ARTICLE

Cricket mate selection as a spatial discounting phenomenon without learning

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Abstract
Many animals prefer small local benefits to large but temporally or spatially distant benefits, and this preference is termed "temporal discounting" or "spatial discounting." Although temporal discounting has been studied in many taxa, only a limited number of papers have primarily focused on spatial discounting. Here, a mate-choice experiment was conducted using female house crickets (*Acheta domesticus*) tasked with selecting between a non-attractive local male and an attractive distant male; training procedures were not performed. The results showed that females that had never heard the calling songs of males exhibited spatial discounting behavior. This finding may be key to determining the fundamental differences between temporal and spatial discounting.

Keywords Decision making · Temporal discounting · Mate-choice experiment · *Acheta domesticus* · Discount rate

Introduction

Many animals, including humans, usually prefer small benefits that can be accessed instantly, even if they have an access to much larger benefits that are temporally distant (Shane et al. 2002). Individual decision-makers appear to discount the absolute value of benefits caused by temporal delays, a phenomenon termed "temporal discounting".

Another concept of discounting is introduced to explain decision-making in animals: spatial discounting considers distance to the reward, whereas temporal discounting considers the time delay to the reward. Empirical evidence of spatial discounting has been reported in a New World monkey (Stevens et al. 2005) and guppies (Mühlhoff et al. 2011).

In ethology and evolutionary biology, there is only a limited number of explanations for the way temporal discounting behavior could be adaptive, where it is considered to be risk hedging against an uncertain future (Sozou 1998; Fawcett et al. 2012). However, these hypotheses have not been directly tested with empirical data. Although temporal discounting behavior has been reported in many vertebrates, including birds (Ainslie 1974; Bateson and Kacelnik 1996; Stephens and Anderson 2001; Mizuyama et al. 2016) and mammals (Richards et al. 1997; Pelé et al. 2010, 2011), the fundamental reason animals exhibit temporal discounting behavior remains unresolved.

Although spatial discounting has been treated as similar to temporal discounting, except for the differences in the discounting units (temporal delay or spatial distance), some studies have suggested that temporal discounting and spatial discounting are completely different processes. Stevens et al. (2005) used two New World monkey species and adopted a similar experimental design for both temporal and spatial tasks, and their results revealed that a difference in context (whether subjects experience a temporal delay or spatial distance) affected how subjects discount rewards. While a temporally distant reward is discounted according to a hyperbolic function (decaying discount rate), a spatially distant reward is discounted according to an exponential

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function (constant discount rate). Thus, temporal and spatial discounting might be fundamentally different phenomena selected by a different evolutionary process. However, a limited number of studies have discussed whether temporal and spatial discounting are different phenomena.

This lack of research is partly related to the limited number of reports on spatial discounting. The lack of attention paid to spatial discounting may be related to the history of research into temporal discounting. Most empirical research on temporal discounting has been conducted by animal psychologists using an operant learning procedure (Ainslie 1974; Bateson and Kacelnik 1996; Stephens and Anderson 2001; Mizuyama et al. 2016). Therefore, the subjects were implicitly restricted to vertebrate animals with high cognitive ability. Though spatial discounting experiments need not be based on operant learning in theory, it has also been studied only in vertebrates (Stevens et al. 2005). This might be just because the concept is influenced by temporal discounting.

For the fundamental difference(s) between temporal and spatial discounting to be discussed, additional empirical data on spatial discounting are needed. If spatial discounting is an innate trait, we can expect this behavior in wide-ranging taxa. Identifying non-vertebrate discounting behavior enables a more thorough examination of the fundamental differences between temporal and spatial discounting. Therefore, this paper aims to examine the potential for spatial discounting in non-vertebrate animals that lack higher cognitive ability.

Male house crickets (*Acheta domesticus*) use calling songs to attract females, and these songs usually consist of 1.5–3.0 pulses per chirp (Stout et al. 1983; Gray 1997). Female crickets prefer more pulses per chirp as an indication of larger body size and higher immune capacity (Gray 1997; Ryder and Siva-Jothy 2000; Rantala 2003), which correspond to indirect fitness through the improved quality of offspring. In this study, we conducted playback experiments and recorded whether females selected distant songs with higher pulse rates or local songs with a lower number of pulses. In these experiments, the pulses per chirp represented an index of the absolute value, and the discounting behavior was tested without pre-training procedures. Female preference for a local song with fewer pulses per chirp over a distant song with more pulses would demonstrate that the female crickets discount absolute values without learning.

