

EVOLUTIONARY SIGNIFICANCE OF PREDATION ON SEXUALLY SIGNALLING MALES

T. BURK*

"There are several very good reasons why courtship displays should not exist at all. Firstly, they render the animal performing them conspicuous, and therefore may attract predators. Secondly, they are usually performed with such intensity that they not only attract predators, but also claim the attention of the displaying animal to such a degree as to make it particularly vulnerable to attack from predators . . ."

(Morris 1956)

"Empirical evidence of increased mortality associated with intersexual selection is uncommon."

(Gwynne & O'Neill 1980)

The male-female dichotomy has far-reaching implications. In most species, females invest more heavily in offspring than males do. The factor limiting a female's number of offspring is likely to be a resource affecting how many eggs she can manufacture or safely deposit. For males, the limiting factor is often simply the number of females impregnated. This disparity has led to tremendous differences in mating behavior of the two sexes, differences which have been discussed in a number of previous papers (Trivers 1972, Thornhill 1980).

Compared to females, males vary widely in the number of offspring they leave (Bateman 1948). For males, sex is an all-or-nothing, high stakes game, where he who hesitates leaves few or no genes in the next generation. Selection favors male adaptations that lead to high reproductive success, such as elaborate physical ornaments and conspicuous displays, even at the cost of increased mortality (Fisher 1958, Trivers 1972). In this paper, I will examine what is possibly the most important mortality factor on sexually active males, predation.

The importance of predation in the evolution of sexual behavior has been somewhat unclear, as the two quotations given above indicate. I hope to show that male-biased predation is both a common and an important factor in the evolution of sexual behavior and communication.

CAUSES OF MALE-BIASED PREDATION

In this section, classes and some examples of male-biased predation are given. Most of these concern insects, but where no clear insect examples have been reported of a particular type of predation, relevant examples are given from vertebrate literature. Examples are grouped into categories corresponding to the causes of male vulnerability (Table 1). I have restricted myself to heterospecific predation, including parasitoids as functionally

*Theodore Burk is a Postdoctoral Fellow employed through a cooperative agreement between the Insect Attractants, Behavior, and Basic Biology Research Laboratory, ARS, USDA and the Department of Entomology and Nematology, University of Florida, Gainesville. He obtained his D. Phil. in 1979 in the Animal Behavior Research Group, Oxford University, where he was a Rhodes Scholar from Kansas. His research interests are in insect social behavior, especially aggressive behavior and acoustic communication.

TABLE 1. CAUSES OF MALE VULNERABILITY TO PREDATORS.

-
1. Exposure
 - A. Active in open or conspicuous areas
 - B. Active at dangerous times
 2. Spacing pattern
 - A. Clumped—economical to exploit
 - B. Regular—predictably encountered
 3. Unwariness
 4. Lack of accurate discrimination (“aggressive mimics”)
 5. Dangerous mating activities
 6. Conspicuous displays
-

equivalent to predators. Cannibalism of males by females, reported in spiders (Christenson and Goist 1979), mantids (Roeder 1963), ceratopogonid flies (Downes 1978), and sphecid wasps (O'Neill and Evans 1981) could easily fall into the general range of this paper but is not considered here.

One cause of male vulnerability to predation is the greater likelihood of male activity in exposed areas or at high-risk times. The male mating swarms of nematoceran Diptera and Ephemeroptera usually occur over streams, in clearings, or adjacent to some conspicuous landmark (Downes 1969, Sullivan 1981). Such locations are found not only by receptive females, but also by dragonflies, wasps, ceratopogonid and empidid flies, birds, and bats (see references in Sullivan 1981). Downes (1970, 1978) has shown that empidids and ceratopogonids respond to “swarm marker” topographical features, hunting in appropriate spots even before prey males begin to swarm. Big brown bats (*Eptesicus fuscus*) find likely areas by orienting to the choruses of calling frogs or katydids, which occur in areas where other insects are swarming (Buchler and Childs 1981).

Other male insects are also active for long periods in exposed locations. Male *Drosophila* chase and court females on pieces of rotting fruit, where they are vulnerable to predation by insectivorous birds (Spieth 1968). Davies (1977) has shown that two British birds, the pied and gray wagtails, specialize on various flies, especially dung flies (*Scatophaga stercoraria*), whose males are present in large numbers on fresh dung pats.

Male insects may also be active at times when the risk of predation is high. Female forest tent caterpillar moths (*Malacosoma disstria*) emerge from cocoons and are receptive in early evenings. Male *M. disstria* must search out and mate with newly emerging females before they are found by competitors. This mate competition forces male moths to begin searching for female cocoons during the daylight hours, and results in the capture of many male moths by birds (Bieman 1980).

A second reason for male vulnerability lies in male spacing patterns. For reasons discussed by Alexander (1975), displaying male insects often gather into swarms or display groups. This clumping may make it more economically worthwhile for large predators to prey on displaying males. Bats probably look for areas where insects are swarming because they are likely to obtain high rates of energy intake with low searching and handling costs. On the other hand, males that are regularly spaced throughout an area, rather than aggregated into clumps, may also be vulnerable. Estes (1973) has reported that male wildebeest are especially vulnerable to predation by

lions because their territorial fidelity results in regular male spacing. Lions only move a short distance in any direction without encountering a territorial male wildebeest, and male wildebeest are strongly attached to their territorial sites and unwilling to flee from them.

Third, males may be less wary when involved in rigorous competition with other males for mates. Nagamine and Ito (1980) reported on their attempts to capture cicadas (*Mogannia minuta*) that sometimes reach epidemic proportions in sugarcane fields. In areas of low male density, with few males calling, only about 60% of males could be captured. However, in high density areas, where many males were calling, nearly 90% of males could be captured. No such density differences in vulnerability were observed in female cicadas. Schaller (1972) has given another example involving lions and their prey: he observed male warthogs falling prey to lions because they were preoccupied with fights over access to females.

