



Nutritional effects on male calling behaviour in the variable field cricket

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In the variable field cricket, *Gryllus lineaticeps*, females prefer higher chirp rates and longer chirp durations in male calling song. Higher chirp rates are energetically more expensive to produce, but the energetic cost of calling does not vary with chirp duration. We tested the hypothesis that nutrition affects male chirp rate and chirp duration. Full-sibling brothers of similar age were placed on high- and low-nutrition feeding regimes. There was no effect of feeding regime on male weight; neither group showed a significant change in weight, and the two groups did not differ from each other in weight change. However, males on the high-nutrition feeding regime both called more frequently and called at higher chirp rates when they did call. The two groups did not differ in chirp duration, the duration of pulses within chirps or chirp dominant frequency. These results suggest that females select mates based on one nutrition-dependent call character (chirp rate) and one nutrition-independent call character (chirp duration). In addition, because males in the two groups did not show significant differences in weight change, and because males on the high-nutrition feeding regime engaged in energetically more expensive calling, these results suggest that males invest any excess energy above their basic maintenance requirements in the production of call types that increase their attractiveness to females. The absence of a relationship between body condition and calling song structure for males in the field may be a consequence of this pattern of energy allocation.

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Females in many species of animals prefer to mate with males that produce more energetically costly displays (reviewed by Ryan 1988; Andersson 1994). In acoustic animals, for example, females often prefer calls that are produced at higher rates, that are longer in duration, and that are higher in amplitude (reviewed by Ryan & Keddy-Hector 1992). These call types tend to be energetically more expensive for males to produce (reviewed by Prestwich 1994), although female preferences for more energetically expensive displays have been shown in only a small number of animals (see Watson & Lighton 1994; Reinhold et al. 1998).

Energetically costly displays can potentially provide information to females about male phenotypic or genetic quality. For example, many of the traits preferred by females are not only energetically expensive for males to produce, but they also vary with male diet or body condition (e.g. Endler 1983; Milinski & Bakker 1990;

Galeotti et al. 1997). Male condition can be correlated with the quality of a number of direct benefits that males provide to females. Males in better condition may provide (1) more sperm or more viable sperm to females (Matthews et al. 1997), (2) more nutritional nuptial gifts to females (Wedell 1994; Belovsky et al. 1996), (3) better care for offspring, or (4) may be less likely to transmit parasites to females (Borgia & Collis 1990). In addition, male condition may be correlated with the quality of indirect benefits that males provide to females. Males in better condition may be of higher fitness, and by mating with such males, a female's offspring may receive higher fitness alleles, if fitness is heritable (Zahavi 1975; Pomiankowski 1988; Iwasa et al. 1991). The reliability of condition-dependent signals is thought to be maintained, in part, by the cost of producing attractive signals and by the inability of males in poor condition to sustain high signalling costs.

While much is known about preferences based on condition-dependent traits, little is known about how males partition energy between body condition and signals used for mate attraction. Males of higher quality may obtain more nutrients and may be able to invest more in both body condition and signal production. Under such a

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circumstance, there may be a correlation between body condition and signal structure. However, there may be situations in which males should invest all energy above their basic maintenance requirements in signal production. For example, when adult survivorship is low, selection should favour investment in current reproduction rather than conserving resources for later reproduction (Williams 1966; Stearns 1976; Charlesworth 1980). Thus, when adult survivorship is low, males might invest more in attractive signals than in body condition. Under such a circumstance, there may be no correlation between body condition and signal structure, even though males that obtain more food produce more attractive signals.

In this study we examine the nutrition-dependence of male calling behaviour in the variable field cricket *Gryllus lineaticeps*. Male field crickets produce three qualitatively different types of songs: calling song, courtship song and aggressive song (Alexander 1961). Calling song is used to attract females at a distance, and courtship song is used to entice a female to mate once a female has approached a male. In the variable field cricket, females prefer male calling songs with higher chirp rates and longer chirp durations (Wagner 1996). There are, however, important costs associated with producing the preferred calling song. First, higher chirp rates and longer chirp duration increase a male's probability of attracting acoustically orienting parasitoid flies (Wagner 1996). Second, some preferred call types are energetically more expensive to produce. Calling, on average, increases male metabolic rate 2.7 times above noncalling metabolic rates, and the cost of calling is positively correlated with chirp rate (Hoback & Wagner 1997). In contrast, the energetic cost of calling does not vary with chirp duration. Because higher chirp rates are energetically more expensive to produce, food-limited males may be incapable of producing higher chirp rates. Because variation in chirp duration does not affect the cost of calling, chirp duration may be independent of food intake.

