

PSYCHE

Vol. 88

1981

No. 1-2

ANTI-PREDATOR STRATEGIES.
II.* GRASSHOPPERS (ORTHOPTERA, ACRIDIDAE)
ATTACKED BY *PRIONYX PARKERI* AND SOME
TACHYSPHEX WASPS (HYMENOPTERA, SPHECINAE
AND LARRINAE): A DESCRIPTIVE STUDY

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INTRODUCTION

Predator and anti-predator adaptations, strategies, have been studied extensively in recent years (see for instance Curio 1976 and Edmunds 1974 for some recent reviews). Problems of predator-prey coevolution, mimicry, protective coloration (e.g., Cott's monumental work, 1940), optimal strategies, etc., have received a great deal of attention. Defense mechanisms are extremely diverse and can even involve use of a commensal species (e.g. Ross 1971). A variety of sensory channels can be used such as visual (e.g. Cott 1940; Robinson 1969), acoustical (e.g. Roeder 1965), chemical (e.g. Eisner and Meinwald 1966; Eisner 1970), mechanical, vibratory (e.g. Tautz and Markl 1975) to mention only a few examples. Predators such as mammals, birds, reptiles (e.g. Curio 1970), fish, mollusks have been extensively studied.

Among insects, solitary and social wasps have also been intensively studied but on the whole surprisingly little is known about the defensive mechanisms of their "helpless" prey. Prey capture is often very difficult to observe and even more so to study extensively in natural conditions. The few exceptions mostly deal with prey that represent a potentially formidable opponent (e.g. spider, praying

*For part I see Steiner 1968 in the Literature Cited.

Manuscript received by the editor May 11, 1981

mantis, etc.). Counter-attacks by such prey and occasional killing of the predator have even been reported (e.g., Deleurance 1941, pp. 287–288, for a praying mantis attacked by the sphecid wasp *Stizus distinguendus*; also 1945, p. 29 for *Tachysphex costai* Dest.). Dead spider wasps have also been found in spider webs in natural conditions (pers. obs.). Non-predaceous prey can also exhibit defense reactions, however, as shown before for crickets attacked by *Liris nigra* wasps (Steiner 1968).

The anti-predator system of acridid grasshoppers is now described, analyzed, as observed both in nature and captivity (summarized in Steiner 1976). The prey are: (1) mainly adult or subadult Oedipodinae, but also a few Cyrtacanthacridinae, all attacked by the sphecid wasp *Prionyx parkeri* Bohart and Menke, (2) to a much lesser extent smaller, earlier, instars preyed upon by *Tachysphex* wasps (details in next section). For the latter prey, defense reactions were essentially the same, except for the ones involving the wings, undeveloped at these stages. Prey hunting and stinging by *Prionyx parkeri* are described in detail in Steiner 1981 (in press).

MATERIALS AND METHODS

Field observations

Prionyx parkeri wasps were observed mainly in the grassland desert and adjacent riparian habitat of S.E. Arizona, U.S.A., at the foot of the Chiricahua Mountains, East of Willcox, during the summer of 1972.

Observations in captivity

Individually marked *Prionyx parkeri* and *Tachysphex* [mostly *tarsatus* (Say)] wasps were observed in controlled laboratory units about 60 × 50 × 50 cm (general method described in Steiner 1965): (1) at the Southwestern Research Station, Portal, Arizona, during the spring and part of the summer 1973 (= Arizona study); (2) in central Oregon, U.S.A., near Bend, using a field trailer, during the summer of 1977 (= Oregon study). The following acridid grasshoppers taken from the wasps' habitats were used in the Arizona study; (1) for *P. parkeri*, adult or last instar nymphs of: Oedipodinae, mostly *Trimerotropis pallidipennis* p. (Burm.), also *Conozoa carinata* Rehn, a few *Cibolacris parviceps* (Walker) — Cyrtacanthacridinae, a few *Psoloessa delicatula* Scudder and an occasional

Eritettix variabilis Bruner; (2) for *Tachysphex* wasps, small acridid nymphs of: Oedipodinae, mostly *Conozoa carinata* Rehn and also a few *Trimerotropis pallidipennis* p. (Burm.); Cyrtacanthacridinae, a few *Psoloessa delicatula* and an occasional *Melanoplus* sp., *Derotmema* sp., *Rehnita* sp. Rather similar but un-determined grasshoppers were used in the Oregon study, in captivity. The grasshoppers were provided either ad libitum, or in staged encounters.

Observations were mostly continuous, with "all occurrences" sampling of wasp-prey interactions. Precise quantifications were difficult or impossible because initial stages of encounters were often sudden and unpredictable. Generally speaking proof of effects of escape-defense reactions is often very difficult to establish (e.g. Edmunds 1974, p. 240). This study is basically descriptive.

Total observation times were; (1) for captive *P. parkeri* in the Arizona study about 178 h over a period of 30 observation days (\bar{X} = about 6 h-day) and in the Oregon study about 142 h for 14 observation days (\bar{X} = about 6½ h-day); (2) for captive *Tachysphex* wasps in the Arizona study about 224 h for 37 observation days (\bar{X} = about 6h-day) and in the Oregon study about 224½ h for 35 observation-day (\bar{X} = 6¼ h-day).

