body size and calling behaviour between third- and fourth-generation males. However, our attempt to even out the dietary sample sizes during the experiment resulted in a significant difference in juvenile diet sample size between the two generations; the third generation contained a higher proportion of males on the high juvenile diet while the fourth generation contained a higher proportion of males on the low juvenile diet (chi-square test: $\chi^2_1 = 26.05$, $P < 0.0001$). Controlling for generation in our analyses of body size and calling behaviour did not change the effects of adult diet or the effects of juvenile by adult diet interactions; however, it did lower the significance of the effects of juvenile diet. Thus, we concluded that body size and calling behaviour differed between the two generations because of the uneven distribution of juvenile diet, rather than an underlying difference between the two generations, and we did not control for generation in our final analyses. Adult diet sample size did not differ between the two generations (chi-square test: $\chi^2_1 = 0.039$, $P = 0.843$).

RESULTS

Males on the low juvenile diet took significantly longer to eclose (mean \pm SE = 10.38 ± 0.60 days) than males on the high juvenile diet (mean \pm SE = 8.177 ± 0.67 days) (one-way ANOVA: $F_{1,141} = 6.003$, $P = 0.0155$). Pronotum area (Table 1) was not significantly affected by diet, although the model did indicate a nonsignificant effect of juvenile diet (Table 2). However, when we tested the prediction that mean pronotum size was smaller for males that had been on the low juvenile diet than for males that had been on the high juvenile diet, the result was statistically significant (one-tailed t test: $t_{139} = -1.771$, $P = 0.039$). As pronotum size in crickets is affected by juvenile condition, this test provided the first indication that juvenile condition was successfully manipulated by our dietary treatments. Furthermore, we found that condition at 1–2 weeks of adult age (Table 1) was significantly affected by both juvenile and adult diet; males that had been on the low juvenile diet were in poorer condition than males that had been on the high

Table 1
Morphological and calling data for Jamaican field crickets, *Gryllus assimilis*, fed one of four diets (HH, HL, LH, LL) (values are means \pm SD)

Variable	Diet				
	Juvenile	H	H	L	
	Adult	H	L	L	
Pronotum area (mm ²)		19.53 \pm 2.96	20.21 \pm 2.19	19.32 \pm 2.63	18.72 \pm 2.84
Condition at 1–2 weeks posteclosion (mg/mm ²)		26.52 \pm 53.12	–9.51 \pm 42.50	0.882 \pm 49.03	–18.34 \pm 49.57
Condition at 4 weeks posteclosion (mg/mm ²)		27.36 \pm 67.98	–22.73 \pm 58.19	7.09 \pm 38.77	–14.44 \pm 37.73
N		32	30	44	35
Pulse duration (ms)		10.14 \pm 1.20	10.36 \pm 1.30	10.74 \pm 1.19	10.09 \pm 1.51
Interpulse duration (ms)		15.21 \pm 2.11	15.46 \pm 1.76	16.44 \pm 2.07	15.70 \pm 1.85
Pulse rate (per min)		4245 \pm 445	4134 \pm 382	3955 \pm 462	4129 \pm 400
Pulses per chirp		8.31 \pm 0.75	8.28 \pm 0.62	8.46 \pm 0.58	8.24 \pm 0.93
Chirp duration (ms)		118.7 \pm 17.3	121.0 \pm 15.8	130.0 \pm 18.3	120.4 \pm 16.9
Interchirp duration (ms)		1055 \pm 503	1012 \pm 420	1159 \pm 510	1128 \pm 524
Chirp rate		61.72 \pm 23.71	61.50 \pm 20.97	55.05 \pm 20.55	58.15 \pm 23.98
Amplitude (dB)		60.60 \pm 8.45	63.30 \pm 11.80	57.74 \pm 9.93	59.37 \pm 12.84
Frequency (Hz)		3719 \pm 223	3737 \pm 226	3615 \pm 122	3791 \pm 305
Calling bout number		17.66 \pm 5.70	17.86 \pm 5.14	16.24 \pm 4.94	20.84 \pm 6.61
Calling bout duration (min)		10.61 \pm 5.98	12.43 \pm 9.09	8.781 \pm 4.031	9.382 \pm 5.242
Calling time/night (min)		176.6 \pm 117.0	221.5 \pm 154.3	148.5 \pm 85.4	192.0 \pm 106.5
N		31	29	44	33

