OBSERVATIONS OF PREY CAPTURE IN MANTIDS

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Several investigations have considerably enlarged our knowledge of the behavior of mantids. Although their predatory behavior is common knowledge, less well known is the fact that these insects are in turn preyed upon by other animals, including lizards, birds and mammals (Gurney, 1951). In a comparative and experimental study of mantid displays, Crane (1952) described and analyzed the innate, defensive behavior patterns which 15 species of Trinidad mantids utilize against these enemies. These defensive reactions were found to consist of four general types: 1) protective resemblance in structure and behavior (motionlessness and body attitude); 2) active escape; 3) startle display (raising of wings and tegmina and other movements); and 4) active attack. For the first time, the postembryological development of such behavior in the adults was observed from the early nymphal instars, and comparisons between species were made. As a result she was able to provide valuable insight concerning the evolution of these inherited patterns of behavior, much as the comparative morphologist provides understanding of the evolution of specific structures.

Mittelstaedt (1953, 1957), was able to analyze the sensory-motor coordination which enables mantids to hit their prey. The strike of a mantid occupies a duration of about 10–30 milliseconds. In this short duration there is clearly no opportunity for the mantid to control the efficacy of its strike by watching the difference between its direction and that of the prey. How it achieves this phenomenon of absolute optic localization has long been a problem. Although the mantid usually tends to bring its head and prothorax into one line with the prey, it is also able, as Mittelstaedt has shown and as the author has observed, to hit prey which has considerable lateral deviation from the median plane of the prothorax. The direction of the strike must therefore be based on information involving the position of the head in relation to the prothorax, as well as the position of the prey in relation to the head. Knowledge of the position of the head in relation to the body depends on proprioceptors supplied to tens of hundreds of hair sensillae on two pairs of cervical plates. Normal mantids (*Parastagmatoptera unipunctata*) hit about 85% of the flies they attempt to capture, but if the proprioceptors of the neck region are eliminated by nerve section, the hitting performance is irreversibly reduced to 20–30%. This, however, is not the complete story, for it turns out that the head fixation line does not exactly center the prey, but deviates from it by an amount proportional to the angle between the prey and the body axis. The difference between the optic center message (a function of the angle Φ between the prey and the fixation line), and the proprioceptive center message (a function of the angle μ, between the head and the body axis), determine the fixation movements of the head which precede the release of the strike (Fig. 1). After the fixation movements have come to rest, the

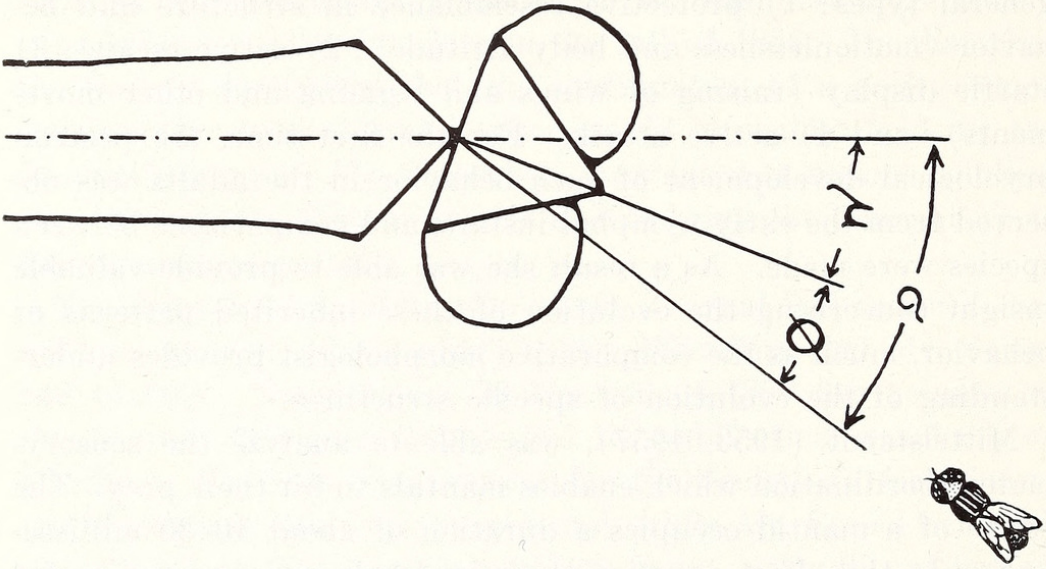

FIG. 1. Head fixation of prey which deviates by an angle σ from the line of the body axis. μ, angle between fixation line and body axis; Ø, deviation of prey from fixation line. (After Mittelstaedt, 1957).

direction of the strike is determined by information from both the optic center and (to a smaller extent) the proprioceptive center of the cervical sensillae.