RESULTS: DESCRIPTION OF RESPONSES, CONDITIONS

*Common responses: escape by jumping (flying) away,
staying put = first line of defense.*

a) Field observations

Visually hunting *Prionyx (parkeri?)* wasps were observed in the short and sparse grassy vegetation, characteristic of the upper Sonoran desert grassland. Acridid grasshoppers were abundant, particularly Oedipodinae such as *Mestobregma plattei rubripenne* (Bruner) adults, also found stored in the nests of these wasps. The most common response to wasps approaching or pouncing was a very sudden, even startling, escape by jumping (Fig. 5a) and flying away (Fig. 5b). The bright flash of the colorful banded wings came in sharp contrast with the sudden disappearance from sight, after landing (crypticity: Fig. 5c). The wasps seldom followed the escaping grasshoppers in flight, but occasionally did so (Fig. 5b) and even managed to cling to them in mid air and to deliver stings before landing. Most stung grasshoppers were apparently caught by surprise or at the preparatory stages of escape. Close range and

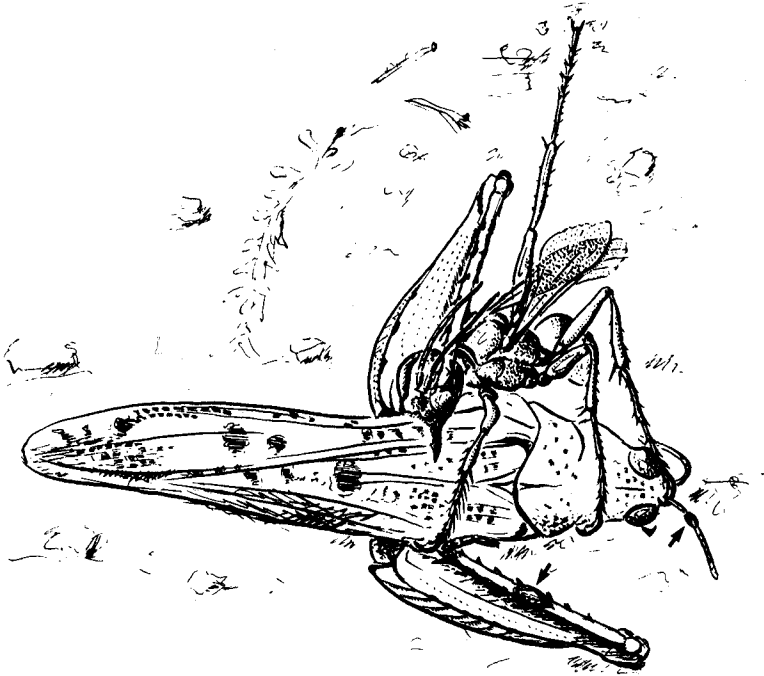


Fig. 1: Attack of an adult acridid grasshopper (Oedipodinae) by a *Prionyx parkeri* wasp. The wasp uses both the strong mandibles and long, powerful legs, to firmly hold the prey and prevent escape. The grasshopper tries (in vain) to push away the wasp with both powerful hind legs by applying strong pressure on the points where the wasp is anchored (head and one fore leg). Several drops of regurgitated repelling fluid are indicated by arrows. The wasp already assumes the appropriate posture for the first paralyzing sting, delivered in the throat of the victim.

quantitative observations were almost impossible. At times the grasshoppers stayed put instead of escaping, for no apparent reason. Attack of the wasp does not necessarily follow detection of a suitable prey, however, since hunting wasps go through periods of temporary refractoriness (Steiner 1962, 1976, 1978, 1979). This considerably complicates the study of possible effects of prey-defenses on the wasps.

b) Observations in captivity

The same responses were also recorded in captivity. Flying away

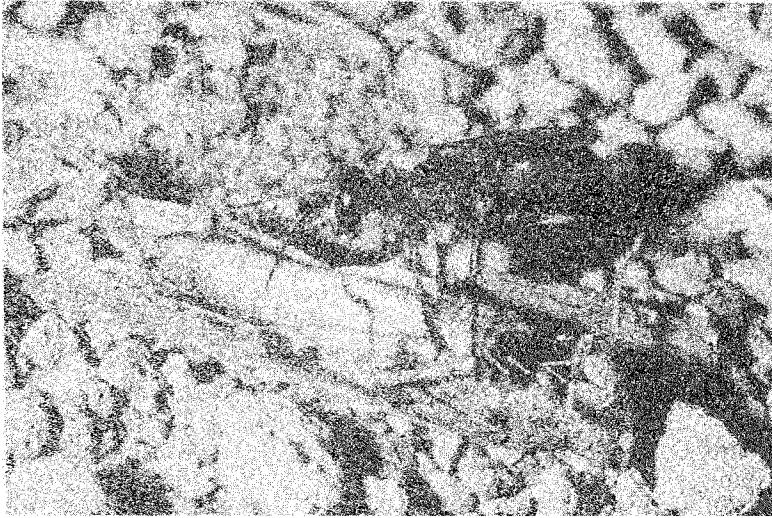


Fig. 2: Regurgitation of a repelling fluid. An acridid grasshopper (*Oedipodinae*), just paralyzed by a *Prionyx parkeri* wasp, lies on its back and a huge drop of fluid covers a large surface of the ventral thoracic area where all four stinging sites are located (indicated by white dots and arrows). Wasps often hesitate to dip their abdomen tip into this viscous, probably offensive, fluid. Accidental contact triggers vigorous body rubbing in an attempt to eliminate the unpleasant fluid from the body surface.

and long-range escape were impossible, however, because of space limitations.

There was no evidence of active avoidance of *Prionyx* or *Tachysphex* wasps by grasshoppers ("predator recognition"), even after repeated attacks. Escape was always in direct response to attack, imminent attack, or at least sudden movements such as a wasp running and/or pouncing. Thus predator and prey were often seen basking together. Immediately following an attack, the escape threshold was clearly lowered, however.

