

# Adaptive significance of death feigning posture as a specialized inducible defence against gape-limited predators

Atsushi Honma<sup>1,\*</sup>, Shintaro Oku<sup>2</sup> and Takayoshi Nishida<sup>1</sup>

<sup>1</sup>Laboratory of Insect Ecology, and <sup>2</sup>Laboratory of Forest Ecology, Graduate School of Agriculture, Kyoto University, Kyoto 606-8502, Japan

Death feigning is fairly common in a number of taxa, but the adaptive significance of this behaviour is still unclear and has seldom been tested. To date, all proposed hypotheses have assumed that prey manage to escape predation by sending a death-mimicking signal, although death-feigning postures are markedly different from those of dead animals. Moreover, the efficacy of this technique may largely depend on the foraging mode of the predator; death feigning seldom works with sit-and-wait predators that make the decision to attack and consume prey within a very brief time. We examined whether death feigning in the pygmy grasshopper *Criotettix japonicus* Haan was an inducible defence behaviour against the frog *Rana nigromaculata*, a sit-and-wait, gape-limited predator. The characteristic posture assumed by the grasshopper during death feigning enlarges its functional body size by stretching each of three body parts (pronotum, hind legs and lateral spines) in three different directions, thereby making it difficult for the predator to swallow the prey. Our result is the first consistent explanation for why death-mimicking animals do not always mimic the posture of dead animals.

**Keywords:** death-feigning; adaptive significance; anti-predator response; gape-limited predator

## 1. INTRODUCTION

In theoretical predator–prey interactions, predators have traditionally been regarded as abstract sources of risk to prey, rather than participants in behavioural interactions (Lima 2002). If predators are allowed to respond to prey behaviour, the expectations about prey behaviour can change radically (Lima 2002). Here, we examine the adaptive significance of death-feigning behaviour, the function of which has seldom been examined using purpose-designed experimentation (Miyatake *et al.* 2004; Ruxton *et al.* 2004), from a novel viewpoint that includes the foraging modes of predators.

Death feigning has been observed in a number of taxa (e.g. mammals, Francq 1969; birds, Rovee *et al.* 1976; reptiles, Greene 1988; insects, Holmes 1906, Edmunds 1972), and is a type of hypnotic reaction or immobility elicited by the presence of predators (Ratner 1967). Although there are many similar types of reaction, death feigning is distinguishable in that it constitutes a secondary defence elicited only after encountering a predator (Edmunds 1974; Ruxton *et al.* 2004) and is associated with a characteristic fixed posture (Ratner 1967; Chemsak & Linsley 1970; Miyatake 2001). Because the posture is sometimes markedly different from that of dead animals, the behaviour is an imperfect mimic of death. However, there is currently no explanation for this discrepancy.

Several hypotheses have been proposed to explain the adaptive significance of death feigning. For example, prey animals feign death: (i) to reduce the motivation of predators which specialize in capturing live prey (Rovee *et al.* 1976), (ii) to enhance escape opportunities from

predators which handle prey gently or momentarily release them prior to feeding (Ratner & Thompson 1960) and (iii) to get opportunities of escape from predators which briefly store their prey after they have ‘killed’ it (Rovee *et al.* 1976). All of these hypotheses tacitly assume that prey manipulate predators by sending the false information that they are dead. However, the success or failure of death feigning depends largely on the foraging mode of the predator. For instance, by sending a death-feigning signal, prey may be able to stop the subjugating behaviour of predators that handle prey gently for a relatively long time before consuming them. In contrast, death feigning may be very ineffective against sit-and-wait predators that make the decision to attack and then consume prey within a very brief time, because prey may recognize predators only after being attacked, and thus may not have time to feign death. Moreover, no convincing explanation accounts for the adaptive significance of sending false death information to predators during subjugation. Rather, an immobility reaction would help the predator in handling the prey. Does death feigning truly confer no adaptive significance against sit-and-wait predators, particularly during subjugation, or does it provide another selective advantage that has yet to be explored?