We report that moderate differences in nutrient intake did not affect male weight, but that males provided with a higher-quality diet called more frequently and produced higher chirp rates when they did call. Diet quality, however, did not affect chirp duration, the duration of pulses within chirps, or chirp dominant frequency. Males that obtain more energy thus appear to both increase calling activity and to invest in call types that are more energetically expensive to produce, but they do not appear to invest additional energy in body condition. This result is reinforced by observations that there is no correlation between calling behaviour and body condition for males in the field.

MATERIALS AND METHODS

Effect of Nutrition on Male Weight and Calling Behaviour

The male *G. lineaticeps* used in the nutrition study were the second-generation offspring of field inseminated females collected from Tucker's Grove County Park, Santa

Barbara County, California in August 1995. We arranged matings to minimize inbreeding in the experimental population. All males were housed in family containers until the penultimate instar, at which time we transferred them to individual containers. All containers were provided with a paper towel substrate, a cotton-plugged water vial, and ad libitum Purina cat chow. The colony room was maintained on a 16:8 h light:dark light cycle at approximately 24°C.

To examine the effect of nutrient quantity on male calling behaviour, we used pairs of full-sibling brothers that had been sexually mature for at least 7 days and had reached sexual maturity within 1 day of each other. We randomly chose one brother of each pair to be placed on a high-nutrition feeding regime, and placed the other brother on a low-nutrition feeding regime. We used this paired design to minimize any effects of genetic differences, age differences and uncontrolled environmental differences on male calling behaviour. Each full-sibling pair used in the experiments was from a different sibship, thereby ensuring the representation of numerous genotypes in the experimental animals. The diets consisted of 14.3% casein, 40% bran, 28.6% baker's yeast, and 17.1% wheat germ, by weight. Males of both treatment groups received 25 mg of dry food per day, but the food of males on the low-nutrition feeding regime was cut with 33% non-nutritive cellulose. Preliminary tests showed that an average male eats a mean (\pm SE) of 26.6 ± 2.0 mg of the uncut diet per day ($N=9$); there was no effect of male size on the amount of food eaten per day: $r=0.175$, $N=9$, NS). We placed males on the experimental diets for 7 days and provided them with cotton-plugged water vials. We weighed the males each day to the nearest 0.1 mg using a Sartorius BP61 scale, removed any uneaten food, and added new food. No male in either treatment group died during the feeding period.

We assessed male calling behaviour 8 days after males were placed on the feeding regimes. We placed the containers housing the two pairs of males on the experimental diets with those housing the two males that had not been fed an experimental diet. We randomly arranged the containers in a 2×3 pattern, with 61 cm between each container. We broadcast taped calling song for 1 h prior to the tests to stimulate calling. We included the two unmanipulated males because preliminary observations suggested that the presence of additional males increased the probability that the experimental males would call during the period of data collection.

We observed the males for 3 h. Every 10 min we noted which of the experimental males was calling (total point samples=18 per male). In addition, if a male called, we recorded at least 2 min of consecutive calling using a Sennheiser ME-80 microphone with a K3-U power module and a Sony TCD-5M stereo cassette recorder.

We analysed calls on a Macintosh Quadra 840AV computer using Canary software. We measured chirp rate (chirps/s) over a 2-min interval, and randomly chose six calls for analysis of chirp duration (ms), average pulse duration (ms), and dominant frequency (Hz). While male calling behaviour in this species varies with temperature (Hoback & Wagner 1997), the paired design eliminated

the need to adjust for the effect of temperature on male calling behaviour.

Some of the males on the low-nutrition feeding regime did not call, and some of the taped calling songs were not analysable. As a result, the number of full-sibling pairs for which calling song data were available was smaller than the number of pairs used in the experiment. In addition, we obtained chirp rate data for one pair of males, but because other males called simultaneously, we did not obtain accurate information on the temporal structure of their chirps. As a result, the sample size for the chirp rate comparison is slightly larger than that for the other comparisons.