Mittelstaedt's experiments, summarized above, are confined to one aspect of the problem of prey localization and capture—that of analyzing the determining factors in establishing the direction of the strike. As he himself has pointed out, there are other factors involved in prey capture, namely that of gauging the distance of the prey, as well as other ethological questions about appetitive behavior, drives and the factors responsible for releasing the prey capture response. The following observations of prey capture in mantids, made by the author over a period of several years, should serve to illustrate the nature of some of these additional factors.

During the late summer of 1954, six adult narrow-winged mantids (*Tenodera angustipennis*) were captured by the author one evening at La Guardia Airport in New York City, apparently attracted there by the airport lights. These were kept isolated in gallon jars, and fed from time to time on late instar nymphs and adults of the cockroach, *Nauphoeta cinerea*. It soon became apparent that the response to prey varies with the physiological state of the mantid.

When a cockroach approaches or is placed before a "hungry" mantid, the mantid cocks its head in the direction of the cockroach (Fig. 2), then, when at all possible, generally moves its body

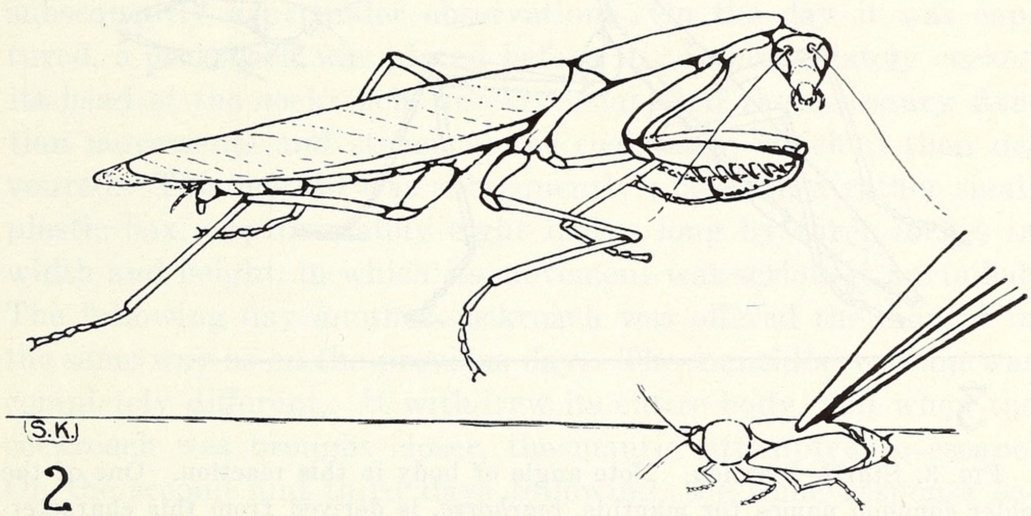

FIG. 2. Predatory response. Note movement of head towards prey.

in line with its head, so that the axis of the head, thorax and abdomen form a straight line in the direction of the cockroach. At the same time the mantid draws its forelegs towards its prothorax, and, when the fixation movements are complete, strikes at and catches the cockroach which it then proceeds to devour. Sometimes such a mantid will strike at, catch and devour a second cockroach. When it is apparently satiated, however, its response to a cockroach is completely different. It now not only draws its forelegs up, but tilts its head and thorax up, rearing back on its mid- and hindlegs, as shown in Fig. 3, so that the body of the mantid makes a large angle with the surface on which it rests.[1] In this position the mantid remains motionless and makes no attempt to strike. After the cockroach is withdrawn, or walks away if it is free, the mantid resumes its horizontal position and also walks away. Following Crane, I have termed this a startle reaction.