Each treatment consisted of either a high (H) or a low (L) juvenile diet, followed by a high (H) or a low (L) adult treatment (resulting in a full factorial design of juvenile diet–adult diet: HH, HL, LH, LL). Sample sizes differ between morphological and calling behaviour data because four males were identified as noncallers and were thus included in the morphological analyses but not in the calling behaviour analyses.

juvenile diet; similarly, males currently on the low adult diet were in poorer condition than males on the high adult diet (Table 2). By 4 weeks of adult age, male condition (Table 1) was significantly affected by adult diet alone (Table 2); males on the high adult diet were in better condition than males on the low adult diet. There was no effect of juvenile diet on condition at 28 days of adulthood (Table 2). Therefore, we concluded that past condition had been successfully manipulated by the juvenile diet and that current condition had been successfully manipulated by the adult diet.

Of the 141 males that survived to 28 days of adulthood, four never called for more than 3 min in a single recorded hour (all other males called for at least 26 min in a single recorded hour). These four males also spent less than 1 min calling on average per night (all other males called longer than 5 min on average per night), and called for less than 16 min in total throughout their adult lives (from 7 to 28 days of adulthood) (all other males called longer than 125 min total). These four outlier males were therefore identified as noncallers (e.g. Cade 1979) and were excluded from all other calling behaviour analyses. There was no effect of dietary treatment on whether males showed noncalling or calling behaviour (chi-square test: $\chi^2_3 = 3.384$, $P = 0.336$).

The principal components analysis yielded four eigenvectors with percentages over 5% each, describing 93% of the variation in calling behaviour (Table 3). PC1 was related to chirp duration in that increasing interpulse duration and decreasing pulse rate were both associated with increasing chirp duration. PC2 was composed of chirp characteristics in that increasing pulses per chirp and decreasing interpulse duration were both associated with increasing chirp rate, as well as increasing amplitude. PC3 was also associated with chirp rate, but in a different way; in this case, increasing pulses per chirp and increasing interchirp duration were both associated with decreasing chirp rate. PC4 was described by increasing mean dominant frequency and pulses per chirp. Only PC1 was affected by diet (Fig. 2, Table 2); adult males that had been on the low diet as juveniles produced calls with longer interpulse durations, lower pulse rates and longer chirp durations than males that had been on the high juvenile diet, particularly if they subsequently received the high diet as adults.

The call components describing pulse, interpulse, chirp and interchirp duration, and thus, pulse and chirp rate (Table 1) were necessarily highly correlated and therefore loaded quite heavily into the PCA (Table 3). However, dominant frequency, amplitude and the measures of calling output (number of calling bouts per night, calling bout duration and time spent calling per night; Table 1) were at least partly independent of one another. Therefore, we also examined the effects of juvenile and adult diet on these individual call components (Table 2). Both dominant frequency and the number of calling bouts per night were significantly affected by diet at a FDR_{BY} adjusted alpha of 0.0157. Dominant frequency was lower for males on the high adult diet, particularly if those males had received the low diet as juveniles (Fig. 3). Males on the low adult diet produced more calls per night than males on the high diet (Fig. 4).

We also examined the correlations between adult body size (pronotum area) and condition and calling behaviour (Table 4). Pronotum area was positively correlated with PC1 and amplitude and negatively correlated with dominant frequency. Condition at 28 days of adulthood was positively correlated with amplitude and mean time spent calling per night.

DISCUSSION

Our results are consistent with both content- and efficacy-based selection. Several components of the male *G. assimilis* long-distance calls behaved in a way consistent with that predicted for traits under content-based selection. The calling components associated with PC1 (interpulse duration, pulse rate and chirp duration) were affected by juvenile condition, while dominant frequency was affected by adult condition; thus, these call components have the potential to function as multiple messages of male quality. The number of pulses per chirp, interchirp duration and chirp rate were not affected by condition and may, therefore, function in species recognition. Call duration increased with decreasing adult condition, and was, thus, consistent with efficacy-based selection. None of our results were consistent with the hypothesis that any components of the male's call function as redundant signals, either

Table 2
Effects of juvenile and adult diet on body size, condition and calling behaviour of Jamaican field crickets, *Gryllus assimilis* (all morphological, $N = 141$; all calling, $N = 137$; all $df = 3$ for whole model)