Mechanical defenses after contact: kicking, pushing and/or brushing away the wasp; biting; wing fluttering and flying
= second line of defense (Fig. 1)

After contact, *Prionyx* wasps attempt to anchor themselves to the struggling or escaping grasshopper. They try to gain a firm grip

using their powerful spinose legs, terminal claws, and also mandibles. These wasps tightly “embrace” the grasshopper, in an anti-parallel posture and strongly cling to them (Fig. 1). In contrast, many larrine wasps (e.g. *Liris*, *Tachysphex*) are comparatively frail, short-legged, and cannot physically overpower their prey as successfully as *Prionyx* wasps do. Their prey often struggles free, in contrast to *Prionyx* prey which seldom succeed, after the “embracing” stage, in spite of frantic efforts to kick and/or brush, push away the attacker with the powerful hind legs. *Prionyx* prey also try to deny free access of the wasp to the dorsal side by raising their long, folded, hind legs, often beyond the vertical, headwards (hind leg raising: Fig. 5e). Powerful kicks (Fig. 5e) sometimes send the wasp a few cm from the grasshopper, but this works mostly before the wasp can secure a firm grip. Pushing action with the tarsi of the powerful hind legs can also be recorded. They are very precisely directed at the points seized by the wasp as shown in Fig. 1. In the latter, drawn from a photograph, the grasshopper tries, with its right hind leg, to push away the left front leg of the wasp while it attempts, with the left hind leg, to exercise strong pressure on the head, jaws, of the attacker and presumably get the wasp to release its mandibular grip (in Fig. 5f these “points of pressure” have been circled). Wing fluttering and even flying attempts can also be observed in reponse to the grasping action of the wasp. The orthopteran also performs snapping motions with the jaws but is seldom able to bite the wasp. The very globulous abdomen of *Prionyx* wasps appears to be especially well adapted to prevent such biting. The abdomen is particularly exposed since the wasp delivers the first sting in the throat of the prey, dangerously close to the powerful jaws (Fig. 5g).

Chemical defenses: regurgitated fluid (Fig. 2)

In addition and often as a last ditch defense the grasshopper regurgitates through the mouth a large drop of dark fluid (“tobacco juice”) that usually spreads rapidly over the body areas closest to the mouth, ventrally, namely the thoracic surface (Fig. 2). This surface sometimes becomes completely covered with the substance. From there it can spread to other body areas, if struggling is intense enough. On Fig. 1 one drop can be seen on the right antenna of the grasshopper and one on the tibia of the right hind leg (arrows).



Fig. 3: Postural defense replacing escape (startle and/or death feigning display?). The attacked grasshopper froze into a hunched posture, with appendages tucked in, thus protecting the vulnerable ventral surface. The colorful wings, showing striking semi-circular dark markings, are fully extended and/or flutter convulsively. The wasp, after many vain efforts, managed to slip under the grasshopper (one leg is still visible on the right of the grasshopper head) and will attempt to reach the vulnerable ventral surface of the thorax made less accessible by the posture and interposition of appendages (obstruction behavior).

*Uncommon and odd postural defenses replacing escape:
stationary wing flashing or extension; body arching; freezing
(Fig. 3) = first line of defense.*

a) Field observations

These rare occurrences guarantee that such responses are not reducible to captivity artifacts.

The first observation was made on Sept. 4, 1972, near the end of the morning, in the Arizona grassland desert. One hunting *Prionyx (parkeri?)* suddenly pounced on a motionless grasshopper. Instead of trying to escape, as usual, the latter was seen with the colorful wings open, fluttering convulsively, with a startling suddenness, thus producing a striking color flash. The hind legs were rigidly extended behind like in the flying posture (Fig. 5b). However the

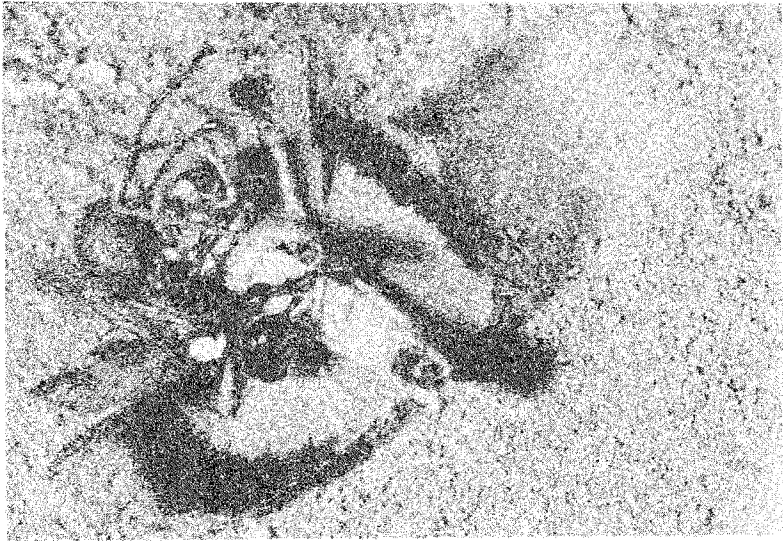


Fig. 4: A *Prionyx parkeri* wasp succeeded in overturning a "frozen" oedipodine grasshopper. This makes the ventral surface of the thorax more accessible to the stings of the wasp. One small drop of repellent fluid can be seen on the abdomen of the wasp. After stinging is over, the wasp will vigorously rub its abdomen on the substrate, in an effort to eliminate this unpleasant, perhaps noxious, fluid. Note (also in Fig. 2) the dot of Testor paint on the dorsal surface of the wasp thorax, for individual identification.

