Behavioral Response of Mantid *Hierodula patellifera* to Wind as an Antipredator Strategy

H. WATANABE¹ AND E. YANO

Entomological Laboratory, Faculty of Agriculture, Kinki University, Nara, 631-8505 Japan

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ABSTRACT We tested the hypothesis that the mantid *Hierodula patellifera* (Serville) sways its body to mimic trembling leaves in the wind as an antipredator strategy. In the field, walking and body-swaying behavior were observed more frequently when the wind blew harder; mantids began walking and swaying as wind velocity increased. In the laboratory, walking and swaying behavior were observed more frequently under windy than under windless conditions, and mantids walked and swayed more frequently when wind velocity was variable than under constant velocity conditions. The discovery rate of the prey mantids by predators was significantly lower on swaying leaves than on fixed leaves. Our results thus indicate that mantids responded actively to wind, and we suggest that walking and body-swaying behaviors are adaptive in reducing the risk of predation.

KEY WORDS mantid, wind, crypsis, antipredator strategy, behavior

Crypsis is one of the most frequent antipredator strategies throughout the animal kingdom; it occurs in amphibians (Laurila et al. 1997, Petranka and Hayes 1998), reptiles (Lopez and Martin 2001), and insects (e.g., orthopterans, Hatle and Faragher 1998). Crypsis is the resemblance of an animal to its background, and its simplest form is color matching. Crypsis and mimicry seem to be distinct, although leaflike insects such as mantids are described by some researchers as being cryptic and by others as mimetic (Edmunds and Brunner 1999). Special resemblance includes adoption of a specific morphological resemblance to an inedible object (Cott 1957). It is useful to distinguish camouflage involving a general resemblance to the background (crypsis) from camouflage involving a very close resemblance to some specific object that a predator may recognize but not associate with food (special resemblance, Robinson 1969a, b). The main types of special resemblance in mantids are resemblance to leaves, flowers, sticks, and grass (plant-part mimics), and many species of praying mantids are protected in this way (Edmunds and Brunner 1999), because predators often fail to recognize them. Protective resemblance is the basic means of defense among mantid species (Crane 1952).

Among animals that use crypsis to avoid predators, immobility reduces the risk of detection. The benefit of immobility will also depend upon the animal’s background or substratum, because animals on a matching substratum have a higher level of crypticity than those on nonmatching substrata and have more to gain by remaining still (Houtman and Dill 1994). Immobility is most effective at a distance, when there is less chance of a predator having already seen the mantid. The remarkable adaptations of leaf mimics include not only morphological resemblance, but also a special behavior involving adaptive stillness during daylight, or imitation of a leaf swaying in the wind (Cott 1957). Mantids face a dilemma because they must move to capture prey and find mates. They have evolved a variety of behavioral adaptations to avoid predation when primary defenses such as crypsis fail (Curio 1976). For many predators that actively pursue their prey, cryptic behavior (in particular immobility) is at conflict with successful foraging (Edmunds and Brunner 1999). Swaying movement may help to conceal an animal because it resembles the movement of leaves disturbed by a gentle breeze (Robinson 1969a). Mantids often move slowly in such a manner (Edmunds and Brunner 1999), and body-swaying behavior probably enhances resemblance to leaves moving in the wind (Cott 1957, Bedford 1978). Although several researchers have shown that mantids respond to blowing wind, little is known of their sensitivity and responses to wind velocity or indeed whether the response to wind has cryptic effects against predation on mantids.

We focused on responses of the mantid *Hierodula patellifera* (Serville) to changes in wind velocity. The species is arboreal and experiences strong and variable wind conditions high in tree canopies. We hypothesized that mantids change their activity with wind velocity and use the effect of wind to reduce predation risk. We conducted experiments to study mantid responses to wind, and the efficacy of cryptic walking behavior and body swaying under windy conditions.
against predation by cannibalistic conspecifics and adult Japanese five-lined skink, *Plestiodon japonicus* Peters.