Variable	Whole model	Diet effect	F	P	Least squares means	
					Diet	
					High	Low
Pronotum area (mm ²)	$R^2=0.036$	Juvenile	3.479	0.064	19.87±0.34	19.02±0.30
	$F=1.714$	Adult	0.006	0.938	19.43±0.31	19.46±0.33
	$P=0.167$	Juv*adult	1.999	0.160	HH: 19.53±0.47	LH: 19.32±0.40
					HL: 20.21±0.49	LL: 18.72±0.45
Condition at 1–2 weeks posteclosion (mg/mm ²)	$R^2=0.102$	Juvenile	4.201	0.042	8.506±6.248	–8.731±5.628
	$F=5.035$	Adult	10.79	0.001	13.70±5.78	–13.93±6.11
	$P=0.003$	Juv*adult	0.997	0.320	HH: 26.52±8.76	LH: 0.882±7.529
					HL: –9.50±8.91	LL: –18.34±8.37
Condition at 4 weeks posteclosion (mg/mm ²)	$R^2=0.121$	Juvenile	0.476	0.492	2.089±6.464	–3.884±5.761
	$F=6.308$	Adult	17.11	<0.0001	17.01±5.91	–18.80±6.33
	$P=0.001$	Juv*adult	2.725	0.101	HH: 27.14±8.99	LH: 6.874±7.669
					HL: –22.96±9.29	LL: –14.64±8.60
PC1	$R^2=0.085$	Juvenile	4.868	0.029	–0.4387±0.2396	0.2694±0.2135
	$F=4.128$	Adult	1.694	0.195	0.1242±0.2174	–0.2935±0.2360
	$P=0.008$	Juv*adult	3.942	0.049	HH: –0.549±0.333	LH: 0.797±0.280
					HL: –0.329±0.344	LL: –0.258±0.323
PC2	$R^2=0.013$	Juvenile	0.444	0.506	0.0951±0.2246	–0.1045±0.1994
	$F=0.589$	Adult	0.222	0.638	0.0660±0.2030	–0.0753±0.2203
	$P=0.624$	Juv*adult	1.108	0.295	HH: 0.008±0.311	LH: 0.124±0.261
					HL: 0.182±0.322	LL: –0.333±0.301
PC3	$R^2=0.007$	Juvenile	0.001	0.981	–0.0104±0.1261	–0.0063±0.1124
	$F=0.323$	Adult	0.935	0.335	0.0734±0.1145	–0.0900±0.1243
	$P=0.809$	Juv*adult	0.003	0.958	HH: 0.067±0.175	LH: 0.080±0.147
					HL: –0.088±0.181	LL: –0.092±0.170
PC4	$R^2=0.014$	Juvenile	0.093	0.761	–0.0151±0.1155	0.0322±0.1030
	$F=0.632$	Adult	1.064	0.304	–0.0712±0.1048	0.0884±0.1138
	$P=0.595$	Juv*adult	0.594	0.442	HH: –0.035±0.161	LH: –0.107±0.135
					HL: 0.005±0.166	LL: 0.172±0.156
Amplitude (dB)	$R^2=0.036$	Juvenile	3.222	0.075	62.06±1.39	58.72±1.24
	$F=1.636$	Adult	1.471	0.227	59.26±1.26	61.52±1.37
	$P=0.184$	Juv*adult	0.157	0.693	HH: 60.56±1.93	LH: 57.96±1.62
					HL: 63.55±1.99	LL: 59.48±1.87
Dominant frequency (Hz)	$R^2=0.088$	Juvenile	0.491	0.485	3728±29	3701±26
	$F=4.295$	Adult	6.506	0.012	3665±26	3763±28
	$P=0.006$	Juv*adult	4.011	0.047	HH: 3717±40	LH: 3613±34
					HL: 3738±41	LL: 3788±39
Number of calls per night	$R^2=0.113$	Juvenile	2.800	0.097	16.97±0.70	18.54±0.63
	$F=5.666$	Adult	11.53	0.001	16.16±0.64	19.35±0.69
	$P=0.001$	Juv*adult	2.247	0.136	HH: 16.08±0.98	LH: 16.24±0.82
					HL: 17.86±1.01	LL: 20.84±0.95
Call duration (min)	$R^2=0.050$	Juvenile	5.315	0.023	11.52±0.79	9.081±0.703
	$F=2.314$	Adult	1.318	0.253	9.693±0.716	10.91±0.78
	$P=0.079$	Juv*adult	0.336	0.563	HH: 10.61±1.10	LH: 8.781±0.921
					HL: 12.43±1.13	LL: 9.382±1.063
Time spent calling per night (min)	$R^2=0.053$	Juvenile	2.102	0.150	199.1±14.8	170.3±13.2
	$F=2.495$	Adult	4.951	0.028	162.6±13.5	206.8±14.6
	$P=0.063$	Juv*adult	0.001	0.973	HH: 176.6±20.6	LH: 148.5±17.3
					HL: 221.5±21.3	LL: 192.0±20.0