whole body was strongly arched downward as in Fig. 3. For the observer, it looked as if the "frozen" grasshopper was disabled or dying. The wasp left the grasshopper alone and pursued her hunting trip. Under the impression that the prey had received a sting or two, I picked it up only to see it instantly recover without the slightest trace of paralysis. Obviously the grasshopper, later identified as an adult *Mestobregma plattei rubripenne* (Bruner), had not been stung and was not disabled at all. This species is an acceptable prey since it was also found in two nests dug up the same day, nearby. In another, similar, instance the upper wings (tegmina) opened only slightly, just enough to uncover the triangular base of the vivid red wings that remained folded. Again the wasp failed to paralyze the frozen grasshopper which later escaped just as suddenly as the first one, unharmed. The latter case might be a less intense version of the first case. Presumably all gradations could be observed.

The eliciting stimuli of such reactions could not be determined, because of the suddenness and unpredictability of such encounters. Sight of the rapidly approaching predator and/or mechanical contact are likely candidates.

b) Observations in captivity (Figs. 3 and 4)

Similar or identical responses were also observed in captivity at close range and in better conditions. Confinement seemed to even somehow favor appearance of this behavior perhaps because of restricted escape and/or greater concentration of attacks. Often the extended wings and whole body were also strongly curved downwards, sometimes even tightly pressed against the substrate (Fig. 3). The appendages and head were tucked in and more or less invisible under the protective "umbrella" of the wings. The sudden flash of the colorful wings and dark semi-circular markings, followed by the appearance of convulsive movement and finally the illusion of a disabled or dying grasshopper were, indeed, an arresting sight, at least for a human observer.

Curiously such frozen grasshoppers mostly failed to suddenly "resuscitate" and escape after it had become evident that their postural defense had failed to stop the wasp attack. Such misfiring might be a cost of this strategy because of the strong inhibitory influences apparently involved. Sometimes wing fluttering resumed as the wasp attempted to deliver the paralyzing stings. If left alone by the wasp the grasshoppers would however invariably recover without any sign of discomfort, like in the wild.

Such displays were never observed with *Tachysphex* wasps, perhaps because the much smaller grasshopper nymphs they attack have undeveloped wings . . . that cannot be used.

If the *Prionyx* wasps succeed in overcoming all these various defense mechanisms or hurdles, as they often do, they then attempt to deliver an average four successive stings, always on the same stinging sites and in a predictable order (summarized in Steiner 1976; details in Steiner 1981). The paralyzed grasshopper can then be safely and freely manipulated and stored in the nest, without any resistance, obstruction.

ANALYSIS, DISCUSSION, COMPARISONS

Discussion is concerned mainly with possible or plausible interpretations and evolutionary significance of these various defense

reactions, their degree of predator-specificity. Comparisons are made with other orthopterans, with similar and different anti-predator strategies. Effectiveness, always difficult to prove, particularly when attacks or lack thereof depend on the internal state of the predator like in the present case, will be assessed rather than analyzed mathematically.

All defenses described before (except crypticity) are secondary rather than primary defenses since they are exhibited during encounters (Edmunds 1974, pp. 1, 136). Defenses are often anti-location, anti-capture or anti-consumption devices (i.e. Alcock 1975, p. 333). Furthermore, many species have several lines of defense (integrated defense systems: Edmunds 1974, p. 243). Thus the mantid *Polyspilota aeruginosa* may run, fly, give a startle display, slash at the attacker. It can also feign death if persistently handled in a rough way. It soon recovers, however. The brightly colored abdomen might also represent flash behavior (in Edmunds 1974, p. 245). Each aspect of the defense system will now be discussed separately.

Escape by jumping, flying away

This is a classical and common case of sudden startling (flash or deimatic behavior Fig. 5b) followed by sudden disappearance into crypsis (landing; Fig. 5c) (Edmunds 1974, pp. 146–148) by using protective colors (e.g. Isely 1938). This is usually a very efficient mechanism but *Prionyx* wasps occasionally dash at flying grasshoppers (Fig. 5b), even sting them in mid air, or take them by surprise before they can escape. Pygmy mole crickets that escape by flying away are also grasped and/or stung during flight by the sphecid wasp *Tachytes mergus* (Yoshimoto, in Krombein and Kurczewski 1963, p. 147) and also by *Tachytes minutus* (Kurczewski 1966). This defense is not especially aimed at digger wasp predators.

Detection of the predator is probably visual but could also be based on hairs sensitive to airborne vibrations, as in some caterpillars such as *Barathra brassicae* (Tautz and Markl 1978).

Use of hind legs other than for jumping: kicking or obstructive behavior such as hind leg raising or interpositions, brushing away, pushing away

Hind leg autotomy used by crickets (Steiner 1968) was never observed in grasshoppers in the present study but *Prionyx* wasps

