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EXPLOITATION OF SEXUAL SIGNALS
BY PREDATORS AND PARASITOIDS

MARLENE ZUK AND GITA R. KOLLURU

Department of Biology, University of California
Riverside, California 92521 USA
E-MAIL: MZUK@CITRUS.UCR.EDU *and* GITAK@CITRUS.UCR.EDU

ABSTRACT

Signals used to attract mates are often conspicuous to predators and parasites, and their evolution via sexual selection is expected to be opposed by viability selection. Many secondary sexual traits may represent a compromise between attractiveness and avoidance of detection. Although such signal exploitation appears to be widespread, most examples come from species that use acoustic or olfactory mating signals, and relatively few cases of visual signal exploitation can be substantiated. Because males are usually the signaling sex, they are more at risk from predators or parasitoids that locate prey or hosts by sexual signals; this differential selection on the two sexes can affect the intensity of sexual selection on male ornamental traits. The notable exception to male signaling and female attraction occurs in pheromone-producing insects, particularly lepidopterans, which show an opposite pattern of female odor production. Exploitation of such sex pheromones is relatively rare. We discuss reasons for the reversal in sex roles in these species and its implications for signal exploitation. Changes in signals that appear to be adaptations to avoid predation include the use of different signal modalities, changes in signaling behavior, loss of signals, and alteration of signal characteristics such as pitch. Selection pressure from signal exploiters could lead to the production of a novel signal and thus facilitate speciation. Relatively little work has been done on adaptations on the part of the exploiting species, but such adaptations could indirectly influence the mating system of the predator or parasitoid. Signal exploitation is also expected to be a fruitful source of examples of coevolution. Finally, plants emit attractants analogous to secondary sex characters in animals, and may also be vulnerable to signal exploitation.

INTRODUCTION

MANY SCIENTISTS have recognized that the signals used by animals to attract mates are also conspicuous to potential predators and other natural enemies (Darwin 1871; Burk 1982; Sakaluk 1990; Verrell 1991; Endler 1992). Otte (1974) called such unintended recipients "illegitimate receivers," and Dicke and Sabelis (1992) discussed further subdivisions of signal interception, including "spies," "stowaways" and "boasters." Most researchers

agree that animals producing mate attraction signals are faced with a conflict between mating success and survival, and many secondary sexual traits are thought to represent a compromise between attractiveness to mates and avoidance of detection by enemies. This risk has been examined in a wide range of taxa using several signaling modalities, including acoustic (e.g., calling crickets attracting parasitoid flies; Cade 1975), visual (e.g., coloration in guppies associated with presence of visual predators; Endler 1980), and olfactory/pheromonal (e.g., use of pheromones by egg parasitoids; Noldus et al. 1991a, 1991b).

Recent work, in particular on acoustically-orienting parasitoids of calling insect hosts, has highlighted several issues of evolutionary significance. These parasitoid flies use the song of male crickets or other orthopterans to locate a host; the female fly then deposits larvae on the cricket. The larvae burrow into the cricket's body cavity and develop for 7 to 10 days, after which they emerge and pupate in the soil (Cade 1975; Walker and Wineriter 1991; Zuk et al. 1995). The auditory system of one species of ormiine, *Ormia ochracea*, is closely tuned to the peak of the energy emission spectrum of the calling song of the host species (Robert et al. 1992, 1994), suggesting evolutionary convergence between the parasitoid and its host. This specificity provides an opportunity for studies not only of the convergence itself, but also of the potential for speciation based on variation in host signaling and on differential attractiveness of signals to females.

Despite questions raised about signal exploitation, much of the literature on the subject has appeared in works that have either a taxonomic or a sensory modality focus; workers on sex pheromones of moths, for example, and those who study visual or acoustic signals, particularly in vertebrates, rarely if ever cite one another's research. It is therefore difficult to determine how general the findings from research on a particular taxon are likely to be. Such a restriction has also hindered the development of general theory about the evolution of sexual signals in the context of exploitation. Similarly, those who study signals and their use by prospective mates and potential enemies sometimes neglect the literature on sexual selection, much of which is concerned with the

nature of sexual signals and the possible constraints on their evolution (Zuk 1991).

In this article we attempt a comprehensive review of the phenomenon of exploitation of mating signals by other species, and address the following questions:

1. To what extent does the sensory modality of a signal determine its likelihood of being exploited?
2. How has selection by the exploiter shaped the evolution of the victim's sexually selected signal?
3. Does selection act differently on the signaling sex and the responding sex?
4. What are the adaptations for exploiting and for avoiding exploitation?

The topic of signal evolution in the context of exploitation has many implications in addition to those mentioned above. We will not include interesting but tangential topics, such as the exploitation of host plant chemicals by insects; the general risks of copulation and mate searching, including the attraction of rivals; the energetic or aerodynamic costs of signals; the causes of differential mortality of the sexes; the exploitation of nonmating signals, such as aggregation pheromones, by natural enemies; and the evolution of reduced conspicuousness of predators to their prey. Some of these issues are covered in more specialized reviews, including those of Verrell (1991), Magnhagen (1991), Sakaluk (1990), Burk (1982), and Stowe et al. (1995). We consider only those signals that appear to be the results of sexual selection via either intrasexual competition or intersexual mate choice, and not simply primary sexual traits used in mating. Note that our use of the word "exploitation" is distinct from the idea of sensory exploitation or sensory bias (Ryan and Rand 1990), which we will discuss in a later section.

SURVEY OF SIGNAL EXPLOITATION

Since at least the 17th century, naturalists have recognized that predators may be attracted to the mating signals of their prey (Lloyd 1966 and references therein). Erasmus Darwin, for example, described frogs that attacked live coals they presumably mistook for flashing fireflies (cited in Lloyd 1966). More recently, exploitation of mating signals by predators and parasitoids has been reported

TABLE 1

Exploitation of victim-produced mating signals by predators and parasitoids

Signal type	Exploiter	Victim	References
Visual	firefly (*Photuris* sp.)	firefly (*Photinus* sp.)	1
	firefly (*Photinus collustrans*)	various lycosid spiders	2
	trout (*Salmo clarki*)	stickleback (*Gasterosteus aculeatus*)	3
	prawn (*Macrobrachium crenulatum*), several predatory fishes	guppy (*Poecilia reticulata*)	4
	Sparrowhawk (*Accipiter nisus*)	Pied Flycatcher (*Ficedula hypoleuca*)	5
Acoustic	*Arthropods*		
	tachinid fly (*Euphasiopteryx ochracea* = *Ormia ochracea*)	field crickets (*Gryllus rubens, G. lineaticeps, G. integer*)	6
	tachinid fly (*Euphasiopteryx depleta* = *Ormia depleta*)	mole cricket (*Scapteriscus* spp.)	7
	tachinid fly (*Ormia ochracea*)	field cricket (*Teleogryllus oceanicus*)	8
	tachinid fly (*Ormia lineifrons*)	tettigoniid orthopteran (*Neoconocephalus robustus*)	9
	tachinid fly (*Homotrixa* sp.)	tettigoniid orthopteran (*Sciarasaga quadrata*)	10
	tachinid fly (*Therobia leonidei*)	tettigoniid orthopteran (*Poecilimon* spp.)	11
	sarcophagid fly (*Colcondamyia auditrix*)	cicada (*Okanagana rimosa*)	12
	tachinid fly (*Euphasiopteryx ochracea* = *Ormia ochracea*), chaoborid fly (*Corethrella wirthi*)	mole cricket (*Scapteriscus acletus*)	13
	chaoborid fly (*Corethrella* spp.)	tree frog (*Hyla avivoca*)	14
	Vertebrates		
	gecko (*Hemidactylus tursicus*)	cricket (*Gryllodes supplicans*)	15
	snapping turtle (*Chelydra serpentina*)	bullfrog (*Rana catesbeiana*)	16
	Little Blue Heron (*Florida coerulea*)	short-tailed cricket (*Anurogryllus celerinictus*)	17

