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MIMICRY, MATE CHOICE, AND THE SENSORY TRAP HYPOTHESIS

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Abstract.—Sensory traps affect mate choice when male courtship signals mimic stimuli to which females respond in other contexts and elicit female behavior that increases male fertilization rates. Because of the supernormal stimulus effect, mimetic signals may become quantitatively exaggerated relative to model stimuli. Viability selection or a decrease in responsiveness to signals that are exaggerated beyond their peak supernormal effect may limit signal elaboration. Females always benefit by responding to models and they may often benefit by responding to mimetic courtship signals. If the response as a preference is costly, it may be maintained by frequent and strong selection for the response to the model. I review five examples of courtship that illustrate the kinds of studies that can provide evidence of sensory traps. The strategic designs of mimetic courtship signals arise not from selection of responses to them but from selection for responses to models. This results from deceit by mimicry and the evolution of sensory trap responses before the signals that elicit them as preferences.

Evolutionary biologists cannot yet fully explain the diverse designs of male courtship signals (Pagel 1993). Several recent discussions of signal evolution (e.g., West-Eberhard 1984; Kirkpatrick 1987; Ryan 1990; Guilford and Dawkins 1991; Endler 1992; Ryan and Keddy-Hector 1992; Searcy 1992; Williams 1992; Arak and Enquist 1993; Ryan and Rand 1993; Weary et al. 1993) restate a view long held by ethologists (Hinde 1970; Smith 1977): receivers' perceptions of, processing of, and responses to stimuli strongly affect signal design. Though they share this basic view, these arguments emphasize the effects of different receiver characteristics on signal design. For example, Ryan and colleagues (Ryan 1990; Ryan and Rand 1990, 1993; Ryan et al. 1990) focus on the effects of sense organ response thresholds, while Guilford and Dawkins (1991) argue that properties of a receiver's "psychological landscape" influence signal design.

These arguments also share an important historical view. Because of phenotypic evolution, the sensory-response systems of receivers of new signals will already have characteristics that affect which new signal designs are effective. Signals that "manipulate" (West-Eberhard 1984) or "exploit" (Ryan 1990) these preexisting characteristics will be favored. Though these terms refer to this sequence in signal evolution and do not imply that signals elicit costly responses, here I use the less provocative terms "play to" and "address" for "exploit" and "manipulate," respectively.

The diversity of female traits that signal address may explain in part (Endler 1992) the diversity of courtship signal designs. Further, the evolutionary pro-

cesses affecting both the design of signals and responses to them may depend on which receiver traits signal first address. Some traits that mediate mate choice may never be used in other contexts or, if they are, selection of them in these contexts may be weak. Such traits may establish initial biases in signal design and then evolve rapidly under the effects of Fisher's (1958) process or a "good genes" process (see, e.g., Zahavi 1975; Hamilton and Zuk 1982; Pomiankowski 1988; Grafen 1990) of signal-preference coevolution (Maynard Smith 1991). Thus, the current design of a preferred signal may differ substantially from its initial design and reveal little about the female trait it first addressed. Other female traits that affect preferences may be strongly selected in different contexts (West-Eberhard 1984) and resist change through signal-preference coevolution. Signals that elicit responses with other functions may catch receivers in a "sensory trap" (West-Eberhard 1984).

Ryan (1990) proposed the term "sensory exploitation" to describe cases in which signals address preexisting receiver traits. Hence, sensory exploitation is a historical pattern that occurs in several very different modes of signal evolution. These modes, but not sensory exploitation itself, make specific predictions about which signal designs will evolve and how they may be affected by signal-response coevolution.

The sensory trap hypothesis is a mode of signal evolution. Here I discuss the design of sensory trap courtship signals and how selection may act on the responses they elicit. I describe the kinds of studies that can provide evidence of sensory traps and present examples of courtship in which sensory traps may be operating. Finally, I discuss the tactical and strategic design (Guilford and Dawkins 1991) of sensory trap signals.

THE SENSORY TRAP MODE OF SIGNAL EVOLUTION

Signal Design

A male structure or movement revealed during courtship may produce stimuli that are qualitatively similar to those to which females respond in another context. A sensory trap arises when the resemblance is sufficient to elicit an out-of-context response, thus establishing a mimetic relation between the male trait and some other stimuli (Wickler 1965). If the female's response increases the male's fertilization rate, it will select for more effective mimetic signals.