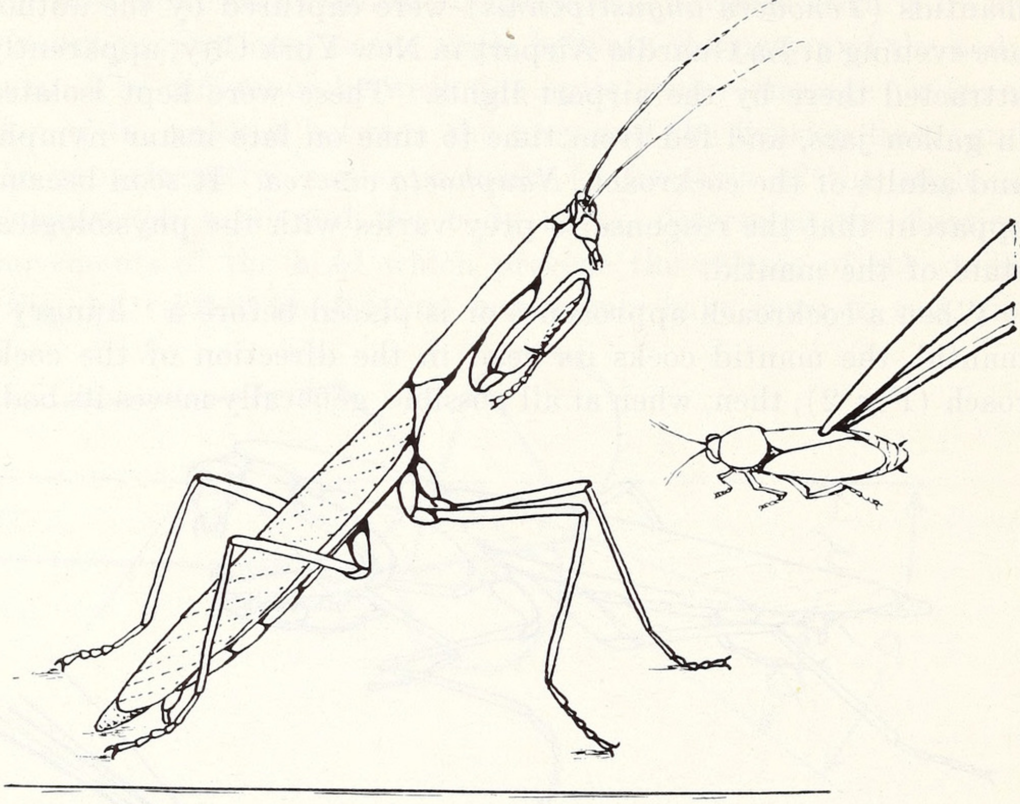

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FIG. 3. Startle reaction. Note angle of body in this reaction. One of the older common names for mantids, *rearhorse*, is derived from this characteristic behavior.

In one instance when a cockroach was placed on the floor before a satiated mantid, the mantid reared back rigidly as described above, and remained motionless. When the cockroach moved towards the left midleg of the mantid, the otherwise motionless mantid raised this leg and permitted the cockroach to

[1] According to the Century Dictionary (1889), one of the common names for these insects, *rearhorse*, is derived from this behavior. Blatchley (1920, p. 115) similarly assigns this common name to this characteristic body attitude.

crawl under it. After a short duration, the mantid walked away in the opposite direction.

These observations make it clear that the sight of moving prey may provoke two distinct responses on the part of the mantid, depending on the physiological state of the mantid. It may react with either the normal fixation response which leads to predation, or with the startle response, generally followed by escape (this latter response may also depend on the size of the prey).[2] In this and the other species of mantids described in this paper, the startle position differed from the defensive reactions described by Crane for numerous species of Trinidad mantids, in that the wings were never displayed in the many instances in which it was observed. It should be mentioned, however, that Judd (1950) has recorded that the spreading of the wings does occur in the startle response of *Mantis religiosa* described below.

In another instance a female adult of the related but larger Chinese mantid (*Tenodera aridifolia sinensis*) was captured and subsequently kept under observation. On the day it was captured, a cockroach was placed before it. It immediately cocked its head at the cockroach, quickly completed the necessary fixation movements and struck at the cockroach, which it then devoured. This mantid was subsequently placed in a rather small plastic box, approximately eight inches long by three inches in width and height, in which its movement was seriously curtailed. The following day another cockroach was offered the mantid in the same way as on the previous day. The mantid's reaction was completely different. It withdrew its entire body, and when the cockroach was brought closer, the mantid attempted to escape. On the second and third days following, the same response occurred, but on the fourth day it captured and devoured the cockroach placed before it. Again for three days, it withdrew

[2] It is possible that under more natural circumstances a mantid would not respond to an approaching insect the size of a cockroach with a startle reaction. The startle reaction in this case may, in part, be due to the method of presentation, i.e. at the end of a pair of forceps, by hand. This fact, however, by no means removes the problem, but reverses it. For when "hungry", the mantid no longer responds to the same stimulus with a startle reaction, but with fixation movements and predation. This same ambiguity has been observed when a cockroach was thrown into a jar with a mantid. The scurrying cockroach sometimes provoked escape movements, and sometimes fixation movements and predation.

from the cockroaches proffered it, but on the fourth day, it responded with fixation movements, struck at, captured and devoured the cockroach. For several days it again withdrew from insect prey.