In this paper, we show that death feigning by the pygmy grasshopper *Criotettix japonicus* Haan is a specialized inducible defence against predation by frogs. We propose and support a novel hypothesis of death feigning; specifically, a prey species can avoid being swallowed by sit-and-wait, gape-limited predators by assuming a characteristic rigid position. In this sense, some so-called death-feigning behaviours do not mimic death *per se*, but rather, enlarge the operational body size of the prey

\* Author for correspondence (honma@kais.kyoto-u.ac.jp).

through a characteristic rigid posture. Our findings may provide the first consistent explanation of these characteristic positions adopted by animals during death-feigning behaviour in a broad range of taxa.

## 2. MATERIAL AND METHODS

### (a) *Experiment 1: the grasshopper feigns death in response to which predator(s)?*

First, we performed an experiment to determine towards which predator(s) the pygmy grasshopper feigns death. Thus, potential predators were examined to determine whether they elicited death-feigning behaviour in the pygmy grasshopper. Adult male pygmy grasshoppers were introduced individually to cages in which a predator had been reared. Each predator was used only once to eliminate possible effects of learning.

#### (i) *Prey: pygmy grasshopper*

*C. japonicus* is a large (15–20 mm in body length) pygmy grasshopper that inhabits wet habitats, such as the fringes of ponds and paddy fields. It lives on the soil surface and feeds on detritus and algae. This species is characterized by an extremely long, hard pronotum with a pair of lateral spines. Pygmy grasshoppers were collected in old paddy fields in Iwakura, in the northern suburbs of Kyoto, western Japan, and held in the laboratory with ample amount of detritus (dead leaves) as food and water absorbed in cotton, at 30 °C with 16 h light : 8 h darkness for at least 24 h before the experiment. Only male grasshoppers were used.

#### (ii) *Predators: bird, amphibian, insect and spider*

Japanese quail (*Coturnix japonica*) are small omnivorous gallinaceous birds that are widely distributed in eastern Asia. Ten birds about 30 days old were acquired from Shimizu Laboratory Supplies (Kyoto, Japan). In the laboratory, all birds were housed in an open-air cage (180 × 180 × 180 cm), where they had *ad libitum* access to water and food (Nippon Formula Feed, Yokohama, Japan).

The frog *Rana nigromaculata* Hallowell is the most abundant potential predator of *C. japonicus* in paddy fields. This frog is a relatively large generalist (less than 90 mm in snout-vent length, SVL) and is widely distributed in paddy fields throughout western Japan (Hirai & Matsui 1999; Maeda & Matsui 1999). We collected 20 *R. nigromaculata* of various sizes from old paddy fields in Iwakura. Captured frogs were held individually in plastic cages (23 × 12 × 12 cm) and maintained in the laboratory at 30 °C with 16 h light : 8 h darkness. Mealworms (*Tenebrio molitor*) were provided as food, although frogs were starved for 24 h before a feeding experiment to standardize their level of hunger. After the experiments, all frogs were returned to their habitats.

The praying mantis *Tenodera angustipennis* Saussure is a large predator (60–90 mm in body length) that inhabits grasslands and is broadly distributed across Japan. Nine adult mantids were collected from a greenhouse belonging to the Itami Museum of Insects, Osaka Prefecture, western Japan. Captured mantids were housed individually in plastic cups (12 cm diameter, 10 cm height) and maintained outdoors in the natural temperature and light conditions. Cabbage white butterflies (*Pieris rapae* L.) were provided as food once a day.

The wolf spider *Pardosa pseudoannulata* is the most common spider inhabiting rice fields in Japan and is an important predator of plant and leaf hoppers. Because wolf spiders spend most of their time on the ground, they are expected to encounter pygmy grasshoppers often. Twenty adult female spiders (10–13 mm in body length) were collected from old paddy fields in Iwakura. They were housed individually in plastic cups (12 cm diameter, 5 cm height) and maintained in the laboratory at 30 °C with 16 h light : 8 h darkness. Mealworms were provided as food. All frogs, praying mantis and spiders were starved for 24 h before a feeding experiment to standardize their hunger levels.