Fourth, males may become prey because they are not very rigorous in the orientation of their sexual behavior. Selection against missing even remote mating possibilities may lead males to court inappropriate objects. Many male insects perch on vegetation and fly out to approach passing insects of approximately the right size and shape; they then drive off conspecific males and court females. Gwynne and O'Neill (1980) have described the fate of male *Philanthus* wasps with this "perch-and-intercept" mating strategy: many are eaten by passing robberflies (Asilidae). (O'Neill and Evans (1981) have also shown that female *Philanthus* hunt and eat intercepting males.) Similarly, the prey of female *Oxybelus* sphecids are mainly male flies with this type of mating strategy (Table 2) (Peckham and Hook 1980).¹

Lack of accurate discrimination accounts for the success of a small but remarkable class of predators called "aggressive mimics." These predators mimic females of a prey species in order to capture and eat unwary responding males. The cues used may be visual or chemical. Some species of ceratopogonids have unusual abdominal appendages: these probably mimic the cerci of mayflies, allowing these flies to enter mayfly swarms without

¹Superscripts refer to notes in the appendix.

TABLE 2. MALE-BIASED PREDATION BY *Oxybelus* FEMALES (SPHECIDAE).

Species	No. of prey		Prey
	Males	Females	
<i>Oxybelus laetus</i>	133	0	Calyptrate flies
<i>O. packardi</i>	55	1	Calyptrate flies
<i>O. exclamans</i>	16	0	<i>Senotainia</i> flies
<i>O. subulatus</i>	548	0	Therevid flies
<i>O. subcornatus</i>	568	0	Syrphid flies
<i>O. uniglumis</i>	429	7	11 Fly families
<i>O. bipunctatus</i>	787	5	14 Fly families
<i>O. sparideus</i>	80	16	Calyptrate flies
<i>O. cressonii</i>	37	1	Stratiomyid flies

References: Peckham and Hook 1980, Peckham et al. 1973, Bohart et al. 1966, Kurczewski 1972.

provoking evasive maneuvers (Downes 1978). Bolas spiders (*Mastophora dizzydeani*) catch flying moths with a sticky ball on the end of a silken thread, resembling the bolas used by South American gauchos. Eberhard (1977, 1980) showed that bolas spiders only capture male moths of a limited range of species, by producing attractants that mimic the sex pheromones of the female moths. Horton (1979) and Eberhard (1981) have provided other examples of possible aggressive chemical mimicry. The best-studied case of aggressive mimicry involves visual signals. Lloyd (1981) has made a series of elegant studies of predation by female *Photuris* fireflies on males of other firefly species. These "femmes fatales" answer the flashes of searching male fireflies with appropriate flash responses, and eat the attracted males: they have broken the "species-specific" flash codes of the prey species.²

The fifth category of male vulnerability includes species whose males are required to perform dangerous precopulatory tasks. In many species of insects, females only mate with males who provide them with a "nuptial gift" of food, often a dead insect. Thornhill's (1978) study of scorpionflies showed that such female-choice requirements lead males into danger. In two nuptial-feeding species, one that hunts for prey to present to females (*Panorpa* sp.) and another that robs prey from spider webs (*Bittacus apicalis*), males are significantly more likely than females to be caught in spider webs. A third species, *Bittacus strigosus*, is a natural control: no nuptial feeding occurs, both males and females actively hunt for prey, and equal numbers fall prey to spiders.

Sixth, predators and parasites may cue in on the conspicuous "calling signals" or courtship displays of male insects. Such predators can be called "signal interceptors." In insects, chemical, acoustic, and visual signals have been most extensively studied, and signal interceptors have been found exploiting all three types.

Males of the Southern green stinkbug, *Nezara viridula*, produce a sex pheromone that attracts female stinkbugs. Unfortunately for stinkbugs, it also attracts a tachinid fly, *Trichopoda pennipes*, which oviposits on stinkbug bodies (Harris and Todd 1980). Large numbers of stinkbugs fall victim: in a Hawaiian population 64% of females and 71% of males (Mitchell and Mau 1971), in a Georgian population 35% of females and 44% of males (Todd and Lewis 1976) were parasitized.

Male bark beetles of the genera *Ips* and *Dendroctonus* produce attractant pheromones that not only attract other bark beetles (see Alcock, this symposium), but also a wide variety of predators and parasites. These include clerid and ostomid beetles, dolichopodid flies, and anthocorid bugs that prey on adults and dipteran and hymenopteran parasitoids which attack immature stages of bark beetles (Birch 1978, Dixon and Payne 1980, Greany and Hagen 1981).

Females of several *Photuris* firefly species, previously mentioned as aggressive mimics, are also visual signal interceptors (Lloyd and Wing ms.). They fly after and catch flashing male fireflies; Lloyd and Wing were able to attract *Photuris* females to a flashing light-emitting diode on the end of a moving fishpole.

A recently discovered and exciting group of signal interceptors includes those who respond to insect acoustic signals. Walker (1964) first noticed housecats feeding on calling crickets and katydids. Subsequently, herons

TABLE 3. PARASITIZATION RATES OF *Neoconocephalus triops* BY *Ormia lineifrons*.