At this point, I removed this mantid from its small box and permitted it to crawl about freely on the window screen of my study. Henceforth, its reactions to cockroaches changed, so that it now responded with fixation movements and captured at least one cockroach each day, and sometimes two a day. This suggests that other activities (energy output) influences the physiological state of the mantid, which in turn quantitatively determines the number of positive responses made to prey.

In the following year, several adult females of the European mantis (*Mantis religiosa*) were captured on September 4, 1955 in Taghkanic State Park, New York. One of these female mantids, with a gravid abdomen, refused all cockroach nymphs placed in front of it, and reacted with a modified startle reaction (it reared back, but not with as great an angle formed between it and the floor as in *T. aridifolia sinensis*) each day for a week. Two other females of the same species, kept in separate jars, reacted with a positive predatory response and ate at least one cockroach each per day. After one week I placed the above gravid female in a larger glass jar, together with grass reeds and twigs on which she might deposit her ootheca. Before doing so, however, I again tried to entice her to feed on a nymphal cockroach. This time she made several weak attempts to strike at the cockroach, but could not hold on to the prey even when she once succeeded in getting her forelegs on the cockroach. Her strike was no longer the lightning-like thrust, but considerably enfeebled. I had the impression that the mantid was debilitated and dying. Thinking she might be starved, I placed some fresh insect viscera in contact with her mouthparts. This she began to eat for a brief period with no great avidity, then shortly turned away from this food.

The mantid was now placed in its new jar. Three hours later I looked in and noticed a freshly formed ootheca around a grass reed, still moist and frothy. Once again I placed a nymphal cockroach, at the end of a pair of tweezers, in front of the mantid. The mantid's response was immediate. She quickly cocked her head towards the cockroach, drew her forelegs up and struck at the cockroach effectively with the usual lightning-like stroke. She then devoured the cockroach avidly. Thereafter, the mantid continued to react to cockroaches with a precise and effective predatory response, often eating two or more nymphal cockroaches per day. This preoviposition period appears to be another instance in which the physiological state of the mantid strongly influences the predatory response.

In those instances above, in which prey was refused, it was noticed that the mantid also drew her forelegs towards the prothorax, as if to strike, but in this pose she never cocked her head in the direction of prey. The mantid seemed to grow rigid, and with the first opportunity, attempted to escape.

In view of the above, the following observations of early instar nymphs of the mantid, *Tenodera aridifolia sinensis*, made during the spring of 1951, 1952 and 1953, also are of interest.

Several mantid oothecae were obtained from a biological supply house each year and kept in a crystallizing dish until they hatched in the spring. In these instances the oothecae generally hatched in March and produced from 80–100 nymphs. Fairly frequent observation of these oothecae produced the impression that when they did hatch, large numbers of young mantids emerged over a short period of time. Rau and Rau (1913) similarly recorded short emergence periods for the nymphs from the oothecae of *Stagmonantis carolina*. (See also Gurney, 1951).

As they come into contact with one another, the newly emerged nymphs show a tendency to assume a "defensive rearing back attitude" during the first day of their lives, which suggests the startle response in the adults described above. If the newly emerged nymphs from a single ootheca are permitted to remain together in a single crystallizing dish, there is an almost ceaseless pattern of activity. Young mantids scramble over and around each other, sometimes rear back defensively, and rush away from each other. When several score of adult *Drosophila* flies were introduced into such dishes, on the second day of emergence, only an occasional attempt by some mantids to catch flies was observed, and few were successful. Several mantids struck at flies, but released or lost them as the flies struggled.

By the afternoon of this second day, very few flies had been captured and eaten, judging by the number of wings on the white filter paper floor of the dish in which they were kept, and by the numbers of flies still present. Several of these same mantids, however, were isolated together with 2 or 3 flies in small homeopathic vials, with a strip of filter paper serving as a floor. Kept in this way, many of the day old (actually about 30 hours old) mantids caught and ate flies in their vials within the first hour of isolation. One mantid placed in such a vial made an immediate attempt to strike at a fly which came within its reach, but lost it as the fly struggled away. Within 30 seconds, however, it succeeded in capturing a fly which it devoured. These observations indicate that the predatory response to moving prey is innate, although one or two attempts may be required in some instances to perfect it.