Sensory trap signals may, however, become quantitatively exaggerated because of the supernormal stimulus effect (Tinbergen 1951; O'Donald 1983; West-Eberhard 1984; Rowland 1989; Ryan and Keddy-Hector 1992; Williams 1992; Enquist and Arak 1993). Exaggeration will stop when the trait exceeds perceptual limits (Magnus 1958) or is no longer mistakenly categorized as the model (Rowland 1975; Baerends and Drent 1982). Viability selection also may limit signal exaggeration (see, e.g., Fisher 1958).

Sensory Trap Responses

Selection in multiple ecological, social, and physiological contexts produces an array of female responses, any of which may be elicited by a mimetic courtship

signal. Once such a response mediates mate choice, its evolution depends on its selection as a mate preference and as a behavior with some other function.

Selection always favors the response to the model and may often favor the response to the mimic. For example, male signals may mimic resources for which selection favors efficient search and discovery; deceived females may have lower mate search costs than those that discriminate against the mimetic signal. If mimetic signals are condition-dependent, females that respond to these signals may gain by mating good-condition males. These and other selective effects may favor sensory trap responses as preferences (Smith 1986).

If the response as a mate preference is costly, selection may favor females that discriminate against the mimic, leading to better mimicry and discrimination. Discrimination may itself be costly, however, because females that ignore the mimic may mistakenly ignore the model and lose the fitness benefits of responding to it. Hence, the benefit of discrimination may decline as signals become better mimics. In general, the more variable the model stimuli, the more frequently they are encountered compared with the mimic, and the greater the fitness cost per encounter of not responding to them, the more likely are sensory trap responses to persist as mate preferences (Wiley 1983; West-Eberhard 1984; Markl 1985; Harper 1991).

RESEARCH APPROACHES

At least five kinds of studies (examples follow; the species for which the tests have been applied are given in parentheses) can provide evidence that a sensory trap is operating.

First, neuroethological studies can determine whether a proposed mimetic male signal and model evoke the same pattern of activity in the female sensory-motor system (bush crickets, oriental fruit moth).

Second, model stimuli, female responses to them, and mimetic signal designs may vary on any spatial or temporal scale. Descriptions of covariation between model, response, and mimic within and between populations can document these patterns in ecological time (fireflies).

Third, comparative phylogenetic studies (e.g., Brooks and McLennan 1991) can determine whether responses and mimics coevolve with changing models (water mites). Unlike some sensory biases that affect signal design (Ryan and Rand 1993), sensory trap responses and signals may often change rapidly with changing models as populations and species diverge. Comparative studies can reveal the preexistence of sensory trap responses only if the taxa compared share a common model and female response to it.

In sensory traps, both mimic and model stimuli must elicit the same female response. This condition suggests two experimental approaches. Fourth, an experimental change in the female response threshold to the model should produce an equal change in her response threshold to the mimic (water mites). Fifth, mimic and model stimuli can also be contextually transposed and the female response to each recorded. If there is a qualitative difference in the response to the stimuli in their transposed and usual contexts, the sensory trap hypothesis can be rejected (fiddler crabs, bush crickets).

EXAMPLES OF SENSORY TRAPS

Fireflies

Male *Photinus*, *Photuris*, and *Pyractomena* fireflies court females on vegetation near the ground by emitting patterned flashes of light as they fly above them (Lloyd 1986 and references therein). Females respond with their own flash patterns whereby males locate potential mates. However, female *Photuris* respond to courting male *Photinus* and *Pyractomena* by mimicking the flash patterns of females of these genera. When these courting males land or as they approach in the air, female *Photuris* catch and eat them.

Male *Photuris* often locate their own usually rare females by mimicking the male courtship signals of the species their females eat. Males of some *Photuris* species emit their mimetic flashes only at locations in the vegetation and times of the night and season at which their females' prey court. Female *Photuris* respond with their own mimetic signals as if they were hunting. The behavior of both sexes following this signal exchange has not been described. However, some *Photuris* species have lost their own courtship signals and rely entirely on mimicry for locating potential mates. Hence, this remains an unsubstantiated but highly probable case for a sensory trap.