Month	1980		1981	
	Number katydids	Percent parasitized	Number katydids	Percent parasitized
A. Gainesville, FL				
February	—	—	2	0
March	35	20	15	0
April	54	54	60	38
May	—	—	1	100
June	—	—	—	—
July	47	38	40	43
August	34	59	43	53
September	3	100	1	100
Total	173	45	162	40
B. Homestead, FL				
June			9	89
July			11	91
August			10	90
September			9	89
Total			39	90

(Bell 1979) and spadefoot toads (Walker 1979) have been added to the list of potential acoustically-orienting predators. Tuttle and Ryan (1981) have shown that certain bats in tropical America cue in on the choruses of frogs: J. J. Bellwood (pers. comm.) has demonstrated that at least four species of neotropical bats are attracted to the calling songs of acoustic Orthoptera.

Insect parasites and parasitoids are also acoustic signal interceptors. *Corethrella* flies locate and bite calling *Hyla* tree frogs (McKeever 1977). A sarcophagid, *Colcondamyia auditrix*, parasitizes a cicada, *Okanagana rimosa*, by orienting to cicada calling song and larvipositing on the cicada (Soper et al. 1976).³

One tribe of tachinid flies, the Ormiini, are specialized acoustically-orienting parasitoids of calling Orthoptera (Sabrosky 1953). Nutting (1953) found that 72% of 18 calling *Neoconocephalus robustus* katydids collected on Cape Cod were infested with the ormiine *Euphasiopteryx brevicornis*. Cade (1975) demonstrated that *E. ochracea* orients to the calling song of a field cricket, *Gryllus integer*, upon which it larviposits. Cade found parasitization rates of calling males as high as 80%. I have been studying parasitization of the katydid *Neoconocephalus triops* by another ormiine, *Ormia lineifrons*. Like *E. ochracea*, *O. lineifrons* can be attracted to tape recordings of its host's calling song. In two widely separated areas in Florida, *O. lineifrons* takes a heavy toll of *N. triops* males. In Gainesville, *N. triops* is bivoltine; in both generations parasitization of calling males is low early in the season and high late in the season (Table 3a). In Homestead, 300 miles further south, *O. triops* is less seasonal and suffers very high parasitization for extended periods (Table 3b). *O. lineifrons* larvae silence calling katydids in about 5 days, killing them in 7-9 days. At times of heavy infestation, the

reproductive lifetime of a calling male katydid is reduced from a potential 2-3 months to an average of 1-2 weeks.

EVOLUTIONARY CONSEQUENCES OF MALE-BIASED PREDATION

Not surprisingly, males subject to male-biased predation have evolved a variety of counter-measures. Table 4 lists a number of these.

In some cases, predation may have to be borne by males as an added cost of mating effort. Female mate choice may limit the options available to males. For example, if female katydids are only active at certain times of the night and will only mate with calling males, male katydids may have to go on calling in spite of the risk of predation or parasitization. Even in such cases, however, predation may have important effects on male sexual behavior. For example, heavy predation may reduce the variance in male mating success, affecting the amount of male-male aggression present.

Males of many species evolve greater caution or specialized antipredator maneuvers. At the approach of *Bembix* wasps, swarming male syrphid flies (*Volucella pusilla*) drop down to vegetation, and male horseflies (*Tabanus bishoppi*) dart rapidly from place to place rather than hovering in one spot (Blickle 1959). Male mosquitoes of the species *Aedes vexans* and *A. impiger* "mob" predatory ceratopogonids (*Probezzia concinna*) and empidids (*Rhamphomyia nigrita*), respectively, by switching flight patterns and closely circling the predators (Downes 1970, 1978). Males of the dung fly, *Stercoraria scataphaga*, scatter from dung pats into the surrounding grass when wagtails approach (Davies 1977).⁴ One thing to note about all of these escape behaviors is that they add to the cost of mating for prey males—they inevitably reduce the amount of time available for mating.

Some species have evolved physical defenses against predators. Fireflies may be at least partially protected against vertebrate predators by chemical defense (Lloyd 1973, Eisner et al. 1978). Rentz (1975) noted the exceptionally long antennae of neotropical forest-canopy dwelling katydids, which may aid in tactile detection of hunting bats. Morris (1980) and Morris and Beier (1982) have noted that these katydids also have sharp spines, capable of drawing blood.

Prey males may avoid predation by evolutionary changes in location or spacing. First, they may display in safer locations. Hawaiian *Drosophila*, unlike most other flies in that genus, do not court females on food sites, but

TABLE 4. ANTIPREDATOR ADAPTATIONS OF DISPLAYING MALES.

-
1. None—Predation unavoidable cost of mating
 2. Evasive behavior
 3. Physical defenses
 4. Spatial changes
 5. Temporal changes
 6. Alteration of signals
 7. Signal loss
 8. Alternative strategies
 - A. Seasonal display differences
 - B. Dimorphism
 - C. Alternative behavioral strategies
-

instead call from vegetation (Spieth 1968). Spieth has proposed that this is an adaptation to heavy predation by native insectivorous birds. Similarly, Borgia (1979) has noted that many small dung-breeding flies have sexual encounter sites away from dung pats because of the presence of predatory *Scatophaga stercoraria* on dung pats.

Lack (1968) suggested that predation was a major factor in the evolution of lekking, or communal displaying by males in areas removed from female-required resources. Lack noted many antipredator adaptations by lekking birds, and suggested that the presence of "many eyes" would lead to less predation on aggregated males. Hamilton (1971) called such aggregations "selfish herds," and suggested that an additional benefit to individual males would be the possibility, in case of predator attack, of putting a competitor between the predator and oneself. Also, when many prey are escaping, predators may be confused and have difficulty selecting individual prey (Neill and Cullen 1974).