Each treatment consisted of either a high (H) or a low (L) juvenile diet, followed by a high (H) or a low (L) adult treatment (resulting in a full factorial design of juvenile diet–adult diet: HH, HL, LH, LL). Significant values are shown in bold: $P < 0.05$ (model effects; whole model, morphological measurements); $P < 0.024$ (whole model, FDR_{BY} corrected for principal components); $P < 0.022$ (whole model, FDR_{BY} corrected for individual calling components).

of overall condition, or as backup signals of the same aspect of condition.

Juvenile and adult condition were successfully manipulated by the dietary treatments. Adult body size, which is affected by and is, therefore, an indicator of past condition, was significantly affected by juvenile diet; males that received the low juvenile diet were smaller as adults than males that received the high juvenile treatment. Similarly, current body condition was significantly affected

by adult diet; males on the low adult diet were in poorer condition than males on the high adult diet.

Several call components were affected by condition at the two different life stages, and, thus, have the potential to act as multiple messages of male quality. PC1, which was composed mainly of interpulse duration, pulse rate and chirp duration, was significantly affected by juvenile diet, and by an interaction between juvenile and adult diet. Males that received the low diet as juveniles

Table 3
Principal components analysis of calling parameters of Jamaican field crickets, *Gryllus assimilis*

Call parameter	PC1	PC2	PC3	PC4
Pulse duration	0.387	0.317	-0.038	-0.186
Interpulse duration	0.472	-0.062	-0.359	0.022
Pulse rate	-0.484	0.051	0.305	0.011
Pulses per chirp	0.111	0.404	0.474	0.538
Chirp duration	0.452	0.217	0.055	0.338
Interchirp duration	0.237	-0.427	0.455	-0.120
Chirp rate	-0.249	0.407	-0.496	-0.020
Amplitude	-0.149	0.476	0.175	-0.104
Dominant frequency	-0.189	-0.328	-0.255	0.731
Eigenvalue	3.677	2.970	0.939	0.793
Cumulative %	40.856	73.860	84.295	93.107

Loadings above 0.400 are shown in bold.

produced calls with longer interpulse durations, lower pulse rates and longer chirp durations than males that had received the high juvenile diet, especially if they were subsequently placed on the high diet as adults. These findings are consistent with studies of other cricket species in which pulse rate is determined by juvenile environment. For example, *G. rubens* males reared at higher temperatures produce calls as adults with significantly higher pulse rates than individuals reared at a lower temperatures (Walker 2000). Pulse rate also increases with ambient temperature due to an increase in the rate at which the cricket opens its wings (Martin et al. 2000). Since temperature did not differ between treatments, temperature cannot explain the difference we observed in pulse rate between males on the high and low juvenile diets. Instead, males that received unlimited access to food as juveniles may have been in better physiological condition as adults than males that had been food limited; thus, they were able to call at higher pulse rates (i.e. able to open their wings at a faster rate), leading to subsequently shorter interpulse and chirp durations. Insect metabolism increases with increasing ambient temperature; similarly, the differences we observed in interpulse duration, pulse rate and chirp