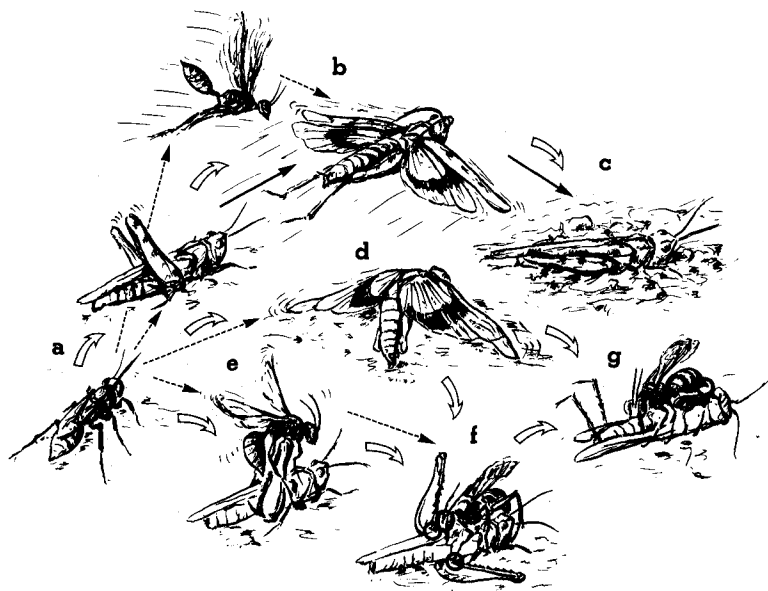


Fig. 5: Summary of oedipodine grasshopper anti-predator actions and *Prionyx*-prey interactions. a: the wasp detected a grasshopper which is at the preparatory stage of jumping (J); b: the prey flies away (F), suddenly opening very colorful wings with conspicuous semi-circular dark markings (startle display) and in some cases the wasp follows the grasshopper in flight and even stings it in midair; c: the escaping prey suddenly lands and blends with the substrate (crypsis); d: instead of escaping the grasshopper sometimes "freezes" into an odd posture somewhat remindful of an inhibited flying action; the posture and convulsive wing fluttering give the impression that the orthopteran is disabled, dying (disablement display? thanatosis?); at the same time the posture and hunching appear to emphasize the semi-circular dark markings on the wings (eyespot intimidation display, "bluff"?); furthermore in this posture, access of the vulnerable ventral side of the thorax, where stings are delivered, is reduced or impossible for the wasp (obstruction behavior); e: hind leg raising (HLR) is another obstructive behavior that makes initial posturing of the wasp difficult or impossible; kicking can also send the wasp a few cm away; f: hind legs are also used for brushing (B) and/or pushing away (P) the wasp; pressure is applied on the circled areas so as to try to force the wasp to release her mandibular and leg grip; g: as a last ditch defense the grasshopper can release a repellent fluid through the mouth, which rapidly spreads over the ventral thoracic surface where all stinging sites are located; the wasp often hesitates to dip into this pool her abdomen tip (circled); the latter is also exposed to powerful bites from the grasshopper; therefore the throat of the prey must be quickly stung to stop these mouth-based defenses. Solid and dashed arrows indicate prey and wasp movements, respectively; open arrows show possible sequences of events but these sequences can also be broken if the defenses are effective and the wasp gives up.

usually seize the wing base(s) or abdomen rather than one hind leg (Fig. 1). Hind legs of crickets, grasshoppers, sometimes phasmids, often covered with strong spines, are one of their major systems of escape and/or defense. Some wingless phasmids can jab the spines into an aggressor (Robinson 1968b). Overt defense by kicking has also been described in some large aphids (in Edmunds 1974, p. 245) and in a number of orthopterans such as crickets (Steiner 1968) and *Locusta migratoria* for instance (Parker et al. 1974). In the latter case it can be so violent that the attacker is knocked 20–30 cm away. According to Parker et al. (1974) hind leg raising often precedes kicking (threat?). It is also part of the defense postures of male *L. migratoria*, the giant weta (*Deinacrida*) of New Zealand (in Sebeok 1977, Fig. 5a, p. 342) and mormon crickets when attacked by the digger wasp *Palmodes laeviventris* (Parker and Mabee 1928, p. 9). In the latter case, as in *Prionyx* and *Tachysphex*, the wasps succeeded in stinging only with considerable difficulty. In the present study hind legs were often raised past the vertical line (Fig. 5e) and even as far forward as the level of the head, as in Fig. 1 for instance, in addition to tail or body raising. This was also observed once in response to an approaching *Tachysphex tarsatus*. Freezing into such postures made access to the dorsal area and wasp posturing very difficult, sometimes impossible (Fig. 5e) (obstructive behavior) and the efficiency of this behavior appeared even to increase as a result of repeated attacks. Interposition of legs (obstruction behavior) was also observed in mole crickets attacked by *Larra* wasps (Williams 1928).

Brushing and pushing away (Figs. 1 and 5f) are more difficult to evaluate since they are more graded and variable responses which are not easy to detect, let alone quantify, in the confusion of the attack. Plausibly these responses work best (if at all) at early stages of contact with the wasp, also if the prey is very large and vigorous or if the wasp is more likely to easily give up, for instance at early stages of hunting (Steiner 1976). It is doubtful that a firmly anchored wasp can easily be dislodged in this way.

[Remark: some orthopterans extend or raise their fore legs, vertically, as part of a threat-intimidation posture (e.g., *Neobarettia*: Cohn, in Sebeok 1977, p. 342, Fig. 5b)].

Orthopteran hind legs are often given special attention and are paralyzed first by some predatory wasps such as *Liris* and *Tachysphex* (Steiner 1962, 1976). *Prionyx* wasps can give priority to the

mouth-based defenses (biting, regurgitating), now discussed, since they effectively neutralize hind leg defenses with their powerful “embracing” legs. Correspondingly, these wasps deliver the first sting in the throat, not around the hind legs (Steiner 1976).

*Biting and retaliation (aggressive defense:
Edmunds 1974, p. 182)*

Orthopterans commonly use their powerful jaws for threat, intimidation or even active defense, retaliation, if not for predation. The predaceous North American katydid *Neobarettia* severely bites and displays the open mandibles as part of the threat-intimidation display (Cohn, in Sebeok 1977, p. 342, Fig. 5b).