The general impression gained from these observations was that the nervous activity of large numbers of newly emerged nymphs, when kept together, prevented the alert attitude which precedes fixation movements and the subsequent capture of flies. When young mantids are isolated in separate vials they are capable of catching prey by the thirtieth hour of their lives, and possibly earlier. If large numbers of newly hatched mantids continue together, however, they begin during the second, third and fourth days to prey on each other until their numbers are sharply reduced within a short period.

Kept in isolation in these homeopathic vials, individual mantids were easily reared through the second, third and even later instars, and their behavior observed. Three or four *Drosophila* were placed in each vial every day, and these were soon caught and devoured. The response of a young mantid to a fly, however, likewise differs, depending on its physiological state. A "hungry" young mantid immediately cocks its head on seeing a fly, and even continues to follow the fly with its head if the fly moves away from it. If the fly approaches, it also draws its forelegs up preparatory to striking. By contrast, a young mantid that has eaten its fill, no longer cocks its head at passing flies, and does not assume a preparatory striking position. If a passing fly comes too close to a satiated mantid, the latter sometimes remains rigid or moves away. It is a striking behavioral observation to introduce half a dozen fruit flies into a vial and watch the young mantid cock its head, fix, strike and devour first one fly, then repeat this response towards a second and third fly, possibly a fourth, then completely ignore the other two flies in the vial. Here again it is clear that the physiological state of the mantid very early modifies the predatory reflex.

Further observations on these early instar mantids suggest that the response to a fly is a complex one, and not only differs from satiation to hunger, but also from moderate to extreme hunger. Flies introduced into these vials often walked on the clear, glass roof side of the vial, and cast a moving shadow on the filter paper floor, in the lighted windowless room in which they were kept. Moderately hungry mantids, that is, mantids fed every 24 hours, were never seen to respond to the moving shadows of flies. On the other hand, extremely hungry young mantids, which had not been fed in 48 or more hours, were sometimes observed to strike at the shadows of moving flies, two or three times in succession in some instances. Since these mantids had had prior fly catching experience, it cannot be assumed that the mantids had not "learned" to differentiate between moving flies and moving fly shadows. This suggests that an extremely hungry mantid responds with a predatory response to fewer releaser signals, than a moderately hungry one.

In addition, extremely hungry young mantids (fed after an interval of 48 or more hours) were sometimes seen to actively pursue flies, that is, to follow them by actively moving in their direction, whereas moderately hungry mantids were content to wait patiently in position until the fly approached within striking distance of the mantid. (See also, Gurney, 1951, p. 343.)

SUMMARY

Adult mantids (*Tenodera angustipennis*) will fix, strike and devour prey (cockroaches) presented to them when hungry; when not hungry they respond with a startle reaction to the same stimulus.

One adult mantid (*Tenodera aridifolia sinensis*), confined in a small cage so that its movements were limited, reacted with a predatory response and devoured a cockroach presented to it about every fourth day; on the days between it responded to the same stimulus with a startle reaction and escape movements. The same mantid allowed to roam freely around a window screen, gave a predatory response at least once and sometimes twice a day, to the same cockroach stimulus.

A gravid female mantid (*Mantis religiosa*) reacted with a startle response or made ineffective, enfeebled strikes at a cockroach presented to it daily for one week prior to oviposition. Immediately after oviposition she effectively fixed, struck and avidly devoured cockroach nymphs daily. Two other non-gravid female adults of this species gave positive predatory responses to cockroaches almost daily.

Newly hatched first instar nymphs of *Tenodera aridifolia sinensis* fix, strike and catch *Drosophila* after isolation in a vial, when presented with flies for the first time at 30 hours of age, possibly earlier. The first predatory response may be completely successful or soon becomes successful after one or two failures.

Thereafter, moderately hungry mantid nymphs (fed every 24 hrs.) fix, strike and devour from 1–4 passing *Drosophila* in fairly quick succession but when satiated they ignore *Drosophila* which walk past them.

Extremely hungry mantid nymphs (fed every 48 hrs.) will strike at moving shadows of *Drosophila* (which moderately hungry mantids were never observed to do) even after considerable, previous fly-catching experience.

Extremely hungry nymphs will actively crawl after and pursue moving prey, whereas moderately hungry nymphs normally wait quietly in place until a fly comes within striking distance.

These observations indicate that the predatory response (consisting of fixation movements at the sight of prey, and the rapid strike) is very early integrated with and modified by various physiological states of the mantid.

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