**Materials and Methods**

**Mantids.** An ootheca of the mantid *H. patellifera* was collected from the field at the Faculty of Agriculture, Kinki University, Nara, Japan, in September 2006. It was kept in a plastic cage (12.5-cm top diameter by 10-cm bottom diameter by 10 cm in height) in a temperature-controlled cabinet at 10 ± 0.5°C, 50% RH, and a photoperiod of 12:12 (L:D) h. The cage was moved to a constant temperature room (30°C) in April 2007 to promote mantid hatching from the ootheca. Larvae hatched on 21 May 2007 were used in all experiments. Sixty larvae were selected and reared individually in plastic cages (dimensions similar to the hatching cage) until they reached the seventh instar. They were fed the fruit fly *Drosophila* sp. (*Drosophila* sp., Sphero Aqua Company, Shizuoka, Japan). Sev- enth-instar larvae were moved individually to acrylic fiber cages (10 cm in diameter by 20 cm in height) whose top and side openings were covered with screen to enable nymph walking and molting. They were reared in the laboratory at 26 ± 0.5°C, 70% RH, and a photoperiod of 12:12 (L:D) h. These larvae were fed the house crickets, *Acheta domesticus* (L.) (Sphero Aqua Company). Prey items were supplied to each mantid every other day, ensuring adequate nutrition. Drinking water was sprayed on the cages several times every other day.

**Japanese Five-Lined Skinks.** Adults of *P. japonicus* were collected in the field at Nara campus, Kinki University, in August 2007. They were maintained in the laboratory at 26 ± 0.5°C, 50% RH, and a photoperiod of 12:12 (L:D) h. They were reared in a plastic cage (20 cm in length by 38 cm in width by 26 cm in height).

**Wind-Induced Behavioral Changes in the Field.** The experiment was conducted at the Faculty of Agriculture, Kinki University, Nara, Japan. The campus contains secondary woodlands with high tree density (Bamba and Itawutbo 2001), as well as ponds and paddy fields (Inamoto and Sakuratani 2008). Our field research was conducted in July 2007 in an open the goldenrod *Solidago canadensis* variety *scabra* (L.) community on the campus. This plant species was selected because many mantid larvae were found on it. We placed one individual mantid larva in the fifth or sixth instar on a leaf of *S. canadensis* (=50 cm in height, with 29 leaves) that had been collected on the campus. The plant was placed on a table facing a fan that was operated at three speeds. We controlled the wind conditions by a remote controller. But because it is a simple fan, we could not simulate the natural air current. We tested the effects of simple wind conditions such as windless, constant, changing conditions. The experiments were conducted for 500 s under four wind velocity conditions.

i) Windless. ii) Constant wind velocity of 1.34 m/s. iii) Variable wind velocity: changed in order from weak (1.34 m/s), to intermediate (1.96 m/s), to strong (2.84 m/s), to intermediate (1.96 m/s) every 25 s. This cycle of changing wind velocity was continued for 500 s. We defined the increasing phase as the change from weak to intermediate speeds, and the decreasing phase as the change from intermediate to weak speeds. iv) Alternately changing conditions, namely, between the windless phase and the constant phase with average wind velocity of 1.34 m/s. The conditions were alternated every 25 s.

We videorecorded three larval behavioral components (resting, walking, and body swaying) in the laboratory at 23–26°C between 1300 and 1700 hours in July 2007.

**A Kruskal-Wallis nonparametric analysis of variance (ANOVA)** was used to compare durations of walking and swaying behaviors under the four wind velocity conditions. A Bonferroni test was used for multiple comparisons among treatment combinations. A Wilcoxon rank sum test was used to compare durations of walking and body-swaying behavior be-
tween increasing and decreasing wind velocity phases, and between the windless and constant phases.

Responses of Natural Enemies: Responses of Conspecific Mantids to Moving Mantids on Leaves. Experiments were conducted using conspecific mantids as natural enemies. There were two reasons for using conspecific mantids. First, recognition of prey mantids by predator mantids was easily detected by the predator mantid’s head movement toward moving prey mantids. The mantid reacts to the moving object first by turning their heads, which is followed by the reaction to retract their raptorial legs close to the front part of the body and align their antennae. Therefore, we adopted the first reaction to the moving as the sign of discovery. Second, cannibalism is common in the wild.

An individual sixth- or seventh-instar larva was selected as the prey item and placed on a leaf of the kudzu vine *Pueraria lobata* (Willd.) Ohwi in front of the fan. Another sixth or seventh instar was selected as the predator and placed on a paper cup (12.5-cm top diameter by 10-cm bottom diameter by 10 cm in height) in front of the prey. The predator mantid was set where the wind effect was small, preventing wind-induced movements (Fig. 1). The prey mantid was released from the starting point on the end portion of a leaf and began walking under the influence of the wind stimulus. After the mantid had reached the basal portion of the leaf, it was removed and was placed at the starting point again. This procedure was repeated ten times for each individual. We recorded the times of prey recognition by the predator mantid through 10 prey leaf-length traverses.