In one observation in captivity (Arizona, June 24 1973, 1335 h) a wrongly positioned *Tachysphex tarsatus* (No + 1042) was clearly and severely bitten by a nymph *Trimerotropis pallidipennis* p. (Burm.) (No + 1098) during a stinging attempt. This suggests that the wasp is particularly vulnerable before proper positioning is achieved and that strong selection pressures in the direction of minimum risk must have shaped the usual stinging postures. The penalty for wrong posturing can be very heavy. Thus the above wasp was found dying in the cage the next day, June 25, most likely as a result of this violent retaliation of the prey.

Importance of mouth-based defenses is confirmed by the fact that many orthoptera-hunters deliver a special throat sting (Steiner 1962, 1976) sometimes even before any other sting (e.g. *Prionyx parkeri*). This also eliminates opposition to prey-transport and storage in the nest (and furthermore “de-activates” the prey that recovers in part from paralysis, later: Steiner 1963a). In sharp contrast, *Oxybelus uniglumis* wasps omit the throat sting when they paralyze their non-recovering fly-prey devoid of subesophageal ganglion and of potentially dangerous mouth parts (Steiner 1978, 1979). Orthoptera-hunting wasps with missing legparts or damaged antennae are often found, particularly late in the season. This might be a testimony to the efficiency of bites of their prey but also result from intra-specific fighting (see for instance Brockmann and Dawkins 1979, for *Sphex ichneumoneus*) and/or accidents during nesting. A female *Palmodes carbo* with two deep dents on the back of her abdomen was found in southern British Columbia. It is probable that this represented severe bites received from one of their large, often

predaceous, decticine grasshopper-prey rather than beak marks of some bird.

Chemical defenses: regurgitated fluid (R)

Chemical defenses are particularly widespread among insects (see for instance Eisner and Meinwald 1966; Wallace and Blum 1971, etc.) including Othoptera. Some of them have specialized glands and the substance can be ejected with considerable force (e.g. *Poecilocus buforus*, from an opening located on the first abdominal tergite: Fishelson 1960). A froth can also be discharged through a thoracic spiracle (e.g. *Romalea microptera*: in Eisner and Meinwald 1966). Such repellents make their owner distasteful or unpalatable. The same apparently holds for fluids regurgitated from the gut through the mouth (Edmunds 1974, p. 199) by grasshoppers for instance = enteric discharges (Matthews and Matthews 1978, p. 335). Digger wasps, however, do not consume their prey usually but avoid contact with this fluid which is apparently a contact repellent. Functioning of the receptors located around the stinger could be impaired (jamming effect?) chemically and/or mechanically (Steiner 1976). Stinging remains possible, however, even with stinging sites covered with the fluid (Figs. 2 and 5b) but the wasp clearly hesitates or even gives up half way through stinging. Contact triggers vigorous, sometimes frantic, rubbing against the ground and/or hyper-grooming as in ants (Matthews and Matthews 1978, p. 335) as in hunters of regurgitating caterpillars like cutworms (e.g., *Amomphila*, *Podalonia* wasps). Body contact is clearly unpleasant if not deleterious, particularly for some small *Tachysphex* wasps (Steiner 1976).

One of the latter (*tarsatus* No + 874) had her abdomen tip covered with a thick coat of sand particles as a result of her attempts to rub off the sticky substance. The wasp was found dying the next day, June 19 (Arizona study) (the same probably happened to another *tarsatus* (No + 887) which died on June 6).

The same wasp (No + 874) was also observed the day before (June 18, 1405 h) in the process of carefully removing with the mandibles, bit by bit, a large crust of dried up fluid, from the ventral surface of the thorax and throat of a grasshopper. This was done right after "malaxation" of the fore leg bases which in some larrine wasps is a preparatory stage of egg-laying (details in Steiner 1971). Since the

egg is invariably glued right behind the fore legs, where the crust was also located, this would indicate that the regurgitated fluid could also be a serious obstacle to egg-laying or egg development. *Prionyx* wasps lay their egg at the base of one hind leg . . . where the risk of such "flooding" is clearly much reduced or even nil! Furthermore, paralyzed grasshoppers cannot remove the spilled fluid by grooming, as they normally do. Consequently "cleaning" of the soiled prey can be done only by the wasps, if at all.

This chemical defense is apparently even more effective in mole crickets against another larrine wasp: *Larra* (Williams 1928). Thus *Larra sanguinea* wasps were found with their mouthparts completely glued together by the very viscous fluid. Remarkably, some of these wasps managed to catch their mole cricket in spite of such crippling handicap! Ants are repelled by fecal material or chryso-melid beetle larvae (in Matthews and Matthews 1978, p. 343), and refuse to carry away pieces of grasshopper treated with their own repelling fluid (Eisner 1970).

In conclusion, the importance of mouth-based regurgitative defenses can be assessed by (1) the care with which these wasps try to eliminate the fluid from the prey and from their own body, (2) evolution of a specialized sting in the throat that abolishes mouth-based defenses, (3) the priority given by *Prionyx* wasps to mouth-based defenses (first sting in the throat), (4) dramatic effects, including death, observed on some wasps like small *Tachysphex*, (5) toxic effects reported in the literature, for mammals, such as topical irritation of eyes, vomiting when swallowed and severe symptoms caused by injection (Matthews and Matthews 1978, p. 335).

Such defenses are therefore particularly efficient against smaller predators like arthropods, wasps included. More experimentation is clearly needed, however.