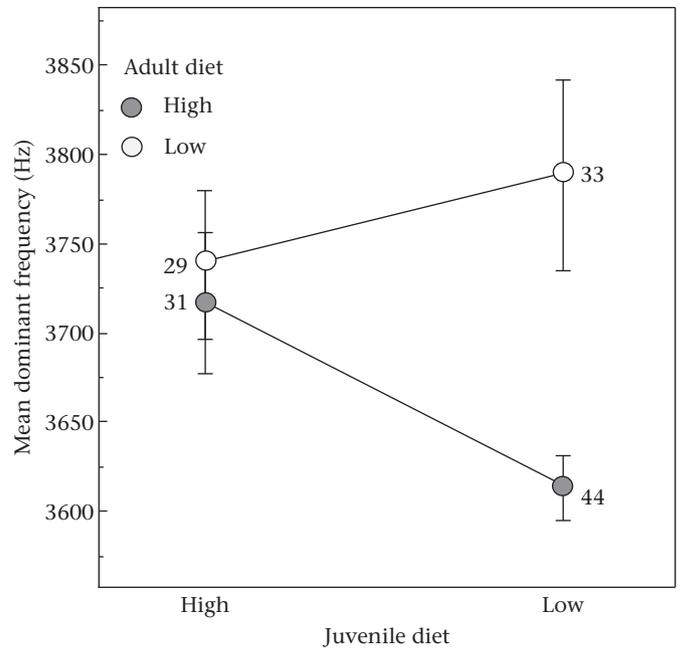


Figure 3. Effects of juvenile and adult diet on mean dominant frequency. Bars indicate standard error; numbers within figure indicate sample sizes.

duration between individuals on high and low juvenile diets may have resulted from changes in either neural or muscular development or function.

Dominant frequency, on the other hand, was significantly affected by adult diet. Males on the high adult diet produced lower-frequency calls than males on the low adult diet. Dominant frequency is partially determined by the size of the body and harp (the resonant structure found on the male forewings; Bennet-Clark 1999; Martin et al. 2000; Bailey et al. 2001), both of which are determined by juvenile condition and do not change significantly posteclosion. Surprisingly, although we observed an effect of

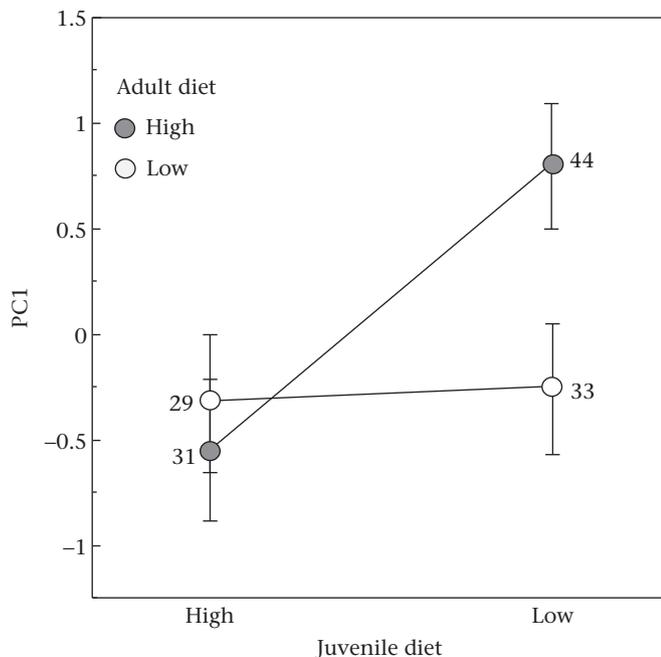


Figure 2. Effects of juvenile and adult diet on principal component 1. Bars indicate standard error; numbers within figure indicate sample sizes.

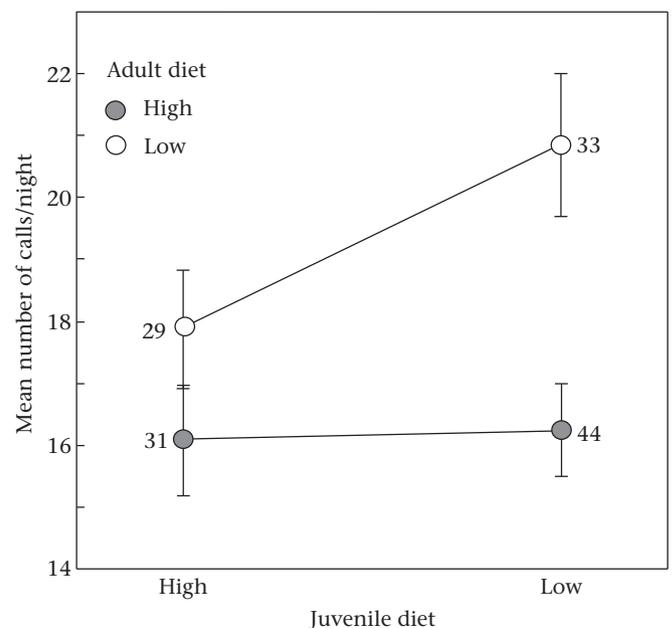


Figure 4. Effects of juvenile and adult diet on mean number of calling bouts per night. Bars indicate standard error; numbers within figure indicate sample sizes.