Water Mites

Leg trembling by courting males of the epibenthic predaceous water mite *Neumania papillator* causes females hunting in the net-stance posture to orient toward and clutch males as they do their copepod prey, a response that increases the rate of spermatophore transfer (Proctor 1991). Two kinds of evidence support the hypothesis that leg trembling mimics prey vibrations and elicits a hunting response. First, hungry females more often orient toward and clutch both copepods and leg-trembling males than do sated females (Proctor 1991). Second, leg trembling evolved either after or concurrently with net-stance hunting (Proctor 1992).

Fiddler Crabs

Courting male *Uca beebei* often build mud pillars at the entrances to their burrows (Christy 1988a) to which they attract females for mating, oviposition, and incubation (Christy 1987). Female choice is not based on the quality of burrows for breeding (Christy and Schober 1994). Females are differentially attracted to males that build pillars (Christy 1988b), and both behavioral displays (J. Christy and U. Schober, unpublished data) and pillars (Christy 1988b) contribute to male attractiveness. Pillars may elicit landmark orientation (Altevogt 1965; Herrnkind 1968, 1972, 1983; Langdon 1971; Langdon and Herrnkind 1985), a response used by crabs that wander on the surface, as do receptive females, to escape predators by running to and hiding behind objects (Crane 1975; Christy 1988b).

Transposition experiments were used to test this sensory trap hypothesis. Male and female *U. beebei* and female *Uca deichmanni*, *Uca musica*, *Uca panamensis*, and *Uca stenodactylus* were released individually in the center of a circle with

TABLE 1
RESPONSES OF FIDDLER CRABS TO APPROACH OF A MODEL PREDATOR

CRAB SEX AND SPECIES	RESPONSE			TOTALS	PERCENTAGE OUT	G_1^*	PERCENTAGE TO BURROW WITH PILLAR	G_2^*
	Ran out of Circle	Ran to Burrow with Pillar	Ran to Burrow without Pillar					
<i>Uca beebei</i> :†								
Female	49	66	34	149	33	289.8	66	10.4
Male	38	51	29	118	32	234.3	64	6.1
<i>Uca deichmanni</i> :								
Female	45	72	30	147	31	305.2	72	17.7
<i>Uca musica</i> :								
Female	29	92	35	157	18	449.8	72	26.4
<i>Uca panamensis</i> :								
Female	42	91	19	152	28	344.8	83	51.3
<i>Uca stenodactylus</i> :								
Female	56	53	30	139	40	212.9	64	6.5

* For G -tests of goodness-of-fit, G_1 to expected relative frequencies of 0.904 runs out of the circle and 0.096 runs to burrows. These frequencies are the proportions of the circumference of the circle occupied by clear space and by burrows. Value G_2 to expected relative frequencies of 0.50 runs to burrows with and without pillars. All G values are significant at least at $\alpha = 0.05$.

† Data are from Christy (1988b).

16 empty burrows, alternately with and without pillars, at even distances along its circumference. Crabs were chased with a model bird predator, and their responses were recorded (see Christy 1988b). Courting male *U. musica* build hoods (Zucker 1974) that, like pillars, attract females (J. Alcock, unpublished data). Males of the other species do not build courtship structures, at least in the Panamanian populations used in these tests.

The results broadly support the sensory trap hypothesis (table 1). All crabs differentially oriented to burrows with pillars, showing that pillars effectively mimic objects to which crabs orient to escape predators. Female *U. musica* showed the response, even though the broad, cupped hoods that males of this species build are structurally very different from pillars. In another experiment, there was no significant difference in the mating rates of hood-building male *U. musica* with their hoods intact and those with their hoods replaced by pillar models (hoods, 48/247 [19%]; pillar models, 33/237 [14%]; $G = 2.649$, $P > .10$). Hence, the mimetic stimulus properties of hoods and pillars are similar, and these courtship signals may differ for reasons other than interspecific differences in female mate preferences that are mediated by their responses to these structures. Male *U. beebei* and females of three species that do not build structures showed the response indicating that its selection as a behavior mediating mate choice is unnecessary for its maintenance. Landmark orientation for predator escape is a common trait in the genus *Uca* that may have affected courtship signaling in several species (Christy 1988a, 1988b; Christy and Salmon 1991).