### (b) *Experiment 2: what is the function of death feigning in the pygmy grasshopper?*

We collected 9, 20 and 19 *R. nigromaculata* of various sizes from old paddy fields in Iwakura, Sizuvara and the Kyoto University experimental rice field, respectively. All three sites were located in the northern suburbs of Kyoto, western Japan. Forty-eight male pygmy grasshoppers were obtained from the same site in Iwakura. Captured frogs and pygmy grasshoppers were maintained as in experiment 1.

We examined how the death-feigning posture, in conjunction with the long pronotum and/or lateral spines, prevented frogs from swallowing grasshoppers. We manipulated the posture of grasshoppers by altering their hind legs, pronotum and lateral spines. The hind legs were left either intact or tied to the pronotum with thin fishing line (Toray Syorin, 0.049 mm in diameter, Tokyo, Japan) so that the death-feigning posture could not be assumed. The pronotum was cut at one of three different locations with a knife to produce three lengths: 15 mm (intact control, cut at the very tip of the pronotum), 11 mm and 7 mm. The lateral spines were either left intact or cut. Removal of the pronotum and lateral spines did not appear to have a detrimental effect on the behaviour or survival of grasshoppers. In addition, frogs were divided into two classes according to body size at 40 mm (SVL). An SVL of 40 mm represents the maximum size to which newly metamorphosed frogs grow in the first season. Thus, in total we had 24 treatment combinations: 2 frog body sizes × 2 hind leg treatments × 3 pronotum lengths × 2 lateral spine treatments.

Each of the 48 pygmy grasshoppers was assigned to one of these treatment combinations and treated grasshoppers were then presented to *R. nigromaculata* of various sizes. Although we did not collect a large number of frogs, each frog was used for the experiment only once to eliminate possible effects of learning. Thus, we only attempted each treatment twice.

The experiment was conducted in the frog holding room to minimize disturbances. One adult male grasshopper was introduced to each of the 48 frog cages and the resultant predatory behaviour was recorded using a video camera (SONY Digital Video Camera Recorder DCR-TRV10, Tokyo, Japan). A predation event occurred when a frog attacked a grasshopper; predation was successful when the grasshopper was swallowed. All other interactions were considered predation failure.

We categorized the prey-holding orientation of frogs into two patterns: lateral and dorso-ventral. In the lateral orientation, the lateral sides of the grasshopper were facing

up and down inside the mouth of the frog; in the dorso-ventral orientation, the dorsal and ventral sides of the grasshopper were facing up and down inside the mouth of the frog. The holding orientation was determined by viewing the video tape of each trial. In addition, when predation was successful, the handling time was compared between treatments in which the hind legs were intact or tied.

All statistical analyses were performed using JMP 4.0 (SAS Institute Inc. 2000). Multiple logistic regression was conducted to test for treatment effects. The whole-model test indicated that the model was significant ( $p=0.0074$ ), whereas the lack-of-fit  $\chi^2$  test was not significant ( $p=0.70$ ) and supported the conclusion that little was gained by introducing variation in the regressor variables. Consequently, the model was adopted and the effect of each parameter in preventing frogs from swallowing grasshoppers was determined using a likelihood ratio test (table 2).

### 3. RESULTS

#### (a) Experiment 1

Death feigning in *C. japonicus* was elicited only by frogs, not by other potential predators such as birds (Japanese quail), mantids or spiders (table 1).

*C. japonicus* assumed the characteristic rigid position by firmly bending its hind legs downward to form a T-like shape (figure 1) only when attacked and caught by *R. nigromaculata*. Pygmy grasshoppers took this position immediately after capture (figure 2) and maintained the position even after being released. Because of the two features of secondary defence and characteristic posture, this behaviour was regarded as death feigning. Without further disturbance by the frogs, death feigning ended after several minutes (figure 2c). If another type of physical stimulus, other than a predatory attack by a frog, was given, the grasshopper immediately stopped the death-feigning behaviour and resumed normal activity. This allowed us to distinguish between death-feigning behaviour and freezing behaviour, which was elicited before a predator attack and was not associated with a specific posture.

When an avian predator failed to catch the grasshopper during the first attack (8 of 10 times; table 1), the prey jumped away before the second attack. No grasshoppers feigned death in response to an avian predator (table 1). Mantid predators held the grasshoppers with their forelegs and gnawed on them. When subjugated by a mantid, a grasshopper sometimes struggled with its legs to escape, but was only successful in one case (table 1). All spiders attacked the grasshoppers but were never able to consume them and never induced the death-feigning response (table 1). Moreover, some grasshoppers threatened the spiders by swaying the body.