in a number of taxa that use various signal modalities (Table 1). Many of the examples are anecdotal, based on counts of invertebrate predators and parasitoids attracted to host pheromone-baited traps (e.g., Hardie et al. 1991; Mendel et al. 1995). Other researchers have noted the attraction of natural enemies to various acoustically-signaling animals [phorid flies on toads (*Bufo typhonius*), G R Bourne, pers. comm.; sarcophagid flies (*Emblemasoma*) attracted to cicada song, T J Walker, pers. comm.; Florida Scrub Jays (*Aphelocoma coerulescens*) foraging on singing orthopterans, J P Hailman, pers. comm.; grass snakes (*Natrix natrix*) feeding on calling European tree frogs (*Hyla arborea*), P Edenhamn, pers. comm.].

TABLE 1 *continuation*
Exploitation of victim-produced mating signals by predators and parasitoids

Signal type	Exploiter	Victim	References
(Acoustic)	bats (*Micronycteris megalotis, M. hirsuta, Tonatia sylvicola, Trachops cirrhosus*)	tettigoniid orthopterans	18
	bat (*Trachops cirrhosus*)	frogs (*Hyla boulengeri, Physalaemus pustulosus, Smilisca sila*)	19
	bat (*Tonatia sylvicola*)	tettigoniid orthopteran	20
	bat (*Eptesicus fuscus*)	tettigoniid orthopteran (*Pterophylla camellifolia*), frog (*Acris crepitans*)	21
	opossum (*Philander opossum*)	frog (*Physalaemus pustulosus*)	22
	cat (*Felis domesticus*)	various orthopterans	23
	Sharp-shinned Hawk (*Accipiter striatus*)	Song Sparrow (*Melospiza melodia*)	24
Olfactory	tachinid fly (*Trichopoda pennipes*)	pentatomid bug (*Nezara viridula*)	25
	phasiid fly (*Gymnosoma rotundatum*)	pentatomid bug (*Plautia stali*)	26
	tachinid flies (*Euclytia flava, Hemyda aurata*), vespid wasp (*Vespula maculifrons*)	pentatomid bugs (*Podisus maculiventris, P. fretus*)	27
	aphelinid wasp (*Encarsia perniciosi*)	diaspidid scale (*Quadraspidiotus perniciosus*)	28
	braconid wasps (*Praon volucre, P. abjectum, P. dorsale*)	aphid (*Aphis* spp.) (synthetic pheromone)	29
	parasitoid wasps (*Aphytis africanus, A. melinus, A. coheni*)	diaspidid scale (*Aonidiella aurantii*)	30
	trichogrammatid wasps on eggs (*Trichogramma evanescens. T. pretiosum*)	noctuid moth (*Heliothis zea*)	31
	trichogrammatid wasps on eggs (*Trichogramma evanescens, T. pretiosum*)	noctuid moth (*Mamestra brassicae*)	32

Because human interest in controlling agricultural pests has fueled an enormous body of research aimed at new biological control strategies, chemicals are continually being tested for their effectiveness in attracting pests. Often these substances are kairomones, host-produced chemicals that attract enemies (Dicke and Sabelis 1992). Some of these discoveries have been further explored from an evolution-ary perspective to determine whether hosts can escape detection (Tumlinson et al. 1993) by "spies" (Dicke and Sabelis 1992). For example, some hosts have evolved pheromone blends that either reduce the risk of being attacked (Raffa and Klepzig 1989), or represent the result of past selection by parasitoids (Aldrich et al. 1989). Although pheromone studies may not be familiar to evolutionary biologists be-

TABLE 1 *continuation*

Exploitation of victim-produced mating signals by predators and parasitoids

Signal type	Exploiter	Victim	References
(Olfactory)	scelionid wasp on eggs (*Telenomus remus*)	noctuid moth (*Spodoptera frugiperda*)	33
	scelionid wasp on eggs (*Telenomus euproctidis*)	lymantriid moth (*Euproctis taiwana*)	34
	clerid beetle (*Enoclerus lecontei*), ostomid beetle (*Temnochila virescens chlorodia*)	scolytid beetle (*Ips confusus*)	35
	clerid beetle (*Thanasimus formicarius*)	scolytid beetle (*Ips typographus*)	36
	clerid beetle (*Thanasimus dubius*)	scolytid beetle (*Dendroctonus frontalis*)	37
	anthocorid bug (*Elatophilus hebraicus*)	matsucoccid scale (*Matsucoccus josephi*)	38
	various entomophagous and parasitic insects	scolytid beetle (*Dendroctonus frontalis*)	39
Olfactory/ Visual	vespid wasp (*Vespula germanica*)	tephritid fly (*Ceratitis capitata*)	40
	several aphelinid wasps	diaspidid scale (*Quadraspidiotus perniciosus*)	41

References: 1) Lloyd and Wing 1983; Lloyd 1997   2) Lloyd 1973; Daly 1978; Wing 1988.   3) Moodie 1972. 4) Endler 1978, 1980, 1982, 1983, 1991.   5) Slagsvold et al. 1995   6) Cade 1975; Walker 1983, 1986, 1993; Cade et al 1996; Wagner 1996.   7) Mangold 1978; Fowler 1987; Fowler and Garcia 1987; Parkman et al. 1996.   8) Zuk et al. 1993.   9) Burk 1982   10) Allen 1995a, 1995b   11) Heller and von Helversen 1993; Lehmann 1996; Lehmann and Heller 1997.   12) Soper et al 1976.   13) Mangold 1978.   14) McKeever 1977   15) Sakaluk and Belwood 1984. 16) Halliday 1980.   17) Bell 1979.   18) Belwood and Morris 1987   19) Tuttle and Ryan 1981, 1982; Ryan et al 1982; Tuttle et al. 1982   20) Tuttle et al. 1985.   21) Buchler and Childs 1981.   22) Tuttle et al. 1981   23) Walker 1964.   24) P K Stoddard, pers. comm.   25) Mitchell and Mau 1971.   26) Moriya and Masakazu 1984.   27) Aldrich et al. 1984, 1986; Aldrich 1985.   28) Kyparissoudas 1987   29) Hardie et al. 1991; Powell et al 1993   30) Sternlicht 1973; Samways 1988   31) Noldus et al. 1991a, 1991b.   32) Lewis et al. 1982.   33) Nordlund et al. 1983. 34) Arakaki et al. 1996.   35) Wood et al. 1968; Rice 1969.   36) Hansen 1983.   37) Vité and Williamson 1970 38) Mendel et al. 1995.   39) Dixon and Payne 1980.   40) Hendrichs et al 1994.   41) McClain et al. 1990

cause they often appear in taxon-specific or applied entomology sources (e.g., Aldrich 1985; Kyparissoudas 1987), they are extremely valuable in establishing the occurrence and intensity of exploitation of mating signals.