Bush Crickets

Following an exchange of calls, a female bush cricket *Metaplastes ornatus* mounts a male. He inserts his subgenital plate into the female's genital chamber, partly withdraws and reinserts it several times, and then removes it (Helvesen and Helvesen 1991). The bilobate plate has a ventral barbed keel about the size of a cricket egg. When the male removes his plate the barbs hook and evert the genital chamber, which the female licks and replaces. This sequence is repeated several times until the male, with his plate clear of the female's genitalia, transfers a spermatophore. By grooming her everted genital chamber the female consumes about 85% of the sperm stored in her spermatheca from previous matings.

Fertilization occurs when an egg passes from the oviduct into the genital chamber and touches receptors in the chamber wall, causing the spermathecal duct to twitch and dispense sperm onto the egg (Sugawara and Loher 1986; Sugawara 1993). Helvesen and Helvesen (1991) suggested that the form and movement of the male genital plate may mimic stimuli produced by eggs during ovulation and elicit the fertilization response. To test this sensory trap hypothesis, eggs were inserted to the position attained by the plate during intromission, either moved or not, then withdrawn. Hundreds of living sperm were recovered from the moved egg and only one from the stationary egg. If the benefits of receiving new and eating old sperm exceed the costs of prolonged coupling, then selection may favor females who make the fertilization response to the egg-mimicking male subgenital plate (Helvesen and Helvesen 1991).

Oriental Fruit Moth

The male oriental fruit moth *Grapholita molesta* locates a female by odor, walks upwind, extrudes his abdominal hair pencils, fans his wings, then retracts the structure (Baker and Cardé 1979). The female responds by approaching, then touching the male's abdomen with her antennae and head. When touched, the male whirls around and grasps the female's abdomen with his claspers and the pair copulates. The hair pencil odor is the primary stimulus that elicits approach. It contains ethyl *trans*-cinnamate, a compound that elicits significant female electroantennogram activity and approach (Nishida et al. 1982). This chemical occurs in fermented fruit juices to which both sexes are attracted to feed (Nishida et al. 1985). Males that drink water containing ethyl *trans*-cinnamate sequester it in their hair pencils and more successfully elicit approach during courtship than do males that drink untreated water (Löfstedt et al. 1989). By taking up an attractive food odor and releasing it to attract females, males elicit an out-of-context feeding response each time they court.

Males of many Lepidoptera have elaborate scent-producing structures that they use during courtship (Birch et al. 1990). Unlike female odors, male odors usually are similar to or the same as the odors of adult or larval food plants. Although other modes of signal evolution have received more attention (Baker and Cardé 1979; Conner et al. 1981, 1990; Birch et al. 1990), the use of plant odors by males

and their specific effects on female behavior suggest that sensory traps may be common in the short-range chemically mediated courtship of this group (Krasnoff and Dussourd 1989).

DISCUSSION AND CONCLUSIONS

The sensory trap mode of courtship signal evolution has two distinguishing characteristics. First, it predicts that sexual selection by female choice favors mimetic courtship signals. Following the approaches outlined here, the mimetic status of a particular signal can be tested. This makes the sensory trap hypothesis attractive for empirical research in a field beset with alternative hypotheses that are very difficult to reject (Bradbury and Andersson 1987). Second, the hypothesis features responses that have functions outside the context of mate choice. I have summarized examples of sensory trap responses that subserve feeding, predator escape, and fertilization. However, any response, including one made to another signal, can be the basis for a sensory trap.

The sensory trap process has an important implication for understanding how selection on receivers affects strategic signal designs. A signal's strategic design determines whether a receiver responds to a signal at all, while a signal's tactical design affects how well it is transmitted, received, perceived, and processed (Guilford and Dawkins 1991; Endler 1992). Exaggeration of a sensory trap signal due to the supernormal effect changes its tactical design. Guilford and Dawkins (1991) noted that mimetic signals often draw attention to signalers, and they correctly argued that this is a tactical effect. However, it is important to distinguish clearly between what makes a signaler conspicuous and what makes its signals conspicuous. The reasons receivers attend to mimetic signals, and, hence, the animals that use them are conspicuous, relate to the strategic design of these signals.