#### (b) Experiment 2

Positive parameters for tying the hind legs, cutting the pronotum and cutting the lateral spines and negative values for frog body size (table 2) indicated that the three manipulations prevented relatively small frogs from swallowing the grasshoppers. Among the three grasshopper manipulations, however, no independent or

Table 1. The results of predation experiments. (Death-feigning in *Crioteitix japonicus* was elicited by frogs (*Rana nigromaculata*), but not by other potential predators, such as birds (Japanese quail, *Coturnix japonica*), mantids (*Tenodera angustipennis*) or spiders (*Pardosa pseudoannulata*). Different lowercase letters indicate a significant difference (Fisher's exact test,  $p<0.001$ ). The results indicate that death feigning was a specialized adaptation against frog predation. One adult male pygmy grasshopper was placed in each cage in which a predator had been reared. Each predator was used only once to eliminate possible effects of learning.)

	predator			
	bird	frog	mantis	spider
number of attacks	10	20	9	20
death-feigning occurred	0 <sup>b</sup>	17 <sup>a</sup>	0 <sup>b</sup>	0 <sup>b</sup>
predation was successful	2	4	8	0

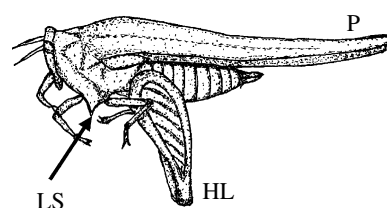


Figure 1. Death-feigning posture in the pygmy grasshopper *Crioteitix japonicus*. This characteristic position enlarges the functional body size in three dimensions by stretching the pronotum (P), hind legs (HL) and lateral spines (LS).

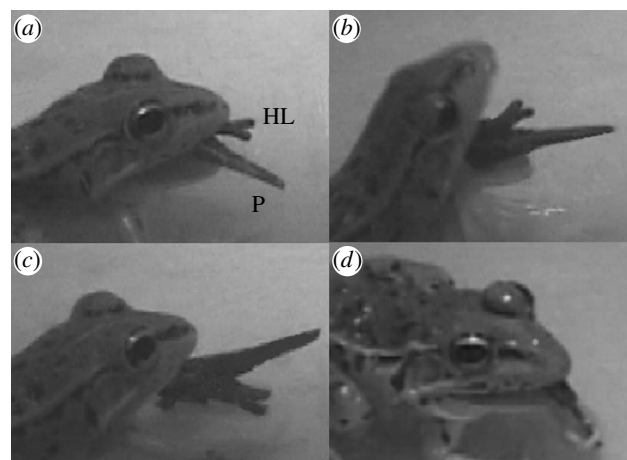


Figure 2. (a) When attacked and caught by a frog (*Rana nigromaculata*), the grasshopper (*Crioteitix japonicus*) assumes a death-feigning position, which forces the frog to hold the grasshopper in a lateral position. (b) The death-feigning position prevents a gape-limited predator from adjusting the orientation of the grasshopper for easier swallowing, and increases the predator's risk of puncturing its upper jaw or tongue with the spines. (c) The spines of the grasshopper project inside the mouth of the predator, causing the frog to reject the grasshopper. Without further disturbance by the frog, death feigning ends after several minutes. (d) Tying the hind legs of the grasshopper allows the frog to hold the prey in a dorso-ventral position, which facilitates swallowing the prey. P, pronotum; HL, hind legs.

significant effect was detected as a result of removing the lateral spines (table 2).