Relationship Between Calling and Condition in the Field

We examined the effect of weight, size and condition on male calling behaviour in the field from 22 August to 16 September 1993 at Tucker's Grove County Park, Santa Barbara County, California. We located calling males, and recorded 2 min of calling song using the same equipment described above. We then captured the males, and we recorded the air temperature at the position from which the male was calling. We transported males back to the laboratory, weighed them to the nearest 1 mg, and measured their pronotal widths to the nearest 0.02 mm with dial calipers. We estimated male body condition using the residuals from a regression of weight on pronotum width (e.g. Galeotti et al. 1997; $r=0.835$, $N=18$, $P<0.001$).

We assessed male calling song as described above. We adjusted calling song characters to a common temperature prior to statistical analysis based on the regression of each calling song character on temperature (see Wagner 1989).

RESULTS

Effect of Nutrition on Male Weight

Neither males on the high-nutrition feeding regime nor males on the low-nutrition feeding regime showed a significant change in weight over the 7-day feeding period (Fig. 1; paired t test: high-nutrition group: $t_{12}=0.831$, NS; low nutrition group: $t_{12}=1.125$, NS). Males on the high-nutrition diet gained an average (\pm SE) of 0.009 ± 0.011 g, a 1.7% increase in weight, and males on the low-nutrition diet gained 0.010 ± 0.009 g, a 2.0% increase in weight. There was no significant difference in weight change by males in the two groups (paired t test: $t_{12}=0.053$, NS).

Effect of Nutrition on Male Calling Behaviour

Males on the high-nutrition diet called during significantly more samples than males on the low-nutrition diet (Fig. 2; paired t test: $t_{12}=6.163$, $P<0.001$). All males on the

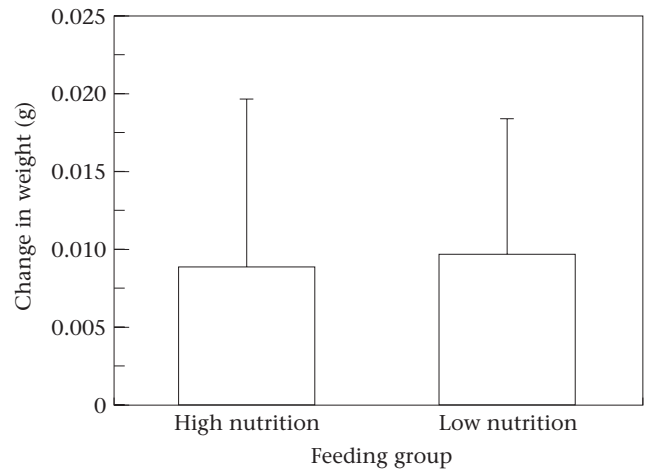


Figure 1. Effect of diet on change in male weight ($\bar{X} \pm SE$).

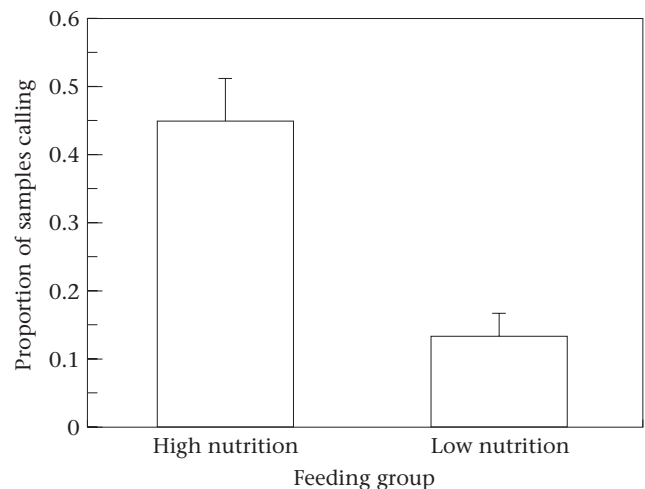


Figure 2. Effect of diet on male calling activity ($\bar{X} \pm SE$).

high-nutrition diet produced calls during some of the sampling periods, and on average, called during 44.9% of the samples. Three of the 13 males on the low-nutrition diet never called (23% of the males); the other 10 low-nutrition males called during an average of 13.2% of the samples.