Postural defenses, displays, replacing escape
(Figs. 3, 4 and 5d)

Such complex postures and displays will be analyzed in terms of their various components or aspects.

a) Color flash, startle response

Sudden display of colored wings, of hidden and bright structures (deimatic behavior) is common in insects, particularly in otherwise cryptically colored moths such as *Catocala scripta*, *Triphaena*

pronuba (in Edmunds 1974) and also many orthopterans. For the latter, wing opening (lifting) is for instance part of the dramatic threat-intimidation display of *Neobarettia* already mentioned (in Sebeok 1977, p. 342) or the one of *Phymateus*. Since these latter species are potentially dangerous and/or distasteful such displays are usually interpreted as warning (in Edmunds 1974, pp. 148, 154; see also for instance Frazer and Rothschild 1962). The first species bites severely while the latter has strong hind leg spines and secretes a repelling fluid if further molested. When exhibited by harmless species such as the stick insect *Metriotes diocles* (e.g. Bedford and Chinnick 1966; Robinson 1968a) or common grasshoppers it is considered as mere "bluff" based on a startle effect and/or an apparent increase in size, height, volume, etc. (intimidation behavior). Similar actions are reported from some cicadas and mantids and are particularly dramatic in the African mantid *Idolium diabolicum* (in Wickler 1968).

b) Display of dark markings or "eyespot"

Eyespots are commonly displayed by moths (see for instance Blest 1957, 1964). If even very imperfect imitations are considered effective then perhaps this also applies to the semi-circular dark markings displayed by grasshoppers (Figs. 3 and 5d). Rarity of the display is essential (in Edmunds 1974, p. 168).

c) Appearance of disabled, dying or dead insect (thanatosis) with freezing, hunching and appendages tucked in (Fig. 5d).

Inhibition of movement in itself or freezing is likely to lower the probability of detection and/or attack by predators that hunt moving live prey visually (e.g., Steiner 1962, 1976 for cricket-hunting *Liris* wasps). This probably includes many digger wasps. Thanatosis is known from a number of insects, also orthopterans (Edmunds 1974, p. 172; Robinson 1968a). The prey might also be considered unsuitable because of the unusual appearance as such (oddity effects). The latter is illustrated by "protean defenses" an unpredictable, erratic and highly diverse behavior (in Edmunds 1974, pp. 144-145; see also Chance and Russel 1959; Humphries and Driver 1971, etc.).

Furthermore, grasshoppers with wings spread, appendages tucked in and body strongly arched (Fig. 3) also seem less exposed because of reduced access to the vulnerable stinging sites, all located on the well protected ventral surface of the thorax (Steiner 1981).

Some *Prionyx* wasps experienced great difficulties in squeezing themselves under such grasshoppers (Fig. 3, one leg of the wasp visible). Sometimes also the wasps succeeded in turning over such grasshoppers, venter up (Fig. 4). Even so, stinging was difficult.

Reduced accessibility might be an accidental by-product of the “disablement” display or a more direct result of wasp-grasshopper coevolution. The apparent immunity of *Acrotylus* grasshopper nymphs to *Tachysphex pectinipes* was also attributed to restricted accessibility linked with dense and long pilosity (Ferton 1910, p. 158). Body arching has also been observed on some other orthopterans and is sometimes associated with the release or violent expulsion of repellent fluid, as in *Poeciloceris buforus* (Fishelson 1960).

d) “Intimidating” and aggressive defensive elements (Fig. 5d).

If the posture shown in Figs. 3 and 5d is also an eyespot display then it has an intimidating as well as “bluff” value.

Sideways rocking, known from some mantids (Crane 1952) and also forward-backward rocking were often observed in crickets, just before or after contact with *Liris* wasps (Steiner 1968), suggesting an intimidating function. This was also observed in *Empusa egea* in response to attacks by the sphecid wasp *Stizus distinguendus* Handl. (Deleurance 1941, pp. 287–288), along with other aggressive responses such as wings open, striking with the raptorial fore legs. Rocking was also observed in some phasmids (Crane 1952) and roaches such as *Periplaneta fuliginosa* (Simon and Barth 1977, p. 307). Crickets also sometimes froze into odd or intimidating erect postures difficult to interpret as “death feigning” (Steiner 1962, 1968). Absence of stinging in such cases, if related at all to the display, might depend on: (1) the oddity of the posture, as Chauvin and Chauvin (1977) suggest (the vertical posture is in sharp contrast with the usual horizontal one), or (2) the possible intimidating effects associated with increased height (bluff behavior), (3) predator mimicry, namely a mantis-like appearance (see Steiner 1968, Fig. i, p. 267). [Remark: this latter possibility was considered far-fetched by one reviewer of the paper cited and consequently eliminated from the text. . . and yet Simon and Barth (1977, p. 307, Fig. 2) describe a somewhat comparable rare posture from the roach *Periplaneta fuliginosa* which they interpreted (probably rightly) as a “Mantis-threat”!]