Males of many species of insects form lek-type display groups (Alexander 1975). Good demonstrations of antipredator benefits of male congregation in insects are lacking, but there are several suggestive examples. Copulating pairs of the ocean skater, *Halobates robustus* (a gerrid bug) form "flotillas" near mangrove edges in the Galapagos Islands. Predators are detected at a greater distance in large groups than in smaller ones (selection for vigilance by female ocean skaters is obviously a factor here) (Treherne and Foster 1980). Periodical cicadas not only synchronize their emergence (see below), but males also congregate in large numbers while calling (Simmons et al. 1971). It has been suggested that the sheer intensity of sound produced by such choruses may act as a repellent to avian predators, as it is so high as to cause partial deafness for several hours in human observers. Other acoustic insects are good candidates for grouping-derived antipredator benefits; Ryan et al. (1981) have shown that predation risk from acoustically-orienting bats is inversely correlated with the number of males within a chorus in a frog, *Physalaemus pustulosus*. For the *Gryllus integer-Euphasiopteryx ochracea* system described earlier, Cade (1981) has shown that aggregated calling crickets are at the least no worse off than isolated ones. The number of parasitoid flies attracted per cricket-song-playing loudspeaker was not significantly higher for groups than for isolates.

However, predation may also break up male aggregations—this will depend on the hunting strategy and social behavior of the predator. Many Asian fireflies form massive aggregations in which thousands of males gather and perch in trees. No such mass sedentary organization is found in the New World; Lloyd (1981) suggested that this is due to the presence of the predaceous *Photuris* in the New World.⁵

Evolutionary temporal shifts analogous to these spatial shifts are another adaptation of displaying males. Sullivan (1981) pointed out that many insect swarms form at dawn and dusk, times when some types of predation should be least (Kacelnik 1979). An impressive example of male display at safe times is the desert cicada, *Diceroprocta apache* (Heath and Wilkin 1970). Physiological and behavioral adaptations allow this insect to be sexually active at the hottest times of day in the hottest months of the year, at temperatures over 40°C. Its main predators, birds and cicada wasps, have

to retire to shelter at temperatures lower than those at which male cicadas start to call.

Just as males concentrate their displays in space, they also may concentrate their displays in time. Predation pressure is generally thought to be the factor accounting for the evolution of 13- and 17-year emergence cycles in periodical cicadas, whose males produce conspicuous acoustic signals (M. Lloyd and Dybas 1966). The synchronous emergence of millions of calling cicadas, usually of three different species, is thought to "swamp" predators, who are literally unable to eat cicadas as fast as they emerge and call. Furthermore, it is extremely common for all males of one insect species to display concurrently during a restricted period of the day; Forrest (1980) provided the example of mole crickets, which call for only about 45 min a night. This should further reduce vulnerability to predators. A further consideration of the antipredator aspects of such "spreeing" is provided by Walker (1982), who has considered diurnal patterns of acoustic displays (he is responsible for the term "spree," temporal equivalent of "lek").

Predator pressure may directly affect the form of signals used by displaying males. Predators may have caused the evolutionary shift from constant glowing to flashing in fireflies, and may account for some of the eccentric flight paths followed by flashing male fireflies (Lloyd 1973, Lloyd and Wing ms.). Morris (1980) and Morris and Beier (1982) have detected several evolutionary changes in signal production by neotropical katydids that are probably counter-adaptations against acoustically-orienting bats. *Copiphora rhinoceros* has shifted from predominantly long-range airborne sounds to short-range substrate vibrations (Morris 1980). A number of other forest canopy species show a coordinated set of adaptations directed against insectivorous bats: (1) extremely low thresholds for elicitation of defensive behaviors; (2) severely curtailed period of time emitting signals; (3) low intensity of signals; (4) lowered duty cycle ratio (low signal output as a percentage of signalling period—i.e., longer intervals between pulses or pulse trains); and (5) use of ultrasonic sinusoidal carrier frequencies. This last adaptation is thought to have evolved as the most efficient type of signal for female katydids to localize quickly. With greatly reduced signal output, females must be more efficient at hearing and localizing male signals (Morris and Beier 1982).

From the reduction in time spent displaying it is a logical next step to the evolution of complete signal loss. Otte (1977) notes that loss of calling songs is a common phenomenon in Orthoptera (it is also reported in frogs). Several authors (Rentz 1975, Morris and Beier 1982, T. J. Walker, pers. comm.) have commented on the relative lack of acoustic activity by forest species of neotropical Orthoptera that are acoustically hunted by bats. In Florida, the only known *Gryllus* field cricket that does not call, *Gryllus ovisopis* (Walker 1974) coincides seasonally with peak populations of the cricket-attacking acoustic parasitoid, *Euphasiopteryx ochracea* (Mangold 1978). Predation pressure is thus strongly implicated as the reason for song loss.

Cade (1980) discussed the presence of alternative mating strategies in insect populations. Predation may be an important factor in the evolution of many of these alternatives (Rubenstein 1980). Alternative strategies may

be present in entire populations at different seasons or in different areas, or may co-exist in a single population at a given place and time.

In some insects male display behavior differs seasonally in ways suggestive of the influence of predation. Returning to *Gryllus* in Florida, both *G. rubens* and *G. firmus* males are primarily silent during their fall generation, when *Euphasiopteryx ochracea* is abundant. An earlier generation in each species, however, is much more active acoustically, even though actual populations may be smaller (T. J. Walker, unpublished data).

Some male insects, such as horned beetles, are dimorphic in physical characteristics, but in no case that I know of has such male dimorphism been reported as being maintained by selective predation. There is one good example of female dimorphism that is relevant. In *Ischnura* damselflies, females are dimorphic in color, one morph being drab (similar in different *Ischnura* species), the other resembling the brightly colored, species-specific male pattern. The dimorphism is maintained by opposing selection pressures. Due to predation, male-like females have only one-third the life expectancy of drab forms. Drab forms, however, are sometimes mated by heterospecific males, resulting in inviable offspring. The proportion of male-like forms is higher in areas of sympatry (Johnson 1975). In some vertebrates predation and sexual selection combine to maintain male dimorphisms. In a fish, the three-spined stickleback, red-bellied and black-bellied males co-exist in some populations. Red-bellied males defend territories and eggs more successfully from conspecific egg predators and are more attractive to females. On the other hand, black-bellied males are subject to much lower levels of predation by trout (Semler 1971). A similar color dimorphism maintained by sexual selection and predation is found in male adders (*Vipera berus*) (Andren and Nilson 1981).