Males on the high-nutrition diet called at a higher chirp rate than males on the low-nutrition diet (109.6 ± 9.3 chirps/s versus 59.8 ± 7.8 chirps/s, respectively; Fig. 3a; paired t test: $t_7=4.276$, $P=0.004$).

There was no significant difference in the chirp durations of males on the two feeding regimes (Fig. 3b; paired t test: $t_6=0.766$, NS). Males on the high-nutrition diet produced an average (\pm SE) chirp duration of 117.5 ± 5.1 ms, while males on the low-nutrition diet produced an average chirp duration of 121.7 ± 8.5 ms.

There was also no significant difference in the pulse durations of males on the two feeding regimes (paired t test: $t_6=0.999$, NS). Males on the high-nutrition diet

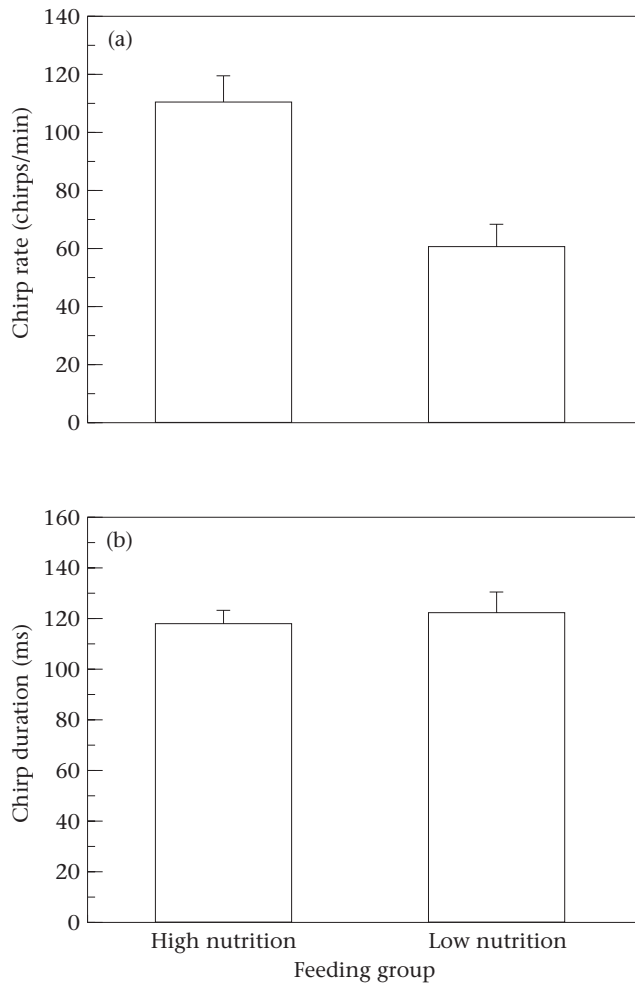


Figure 3. Effect of diet on (a) calling song chirp rate and (b) chirp duration ($\bar{x} \pm \text{SE}$).

produced an average ($\pm \text{SE}$) pulse duration of 11.8 ± 1.0 ms, while males on the low-nutrition diet produced an average pulse duration of 10.8 ± 1.4 ms.

Finally, there was no significant difference in the dominant frequencies of males on the two feeding regimes (paired t test: $t_6 = 1.664$, $P = \text{NS}$). Males on the high-nutrition diet produced an average ($\pm \text{SE}$) dominant frequency of 4.89 ± 0.08 kHz, while males on the low-nutrition diet produced an average dominant frequency of 4.79 ± 0.07 kHz.

For the 3-h measurement period, we estimated total chirp production for each male as the proportion of samples during which males called $\times 180 \text{ min} \times \text{chirp rate}$ (chirps/min). Because males on the high-nutrition diet called more frequently, and averaged higher chirp rates when they did call, males on the high-nutrition diet produced more chirps than males on the low-nutrition diet (Wilcoxon signed-ranks test: $z_6 = 2.366$, $P = 0.018$). We estimated that males on the high-nutrition diet produced an average ($\pm \text{SE}$) of $10\,272 \pm 2006$ chirps, while males on the low-nutrition diet produced an average of 1693 ± 173 chirps.