Table 4
Correlations of call parameters with body size (pronotum area) and condition at 28 days of adult age (all $N = 137$, $df = 1$)

Variable	Pronotum area (mm ²)			Condition by wet mass (mg/mm ²)		
	R ²	F	P	R ²	F	P
PC1	0.047	6.681	0.011	0.028	3.909	0.050
PC2	0.035	4.920	0.028	0.037	5.141	0.025
PC3	0.005	0.672	0.414	0.004	0.530	0.468
PC4	0.019	2.628	0.107	0.009	1.166	0.282
Mean amplitude	0.068	9.822	0.002	0.056	8.025	0.005
Mean dominant frequency	0.065	9.370	0.003	0.010	1.392	0.240
Mean number of calls/night	0.002	0.316	0.575	0.014	1.883	0.172
Mean call duration	0.014	1.985	0.161	0.029	4.078	0.045
Mean time spent calling/night	0.008	1.110	0.294	0.043	6.127	0.015

Significant values are shown in bold ($P < 0.024$ for principal components; $P < 0.022$ for individual call parameters (FDR_{BY} corrected)).

juvenile diet on adult body size, we found no relationship between juvenile diet and dominant frequency. Body size was negatively correlated with dominant frequency, but this relationship was independent of treatment. This result may have occurred because dominant frequency is also affected by the speed of wing closure (Martin et al. 2000). When a male closes his wings quickly, the teeth of the file are hit at a high rate, resulting in a high-frequency sound (Martin et al. 2000). Females of several cricket species prefer calls of low frequency (e.g. Simmons & Ritchie 1996; Gray 1997; Scheuber et al. 2004). This is likely due to a preference for larger males since dominant frequency decreases with body size (Simmons 1995; Scheuber et al. 2003b). However, males in good present condition may also be able to alter their dominant frequency. For example, in male *G. campestris*, dominant frequency decreases, becoming more attractive, with age (Jacot et al. 2007). This may occur through some unidentified costly mechanism that becomes more profitable as the male ages. For example, young males may choose not to pay this cost as it may detract from their future reproductive potential. However, older males facing decreased future reproductive potentials may choose to pay the cost in order to potentially increase their current reproductive success since females prefer calls of lower dominant frequency. Similarly, in *G. assimilis*, it is possible that only males in good current condition may be able to slow their rate of wing closure (at a corresponding energetic cost) while still maintaining other call parameters such as pulse rate and amplitude. Males in poor condition may lack the energetic resources required for this type of muscular control, explaining why only males in good present condition were able to produce calls at lower dominant frequencies. There is some evidence that calling at a low dominant frequency is more costly; in *G. lineaticeps*, the energetic cost of calling increases with increasing pulse duration (Hoback & Wagner 1997). This is interesting since pulse duration is negatively correlated with dominant frequency in both *G. assimilis* and *G. texensis* (E. M. Whattam & S. M. Bertram, unpublished data). This implies that low-frequency pulses (i.e. those with longer pulse durations) are more expensive to produce than high-frequency pulses, again suggesting that dominant frequency is an honest signal of current condition.

Thus, the call parameters involved in PC1 (interpulse duration, pulse rate and chirp duration) may signal past male condition, while dominant frequency may be an honest signal of present condition in *G. assimilis*. Some authors have suggested that long-term signals are probably indicative of genetic suitability to the environment, and, thus, indirect benefits, while short-term signals are more indicative of the direct benefits that a male has to offer (e.g. Gerhardt 1991; Candolin 2003). Here, the components of PC1,

which are indicative of long-term (past) condition, may be more indicative of overall male suitability to the environment; thus, they could indicate indirect genetic benefits to the female. Dominant frequency, on the other hand, being more indicative of short-term (present) fluctuations in condition may advertise direct benefits, such as higher sperm count (Andersson 1994; Candolin 2003).

We did not explicitly investigate the benefits that females may receive by mating with males in good past and present condition. However, males in good current condition may be able to produce more or better sperm (Wagner & Hoback 1999). They may also be less likely to be infected with parasites, thereby decreasing the female's chances of contracting them during mating (e.g. Borgia & Collins 1990; Doucet & Montgomerie 2003). These and other benefits may also be heritable, conferring similar advantages to the female's offspring. Alternatively, Hedrick (2005) suggested that females may acoustically locate to males that have attractive condition-dependent signals in order to find locations with favourable environmental conditions, either for their own benefit, or for the benefit of their offspring. Wagner & Harper (2003) found that female *G. lineaticeps* that mate with males that produce calls with preferred chirp rates and chirp durations receive fertility, fecundity and life span benefits as a result. Further study should be conducted to determine which benefits, if any, are given to female *G. assimilis* that mate with males producing calls indicative of good juvenile and adult condition. This is a topic of ongoing investigation in our laboratory.