In controls, the leaf was fixed by wire to prevent swaying in the wind. Prey recognition was recorded by predator head movements toward the prey. The predator mantids were deprived of food for 3 d to enhance their reactions to the prey.

Predator mantid discovery rates of 10 prey mantids were analyzed by leaf movement category (leaf swaying and leaf fixed) by using one-way ANOVA after arcsine transformation. Forty mantids were used for the experiments.

Responses of Natural Enemies: Responses of *P. japonicus* to Moving Mantids on a Leaf. *P. japonicus* was used as a natural enemy in laboratory experiments. A prey adult mantid was placed on a leaf of *P. lobata* facing the fan. One adult *P. japonicus* was placed in a plastic cage (20 cm in length by 38 cm in width by 26 cm in height) when there was no wind blowing on the prey adult mantid (Fig. 2). The prey mantid began to walk along the leaf as the wind stimulus was applied; we recorded whether the predator discovered and moved toward the moving prey mantid within 10 min. In controls, the leaf was fixed by wire so it could not sway in the wind. *P. japonicus* was deprived of food for 3 d to enhance its reaction to the prey mantid.

![Fig. 2.](image)

Responses of *P. japonicus* to moving mantids on a leaf. The prey mantid on a leaf began walking as the wind stimulus was applied. We recorded whether *P. japonicus* discovered the walking prey mantid within 10 min.

![Fig. 3.](image)

(A) Relationship between mean wind velocity ($x$) and total duration of walking behavior ($y$) ($y = 64.99x - 14.07; r^2 = 0.429; P < 0.001, n = 36$). (B) Relationship between mean wind velocity ($x$) and total duration of body-swaying behavior ($z$) ($z = 73.70x - 6.235; r^2 = 0.423; P < 0.001, n = 36$). Nine individuals were used for the experiments under fine weather conditions between 1300 and 1500 hours in July 2007. We videorecorded the behavior of fifth- or sixth-instar larvae on a plant of *S. canadensis* for 500 s and measured wind velocity every second with an anemometer. The recorded behavioral components were resting, walking, and body swaying. Experiments were conducted under fine weather conditions between 1300 and 1500 hours in July 2007.
Chi-square tests were performed to test the difference in predator discovery rates between treatments. All statistics were analyzed using SPSS 14.0 for Windows (SPSS Inc., Chicago, IL).

**Results**

**Behavioral Response to Changing Wind Conditions in the Field.** The total duration of walking behavior ($y$) during 500 s of observation increased with increasing mean wind velocity ($x$) (Fig. 3A). The total duration of body-swaying behavior ($z$) during 500 s of observation increased with increasing mean wind velocity ($x$) (Fig. 3B).

**Behavioral Response to Wind in the Laboratory.** The total durations of walking behavior were compared under four kinds of wind conditions through 250 s. There were significant differences among wind conditions ($\chi^2 = 91.972$, df = 3, $P < 0.0001$) (Fig. 4A); the longest duration of walking occurred under changing conditions and the shortest under windless conditions. The total duration of walking behavior in the changing condition was significantly longer in the increasing phase of wind velocity than in the decreasing phase (Wilcoxon rank sum test: $U = 269.50$, $P < 0.0001$) (Fig. 5A). The total duration of walking behavior in alternately changing conditions was significantly longer in the constant phase than the windless phase (Wilcoxon rank sum test: $U = 20.50$, $P < 0.0001$) (Fig. 6A).

The total duration of body-swaying behavior differed significantly by wind condition ($\chi^2 = 104.796$, df = 3, $P < 0.0001$) (Fig. 4B), and each treatment was significantly different from all others. Duration was longest under changing wind conditions and shortest under windless conditions. The total duration of swaying behavior was significantly longer as wind velocity increased than when it decreased ($U = 279.00$, $P < 0.0001$) (Fig. 5B), and it was significantly longer in the constant phase than in the windless phase ($U = 1.50$, $P < 0.0001$) (Fig. 6B).