Best studied are alternative behavioral strategies existing within a single population. In many conspicuously displaying species, calling males co-exist with non-displaying males called satellites or sneaks. These males do not display, but attempt to intercept and mate with females attracted to the displays of other males. Cade (1979) demonstrated such behavior in the cricket *Gryllus integer*. Satellite males were usually rejected by females and had much lower mating success than callers, but calling males were subject to heavy mortality from *Euphasiopteryx* flies. In bullfrogs, Howard (1981) has described three alternative male behaviors. "Territorial" males were large, called loudly, and attracted many females. Their territorial fighting and exposed calling locations also exposed them to significant predation by snapping turtles. Intermediate-sized males were "opportunists," who called but did not defend territories, thereby reducing risks of predation. Small males were "parasites" that did not call at all, but attempted to intercept females coming to territorial males. Similar opportunist and satellite behavior probably remains to be detected in many conspicuously displaying species. One prime candidate is the katydid I have been studying, *Neconocephalus triops*, which suffers such high acoustically-mediated parasitization.

OTHER ASPECTS OF MALE-BIASED PREDATION SYSTEMS

It goes without saying that any predator-prey system takes on aspects of an "arms race," with prey evolving defenses against predators, predators

evolving new tactics, and so on (Dawkins and Krebs 1979). It would be pointless to pursue the many possible refinements made by predators to overcome the responses of prey. But several ways in which male-biased predation systems are exploited are unusual and merit brief mention.

Males often congregate in search of females on resources required by those females for the production and deposition of eggs (Burk 1981). The prey of predatory females qualifies as such a resource, so it is not surprising that males of many predator species respond to the sexual signals of males of prey species, not to eat them but to use them as mating rendezvous sites. For example, male tachinids, *Trichopoda pennipes*, are attracted to male sex pheromones of Southern green stinkbugs (Harris and Todd 1980), while male clerid beetles, dolichopodid flies, and anthocorid bugs respond to bark beetle pheromones (Dixon and Payne 1980). Attracted predator males do not attack the prey males, but scramble about searching for predator females.

Some predators may reveal their presence to displaying males. In such cases, competing males of prey species have evolved ways of exploiting anti-predator responses by mimicking the predators! Lloyd (1981) has described such a system in the firefly *Photinus macdermotti*. *Photuris* female predators, in trying to mimic the flashes of several different prey species, sometimes make characteristic mistakes in their responses to *P. macdermotti* males. When *P. macdermotti* males detect a flash dialogue between a *P. macdermotti* male and a *P. macdemotti* female, they sometimes inject flashes similar to the mistakes of the *Photuris* predator. These "false injectors" benefit from this behavior if they cause competing males to hesitate in approaching real *P. macdermotti* females, allowing the injector to get to her first.

The firefly system elegantly demonstrates my earlier point about arms races. Lloyd (1981) has shown that even male *Photuris* get into the mimicry act! What is the best way to find a *Photuris* female? To be a prey *Photinus* male, of course. Remarkably, *Photuris* males of several species fly around searching for females while flashing the signals of various prey species; as many as four different prey species' signals are mimicked in this way by *Photuris cinctipennis*.

PRAGMATICS

Because one of the aims of this symposium series is to demonstrate the pragmatic significance of behavioral ecology, it is appropriate to conclude with some thoughts on the practical significance of male-biased predation. I can think of at least four ways in which it is important. First, a substantial literature exists on the possibility of controlling insect populations by male annihilation (Knipling 1979). Predators, and especially insect parasitoids, may be efficient enough at attacking males to be useful in this way; ormine flies might be of use in controlling pest Orthoptera. Second, in many cases, predators attracted to displaying males remain in the vicinity and also attack females and immatures. This happens, for example, in the stinkbug-attacking tachinid *Trichopoda pennipes* (Harris and Todd 1980). Third, predation may have significant impact on other control methods (Barclay and Mackauer 1980), so must be taken into account. Finally, and most importantly, we can hardly hope to be successful as pragmatic entomologists unless we understand the basic features of a target species' behavior. This

of necessity includes an understanding of those selective forces, such as sexual selection and predation, that have shaped the insect's behavior through the process of natural selection.

SUMMARY

Sexual selection favors male adaptations that lead to high reproductive success, such as elaborate ornaments and behavior, even at the cost of increased mortality. One important mortality factor is sex-biased predation on males. Males are vulnerable because they display at dangerous times or in exposed places, they may be clumped and economical to exploit, they are unwary and indiscriminating, they perform dangerous mating activities, and they produce conspicuous signals. In some cases virtually 100% of displaying males are killed by predators or parasitoids. Male defenses include evasive behavior, physical defenses, shifts in the spacing and timing of displays, alterations in signal form, signal loss, and evolution of alternative mating strategies. Male-biased predation systems take on aspects of an arms race, and provide many interesting examples of predator-prey coevolution.

APPENDIX

¹*Oxybelus exclamans* may be involved in a fascinating case of predator-prey coevolution (Peckham and Hook 1980). Its prey are male milto-graphmine sarcophagids, *Senotainia* spp. Female flies of this genus are kleptoparasites of *Oxybelus* females' nests. As pointed out by Alexander (1975) and Burk (1981), males often concentrate their mating activities in areas where females are active doing other things (this helps to explain why swarming male insects often occur in particular locations, making them localizable for predators). For male *Senotainia*, the best place to find females is around *Oxybelus* nests. But in hanging around *Oxybelus* nests, they have become vulnerable to predation by *Oxybelus* females. Thus the bizarre result comes about that male *Senotainia* flies actually provide the food for developing *Senotainia* larvae! An extreme adaptationist might even argue that this is an unusual form of paternal investment in offspring by *Senotainia* males!