Visual signals are thought to be particularly susceptible to detection by predators (Alcock 1984), and many are classic examples of sexually selected ornaments. Interestingly, however, exploitation of visual mating signals has rarely been demonstrated (Olsson 1993). Notable exceptions include the long-term studies of guppies (Endler 1978, 1980, 1983; Endler and Houde 1995), which have revealed the specific components of male guppy coloration that attract predators, and work on fireflies (Lloyd 1966, 1973, 1997; Lloyd and Wing 1983), which has shown how the females of one species respond to the courtship flashes of the male of a prey species. Although it is unlikely that visual signals are not subject to exploitation, it is probably more difficult to demonstrate their role in attracting predators, perhaps because most visual signals are produced continually. In addition, visual traits such as bright colors often have functions, such as thermoregulation or territorial display (Endler 1978), that are under their own selection pressures; these pressures may mask the effects of selection to avoid predation.

Acoustic mating signals can be detected at night, are easily localized, and travel quickly over long distances (Alcock 1984; Sakaluk 1990). These characteristics make transmission of acoustic signals easy, but also make mating songs, such as those produced by orthopteran insects and frogs, detectable by a variety of invertebrate and vertebrate natural enemies (Table 1). Acoustic signals have been examined both from a mechanistic standpoint, as in the parasitoid ear morphology studies by Robert et al. (1992, 1994) and Lakes-Harlan and Heller (1992), which have shown that tachinid flies have evolved the necessary specialized morphology to detect orthopteran songs, and from an evolutionary perspective (Gwynne and Morris 1983). A well-known example of the latter approach includes work on the túngara frog (*Physalaemus pustulosus*) and its acoustically-orienting bat predator (Tuttle and Ryan 1981; Ryan 1985). Like the guppy studies, work on the túngara frog has revealed the compromise between sexual selection and natural selection that can result from mating signal exploitation, thus demonstrating that the same signal components are attractive both to potential mates and to unintended signal receivers.

ENVIRONMENTAL VARIATION IN SIGNAL CONSPICUOUSNESS

Understanding the evolution of signal exploitation relies on determining how conspicuous a mating signal is to a predator or parasitoid. Both Darwin (1871) and Endler (1978, 1991) emphasized that signal conspicuousness is relative: the same mating display can be noticeable under certain environmental conditions to certain receivers, but cryptic under other conditions to other receivers. Light and turbidity levels, for example, can affect predation on fish (Moodie 1972). Signal detection by predator and prey may differ enough so that a signal conspicuous to a potential mate is not as easily detected by a predator (Endler 1978, 1983, 1991). If this is the case, then certain aspects of a mating signal such as color may be less susceptible to exploitation, and sexual selection may thus favor aspects less easily detected by the predator (Endler 1978, 1992).

Endler (1978) noted that cryptic color patterns must resemble a random sample of the background in which an animal signals, whereas conspicuous patterns must deviate from the background. He then quantified the conspicuousness of guppy color patterns under different backgrounds, and showed that signalers in areas of high predation intensity had better background color matching (i.e., less conspicuousness) than signalers in areas of low predation intensity. Similar variation in conspicuousness of mating signals with predation intensity was found by Heller (1995) for bushcrickets. Female guppies also show reduced preference for bright males under high predation (Endler and Houde 1995; Houde 1997).

Environmental conditions can affect courtship behavior as well. Potential victims may reduce predation risk by signaling in areas where (or at times when) detection by predators is minimized. For example, some lekking birds display themselves in light environments that maximize conspicuousness, but remain inconspicuous at other times (Endler and Théry 1996). Guppies also switch courtship tactics from displaying themselves to sneak copulations performed without courtship, depending on perceived predation risk (Endler 1987; Godin 1995). Furthermore, male guppies from high predation localities are more likely to reduce courtship in the presence of a predator than males from low predation localities (Magurran and Seghers 1990), and within a locality, large males are more likely to reduce courtship displays at high light intensities than small males, possibly because they face a greater risk of predation (Reynolds et al. 1993). Females attracted to conspicuous males can be targets of predation (Sakaluk and Belwood 1984; Pocklington and Dill 1995), and may also alter their behavior under different environmental conditions. Both female crickets and túngara frogs respond differently to male songs, depending on the perceived risk of predation (Hedrick and Dill 1993; Csada and Neudorf 1995; Rand et al. 1997), and female guppies reverse their preference for conspicuous males in the presence of a predator (Godin and Briggs 1996; Gong and Gibson 1996).

Signaling systems using nonvisual cues also provide useful examples of conspicuousness that varies with environmental conditions. A number of studies have addressed the optimal conditions for transmission of acoustic signals

with respect to background noise and the songs of other individuals (Wiley 1991; Endler 1992; Römer 1993; Badyaev and Leaf 1997). Male *Smilisca* frogs, for example, tend to call from areas that have higher ambient noise levels generated by waterfalls, which are avoided by predatory bats, possibly because the noise interferes with the bats' ability to detect calling frogs (Tuttle and Ryan 1982). It would be interesting to know whether other acoustically-signaling animals co-occurring with phonotactic predators or parasitoids signal under conditions that reduce the risk of exploitation (Endler 1993).

THE SIGNALING SPECIES: IMPLICATIONS FOR SEXUAL SELECTION

Mortality sources associated with sexual signaling obviously influence the evolutionary ecology of the target (Burk 1982; Sakaluk 1990). Such effects will differ for males and females because of the ways in which selection acts on the two sexes. According to classical sexual selection theory, males maximize reproductive success by obtaining as many matings as possible, while females are limited by the number of offspring they can produce and rear; male variance in reproductive success is likely to be much higher than that of females because of the larger parental investment by females in most animal species (Trivers 1972; Thornhill and Alcock 1983; Andersson 1994). This dichotomy is often said to account for the usual male role of risky signal production and the usual female role of signal reception, travel to the signaling male, and eventual mate choice. In sexually dimorphic species, males are usually more brightly colored, larger, more likely to possess specialized ornamentation or weaponry (such as horns and antlers), and more commonly produce courtship songs and calls (Andersson 1994). Traits that are absolutely necessary for reproduction, such as the gonads, are not usually considered to be sexually selected characters.