A signal's strategic design embodies its content or meaning to receivers as established by selection of their responses. The importance of different causes of selection of responses, especially those that mediate mating preferences, is much debated (Bradbury and Andersson 1987; Kirkpatrick and Ryan 1991). It is widely (often tacitly) assumed, however, that selection of a response occurs only because it is elicited by a particular signal (Pomiankowski 1988). This assumption is wrong for a sensory trap response because it has another important function. Selection of the response in this context establishes and can change the strategic design of a sensory trap courtship signal. Selection of the response as a mate preference affects the maintenance of the response and the signal's tactical but not strategic design.

There is a two-part reason for this. First, sensory trap signals are mimics, deceitful and false in content. Their strategic designs are antithetical to those of "honest" signals, which reveal the nature of selection for responses to them (Zahavi 1975; Grafen 1990), not to something else. I emphasize, however, that selection may often favor sensory trap responses as mate preferences. Second, the strategic features of sensory trap signals address preexisting responses. Their

meaning, in effect, predates their evolution, and their strategic designs do not result from subsequent selection of responses used in mate choice.

The terms "sensory exploitation" and "sensory trap" may sound as though they refer to the same thing, but they do not. For clarity, I will reiterate their differences. Sensory exploitation occurs when a signal evolves to address a preexisting receiver trait (Ryan 1990). Since sensory-response systems are never featureless (Williams 1992), all signals may initially address preexisting traits and all modes of signal evolution may begin with sensory exploitation. Various processes then immediately affect stasis or change in receiver traits that mediate responses and thereby affect the tactical and strategic designs of the signals that play to them. "Sensory trap" refers to the process of signal evolution that begins with sensory exploitation and then is governed by the special relations between mimics, models, and responses to both.

Unlike sensory trap responses, other preexisting receiver traits have no identified functions other than mate choice (Ryan and Rand 1993). If they are otherwise functionless, then they and the signals that play to them can, and perhaps should, coevolve (Maynard Smith 1991). However, at least one ancestral auditory sensory bias of *Physalemus* frogs has not changed despite its long role in mate choice (Ryan et al. 1990). What accounts for its stasis? Perhaps the mate preference that the bias mediates is a target of selection but the bias itself is not. The component of the male call that plays to this sensory bias may be a tactical embellishment (Rand et al. 1992) that has no strategic design in the specific sense discussed here. Several if not all modes of signal evolution begin with sensory exploitation. Some may even produce purely tactical signal designs (see also Hasson 1989) rather than mimetic designs with false meanings, as does the sensory trap process.

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LITERATURE CITED

- Altevogt, R. 1965. Lichtkompass- und Landmarkendressuren bei *Uca tangeri* in Andalusien. *Zeitschrift für Morphologie und Ökologie der Tiere* 55:641–655.
- Arak, A., and M. Enquist. 1993. Hidden preferences and the evolution of signals. *Philosophical Transactions of the Royal Society of London B, Biological Sciences* 340:207–213.
- Baerends, G. P., and R. Drent. 1982. The herring gull and its egg. II. *Behaviour* 82:1–416.
- Baker, T. C., and R. Cardé. 1979. Courtship behavior of the oriental fruit moth (*Grapholita molesta*): experimental analysis and consideration of the role of sexual selection in the evolution of sex pheromones in the Lepidoptera. *Annals of the Entomological Society of America* 72:173–188.
- Birch, M. C., G. M. Poppy, and T. C. Baker. 1990. Scents and eversible scent structures of male moths. *Annual Review of Entomology* 35:25–58.
- Bradbury, J. W., and M. B. Andersson. 1987. *Sexual selection: testing the alternatives*. Wiley, New York.