²Many of these aggressive mimics and male-attacking predators are examples of the concept of preadaptation: they already behaved in ways that easily led to the evolution of male-biased predation or aggressive mimicry. Note that female ceratopogonids and empidids entered swarms to mate, easily leading to entering heterospecific swarms to feed; also that female *Photuris* were already flashing in response to searching conspecific males, possibly resulting in over-anxious heterospecific males occasionally flying to them, leading to selection for better mimicry.

³*Colcondamyia auditrix* may have evolved a neat way of avoiding subsequent parasitization of an already-parasitized cicada ("superparasitism"). In laboratory observations, Soper et al. (1976) noted that *C. auditrix* females larviposited in the area of the cicada's sound organ. It may be that the larvae immediately destroy the sound organ, preventing further calling, and the attraction of additional *C. auditrix* females. Ormiine flies (below) do not have any such tricks—parasitized crickets and katydids continue to call for up to another week, and superparasitism is common.

⁴The wagtail-dung fly system demonstrates the "arms-race" nature of predator-prey systems (see below). Dung flies have adapted to wagtail predation by immediately leaving the dung pat when wagtails approach; however, wagtails find it easier to pick off individual dung flies when they are in the grass. Davies (1977) observed that wagtails would sometimes make a

sudden rush at swarms of flies on dung pats, not attempting to catch them, but merely scaring them into the surrounding grass where they could then be picked off one at a time.

⁵The situation is actually more complicated. Males of a summer species of *Photuris* in Florida perch in aggregations, apparently as a consequence of the hawking attacks of their own females (Lloyd and Wing ms).

ACKNOWLEDGEMENTS

I thank J. E. Lloyd for inviting me to participate in the Insect Behavioral Ecology Symposium; the staff of the USDA Insect Attractants, Behavior, and Basic Biology Laboratory for their assistance and support of my research; T. J. Walker, G. K. Morris, and J. J. Bellwood for permission to use unpublished data and manuscripts; M. D. Greenfield, T. J. Walker, J. J. Bellwood, J. E. Lloyd, P. D. Greany, and J. C. Webb for commenting on the manuscript; Elaine S. Turner for preparation of the manuscript; and T. J. Walker for uncounted acts of advice and assistance.

LITERATURE CITED

- ALEXANDER, R. D. 1975. Natural selection and specialized chorusing behavior in acoustical insects. Pages 35-77 in D. Pimental, ed. *Insects, Science and Society*. Academic Press, New York.
- ANDREN, C., AND G. NILSON. 1981. Reproductive success and risk of predation in normal and melanistic colour morphs of the adder, *Vipera berus*. *Biol. J. Linn. Soc.* 15: 235-46.
- BARCLAY, H., AND M. MACKAUER. 1980. Effects of sterile insect releases on a population under predation or parasitism. *Res. Popul. Ecol.* 22: 136-46.
- BATEMAN, A. J. 1948. Intra-sexual selection in *Drosophila*. *Heredity* 2: 349-68.
- BELL, P. D. 1979. Acoustic attraction of herons by crickets. *J. New York Ent. Soc.* 87: 126-7.
- BIEMAN, D. N. 1980. An evolutionary study of *Malacosoma americanum* (Fabricius) and *Malacosoma disstria* Hübner (Lepidoptera: Lasiocampidae). M.Sc. Thesis, Univ. of Michigan, 49 pp.
- BIRCH, M. D. 1978. Chemical communication in pine beetles. *American Sci.* 66: 409-19.
- BLICKLE, R. L. 1959. Observations on the hovering and mating of *Tabanus bishoppi* Stone (Diptera, Tabanidae). *Ann. Ent. Soc. America* 52: 183-90.
- BOHART, R. M., C. S. LINN, AND J. F. HOLLAND. 1966. Bionomics of *Oxybelus sparideus* at Lake Texoma, Oklahoma (Hymenoptera: Sphecidae, Crabroninae). *Ann. Ent. Soc. America* 59: 818-20.
- BORGIA, G. 1979. Sexual selection and the evolution of mating systems. Pages 19-80 in M. S. and N. A. Blum, eds. *Sexual Selection and Reproductive Competition in Insects*. Academic Press, New York.
- BUCHLER, E. R., AND S. B. CHILDS. 1981. Orientation to distant sounds by foraging big brown bats (*Eptesicus fuscus*). *Anim. Behav.* 29: 428-32.
- BURK, T. 1981. Signalling and sex in acalyptrate flies. *Florida Ent.* 64: 30-43.
- CADE, W. H. 1975. Acoustically orienting parasitoids: fly phonotaxis to cricket song. *Science* 190: 1312-13.
- . 1979. The evolution of alternative male reproductive strategies in field crickets. Pages 343-79 in M. S. and N. A. Blum, eds. *Sexual*