**Responses of Natural Enemies.** The discovery rate of the prey mantids by conspecific predator mantids was significantly lower in the swaying leaf conditions (12.8 ± 1.9%; mean ± SE) than in the fixed leaf conditions (78.5 ± 2.7%) (ANOVA: $F = 207.233$, df =

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Fig. 4. (A) Total durations of walking and (B) body-swaying behaviors in the laboratory under four wind velocity conditions over 250 s. Fifth- or sixth-instar larvae were placed on a leaf of *S. canadensis* (height, ~50 cm; 29 leaves). The plant was placed on the table in front of a fan that allowed us to apply three levels of wind velocity. The levels of wind velocity were applied for 500 s. Wind velocity levels were as follows. i) Windless condition. ii) Constant condition with average velocity of 1.34 m/s. iii) Changing condition where wind velocity was changed every 25 s in the following order: weak (1.34 m/s), intermediate (1.96 m/s), strong (2.84 m/s), and intermediate (1.96 m/s). This cycle of change in wind velocity was continued for 500 s. iv) Alternately changing every 25 s between the windless and constants phases. The different letters on bars show significant differences ($P < 0.05$; ANOVA and Bonferroni test). Values are means ± SE, $n = 36$.

Fig. 5. (A) Total duration of walking behavior in 125 s as wind velocity increased and decreased. (B) Total duration of body-swaying behavior in 125 s as wind velocity increased and decreased. Values are means ± SE, $n = 36$. 

![Fig. 4](https://academic.oup.com/aesa/article-abstract/102/3/517/8642/fig4)

![Fig. 5](https://academic.oup.com/aesa/article-abstract/102/3/517/8642/fig5)
1, $P < 0.001$). The discovery rate of the prey mantids by *P. japonicus* was significantly lower in the swaying leaf condition than the fixed leaf condition ($\chi^2 = 9.317$, $P < 0.001$) (Table 1).

**Discussion**

In the laboratory experiments, mantids became more active with increasing mean wind velocity (Fig. 3A and B), and activity also increased with changing wind velocity (Fig. 4), markedly so when the wind became stronger (Fig. 5). When the wind stopped blowing, mantids became still. The mantid changed behavior responding to the wind alternately changing condition (Fig. 6). It is necessary to distinguish the effect of the wind from the effect of shaking substratum. However, it is rare that the leaves shake under windless conditions in the field.

It has been considered that the mantid’s body swaying behavior have originated as an adaptation for absolute distance measurements (Walcher and Kral 1994, Poteser and Kral 1995). However, there is no need to react to wind if this behavior is only for this effect. Moreover, mantids show this type of behavior while feeding or grooming their bodies, which are not related to distance measurements. So, it is reasonable to assume the body swaying behavior has been modified by natural selection as an antipredator strategy.

Mantids frequently body sway when searching for prey, moving around, and grooming their bodies (Crane 1952). Predation risk is increased by searching for prey, moving around, and grooming their bodies, but if they sway while they show these behaviors, the risk may be reduced. The movement of females of the South American mantid *Acanthops falcata* Stål is a more or less violent trembling, and the shaking body perfectly resembles the motion of a dried leaf in the wind (Crane 1952). Even walking is likely helpful in reducing insect conspicuousness (Crane 1952). Mantid walking movement is usually accompanied by body-swaying behavior (H.W., unpublished data). Thus, we hypothesize that walking with swaying behavior imparts adaptive significance for moving animals when the wind is blowing.

Natural enemy experiments showed that it was more difficult for a predator to find a moving mantid on a swaying leaf than on a fixed leaf; we therefore suggest that body swaying is an anti-predator strategy in mantids. Such a strategy explains why the frequency of walking with swaying behavior decreased remarkably under still conditions in the laboratory; it is adaptive for animals to keep still when the leaves on which they stand are motionless. Movement of an organism can be important for cryptis, although generally, movement of an organism is not compatible with good matching to the background (Ruxton et al. 2004).

Use of conspecific mantids as natural enemies in our experiments might seem inappropriate. Cannibalism depends on body size (Fagan and Odell 1996); both young and old conspecific mantids battle with each other, with the winner always eating the loser. The size differential between combatants results from differences in hatch time or speed of growth. Mantid nymphs suffer high mortality from starvation and cannibalism (Hurd and Eisenberg 1984). Thus, conspecific mantids may be included among natural enemies. Nevertheless, birds are the most important natural enemies of mantids, and experiments examining effects of bird predation are needed.