SENSORY MODE AND THE SIGNALING SEX

The cost of producing a signal is generally assumed to determine which sex produces it, and for the reasons summarized in the preceding paragraph, males usually bear that cost. Interestingly, however, the type of signal used—

acoustic, visual or olfactory—is also associated with a sex difference in signaling practice. Acoustic and visual signals are most often produced by males at a given location, with females traveling to stationary groups or territorial individuals, as evidenced in taxa as diverse as crickets and katydids (Gwynne and Morris 1983; Thornhill and Alcock 1983), lekking birds and mammals (Höglund and Alatalo 1995), fruit flies (Spieth 1974), and many anuran amphibians (Howard 1988; Sullivan 1989). Even when males do not signal from a fixed position, they are still the sex assumed or found to pay the price of having conspicuous mating signals. For example, singing male crickets use several times more energy than those at rest (Prestwich and Walker 1981), and the metabolic power output of several species of hylid frogs is many times greater than their resting metabolic rate (Prestwich et al. 1989). Energetic costs of visual signals are more difficult to determine, but studies of barn swallows have suggested that males that are more fit are better able to produce the long tail feathers that attract females, which implies that the trait is costly (Møller 1994). Numerous papers in the sexual selection literature are devoted to the origin, measurement and consequences of costly male sexual ornaments and displays.

FEMALE PHEROMONES: FALLACY, FACT, OR TEST OF VIGOR?

In contrast to male visual and acoustic displays, long-range olfactory sex signals—sex pheromones—are usually produced by the female, although odors may be produced by both sexes during courtship (Thornhill 1979). This striking reversal of the usual signaling sex has been met with reactions ranging from astonishment to indifference. Williams (1992: 111) states, "The world is full of males displaying to females with bright colors and loud song and conspicuous actions, and of females displaying to males with odors. This is strange. Or, more likely, wrong." He goes so far as to suggest that the sex-attractant pheromones used by moths and other insects are not sexually selected signals per se, because he does not see that females usually exhibit specialized behaviors or structures for signal emission, and because males appear to have been strongly selected to distinguish even tiny concentrations

of the odor molecules in the air. Hence, he argues, males are merely capitalizing on a trait that happens to reveal sexual receptivity in females, and he terms the phenomenon of female pheromones a "fallacy" because a true sex pheromone should be a signal, like the tail of a peacock, that has itself been subject to sexual selection. The supposed sex reversal of signaling therefore does not exist. Otte (1974) presents a somewhat milder version of this idea.

Perhaps because workers on signaling in one modality or taxon tend to communicate mainly with those in the same area, this radical position has received surprisingly little commentary in the pheromone literature (but see Phelan 1997a, 1997b). At the same time, several authors have addressed the question of role reversal in olfactory signaling (Landolt 1997). Most of them have concluded that producing pheromones is not particularly costly, whereas responding to the odor and traveling to its source involves relatively more risks (Cardé and Baker 1984; Dicke and Sabelis 1992; Svensson 1996; Phelan 1997b). The risky behavior is therefore taken on by males, as usual, while females are not in danger of detection or exploitation by predators and parasites because they emit only minute amounts of highly specific chemicals (Cardé and Baker 1984). Indeed, the intensity of long-range pheromones produced by females is dramatically less than that of male-produced pheromones (Greenfield and Coffelt 1983). Greenfield (1981) concurred with this viewpoint, and suggested that female moths are not competing among themselves in the way that male peacocks or crickets may be by signaling; by emitting such low intensity signals, females might even be presenting a passive filter to test male response, such that only those males able to detect minute concentrations of odors can find a mate. This test would only work, of course, if detection ability is linked to the viability of the male, perhaps because more sensitive males can also locate host plants more easily.

Other authors have not viewed female signaling as a departure from a more conventional pattern, and simply assume that because females invest more in individual offspring, their signals must be canalized mechanisms for ensuring species recognition (Cardé and Baker 1984). Sexual selection, however, is usu-

ally thought to involve more than species recognition (cf. Paterson 1985) because, in addition to being a member of the appropriate species, individuals preferred in sexual selection must also win in sexual competition. This competition will lead to exaggerated ornaments, such as long tails in many birds (Andersson 1994). Contrary to the directional selection producing these exaggerated ornaments, stabilizing selection is usually the form invoked for the evolution of olfactory mating signals (Cardé and Baker 1984; Phelan 1997a). In any case, exploitation of female pheromones is seen to be unlikely by most researchers because odor detection is highly specific to particular compounds or combinations of compounds; therefore predators and parasitoids are less likely to be able to "eavesdrop" on prey signals. Greenfield (1981) and Boake et al. (1996) suggest that pheromones may even have evolved as long-range attractants precisely because they are rarely exploited.

We do not agree with Williams (1992), but are still not convinced that the exploitation of pheromones has been easily or completely explained. Two issues arise from Williams's declaration that female pheromones are not truly signals. First, he suggests that female insects often lack specialized apparatus for the production or transmission of odors, unlike male crickets, for example, which have modified wing structures used to produce and amplify sound. Such a deficiency would imply that, although males can use sex-specific odors to distinguish females in reproductive condition, these odors may not have evolved as an adaptation on the part of females to attract males. Closer examination of the literature on pheromones suggests, however, that although concentrations of sex attractants are indubitably small, females frequently assume particular "calling" postures when emitting pheromones, and many species have glands near the ovipositor that are specialized for pheromone production (Cardé and Baker 1984; Phelan 1997b). In addition, females may adjust the amount of pheromone emitted, depending on how much sperm they have received (McNeil et al. 1997). It therefore seems plausible that selection has acted on females to produce appropriately alluring signals, although the lack of exaggeration of those signals, unlike

those in males, remains intriguing. What would constitute an elaborated scent? Our own relative insensitivity to olfactory cues may hinder our ability to imagine the odor equivalent of a bird of paradise's plumage. Certainly little is known about the ancestral state of pheromones among those insects that produce them, making comparative studies even more problematic.

The second issue is whether a role reversal in signaling occurs in animals using long-range pheromones to attract mates. If the pheromone is not costly to produce, and if males compete with one another by searching and incur costs as they travel to the female, then Greenfield's (1981) idea about using pheromones as a filter to test males is appealing because males are still performing the costly part of mating. The problem is that virtually no data on the energetic costs of pheromone production are available (Dicke and Sabelis 1992). Interestingly, female moths sometimes produce greater concentrations of pheromone as they age (Greenfield 1981); this is consistent with the idea that odor production is expensive since females should be more willing to pay costs as their reproductive value decreases and less of their reproductive lifespan remains (Williams 1975). If increased signal intensity is not costly, but attracts males more effectively, why has selection not increased signal intensity at all ages? Lundberg and Löfstedt (1987) discussed variation in pheromone production in the context of intraspecific competition, and suggested that ecological constraints control emission rate. Phelan (1997a) emphasized the importance of stabilizing selection in the evolution of pheromone signaling, but it seems to us that as long as male responses are linked to female signals, directional selection and subsequent exaggeration of the odor ought to be at least as likely. Information about the costs of manufacturing and releasing pheromones is sorely needed.

The other cost, besides an energetic one, is the subject of this article: exploitation by predators or parasites. If odors are not likely to attract natural enemies, then females take no risks by producing them. Greenfield (1981) suggested that the apparent rarity with which parasitoids locate female-emitted pheromones may reflect the rarity with which parasitoids

attack adult lepidopterans; most such parasitoids attack eggs or larvae. It may be economically unwise for a parasitoid to locate a pheromone-emitting female, only to wait until she mates and lays eggs. Thus, except for a few special cases such as the attraction of egg parasitoids to the noctuid moths, *Heliothis zea* and *Mamestra brassicae*, at the time of oviposition (Table 2; Noldus et al. 1991a, 1991b), most sex pheromones that attract natural enemies are male-produced pheromones in aggregating species such as bark beetles (Table 1; Wood et al. 1968; Hansen 1983). This argument does not explain, however, why predators of adult insects are thought to be unlikely to use odor cues.