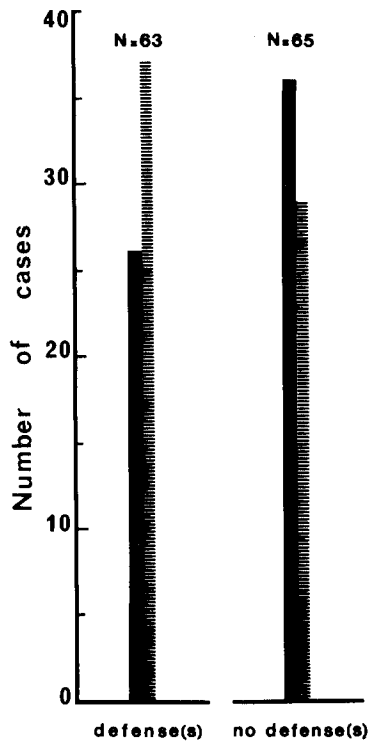


Fig. 6: Proportions of cases where negative effects on the wasp were present (hatched bars = wasp inhibited or stopped, stinging incomplete or no stinging at all) or not present (bars in solid black = complete stinging without apparent negative effects). For cases where prey defenses were recorded (left pair of bars) the proportion of negative effects is greater than no effects, whereas it is the reverse for cases where no defenses were recorded or this information was unavailable (right pair of bars). This indicates that prey defenses (all cases pooled) do have some negative effects on the wasps. It is only a trend, however, since the differences do not reach significance.

It has been suggested that some protective and intimidating displays (e.g. in saturniid and sphingid moths) could have evolved from flight movements (Blest 1957) and can be classified as (1) rhythmic, (2) static, (3) mixed and (4) cryptic. Category (1), that appears to best fit the data (Figs. 3 and 5d) would be closest to the original flight movements. Extension of hind legs, wing beats, even if convulsive, are clearly part of flying which is strongly inhibited.

Similar explanations would seem to apply to the odd cricket postures (Steiner 1968) but in the form of “frozen jumping and/or kicking” rather than “frozen flight” and reduced access to the vulnerable ventral stinging sites is also indicated. Startle displays have also been interpreted in terms of conflict between flying and freezing for some mantids (Crane 1952).

Efficiency of such defenses has been clearly demonstrated in only a few cases. Parker et al. (1974), for instance, showed that defense postures exhibited by *Locusta migratoria* had a significant negative effect on bout continuance between conspecifics. With wasp studies the problem is further complicated by wide moment-to-moment fluctuations in responsiveness of the hunting wasps (Steiner 1962, 1976, 1979). Such variables must be controlled, manipulated or eliminated to get clear answers and this was not done in the present study.

QUANTITATIVE DATA

Quantifications were too limited and inappropriate to make a statistical analysis of the effectiveness of such defenses very meaningful. Only 128 cases were known in sufficient detail to be included in the analysis. In 41.27% ($n = 26$) of the cases the defenses (lumped together) had no apparent effect and complete stinging followed and in 58.73% ($n = 37$) at least some possible effects were recorded, such as temporary, permanent, interruption or even deletion of stinging. When no defenses were observed (or unknown status) the percentages of complete vs incomplete stinging were approximately reversed as predicted: 55.38% ($n = 36$) and 44.62% ($n = 29$). These differences in proportions (Fig. 6) were not significant, however, since the calculated χ^2 was only 3.689 for a critical value of 5.991 ($p \leq 0.05$; $df = 2$; G-test of independence of rows and columns: Sokal and Rohlf 1969, p. 599). A slight advantage can have a decisive selective value in the long run, however.

CONCLUSION

Prey as harmless as herbivorous crickets and grasshoppers possess a rather complex, well integrated, system of anti-predator devices they can use against their wasp enemies. Even if some of these responses are merely obstructive, they do in fact increase the

cost of predation to the wasps by making capture more difficult, more costly, and/or less probable. Natural selection should therefore promote evolution of such anti-predator strategies which in the long run increase the fitness of the prey.

Some components of the system such as flying away and crypticity, perhaps regurgitation, are of a very generalized nature whereas other devices are more predator-specific. Thus startle displays with exposure of dark semi-circular markings are probably most efficient against small avian predators, whereas biting, mouth regurgitation, hind leg raising and obstruction behaviors are presumably more useful against smaller, more vulnerable predators such as other insects, including digger wasps. Matthews and Matthews (1978, p. 352) state that "protective adaptations in insects are intimately related to the behavior and physiology of their predators." This also applies well to wasp predators.

ACKNOWLEDGEMENTS

The Arizona study was part of a sabbatical project, while on an exchange program with the American Museum of Natural History, New York, in 1972-73. Research was conducted at the Southwestern Research Station, Portal, Arizona, and in the surrounding areas, including the Chiricahua National Monument and the Erickson Ranch. Help, advice and hospitality of many persons and friends, I cannot mention individually, are gratefully acknowledged. Wasp specimens were kindly identified by A. S. Menke, U.S. National Museum (Entomology), Washington; R. M. Bohart, University of California, Davis, and W. J. Pulawski, Wroclaw University, Poland, and grasshopper specimens by D. C. Rentz, the Academy of Natural Sciences, Philadelphia, Pennsylvania. The study was supported in part by an operating grant (A3499) from the National Research Council of Canada and funds from the University of Alberta, Edmonton, Canada. I would like to thank J. Scheinas for typing the manuscript.

SUMMARY

Harmless herbivores such as acridid grasshoppers exhibit a complex anti-predator behavior when attacked by *Prionyx* and *Tachysphex* sphecid wasps. Besides jumping and flying away with

exposure of colorful wings (flash behavior) and sudden return to crypticity upon landing, these insects show freezing, often in odd postures, with the colorful wings and dark markings (“eyespot”?) prominently exposed. Such postures also reduce access to the vulnerable ventral surface usually stung by these wasps (obstruction behavior). After contact with the wasp a second line of defense comes into effect such as kicking, brushing and pushing actions. In addition to these hind-leg based defenses, the attacked prey can also use mouth-based defenses: biting and/or regurgitating a repelling, perhaps even noxious, fluid (“tobacco juice”). Such defenses presumably lower the probability of capture or at least increase the cost to the predator and have therefore a selective value.

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