Materials and methods

Study organism

We reared approximately 300–500 house crickets (*A. domesticus*) in plastic cages (430×340×260 mm) according to

their development stages. Each individual had free access to food (Tetrafin; Spectrum Brands, Middleton, WI) and water. To avoid inbreeding, hundreds of new subjects from different local pet supplies were introduced into the laboratory stock two to three times per year. Therefore, the laboratory stock was derived from multiple males and females, and all subjects used for the experiments were hatched in the laboratory.

All subjects were separated into different cages according to their sex and nymphal stages. The cage for reproductive subjects (males and post-experimental females) was placed in a different room, thus eliminating the opportunity for females to hear the males' calling songs.

For the experiments, we randomly selected adult females and transferred them into individual containers 10–14 days after their final molt. All subjects in the experiments were hatched in the laboratory. As the females were never exposed to adult males in their nymphal stage, they had not heard the males' calling songs until the experimental trials began.

To avoid a learning effect, each female was used in only one trial, which included a specific combination of calls with specific distances to speakers. Thus, any learning effect was avoided in our experiments. Thus, the outcomes observed in the experiments (with no opportunities for learning) can be interpreted as innate behavior. Each individual female had free access to food and water. Each treatment (see below) had at least ten individuals.

Recording and editing of calls

A male song was recorded by using a condenser microphone (IK000008; IK Multimedia, Modena, Italy) and transformed into digital data (Audio Kontrol; Native Instruments, Berlin). The calling song consisted of a 3–4 kHz sound, so we eliminated background noise (20 Hz–3 kHZ) using a low-pass filter. The call was edited into three artificial calls with averages of 3.0, 2.3 and 1.7 pulses per chirp. We arranged the timing of pulses so that all calls had the same pulse rate and the same frequency characteristics; therefore, each chirp differed only in the number of pulses. The 3.0 call consisted of only chirps with three pulses; the 2.3 call used chirps with three and two pulses; and the 1.7 call used chirps with two and one pulses. The average chirp rate was 1.5/s, and the interval between chirps was 538 ms. All calls were on a 4-s loop. All these editing procedures were conducted using the software Cubase 6.5 (Steinberg, Hamburg, German).

Experimental procedures

Speakers (8SR-A27; Sony, Tokyo) were set on a plastic board (120 cm×50 cm) enclosed by rectangular pieces of wood. The calls were played using a music player (iPod Classic; Apple, Cupertino, CA). The speakers were covered

with egg cartons and a bundle of newspapers to maintain darkness in the vicinity of the speakers. This method facilitated a swift decision by the females because a darkened area is under lower predation pressure for crickets (Hedrick and Dill 1993). However, the remainder of the experimental arena was not covered.

The trial procedures were as follows: a female cricket was introduced into an empty cup, the distance of which to the two speakers was adjusted for each trial. Then, two types of calls were played from the two opposing speakers. The first speaker was set at a distance of 18 cm from the pudding cup, and the second speaker (placed in the opposite direction) was set at various distances depending on the trial. The calls with a lower number of pulses per chirp were played from the first speaker, and the calls with 3.0 pulses per chirp were played from the second speaker. Note that the calls with a lower number of pulses per chirp were played at a fixed distance in all experiments (Fig. 1). Regardless of the pulses and distances, all calls were played at 50 dB, which was measured at 18 cm in front of the speakers using a sound pressure level meter (CM-130; Galaxy Audio, Wichita, KS).

The two types of 4-s looped calls, i.e., less attractive calls and attractive calls, were played alternately during the 3-min acclimation time so that the female has enough time to evaluate both calls. After acclimation, we quietly removed the cup and measured the call selected by the female and the elapsed time before the female entered the shaded area (location of the speaker). The speaker used for the lower quality call was determined at random, and the surface of

the plastic board was cleaned with ethanol each time a new trial was conducted.

We performed two experiments. In experiment 1 (number of trials = 60; ten trials for each distances), the less attractive calls had 1.7 pulses and were played from the first speaker (18 cm away), and in experiment 2 (number of trials = 83; $n = 31$ for 80 cm and $n = 10$ for 56, 36, and 24 cm, and $n = 11$ for 21 and 18 cm), the less attractive calls had 2.3 pulses and were played from the first speaker. The number of trials differed among experiments and distances. See Fig. 1 for the detailed number of each trial. For both experiments, the 3.0 pulse was played from distances of 18, 21, 24, 36, or 80 in each experiment. Prior to the experiments, we set the following criteria: females that did not approach either speaker within 180 s were eliminated from the dataset. However, all females approached one speaker within 140 s (see Results). Through these experiments, we were able to test whether a female cricket discounted the absolute value of the two options based on their qualities (pulses), which is important because if a female cricket discriminates between calls solely based on quality, then she should show a preference for the more attractive calls at the same distance.