Table 1. Correlations between male calling song characteristics and weight, pronotum width and body condition

Song characteristic	Correlation coefficients		
	Weight	Pronotum width	Body condition
Chirp rate (chirps/s)	0.043	0.185	0.317
Chirp duration (ms)	0.239	-0.028	-0.059
Pulse duration (ms)	-0.108	-0.039	-0.219
Dominant frequency (kHz)	0.107	-0.355	0.077

$N = 18$; all P values were nonsignificant.

Relationship Between Condition and Male Calling Behaviour

For males in the field, there was no significant correlation of any calling song character with either weight or pronotum width (Table 1). Similarly, there was no significant correlation of any calling song character with our measure of male body condition (Table 1).

DISCUSSION

The Nutrition Dependence of Male Calling Behaviour

In *G. lineaticeps*, females prefer higher chirp rates and longer chirp durations (Wagner 1996). Higher chirp rates are energetically more expensive to produce, but longer chirp durations do not appear to be energetically more expensive to produce (Hoback & Wagner 1997). The results reported here suggest that nutritional intake by males has important effects on male calling behaviour; males provided with a diet of lower quality called less frequently, and they called at a lower chirp rate when they did call. As a result, males provided with a diet of higher quality produced more than six times as many chirps, on average, as males provided with a diet of lower quality. Because males that call less frequently will have fewer opportunities to attract females, and because females discriminate against males that produce lower chirp rates, nutrition-dependent changes in calling behaviour should have an important influence on male mating success. In contrast, diet quality did not affect the duration of a male's chirps, and thus, chirp duration may be independent of a male's nutritional status. Therefore, in *G. lineaticeps*, females appear to select mates based on one calling song character that covaries with male nutritional status, and one that is independent of male nutritional status. Other traits preferred by females, such as chirp amplitude (Wagner 1996), may also vary with male nutrition.

Other studies have also manipulated male diet and examined the effect on male signal structure (e.g. Green 1991; Simmons et al. 1992; Backwell et al. 1995). As with *G. lineaticeps*, males produced more attractive signals when provided with diets of higher quality. Some studies have examined the condition-dependence of male traits by examining the correlation between a measure of body

condition and signal structure. In these studies, male body condition has been measured using a wide variety of methods. Some investigators have used weight to estimate a male's condition (e.g. Slagsvold & Lifjeld 1992). This method has the drawback of making condition size-dependent, unless males do not vary in size. Others have used condition indices that are derived by dividing weight by some measure of length (e.g. Nicoletto 1993; Docherty et al. 1995). The reliability of estimates of condition derived from this method can vary depending upon the slope of the relationship between weight and length. A more accurate method may be to use the residuals from a regression of weight on length as an estimate of condition (e.g. Galeotti et al. 1997). As our results illustrate, however, male traits can vary depending upon nutritional intake, without a correlated change in male weight. As a result, it might appear that a trait is not condition-dependent when in fact the trait varies with a male's diet.

Energy Allocation Strategies in Crickets

When nutrients are abundant, there are two potential patterns of energy allocation males could adopt. First, they could invest all energy above their basic maintenance requirements in the production of signals for mate attraction. Second, they could store some of the excess nutrients, either to enhance survival or for later use in mate attraction. Because males on the high-nutrition feeding regime engaged in costlier calling and did not gain weight relative to males on the low-nutrition feeding regime, it appears that males of this species may invest any excess energy above their basic maintenance requirements in calling. This hypothesis is supported by the lack of a relationship between our measure of condition (see Methods) and calling behaviour for males in the field. The observation that males on the low-nutrition feeding regime did not lose weight suggests that both feeding regimes were adequate for the minimum maintenance requirements of most males.

Like *G. lineaticeps*, male bushcrickets, *Requena verticalis*, increase their calling effort when provided with more nutrients (Simmons et al. 1992). Unlike *G. lineaticeps*, however, *R. verticalis* males provided with more nutritional diets gained weight, storing some of the additional energy in body tissue. This difference between the two species may be a result of differences in their natural histories, such as differences in survivorship. If adult survivorship is low, it may pay for males to invest excess energy in current reproductive behaviour, such as calling, rather than storing it for future use (Williams 1966; Stearns 1976). In *G. lineaticeps*, males are attacked by acoustically orienting parasitoid flies (Wagner 1996). The risk of parasitism for males varies both between years and over the course of any given year, but during some periods up to 96% of males may be parasitized (W. E. Wagner, Jr & M. G. Reiser, unpublished data). Because the parasitoids kill their hosts within approximately 7 days after entering a male (Cade 1975), selection may favour investment in current rather than future reproduction by males in this species. Alternatively, female choice

based on nutrition-dependent signals may be stronger in *G. lineaticeps* than in *R. verticalis*, forcing males to invest all available energy in the production of more attractive calling songs.