- Selection and Reproductive Competition in Insects. Academic Press, New York.
- . 1980. Alternative male reproductive behaviors. *Florida Ent.* 63: 30-45.
- . 1981. Field cricket spacing, and the phonotaxis of crickets and parasitoid flies to clumped and isolated cricket songs. *Z. Tierpsychol.* 55: 365-375.
- CHRISTENSON, T. E., AND K. C. GOIST, JR. 1979. Costs and benefits of male-male competition in the orb weaving spider, *Nephila clavipes*. *Behav. Ecol. Sociobiol.* 5: 87-92.
- DAVIES, N. B. 1977. Prey selection and social behaviour in wagtails (Aves: Motacillidae). *J. Anim. Ecol.* 46: 37-57.
- DAWKINS, R., AND J. R. KREBS. 1979. Arms races between and within species. *Proc. Royal Soc. London B205*: 489-511.
- DIXON, W. N., AND T. L. PAYNE. 1980. Attraction of entomophagous and associate insects of the southern pine beetle to beetle and host tree-produced volatiles. *J. Georgia Ent. Soc.* 15: 378-89.
- DOWNES, J. A. 1969. The swarming and mating flight of Diptera. *Annu. Rev. Ent.* 14: 271-98.
- . 1970. The feeding and mating behaviour of the specialized Empidinae (Diptera): Observations of four species of *Rhamphomyia* in the high arctic and a general discussion. *Canadian Ent.* 102: 769-91.
- . 1978. Feeding and mating in the insectivorous Ceratopogoninae (Diptera). *Memoirs Ent. Soc. Canada* 104: 1-62.
- EBERHARD, W. G. 1977. Aggressive chemical mimicry by a bolas spider. *Science* 198: 1173-75.
- . 1980. The natural history and behavior of the bolas spider *Mastophora dizzydeani* sp. n. (Araneidae). *Psyche* 87: 143-169.
- . 1981. The single line web of *Phorocidia studo* Levi (Araneae: Theridiidae): a prey attractant? *J. Arachnol.* 9: 229-232.
- EISNER, T., D. F. WIEMER, L. W. HAYNES, AND J. MEINWALD. 1978. Lucibufagins: defensive steroids from the fireflies *Photinus ignitus* and *P. marginellus* (Coleoptera: Lampyridae). *Proc. Nat. Acad. Sci.* 75: 905-908.
- ESTES, R. D. 1973. Territorial behavior of the wildebeest (*Connochaetes taurinus* Burchell 1923). *Z. Tierpsychol.* 26: 284-370.
- FISHER, R. A. 1958. *The Genetical Theory of Natural Selection* (2nd ed.). Dover, New York. 291 pp.
- FORREST, T. G. 1980. Phonotaxis in mole crickets: Its reproductive significance. *Florida Ent.* 63: 45-53.
- GREANY, P. D., AND K. S. HAGEN. 1981. Prey selection. Pages 121-35 in D. A. Nordlund, ed. *Semiochemicals: Their Role in Pest Control*. John Wiley & Sons, New York.
- GWYNNE, D. T., AND K. M. O'NEILL. 1980. Territoriality in digger wasps results in sex biased predation on males (Hymenoptera: Sphecidae, *Philanthus*). *J. Kansas Ent. Soc.* 53: 220-4.
- HAMILTON, W. D. 1971. Geometry for the selfish herd. *J. Theoret. Biol.* 31: 295-311.
- HARRIS, V. E., AND J. W. TODD. 1980. Male-mediated aggregation of male, female, and 5th-instar southern green stink bugs and concomitant attraction of a tachinid parasite, *Trichopoda pennipes*. *Ent. Exp. & Appl.* 27: 117-26.
- HEATH, J. E., AND P. J. WILKIN. 1970. Temperature responses of the desert cicada, *Diceroprocta apache* (Homoptera, Cicadidae). *Physiol. Zool.* 43: 145-54.
- HORTON, C. D. 1979. Apparent attraction of moths by the webs of araneid

- spiders. *J. Arachnol.* 7: 88.
- HOWARD, R. D. 1981. Male age-size distribution and male mating success in bullfrogs. Pages 61-77 in R. D. Alexander and D. W. Tinkle, eds. *Natural Selection and Social Behavior: Recent Research and New Theory*. Chiron, New York and Concord.
- JOHNSON, C. 1975. Polymorphism and natural selection in ischnuran damselflies. *Evol. Theory* 1: 81-90.
- KACELNIK, A. 1979. The foraging efficiency of great tits (*Parus major* L.) in relation to light intensity. *Anim. Behav.* 27: 237-41.
- KNIPLING, E. F. 1979. The basic principles of insect population suppression. USDA Agric. Handbook No. 512. U. S. Government Printing Office, Washington, DC. 659 pp.
- KURCZEWSKI, F. E. 1972. Observations on the nesting behavior of *Oxybelus cressonii* and *O. exclamans*. *J. Kansas Ent. Soc.* 45: 397-404.
- LACK, D. 1968. *Ecological adaptations for breeding in birds*. Methuen, London.
- LLOYD, J. E. 1973. Firefly parasites and predators. *Coleopt. Bull.* 27: 91-106.
- . 1981. Mimicry in the sexual signals of fireflies. *Sci. American* 245(1): 138-45.
- , AND S. R. WING. 1982. Light-seeking "sidewinder" fireflies: nocturnal aerial predation. (ms submitted).
- LLOYD, M., AND H. S. DYBAS. 1966. The periodical cicada problem: II, evolution. *Evolution* 20: 466-505.
- MANGOLD, J. R. 1978. Attraction of *Euphasiopteryx ochracea*, *Corethrella* sp. and gryllids to broadcast songs of the southern mole cricket. *Florida Ent.* 61: 57-61.
- McKEEVER, S. 1977. Observations of *Corethrella* feeding on tree frogs (*Hyla*). *Mosquito News* 37: 522-3.
- MITCHELL, W. C., AND R. F. L. MAU. 1971. Response of the female southern green stink bug and its parasite, *Trichopoda pennipes*, to male stink bug pheromones. *J. Econ. Ent.* 64: 856-9.
- MORRIS, D. 1956. The function and causation of courtship ceremonies. Pages 261-87 in P. Grasse, ed. *L'Instinct dans le Comportement des Animaux et de L'homme*. Masson, Paris.
- MORRIS, G. K. 1980. Calling display and mating behaviour of *Copiphora rhinoceros* Pictet (Orthoptera: Tettigoniidae). *Anim. Behav.* 28: 42-51.
- , AND M. BEIER. 1982. Song structure and description of some Costa Rican katydids (Orthoptera: Tettigoniidae). *Trans. Phil. Acad. Sci.* in press)
- NAGAMINE, M., AND Y. ITO. 1980. "Predator-foolhardiness" in an epidemic cicada population. *Res. Popul. Ecol.* 22: 89-92.
- NEILL, S. R. ST. J., AND J. M. CULLEN. 1974. Experiments on whether schooling by their prey affects the hunting behaviour of cephalopods and fish predators. *J. Zool. London.* 172: 549-69.
- NUTTING, W. L. 1953. The biology of *Euphasiopteryx brevicornis* (Townsend) (Diptera, Tachinidae), parasitic in the cone-headed grasshoppers (Orthoptera, Copiphorinae). *Psyche* 60: 69-81.
- O'NEILL, K. M., AND H. E. EVANS. 1981. Predation on conspecific males by females of the beewolf *Philanthus basilaris* Cresson (Hymenoptera: Sphecidae). *J. Kansas Ent. Soc.* 54: 553-556.
- OTTE, D. 1977. Communication in Orthoptera. Pages 334-61 in T. A. Sebeok, ed. *How Animals Communicate*. Indiana Univ. Press, Bloomington.
- PECKHAM, D. J., AND A. W. HOOK. 1980. Behavioral observations on *Oxybelus* in Southeastern North America. *Ann. Ent. Soc. America* 73: 557-67.