Through the video analysis, we were able to identify the behavioural mechanism that allowed frogs to easily

Table 2. Results of multiple logistic regression for experiment 2. (Positive (pronotum, hind legs and lateral spines) and negative (frog size) parameters indicate that the three grasshopper manipulations prevented relatively small frogs from swallowing the grasshoppers. This also suggests that these traits represent morphological defences against frogs. Among the three grasshopper manipulations, neither independent nor significant effects were detected for cutting of the lateral spines. Significance was assessed by the change in the likelihood ratio test statistic (which approximates  $\chi^2$ ) when independent variables were removed from the statistical model.)

parameters	estimate	$\chi^2$	<i>p</i> -value
pronotum cut	0.297	5.420	0.020
hind legs tied	0.844	4.082	0.043
lateral spines cut	0.403	0.951	0.329
frog body size	-0.131	5.468	0.019

swallow grasshoppers whose legs were tied. Immobilizing the hind legs allowed frogs to change the orientation with which they held the prey. The frogs held the grasshoppers in significantly different orientation according to the condition of prey's hindlegs ( $p=0.0006$ , Fisher's exact test). The frogs held grasshoppers in a lateral position (figure 2*a*) when the hind legs were free (lateral : dorso-ventral = 17 : 1), but often held the grasshoppers dorso-ventrally (lateral : dorso-ventral = 5 : 9) when the legs were tied (figure 2*d*). Handling time was significantly reduced by tying the legs (tied versus free,  $8.61 \pm 7.1$  versus  $23.25 \pm 17.15$  s, respectively,  $p=0.0025$ , Mann-Whitney *U*-test).

#### 4. DISCUSSION

The results of experiment 1 (table 1) indicate that death feigning in *C. japonicus* is a specialized adaptation against frog predation. The results of experiment 2 suggest that this posture represents a morphological defence against frogs, and support the assumption that armour is a morphological defence trait against frog predators associated with wet habitats, because neither *Tetrix japonica* nor *Euparotetix insularis*, the other two sympatric species in the same family of grasshoppers that live in drier microhabitats with few frogs, have such defensive traits. Moreover, the function of death feigning in the pygmy grasshopper is contrary to all proposed hypotheses, which assume that prey manage to escape predation by sending a death-mimicking signal. This is because the pygmy grasshopper has no time to stop the frog from swallowing it as it begins to feign death when the frog was just about to swallow it.

The predation experiment and video analysis further revealed a combined function of the death-feigning posture and the lateral spines. Frogs usually managed to correct the orientation of the grasshoppers before swallowing them headfirst. Tying the hind legs markedly shortened the handling time, indicating that the death-feigning posture made it difficult for the predator to correct the orientation of the prey, and ultimately prevented the frogs from swallowing the grasshoppers. In addition, a longer handling time may increase the risk that the lateral spines become stuck in the mouth of the frog. After holding prey in the mouth, the frog swallows it by pushing forcefully with the upper jaw and tongue. The death-feigning posture forces the predator to hold the

prey laterally, thus causing the hind legs to project perpendicularly to the head-pronotum and lateral axis and possibly increasing the frog's risk of puncturing its upper jaw or tongue with the spines (figure 2*b*).

It is not clear why the lateral spines, which are obviously defensive, did not significantly affect predation success. Tying the hind legs of the grasshoppers may have neutralized the effects of lateral spines by allowing the frogs to hold the grasshoppers dorso-ventrally, so that the spines did not stick up. That is, if the lateral spines function only when a frog holds the prey in its mouth laterally, then the hind leg treatment may have masked the effect of lateral spines. The lateral spines may not function effectively without the aid of both the pronotum and the characteristic death-feigning posture. Another possibility is that the other defensive traits are effective enough to prevent small frogs from swallowing grasshoppers, whereas even the whole armoury of defensive traits may not work against large frogs. Each frog was given a single opportunity to attack a pygmy grasshopper of a given size. Thus, the experimental design did not allow us to identify such interactions with statistical confidence. Significant effects of lateral spines may be detected if the predation behaviour of medium-sized frogs is examined by providing them with pygmy grasshoppers whose hind legs are either intact or tied.

Which contextual conditions between prey and predator have favoured the death-feigning posture? Endler (1986) reviewed the sequence of predatory stages followed in successful predation events and concluded that earlier interruption during the predatory stages may be advantageous for prey to avoid predation. This is because earlier interruption may reduce predation risk, preserve current energy reserves and resultant future fitness and reduce the relative frequency of predation events (Endler 1991). As a result, there should be a larger frequency of encounters terminated earlier than later (Endler 1991). However, it is the foraging mode of the predator, rather than the anti-predation defences of the prey, that determines the success of early predation interruption. For instance, prey may not detect sit-and-wait predators, which seldom move except when they attack prey within a certain range (Hamilton 1948), before the attack. To avoid the risk of predation by these predators, prey may be obliged to engage counter-defences that are elicited after the attack is initiated.