The number of pulses per chirp, interchirp duration and chirp rate were not significantly affected by diet, condition or body size. These results suggest that these calling components are relatively stereotyped in *G. assimilis* and may function in species recognition (Hebets & Papaj 2005). This result is consistent with the general finding that other chirping cricket species (as opposed to trilling species, which produce large, variable numbers of pulses per trill) show relatively low variability in the number of pulses produced per chirp (e.g. Ciceran et al. 1994; Van Wyk & Ferguson 1995).

Males on the low adult diet tended to produce more calling bouts per night than males on the high adult diet. Thus, males in poor condition appeared to be increasing their calling output. As such, calling bout number does not appear to be an honest signal of male condition. Instead, males in poor condition, which are faced with lowered future reproductive potential relative to males in good condition, may compensate by increasing their investment in current reproduction. Since males that call most often are statistically more likely to be heard by intermittently passing females, males that increase their calling output may be able to increase their current reproductive success (e.g. Cade & Cade 1992; Rodríguez-Muñoz et al. 2010). As such, calling bout number may be under efficacy-based selection (Ryan & Cummings 2005) in *G. assimilis*. Alternatively, calling bout number may honestly signal current male reproductive effort. Males in poor condition, which face low future reproductive potential, may also be willing to invest more in current matings, for example, by increasing the number of copulations, or by giving increased seminal fluid. For example, in the variable field cricket, *G. lineaticeps*, females that mated repeatedly with the same male, or that mated multiply with different males, lived more than 32% longer than singly mated females (Wagner et al. 2007). Since females only receive sperm and seminal fluids from these males, the benefits were probably due to beneficial products present in the males' seminal fluid. Similarly, calling bout duration in *G. assimilis* may indicate a male's willingness to provide a direct benefit to females. However, it is unlikely that females assess calling bout duration, as calling bouts are several minutes long on average; therefore, it is likely that calling bout duration has been selected for efficacy. Future work should determine whether male *G. assimilis* enjoy increased mating

success as a result of increased calling bout duration, and whether females receive benefits by mating with males that produce longer calling bouts.

Body condition was not affected by an interaction between juvenile and adult diet; therefore, it appeared that past condition did not affect current condition. However, several call parameters were affected by an interaction between juvenile and adult diet. Mean dominant frequency was lowest (most attractive) in males on the high adult diet, especially in those males that had received the low diet as juveniles. Thus, it appears that males that had been in poor condition in the past may have compensated for their less attractive long-term signals by increasing investment in signals of their current condition. In doing so, they could remain competitive with males that produced attractive long-term signals. Both phenotypes may then be reproductively successful, explaining the maintenance of variation in multiple sexual signals. Increased investment in current signalling may still be an honest signal to females. These increases are energetically costly and, thus, occur at a cost to long-term reproductive success. As such, a male that increases his investment in a current signal may be willing to invest correspondingly more in current reproduction (e.g. through any of the benefits discussed above). This suggests that multiple messages, while still indicative of separate aspects of male condition, may also be interrelated. For example, two males may signal current condition equally; however, if one male also signals that he was in poor past condition, he may be willing to invest more in current reproduction, since his future reproductive potential is lower. Thus, females should assess all of a male's traits in order to best assess what benefits he has to offer.

We must be careful when considering multiple signals, particularly when they constitute different aspects of a multicomponent signal. For example, in our study we found that interpulse duration, pulse rate and chirp duration were all interdependent; if one parameter changes, at least one other parameter, if not both, will be correspondingly affected. As such, while we are able to measure each call parameter separately, we should not necessarily consider them separate signals. This concern becomes especially important when attempting to distinguish between the redundant signals and multiple messages hypotheses. For example, because interpulse duration, pulse rate and chirp duration were all affected by juvenile diet in our study, we could have interpreted them as being redundant signals of past condition. However, a more accurate interpretation is that the effect of juvenile diet on these parameters resulted from the way in which we parsed a single acoustic signal of past condition. Future studies should consider the interdependency between potential multiple sexual signals before labelling them as such.

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