- , F. E. KURCZEWSKI, AND D. B. PECKHAM. 1973. Nesting behavior of nearctic species of *Oxybelus* (Hymenoptera: Sphecidae). *Ann. Ent. Soc. America* 66: 647-61.
- RENTZ, D. C. 1975. Two new katydids of the genus *Melanonotus* from Costa Rica with comments on their life history strategies (Tettigoniidae: Pseudophyllinae). *Ent. News* 86: 129-40.
- ROEDER, K. D. 1963. *Nerve Cells and Insect Behavior*. Harvard Univ. Press, Cambridge, MA.
- RUBENSTEIN, D. I. 1980. On the evolution of alternative mating strategies. Pages 65-100 in J. E. R. Staddon, ed. *Limits to Action: The Allocation of Individual Behavior*. Academic Press, New York.
- RYAN, M. J., M. D. TUTTLE, AND L. K. TAFT. 1981. The costs and benefits of frog chorusing behavior. *Behav. Ecol. Sociobiol.* 8: 273-278.
- SABROSKY, C. W. 1953. Taxonomy and host relations of the tribe Ormiini in the western hemisphere. *Proc. Ent. Soc. Washington* 55: 167-83.
- SCHALLER, G. B. 1972. *The Serengeti Lion*. Univ. Chicago, Chicago.
- SEMLER, D. E. 1971. Some aspects of adaptation in a polymorphism for breeding colours in the threespine stickleback (*Gasterosteus aculeatus*). *J. Zool., London* 165: 291-302.
- SIMMONS, J. A., E. G. WEVER, AND J. M. PYLKA. 1971. Periodical cicada: sound production and hearing. *Science* 171: 212-213.
- SOPER, R. S., G. E. SHEWELL, AND D. TYRRELL. 1976. *Colcondamyia auditrix* nov. sp. (Diptera: Sarcophagidae), a parasite which is attracted by the mating song of its host, *Okanagana rimosa* (Homoptera: Cicadidae). *Canadian Ent.* 108: 61-8.
- SPIETH, H. T. 1968. Evolutionary implications of sexual behavior in *Drosophila*. *Evol. Biol.* 2: 157-93.
- SULLIVAN, R. T. 1981. Insect swarming and mating. *Florida Ent.* 64: 44-65.
- THORNHILL, R. 1978. Some arthropod predators and parasites of adult scorpionflies (Mecoptera). *Environ. Ent.* 7: 714-16.
- . 1980. Competitive, charming males and choosy females: Was Darwin correct? *Florida Ent.* 63: 5-30.
- TODD, J. W., AND W. J. LEWIS. 1976. Incidence and oviposition patterns of *Trichopoda pennipes* (F.), a parasite of the southern green stink bug, *Nezara viridula* (L.). *J. Georgia Ent. Soc.* 11: 50-4.
- TREHERNE, J. E., AND W. A. FOSTER. 1980. The effects of group size on predator avoidance in a marine insect. *Anim. Behav.* 28: 1119-1122.
- TRIVERS, R. L. 1972. Parental investment and sexual selection. Pages 136-79 in B. Campbell, ed. *Sexual Selection and the Descent of Man, 1871-1971*. Aldine, Chicago.
- TUTTLE, M. D., AND M. J. RYAN. 1981. Bat predation and the evolution of frog vocalizations in the neotropics. *Science* 214: 677-8.
- WALKER, T. J. 1964. Experimental demonstration of a cat locating orthopteran prey by the prey's calling song. *Florida Ent.* 47: 163-5.
- . 1974. *Gryllus ovisopis* n. sp.: A taciturn cricket with a life cycle suggesting allochronic speciation. *Florida Ent.* 57: 13-22.
- . 1979. Calling crickets (*Anurogryllus arboreus*) over pitfalls: Females, males, and predators. *Environ. Ent.* 8: 441-3.
- . 1982. Diel patterns of calling in nocturnal Orthoptera. in D. T. Gwynne and G. K. Morris, eds. *Orthopteran Mating Systems*. Westview Press, Boulder, CO. (in press)