Why do so few examples of odor detection by predators exist, compared to the detection of other sensory cues? We suggest that the difference may lie in a distinction drawn by Maynard Smith (1958, 1991) between "notices" and "advertisements." If the interests of signaler and receiver do not coincide, the evolution of a costly advertisement is likely. Most interactions between males and females fall into this category because of the disparity of parental investment between the sexes and subsequent male competition for females (Trivers 1972). However, some signals, such as the railway timetable or bee waggle dance (Maynard Smith 1991), are not selected to be costly because both sender and receiver benefit from accurate transfer of information. If female moths do not compete among themselves for males, and if odors are not energetically costly to produce, sex pheromones may qualify as notices, and hence not be conspicuous to natural enemies in the way, for example, that cricket song is. It is interesting to note that in the few cases of long-range sex attractants in noninsects, including mammals such as dogs, females are again the sex that produces the odor (Thornhill 1979). Whether predators are attracted to such mammalian-produced scents and whether these odors are similarly less costly to produce remains to be seen.

Finally, it has been suggested that predators might simply find it more difficult to exploit odors because of the precise composition of most pheromones. We are skeptical of this explanation, given the remarkable adaptations

TABLE 2
Exploitation of female-produced pheromone signals by predators and parasitoids

Victim	Exploiter	Pheromone type	References
aphid (*Aphis* spp.)	brachonid wasps (*Praon volucre, P. abjectum, P. dorsale*)	synthetic	1
noctuid moths (*Heliothis zea, Mamestra brassicae*)	trichogrammatid wasps on eggs (*Trichogramma evanescens, T. pretiosum*)	natural	2
lymantriid moth (*Euproctis taiwana*)	scelionid wasp on eggs (*Telenomus euproctidis*)	natural and synthetic	3
noctuid moth (*Spodoptera frugiperda*)	scelionid wasp on eggs (*Telenomus remus*)	natural	4
diaspidid scale (*Aonidiella aurantii*)	aphelinid wasps (*Aphytis africanus, A. melinus, A. coheni*)	natural and synthetic	5
matsucoccid scale (*Matsucoccus josephi*)	anthocorid bug (*Elatophilus hebraicus*)	synthetic	6
diaspidid scale (*Quadraspidiotus perniciosus*)	aphelinid wasp (*Encarsia perniciosi*)	synthetic	7

References: 1) Hardie et al. 1991; Powell et al. 1993. 2) Noldus et al. 1991a, 1991b. 3) Arakaki et al. 1996. 4) Nordlund et al. 1983. 5) Sternlicht 1973; Samways 1988. 6) Mendel et al. 1995. 7) Kyparissoudas 1987; McClain et al. 1990.

seen in other natural enemies with special sensitivities to acoustic frequencies or other properties of signals (Robert et al. 1994). Sanderford and Conner (1995) suggested that the acoustic courtship signals given by both males and females in the moth *Syntomeida epilais* are possible because of a release from predation pressure by bats; whether other species are under similar constraints is as yet unknown. The literature yielded numerous examples of female-produced pheromones that are exploited by parasitoids and predators (Table 2), most of which were discovered in the last few years. More research may lead to the abandonment of the idea that olfactory cues are inconspicuous to unintended receivers. We agree with the conventional view that pheromones are signals, but we also agree with Williams (1992) that the phenomenon of female-produced odors is strange. We hope that future work will address the questions of costs of pheromones and the sensory capabilities of predators that utilize them.

VICTIM ADAPTATIONS

The mating signals of numerous species have been exploited by natural enemies, as detailed in Table 1, and here we consider the avenues of escape taken by the victim. Later we also examine the interaction from the exploiter's point of view. Table 3 contains a summary of signal characteristics that have been suggested to be adaptations for avoiding detection by parasites or predators. Forest-dwelling katydids (Tettigoniidae) subject to predation by foliage-gleaning bats show reduced calling activity and unusually high ultrasonic carrier frequencies, and utilize substrate vibration instead of airborne calling (Morris 1980; Belwood and Morris 1987; Belwood 1990; Morris et al. 1994; Heller 1995). Similarly, members of 11 insect orders produce substrate vibration in lieu of airborne calling songs; such "silent singing" is particularly noteworthy in lacewings (Henry 1994). Other forms of antipredator behavior in acoustically-signaling insects are discussed by Bailey (1991). Surprisingly, incidences of

visual cues modified as a result of predation pressure are harder to document, although the cryptic plumage of females in many sexually dimorphic birds, for example, is often attributed to selection by predators against the conspicuous coloration of males (Promislow et al. 1994). The ancestral state of plumage coloration in sexually dichromatic species is generally supposed to have been dull or cryptic rather than bright, since the usual pattern is for males to be more colorful (Butcher and Rohwer 1989). Although little evidence is available on this point, a striking exception is the work by Endler (1983, 1991, 1992), who demonstrated that male guppies in predator-rich environments have duller orange patches than males in streams relatively free from predators.

An interesting and little considered aspect of escape from predation or parasitism by signaling animals is the possibility that such an escape may include the production of novel signals, which could instigate or facilitate speciation via sexual selection on the new signal (Lande 1981; West-Eberhard 1983; Verrell 1991). If female preference for a signal is correlated with genes for signal production, as many models of sexual selection suggest (Kirkpatrick and Ryan 1991), females may "follow" males as they evade detection by natural enemies. Alternatively, if a risky signal contains elements favored by females, either because they exploit her sensory systems (Christy 1995) or because the risk constitutes a test of male fitness, such rapid isolation of populations is less likely. In the túngara frog *Physalaemus pustulosus*, females prefer the portion of the song most easily detected by predatory bats (Ryan et al. 1982; Ryan 1985), but the generality of this finding remains unexplored. More work on the role of female preference in shaping the opposing selection forces on sexual signals is needed.

In addition to showing altered signals, several taxa modify their behavior in response to predation on the signaling sex (Table 3; Burk 1982). Display sites, spacing patterns, and temporal shifts in signaling of both birds and insects all may reflect selection by predators or parasites (Burk 1982; Lloyd and Wing 1983; Trail 1987; Sakaluk 1990; Endler and Théry 1996). In its most extreme form, such behavioral differences among individuals have led

to the evolution of alternative reproductive behavior, which may involve less risky, "sneaky" means of gaining fertilizations, as shown by some males within a population (Gadgil 1972; Austad 1984; Andersson 1994). The alternatives may yield the same reproductive success, in which case they may be genetically predetermined; or they may not, in which case males with inferior developmental histories may be "making the best of a bad job." For example, female-mimicking males of bluegill sunfish are a smaller, morphologically distinct class that does not defend territories (Dominey 1980). Instead, such males wait until a female is about to deposit eggs onto the nest of a territorial male, then swim quickly into the territory, release sperm, and leave. Adoption of a female-mimic or territorial male strategy appears to be relatively fixed (Dominey 1980). Cade (1975, 1980) found some male field crickets (*Gryllus integer*) that did not call but were seen near callers; this species is subject to an acoustically-orienting parasitoid fly (*Ormia ochracea*), which primarily attacks calling males. Cade (1975) called such silent males "satellites" and suggested that they were intercepting females as they moved toward callers, thus avoiding parasitization. Similar satellite males were observed near male moths (*Syntonarcha iriastis*) producing ultrasound by genital stridulation (Gwynne and Edwards 1986), and females sometimes mated with silent male wax moths (*Achroia grisella*) found near ultrasound-producing males (Greenfield and Coffelt 1983).