All statistical analyses were performed using R (3.2.3) (R Foundation for Statistical Computing, Vienna) and package MuMIn (1.15.6). We constructed generalized linear models and conducted variable selection based on the Bayesian information criterion (BIC). Note that the BIC is an approximate posterior model probability that assumes that all models have the same prior probability (Aho et al. 2014). The dependent variable was the binomial measure of whether the female selected the non-attractive lower pulse (= 1) or not (= 0). Candidate independent variables were the distance to attractive calls (18–80 cm as a numerical predictor) and the quality of the less attractive calls (1.7 or 2.3 as a categorical predictor). Finally, we conducted model averaging based on the BIC.

Fig. 1 Proportion of females that selected a lower pulse rate along the distance to the higher pulse speaker. The lower pulse rate speaker is 18 cm in the opposite direction. Two different pulse rates per chirp, 1.7 pulses (open circle with dotted lines) and 2.3 pulses (closed circle with solid lines), are presented as the lower pulse rate

Results

All females selected one speaker within 140 s (mean = 12.8 s). We found that only the full model was strongly supported (posterior model probability = 99%; see Table 1), indicating that both the distance and the number of the pulses were significant factors in female choice. Indeed, the female crickets preferred the attractive calls when the 3.0 pulses were local (averaged estimate = 0.036) (Table 2), but when the higher pulses were distant, the female crickets tended to select nearby less attractive calls (averaged estimate = 1.43) (Table 2). This result indicated that female crickets devalued the absolute value of the high pulses when the pulses were located at a distance.
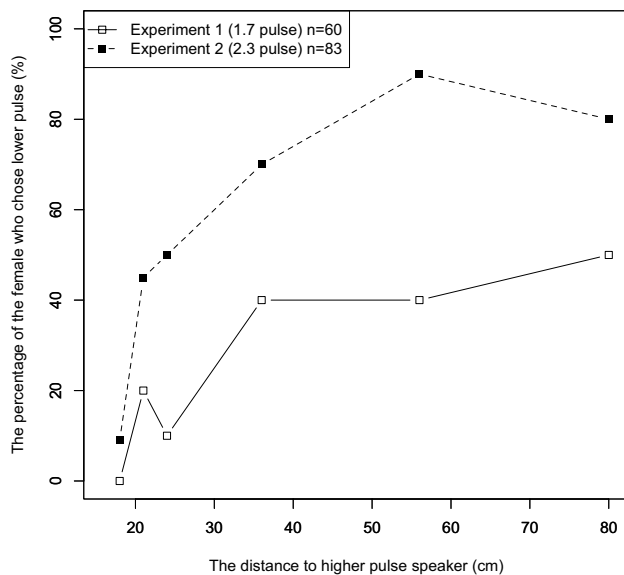
Table 1 Summary statistics of the models in order of Bayesian information criterion (*BIC*) (*n* = 143 integrating both experiments 1 and 2)

Model component	*df*	BIC	ΔBIC	Posterior prob.
Distance to attractive calls and quality of less attractive calls	3	171.09	–	0.99
Distance to attractive calls only	2	179.59	8.50	0.01
Quality of less attractive calls only	2	189.21	18.11	< 0.01
Intercept only	1	202.86	31.77	< 0.01

Model component represents the independent variable(s): *df* degree of freedom of number of free parameters, *BIC* BIC score, *ΔBIC* difference in the BIC score between the indicated model and most supported model, *Posterior prob.* approximate posterior model probability

Table 2 Summary of the model average (*n* = 143 integrating both experiments 1 and 2)

Independent variables	Estimate[a]
Intercept	− 2.57
Distance to attractive calls	0.03
Quality of less attractive calls	1.43

[a]Estimate is the averaged maximum likelihood estimate of each coefficient conditional on the posterior model probability approximated by the BIC

If the sampling size of our experiments was not sufficiently large, a certain model would not have been strongly supported against the others. However, the BIC, which can be used as an approximate posterior probability (Aho et al. 2014), indicated that only the full model was strongly supported (posterior model probability = 99%). In addition, the averaged estimate of the coefficient showed positive values for the distance to attractive calls and the quality of less attractive calls, where positive values indicate that the larger the covariance, the higher the probability of accepting the non-attractive male.