Another characteristic of frogs is that they are gape-limited (Toft 1980), i.e. the body size and width of the mouth determine their feeding habits (Toft 1980; Houston 1987). In *R. nigromaculata*, larger individuals have a larger diet volume comprising fewer prey items (Hirai 2002). A field survey of the stomach contents of *R. nigromaculata* showed that *C. japonicus* was not consumed by small (less than 40 mm SVL) or large (greater than 50 mm SVL) frogs, although the latter easily captured and swallowed grasshoppers in the laboratory. Only 3 of 316 frogs (SVL 20.70–71.28 mm) consumed grasshoppers in the field even though the density of grasshoppers in their microhabitat was  $1.63 \text{ m}^{-2}$  and their SVLs were 42.42, 43.31 and 38.66 mm (A. Honma, unpublished data). These results suggest that *R. nigromaculata* is not only gape-limited, but is also a classical optimal forager (Stephens & Krebs 1986) that ignores small prey items, relative to its own body size, to maximize its energetic gain. Ingle (1968) also reported that ranid

frogs could determine the absolute size of objects and then change their behaviour (attack or ignore). If frogs have an optimal prey size that elicits predatory behaviour and varies ontogenetically, then optimal foraging may be realized. If so, the grasshopper's anti-predator tactic of increasing the functional body size when threatened by a frog may decrease the vulnerability to attack by small, optimally foraging frogs in up to 80% of the population (A. Honma, unpublished data) and increase the survival rate.

A similar adaptive significance of death feigning may be prevalent in a broad range of animal taxa in which predators swallow the prey whole. Nymphs of the stonefly *Pteronarcys dorsata* feign death by curling up into a tight ball when attacked by rainbow trout (*Oncorhynchus mykiss*), allowing them to successfully survive such attacks because the curling behaviour causes the cerci to project outward like spines, reducing the handling success of the trout (Moore & Williams 1990). However, these nymphs are easily eaten by trout shortly after their death (Moore & Williams 1990). In contrast, the experimental removal of cerci greatly enhanced nymph mortality caused by fish (Otto & Sjöström 1983). These results suggest that death feigning by stoneflies has the same function as that of *C. japonicus*. Many coleopterans also feign death in volume- or size-enhancing positions (e.g. Chemsak & Linsley 1970; Oliver 1996; Miyatake 2001). In particular, the death-feigning posture of cerambycid beetles is very similar to that of *C. japonicus* (Chemsak & Linsley 1970). These death-feigning behaviours may also perform the function of preventing prey from being swallowed by specific predators.

Death feigning in *C. japonicus* was elicited only by *R. nigromaculata*, and not by other sympatric predators such as birds, mantids or spiders, even though mantids killed grasshoppers more easily than frogs did (table 1). This suggests that the foraging mode of the predator, rather than its degree of danger, determine whether the death-feigning behaviour is elicited. Specifically, death feigning could be ineffective against mantids, because mantids do not attempt to swallow grasshopper whole. Therefore, in studying the evolutionary dynamics of predator-prey interactions, it is necessary to account for both the foraging and predation-avoidance tactics of the participants, and to examine mutual effects created through the cognitive processes peculiar to each of the participants. Understanding the responses of predators to the reactions of prey may lead to radically different expectations of prey behaviour and may reveal new aspects of behavioural phenomena that occur at large spatial scales (Lima 2002).

We confirmed that prey can prevent predation by gape-limited predators by assuming a characteristic rigid posture, but not by manipulating the predator by providing misleading information. In this regard, several so-called death-feigning behaviours do not actually mimic death, but instead, enlarge the functional body size of the prey. Our findings provide a consistent explanation for why death-mimicking animals often assume different positions than dead animals in a wide variety of taxa. The characteristic posture may have an important function in anti-predator defence.

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