Evasion of predation on the more conspicuous signaling males is often thought to be a benefit of adopting such an alternative strategy, but unless such an advantage is demonstrated, it may be unwarranted to assume that it is. For example, the parrotfish *Sparisoma radians* has both conspicuous territorial and cryptic schooling males within a population (Clifton and Robertson 1993). Although one might assume that the cryptic males enjoy a more risk-free existence, examination of the stomach contents of the major predator of this species, the yellow jack *Caranx bartholomaei*, showed that both male morphs were eaten in proportion to their availability, with a shift over the course of the day to selective predation on spawning males, whether gaudy or cryptic (Clifton and Robertson 1993). Simi-

TABLE 3
Victim adaptations that counter exploitation of mating signals

Signal type	Victim	Victim adaptation	References
Visual	spider (*Dolomedes triton*)	surface-wave mating signal frequency characteristics like that of nonprey rather than prey	1
	firefly (*Photinus* spp.)	evolution of flashing signal instead of constant glow; paucity of sedentary aggregations in the U.S. (where predator occurs); delayed signaling activity until sunlight is reduced during summer (when predator is active)	2
	firefly (*Pyractomena* sp.)	male drops to the ground after female flash response instead of flashing again	3
	poeciliid fishes (guppy, *Poecilia reticulata*; *Phalloceros caudimaculatus*)	evolution of decrease in number and size of sexually selected color patches in populations with high predation intensity; more frequent displays at low light intensities and use of alternative mating tactics at high light intensities; large males more likely to reduce courtship displays at high light intensities than small males, possibly because they face a greater risk of predation; evolution of reduced courtship display in populations with high predation	4
	Guianan Cock-of-the-Rock (*Rupicola rupicola*)	mating displays performed in groups (leks) to reduce raptor predation	5
	lekking birds (*Rupicola rupicola, Corapipo gutturalis, Lepidothrix serena*)	minimized conspicuousness when not displaying; males are either more chromatic or brighter than background, but never both	6
Acoustic	*Arthropods*		
	tettigoniid orthopteran (*Copiphora rhinoceros*)	reduced proportion of time spent calling in presence of predator; reduced airborne calling in favor of substrate vibration in presence of predator	7
	tettigoniid orthopteran (*Sciarasaga quadrata*)	presunset calling; frequent movement, lack of association with any one plant species	8
	tettigoniid orthopteran (*Insara covilleae*)	cessation of ultrasonic mating calls when predator is detected	9
	field cricket (*Gryllus integer*)	some males remain silent and opportunistically mate with females attracted to other males' songs	10

field cricket (*Gryllus rubens*)	phase shifting of pulses in calling song to reduce detection by parasitoid	11
field cricket (*Teleogryllus oceanicus*)	beginning and ending singing more abruptly in parasitized populations; singing more slowly in parasitized populations	12
field cricket (*Gryllus integer*)	delays calling until sunrise and preceding hours when parasitoid is not active	13
mole cricket (*Scapteriscus* spp.)	changes in time of year that signal is produced	14
snowy tree cricket (*Oecanthus fultoni*)	singing in choruses so each individual is less likely to be detected by predator or parasitoid	15
lesser wax moth (*Archroia grisella*)	ceases producing ultrasonic mating calls and switches to pheromone calling when predator is detected	16
eleven insect orders	production of substrate vibrations instead of airborne songs	17

Vertebrates

frogs (*Physalaemus pustulosus, Smilisca sila*)	ceases calling when predator approaches; dives down into water if predator is very close; synchronized calling	18
Olfactory pentatomid bug (*Podisus maculiventris*)	selective release of pheromone during daylight hours; "silent" strategy adopted by some males; males do not signal, but instead mate with females attracted to other males' pheromone; seasonal decline in attraction of bugs to pheromone traps when parasitoid becomes active	19
pentatomid bug (*Nezara viridula*)	evolution of shorter preoviposition period and longer larval period in parasitized populations (may dampen effects of parasitoid)	20
scolytid beetle (*Ips pini*)	ability to produce and respond to a variety of pheromone blends; may enable "escape" from exploitation	21
scolytid beetle (*Ips pini*)	parasitoid more attracted to local than distant prey populations, possibly due to evolution of chemical differences in prey pheromone	22

References: 1) Bleckmann and Bender 1987. 2) Lloyd 1983. 3) Lloyd 1966. 4) Farr 1975; Endler 1978, 1980, 1982, 1983, 1987, 1991; Reynolds et al. 1993. 5) Trail 1987. 6) Endler and Théry 1996. 7) Morris 1980; Belwood and Morris 1987. 8) Allen 1995b. 9) Spangler 1984. 10) Cade 1975. 11) Walker 1993. 12) Zuk et al. 1993; Rotenberry et al. 1996. 13) Cade et al. 1996 14) Mangold 1978 15) Walker 1969 16) Spangler 1984. 17) Henry 1994. 18) Tuttle et al. 1982; Tuttle and Ryan 1982 19) Aldrich et al. 1984; Aldrich 1985; Aldrich 1995. 20) Aldrich et al. 1989. 21) Raffa and Klepzig 1989. 22) Raffa and Dahlsten 1995

larly, the field cricket *Teleogryllus oceanicus* is also subject to parasitization by the same phonotactic parasitoid fly that attacks *Gryllus integer*, and silent males are common in parasitized populations; these silent males, however, are actually more likely to harbor parasitoid larvae than are calling males (Zuk et al. 1995). Perhaps because of the relatively recent association between *Ormia ochracea* and *T. oceanicus*, parasitized males may not have evolved defenses that would allow them to continue calling despite the presence of the parasitoids (Zuk et al. 1993; Rotenberry et al. 1996). Instead, males in populations where the flies are present show shifts in the time of day when calling starts and stops and in the structure of the song, compared with unparasitized populations of the same species (Zuk et al. 1993; Rotenberry et al. 1996).

Finally, although most studies of bright coloration and other sexual signals assume that these evolved via sexual selection, the unprofitable prey hypothesis (Baker and Parker 1979) maintains that conspicuous colors actually serve to indicate unpalatability or awareness of a predator, and hence are not a risk at all (Lloyd 1966; Baker and Parker 1979; Götmark 1994; Götmark and Unger 1994). Andersson (1994) provided a discussion of the recent literature on this topic, and concluded that while a few dichromatic species may show aposematic coloration, and a few others may experience more predation on the less conspicuous sex in accordance with the unprofitable prey hypothesis, this notion is not likely to be a general explanation for the evolution of showy male traits.