In our experiments, the high- and low-nutrition males were provided with a standard quantity of food each day. As a result, the low-nutrition males did not have the option of eating more to compensate for the lower-quality diet. Under natural conditions, such males might spend more time foraging. In some animals, for example, males appear to abandon calling to forage when energy reserves drop below some critical threshold (e.g. Murphy 1994). The observation that 77% of the low-nutrition males produced calling songs during our experiments, however, suggests that many low-nutrition males might continue to call under natural conditions, even though some components of their calling songs are less attractive to females. Whether they would forage during periods when they are not calling, however, is not known. Foraging itself may be costly, particularly in terms of predation risk (Lima & Dill 1990), and whether low-nutrition males forage more than high-nutrition males should depend on a complex set of factors, including the rate of mate attraction when producing less attractive calls, the predation risk associated with additional foraging, the cost of lost mating opportunities during periods of additional foraging, the increase in the rate of mate attraction resulting from the acquisition of additional energy, and the effect of nutritional differences on the reproductive life span of males.

Female Mating Preferences

It has been proposed that there is a general relationship between signal attractiveness and energy expenditure (Ryan 1988). As pointed out by others, however, evidence to support this conclusion is sparse (e.g. Watson & Lighton 1994; Reinhold et al. 1998). In *G. lineaticeps*, females possess preferences based on one trait, chirp rate, that affects the energetic cost of calling, and that varies with male nutritional status. They also possess preferences based on one trait, chirp duration, that does not appear to affect the energetic cost of calling, and that does not appear to vary with male nutritional status. While the production of higher chirp rates and longer chirp durations results in the production of greater acoustic energy, only the former appears to require more metabolic energy to produce. A similar result was found by Reinhold et al. (1998). In lesser wax moths, *Achroia grisella*, females prefer ultrasonic signals with higher pulse rates, higher amplitudes, and longer asynchrony intervals, but only pulse rate affects the energetic cost of signalling.

Without further information it is impossible to assess why preferences based on chirp rate and chirp duration have evolved. While condition-dependent mating preferences are predicted both by some direct and by some indirect benefits models of preference evolution, such preferences are not inconsistent with any model of sexual selection (Kirkpatrick & Ryan 1991; Backwell et al. 1995; Reinhold et al. 1998). There are, however, some obvious

reasons why these preferences may have evolved. Because male field crickets transfer spermatophores to females during mating that the females eventually remove and eat, females may receive nutritional benefits from eating the spermatophores of higher-nutrition males. Females will mate repeatedly with the same male, and they might also benefit from faster spermatophore replacement times by high-nutrition males, either in terms of nutrient intake or reduced mating time. Males that obtain more nutrients are known to produce spermatophores at a faster rate, but the wet mass of spermatophores does not appear to vary with nutrient intake (W. E. Wagner, Jr & M. G. Reiser, unpublished data). If higher chirp rates are easier to localize, females might reduce their search costs by orienting towards such calls. If nutrient intake affects the number of viable sperm that males produce (e.g. Matthews et al. 1997), females might fertilize a higher proportion of their eggs by orienting to higher chirp rates. Females might also prefer males that produce chirps at a higher rate because of fitness benefits that accrue to offspring.

It is not clear why females prefer longer chirp durations. If females prefer males that have higher chirp rates because of the nutrition-dependent benefits that they receive from such males, preferences based on chirp duration may have evolved for a different reason, because chirp duration is independent of male nutritional intake. It is possible that nutritional conditions prior to sexual maturity affect the chirp durations of adult males, and that females mating with such males produce offspring that are better at acquiring nutrients. In other crickets, larval conditions can affect male calling song structure (e.g. Olvido & Mousseau 1995). Females may also receive benefits that are not related to nutrition if, for example, longer chirps are easier to localize.

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