Thus, by integrating these results, we obtained evidence that female selection was strongly affected by both the distance to the attractive calls and the quality of less attractive calls. This result indicates the occurrence of spatial discounting in mate choice.

Discussion

Our results agree with the predictions of the spatial discounting theory, which states that distant benefits are discounted from their absolute values. For example, females showed a greater preference for the 3.0 pulses at 24 cm than the 1.7 pulses at 18 cm but selected the 3.0 pulses at 24 cm at the same rate as the 2.3 pulses at 18 cm. These results can be interpreted as follows. Discounting implies that the value of high-value resources is decreased based on the distance required to reach them (or time required to reach them). The 3.0 pulses at 24 cm decrease in value and become equivalent to the 2.3 pulses at 18 cm, but the 3.0 pulses at 24 cm still have a higher value than the 1.7 pulses at 18 cm.

Female selection could be explained as the females seeking a safe space (covered and darkened area) without recognizing that the distant speaker with the high-quality call is also a safe space. In this paper, our focus is not on whether the females recognize the safe space, so our design does not rule out the possibility of such a cause, especially when the high-quality calls were far away (56 or 80 cm). However, if a female's choice were determined based on only safety (and/or recognition of such a safety), then the difference between experiments 1 and 2 cannot be explained. A comparison between experiments 1 and 2 at the same distance shows that the proportion of females that selected the lower pulse was higher in experiment 2, and this trend was consistent at all distances tested (Fig. 1). Therefore, we conclude that females consider the quality of male calls before making a decision.

Previous studies on discounting have not eliminated the possibility that the observed discounting is a byproduct of learning procedures (Ainslie 1974; Bateson and Kacelnik 1996; Richards et al. 1997; Stephens and Anderson 2001; Pelé et al. 2010, 2011; Mizuyama et al. 2016); however, our experiment was designed to eliminate the chance of learning. Therefore, this study is the first demonstration of discounting without a prior learning process, and our findings demonstrate that spatial discounting is not a product of learning procedures.

In addition, we can reinterpret the results of several studies that did not focus on spatial discounting. Hedrick and Dill (1993) have shown that when the path to the attractive calls is through a brightly lit area (which implies high predation risks) and the less attractive calls are in a dark area, female field crickets (*Gryllus integer*) show a preference for the latter. The chief difference between the experimental designs of their study and ours are the ways risk were represented. Hedrick and Dill (1993) did not alter the distance between the two speakers but instead changed the environmental conditions of the path to the lower quality speaker via shading. Thus, these authors tested the female preference between high-quality males in a brightly lit (dangerous) environment and low-quality males in a darkened (safer) environment, and the shaded degrees (areas) were varied. Their results showed that a female prefers low-quality males in a safer environment over a high-quality male in a riskier environment. In our experiments, the females had to walk through a lit area to reach each type of male, which represented a trade off between a more distant but more attractive reward and a closer but less attractive reward.

The females frequently selected the closer but less attractive call, indicating that spatial discounting occurs in relation to distance (Fig. 1). Because we did not vary the predation risk, our experiments do not indicate whether spatial discounting is an adaptation to avoid predation risks. In the future, we may be able to test this question, such as by changing the brightness (light intensity) of the room.

More importantly, we eliminated the chance that the females would learn male calls in the nymphal stages to determine whether the behavior is a byproduct of learning procedures. Hedrick and Dill (1993) used virgin females that had heard conspecific male calls prior to the experiments.

Murphy showed that there is a trade off between mate quality and distance and concluded that mate choice is adaptive under this trade off (Murphy 2002). He carried out field playback experiments to examine mate choice in female barking treefrog (*Hyla gratiosa*) and showed that females preferred 500-Hz playback calls over 550 Hz calls when the calls were at the same distance; however, almost all females exhibited the opposite behavior when the preferred 500-Hz calls were placed at double the distance. Murphy's (2002) study can be reinterpreted as spatial discounting behavior. However, the female frogs used in his experiments were collected in the wild, and the same females were used several times in his experiments. Therefore, his study could not eliminate the possibility that discounting emerged as a result of learning, whereas the present study eliminated the possibility of learning.

In this study, we tested the mate selection of female house crickets in the absence of learning, and our results provide evidence for spatial discounting without experience or learning. Our results show the existence of non-vertebrate spatial discounting. These findings provide additional empirical data on spatial discounting and indicate that this phenomenon can be studied in a wider range of taxa, thus contributing important insights for identifying the fundamental differences between temporal and spatial discounting.

Compliance with ethical standards

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