THE DETECTING SPECIES: EXPLOITER ADAPTATIONS

The degree of specialization on a particular host or prey type will constrain the sensory system of the parasite or predator, as well as influence the signaling of its prey. Earlier reviews on the exploitation of sexual signals have mainly focused on victim adaptations, but as with other predator-prey interactions, both sides of the relationship are expected to be affected. The "life/dinner principle" (Dawkins and Krebs 1979), which states that the consequences of being eaten (losing one's life) are more important than the consequences of missing a prey item (losing one's

dinner), obviously applies here. We expect stronger adaptations for avoiding predators than for overcoming these avoidance mechanisms. Nevertheless, examining the interaction from the exploiter's viewpoint is also worthwhile, especially when parasitoids specialize on a single host species. Table 4 lists exploiter adaptations in a variety of systems.

The life/dinner principle becomes less applicable as the predator becomes more specialized, and especially when parasitoids are involved (Thompson 1994). The disparity between the costs to each side of losing an evolutionary arms race is lessened in these situations, because highly specialized predators and most parasitoids must find an appropriate prey or host; if one chance is lost, another may not arise. As an example, contrast the feeding of bats on túngara frogs with the use of calling crickets as hosts by ormiine flies. If a bat does not detect a frog, it can eat other prey, or find one by using another means. A gravid female ormiine, however, must locate a calling male cricket from one or a few appropriate species in order to reproduce at all, and her window of time for doing so is probably quite narrow. It comes as no surprise, therefore, that the flies possess a highly unusual tympanal hearing apparatus. As mentioned earlier, the auditory system of female *Ormia ochracea* is closely tuned to the calling song of the host genus (Robert et al. 1992, 1994), suggesting convergent coevolution between the parasitoid and its hosts. Indeed, Robert et al. (1992) pointed out that the female *O. ochracea* must be able to do exactly what a female cricket does, namely, find calling male crickets. To our knowledge, no such coevolved structure exists in the hearing apparatus of bats that feed on túngara frogs.

Having an ear that is similar to a cricket's is obviously helpful for finding a host. But what about the need to find a mate, which is of course not a cricket but another fly? How has selection for prey detection and exploitation of mating signals constrained the signaling abilities, not of the exploited species but of the exploiter? We know of no studies along these lines, but it seems at least plausible that the mating system of the predator or parasitoid could be affected by the need to be sensitive to the visual, auditory or olfactory range emitted by the prey species, as well as to signals

TABLE 4
Predator and parasitoid adaptations for exploiting victim mating signals

Signal type	Exploiter	Exploiter adaptation	References
Acoustic	sarcophagid fly (*Colcondamyia auditrix*)	prey cicadas muted after parasitization to prevent superparasitism	1
	tachinid fly (*Ormia ochracea*)	tympanal ear allows hearing high (4–5 kHz) frequencies	2
	tachinid fly (*Euphasiopteryx depleta* = *Ormia depleta*)	activity period corresponds to victim calling periods	3
	bat (*Eptesicus fuscus*)	ability to hear low frequency, long-range sounds of frog and insect choruses	4
	bat (*Trachops cirrhosus*)	ability to discern suitable prey frogs by their songs	5
	bats (*Trachops cirrhosus, Tonatia sylvicola*)	resource partitioning by exploiting calls of either orthopteran insects or frogs	6
Olfactory	trichogrammatid wasps on eggs (*Trichogramma evanescens, T. pretiosum*)	arrestment of flight in presence of prey pheromone (more advantageous than flying toward pheromone because pheromone is not exactly where eggs are); preferential searching for prey eggs on underside of leaves, where they are deposited	7
	brachonid wasps (*Praon volucre, P. abjectum, P. dorsale*)	ability to recognize sexual female aphids, which may be the last chance for parasitoid to find suitable host for overwintering	8
	clerid beetle (*Thanasimus dubius*)	ability to recognize a variety of prey pheromone blends (expressed as high local variation in response to blends)	9
	clerid beetle (*Thanasimus formicarius*)	antennal olfactory receptors as sensitive as the prey receptors to prey pheromone	10
	aphelinid wasp (*Encarsia perniciosi*)	start of seasonal flight coincident with that of prey males	11
Olfactory/Visual	vespid wasp (*Vespula germanica*)	switch from olfactory detection in morning when victim lekking peaks, to visual detection later in day when victim females are ovipositing	12

References: 1) Soper et al. 1976. 2) Lakes-Harlan and Heller 1992; Robert et al. 1992, 1994; Edgecomb et al. 1995. 3) Fowler 1987. 4) Buchler and Childs 1981. 5) Tuttle and Ryan 1981. 6) Tuttle et al. 1985. 7) Noldus et al. 1991a, 1991b. 8) Hardie et al. 1991. 9) Herms et al. 1991. 10) Hansen 1983. 11) Kyparissoudas 1987. 12) Hendrichs et al. 1994.

produced by the opposite sex. On the other hand, predators may use exploitation to locate potential mates that are also attracted to the victim's mating signal (Vité and Williamson 1970; Dixon and Payne 1980). The situation is complicated by our lack of information about the natural lives of many parasitoids at times other than host location and larval deposition (Godfray 1994). Presumably a predator or parasitoid cannot be finely tuned to two different frequency curves, and so one might expect that it either uses the same sensory window as its prey, or switches to a different sensory modality entirely for locating mates (e.g., olfaction if it locates prey acoustically, or vice versa). This idea is speculative, but worth exploring.

SIGNAL HONESTY

We have discussed the inadvertent attraction of predators or parasitoids as a cost of producing conspicuous mating signals (Magnhagen 1991). Why would signals that are potentially fatal to the signaler evolve? This question may be asked of any costly mating signal, such as a long tail that reduces male flying ability (Evans and Thomas 1992). One convincing answer is that such traits serve as indicators of the signaler's quality to the receiver (Zahavi 1975). If the expense of the signal ensures that it can only be produced by high-quality males, then it is an "honest" indicator of the signaler's quality; signal honesty is therefore advanced as a necessary condition for "good genes" models of sexual selection (Andersson 1994; Johnstone 1995).

As noted already, sexual ornaments are "advertisements," not "notices" (Maynard Smith 1991); the production of advertisements involves a conflict of interest between the signaler and the receiver that is not present in the production of notices. Advertisements thus involve a cost to the signaler because the cost maintains signal reliability and prevents low-quality males from cheating by displaying the ornament without having the accompanying high fitness. The handicap principle (Zahavi 1975) states that exaggerated male ornaments will evolve via sexual selection because they indicate a male's ability to breed despite being burdened with a trait (the handicap) that threatens survival. Theoretical models have shown that costly male ornaments will evolve via the handicap principle even if they pose a cost to the choosing female (e.g., if she is attacked by the exploiter responding to the male's signal), provided the handicap is "revealing" or "condition-dependent" (Grafen 1990; Maynard Smith 1991; Johnstone 1995). In other words, if males can produce the handicap only if they are fit, then the handicap trait will evolve.

COEVOLUTION

Ever since it was first emphasized by Ehrlich and Raven (1964), coevolution has been controversial, largely owing to the lack of a consistent definition (Janzen 1980). Every mutualism or predator-prey association that involves adaptations is not an example of coevolution (Janzen 1980; Schemske 1983). An adequate demonstration of coevolution requires evidence that the traits in question have evolved specifically to aid in the interaction described, and are not the products of past evolution (Janzen 1980). Even this restrictive definition has yielded several convincing examples of reciprocal evolution (Thompson 1994 and references therein).