Our study is the first to demonstrate that movement on shaking leaves is a mantid antipredator strategy that reduces the chances of discovery. Walking was always associated with body swaying, and the significance of these two components of movement should be separated in future work. The mantids we studied live in trees; however, because some mantids inhabit grasslands, it is important that they be studied in a similar manner.

| Leaf condition | No. observations* | Discovery rate (%) |
|----------------|-------------------|--------------------|
|                | Discovered | Not discovered |
| Fixed          | 18        | 12         | 60     |
| Swaying        | 2         | 28         | 7      |

* One prey mantid was used for each 10-min observation, and we recorded whether prey was discovered by the predator. Thirty individuals were observed in total.
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References Cited

Bamba, I., and G. Iwatubo. 2001. An ecological study of actual vegetation at Kinki University’s Nara Campus. Mem. Fac. Agric. Kinki Univ. 34: 113–149.

Bedford, G. O. 1978. Biology and ecology of the Phasmatodea. Annu. Rev. Entomol. 23: 125–149.

Cott, H. B. 1957. Adaptive coloration in animals. Methuen, London, United Kingdom.

Crane, J. 1952. A comparative study of innate defensive behaviour in Trinidad mantids (Orthoptera, Mantodea). NY Zool. Soc. 37: 294.

Curio, E. 1976. The ethology of predation. Springer, Berlin, Germany.

Edmunds, M., and D. Brunner. 1999. Ethology of defenses against predators, pp. 276–299. In F. R. Prete, H Wells, P. H. Wells, and L. E. Hurd [eds.], The praying mantid. The Johns Hopkins University Press, Baltimore, MD, and London, United Kingdom.

Fagan, W. F., and G. M. Odell. 1996. Size-dependent canibalism in praying mantids: using biomass flux to model size-structured populations. Am. Nat. 147: 230–268.

Hatle, J. D., and S. G. Faragher. 1998. Slow movement increases the survivorship of a chemically defended grasshopper in predatory encounters. Oecologia (Berl.) 115: 260–267.

Hurd, L. E., and B. M. Eisenberg. 1984. Experimental density manipulations of the predator Tenodera sinensis (Orthoptera: Mantidae) in an old-field community. I. Mortality, development, and dispersal of juvenile mantids. J. Anim. Ecol. 53: 269–281.

Houtman, R., and L. M. Dill. 1994. The influence of substrate color on the alarm response of tidepool sculpins (Oligocottus maculatus, Pisces, Cottidae). Ethology 96: 147–154.

Inamoto, Y., and Y. Sakuratani. 2008. The aquatic flora and fauna on the Nara Campus of Kinki University. Mem. Fac. Agric. Kinki Univ. 41: 95–122.

Laurila, A., J. Kujasalo, and E. Ranta. 1997. Different antipredator behavior in two anuran tadpoles: effects of predator diet. Behav. Ecol. Sociobiol. 40: 329–336.

Lopez, P., and J. Martin. 2001. Chemosensory predator recognition includes specific defensive behaviours in a fossorial amphibiaenian. Anim. Behav. 62: 259–264.

Petranka, J., and L. Hayes. 1998. Chemically mediated avoidance of a predatory odonate (Anax janius) by an American toad (Bufo americanus) and wood frog (Rana sylvatica) tadpoles. Behav. Ecol. Sociobiol. 42: 263–271.

Poteser, M., and K. Kral. 1995. Visual distance discrimination between stationary targets in praying mantis: an index of the use of motion parallax. J. Exp. Biol. 198: 2127–2137.

Ruxton, G. D., T. N. Sherratt, and M. P. Speed. 2004. Avoiding attack: the evolutionary ecology of crypsis, warning signals, and mimicry. Oxford University Press, New York.

Robinson, M. H. 1969a. The defensive behaviour of some orthopteroid insects from Panama. Trans. R. Entomol. Soc. Lond. 121: 281–303.

Robinson, M. H. 1969b. Defenses against visually hunting predators. Evol. Biol. 3: 225–259.

Walcher, F., and K. Kral. 1994. Visual deprivation and distance estimation in the praying mantid larva. Physiol. Entomol. 19: 230–240.

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