Signaling systems that evolve under selection pressure imposed by exploiters may yield other examples of coevolution. Signaling animals are under selection to avoid detection by illegitimate receivers, and the predators and parasitoids are in turn evolving better ways to eavesdrop on the signals of their victims; the result is a coevolutionary arms race between victim and exploiter (Burk 1988). Both predators and parasitoids may evolve specializations that detect signals, but because parasitoids are forced to live a large part, or all, of the life cycle on a single host individual, they are expected to evolve even more highly specialized abilities to detect suitable, high-quality victims (Thompson 1994). Indeed, many of the examples of exploiter adaptations in Table 4 involve parasitoid insects.

Pheromones are often produced in extremely small quantities, possibly as a mechanism for preventing exploitation (Greenfield 1981; Boake et al. 1996). As a consequence, organisms that use host pheromones as kairomones must evolve specialized mechanisms to detect such minute quantities of chemicals.

For example, Hansen (1983) provided anatomical and electrophysiological evidence suggesting that the antennae of predatory clerid beetles have developed sensitivity to their prey's pheromones that is equivalent to the prey's own antennal sensitivity.

The most striking example of host-detection morphology currently known, however, is the ears of tachinid flies which phonotactically orient to their singing orthopteran hosts (Lakes-Harlan and Heller 1992; Robert et al. 1992, 1994). These flies, particularly *Ormia ochracea,* have evolved tympanal ears that are convergent with the ears of their hosts and that are unlike the auditory organs of other closely related flies (Edgecomb et al. 1995). Orthopterans in turn may have evolved mechanisms to reduce parasitization, such as restricting their singing period to times of darkness and reducing various temporal song components (Zuk et al. 1993; Allen 1995b). Before the association between ormiine flies and their hosts can be called coevolution in the strict sense, however, the heritabilities of the traits involved and the histories of the associations must be elucidated (Schemske 1983).

Many species have evolved adaptations to counter exploitation by natural enemies (Table 3); however, most of these traits, such as remaining silent in the presence of a predator, minimize conspicuousness in general but are not specializations against specific predators or parasitoids. Probably other examples of specific traits that reduce the risk of exploitation will be found in acoustic and olfactory signaling systems, because these signals are produced discreetly and often require specialized structures for detection. Visual signals, on the other hand, are conspicuous to a variety of organisms, and may not require specialized detection organs beyond what most species have evolved in order to see conspecifics. This generalization should be treated with caution, however, because it may reflect human bias towards visual orientation; animals vary, for example, in their abilities to perceive certain wavelengths of light (Endler 1983), and so specialization may be equally possible in visually signaling systems.

CONCLUSIONS

Signal exploitation is widespread among animals. It occurs in many taxa and uses various signaling modes. We suspect that preda-

tion may have constrained the evolution of visual signals in particular, and more than is commonly assumed, but because predation is rarely observed in nature, this has been difficult to document. Taxa that have been neglected in this regard include acoustically-signaling fish, which are conspicuous in their own environment but have been little studied (Bass 1992). Seeking examples of signal exploitation in new situations may help resolve some of the controversies and test hypotheses about its evolution. For example, if pheromone-producing insects have evolved signals in a very narrow "frequency band" because of selection pressure from predators, then pheromone-producing animals that are not subject to such predation should have more generalized signals. Carnivores at the top of the food chain, such as tigers, might be interesting subjects for studies in this regard (Brahmachary et al. 1992), and researchers should look at a diversity of taxa within particular signaling modes.

Studies on coevolution should also look toward signal exploitation for new sources of examples. Much of the current literature on coevolution relies on plant-pollinator relationships, but signal exploitation should yield many other potential cases of reciprocal changes in signal production and detection. As discussed, the high degree of specialization found in many natural enemies of signaling species opens the way for coadaptations. Studies of exploitation of sexual signals may provide tests for some of the currently intractable hypotheses about patterns of coevolution (Thompson 1994).

The role of signal exploitation in speciation was discussed by Verrell (1991), who pointed out that arms races between signalers and natural enemies can lead to rapid divergence of populations in both taxa. If populations of signalers are subject to different exploiters, evasion of the predator or parasitoid might generate isolation from other populations of signalers as the signal changes (Verrell 1991). Although several authors have suggested that sexual selection can drive rapid speciation in certain groups, such as the Hawaiian drosophilids (Kaneshiro and Boake 1987) or in theoretical models (Lande 1981; West-Eberhard 1983), less attention has been paid to signal exploitation as a part of the sexual selection process.

Classical biological control, involving the use of native parasitoids to control pest species, has long been appealing because it does not involve pesticides and because the parasitoids are often host-specific (Pimentel 1963; Nechols and Kauffman 1992). However, more recently researchers have argued that natural enemies may not be as effective in biological control as novel ones, because pests may have evolved adaptations to avoid enemies with which they have co-occurred (Pimentel 1963; Hokkanen and Pimentel 1984). Because parasitoids often exploit mating signals to locate hosts, researchers interested in determining which parasitoid to use in biological control must understand the degree to which native hosts have evolved adaptations to avoid exploitation. For example, some predators are more highly attracted to the pheromones of novel hosts than native ones (Aldrich 1995; Raffa and Dahlsten 1995), and variation among host populations has been suggested to be the result of selection pressure imposed by eavesdropping enemies (Aldrich et al. 1989; Raffa and Klepzig 1989); however, in other cases the natural enemies are more attracted to native hosts (Raffa and Dahlsten 1995). Careful studies of which parasitoids and predators occur with which hosts (Hokkanen 1986), how recent the associations are, and how signal exploitation has evolved are necessary to establish effective control programs.

Finally, signal exploitation has implications for the study of sexual selection itself. For example, geographic variation in secondary sexual characters has received considerable attention in the literature (Endler 1983; Zuk et al. 1993; Endler and Houde 1995; Heller 1995). This variation is of interest partly because it may contribute to speciation, as described already. If the secondary sexual character is subject to detection and exploitation by a natural enemy, variation in its characteristics may arise independently of geography. Conversely, pressure from the exploiter may exaggerate existing variation if the exploiters are present in some areas and not others, as is the case for the phonotactic parasitoid fly *Ormia ochracea* that uses the cricket *Teleogryllus oceanicus* as a host (Zuk et al. 1993). Exploitation of signals will also influence their costliness, and hence their reliability and usefulness as honest indicators.

Although our review focused on animals as both signaling and exploiting species, there is no a priori reason why plants should not emit signals that might be used by exploiters, such as nectar robbers or herbivores, that capitalize on the need to attract pollinators and seed dispersers. Sexual selection in plants is now widely acknowledged (Willson and Burley 1983; Andersson 1994; Grant 1995), and thus perhaps the time has come to recognize the potential for further study of sexually-selected signals in these organisms. Regardless of whether authors agree on the definitions of sexual competition and secondary sexual characters in plants (Grant 1995), conspicuous visual and odor attractants are widespread among them, and should be examined for unwanted visitors. Exploitation of sexual signals is a unifying force in sexual selection that we hope will receive even more attention and synthesis from biologists in many disciplines.

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