- Brooks, D. R., and D. A. McLennan. 1991. Phylogeny, ecology, and behavior. University of Chicago Press, Chicago.
- Christy, J. H. 1987. Female choice and the breeding behavior of the fiddler crab *Uca beebei*. *Journal of Crustacean Biology* 7:624–635.
- . 1988a. Pillar function in the fiddler crab *Uca eebei*. I. Effects on male spacing and aggression. *Ethology* 78:53–71.
- . 1988b. Pillar function in the fiddler crab *Uca beebei*. II. Competitive courtship signaling. *Ethology* 78:113–128.
- Christy, J. H., and M. Salmon. 1991. Comparative studies of reproductive behavior in mantis shrimps and fiddler crabs. *American Zoologist* 31:329–337.
- Christy, J. H., and U. M. Schober. 1994. A test for resource-defence mating in the fiddler crab *Uca beebei*. *Animal Behaviour* 48:795–802.
- Conner, W. E., T. Eisner, R. K. Vander Meer, A. Guerrero, and J. Meinwald. 1981. Precopulatory sexual interaction in an arctiid moth (*Utetheisa ornatrix*): role of a pheromone derived from dietary alkaloids. *Behavioral Ecology and Sociobiology* 9:227–235.
- Conner, W. E., B. Roach, E. Benedict, J. Meinwald, and T. Eisner. 1990. Courtship pheromone production and body size as correlates of larval diet in males of the arctiid moth, *Utetheisa ornatrix*. *Journal of Chemical Ecology* 16:543–552.
- Crane, J. 1975. Fiddler crabs of the world. Princeton University Press, Princeton, N.J.
- Endler, J. A. 1992. Signals, signal conditions, and the direction of evolution. *American Naturalist* 139(suppl.):S125–S153.
- Enquist, M., and A. Arak. 1993. Selection of exaggerated male traits by female aesthetic senses. *Nature (London)* 361:446–448.
- Fisher, R. A. 1958. The genetical theory of natural selection. 2d ed. Dover, New York.
- Grafen, A. 1990. Biological signals as handicaps. *Journal of Theoretical Biology* 144:517–546.
- Guilford, T., and M. S. Dawkins. 1991. Receiver psychology and the evolution of animal signals. *Animal Behaviour* 42:1–14.
- Hamilton, W. D., and M. Zuk. 1982. Heritable true fitness and bright birds: a role for parasites. *Science (Washington, D.C.)* 218:384–387.
- Harper, G. C. 1991. Communication. Pages 374–397 in J. R. Krebs and N. B. Davies, eds. *Behavioural ecology*. 3d ed. Blackwell, London.
- Hasson, O. 1989. Amplifiers and the handicap principle in sexual selection: a different emphasis. *Proceedings of the Royal Society of London B, Biological Sciences* 234:383–406.
- Helversen, D. V., and O. V. Helversen. 1991. Pre-mating sperm removal in the bushcricket *Metaplastes ornatus* Ramme 1931 (Orthoptera, Tettigonoidea, Phaneropteridae). *Behavioral Ecology and Sociobiology* 28:391–396.
- Herrnkind, W. F. 1968. Adaptive visually-directed orientation in *Uca pugilator*. *American Zoologist* 8:585–598.
- . 1972. Orientation in shore-living arthropods, especially the sand fiddler crab. Pages 1–59 in H. E. Winn and B. L. Olla, eds. *Behavior of marine animals*. Vol. 1. Invertebrates. Plenum, New York.
- . 1983. Movement patterns and orientation. Pages 41–105 in F. J. Vernberg and W. B. Vernberg, eds. *The biology of Crustacea*. Vol. 7. Behavior and ecology. Academic Press, New York.
- Hinde, R. A. 1970. *Animal behavior*. McGraw-Hill, New York.
- Kirkpatrick, M. 1987. The evolutionary forces acting on female mating preferences in polygynous animals. Pages 67–82 in J. W. Bradbury and M. B. Andersson, eds. *Sexual selection: testing the alternatives*. Wiley, Chichester.
- Kirkpatrick, M., and M. J. Ryan. 1991. The evolution of mating preferences and the paradox of the lek. *Nature (London)* 350:33–38.
- Krasnoff, S. B., and D. E. Dussourd. 1989. Dihydropyrrrolizine attractants for arctiid moths that visit plants containing pyrrolizidine alkaloids. *Journal of Chemical Ecology* 15:47–60.
- Langdon, J. W. 1971. Shape discrimination and learning in the fiddler crab *Uca pugilator*. Ph.D. diss. Florida State University, Tallahassee.

- Langdon, J. W., and W. F. Herrkind. 1985. Visual shape discrimination in the fiddler crab, *Uca pugilator*. *Marine Behavior and Physiology* 11:315–325.
- Lloyd, J. E. 1986. Firefly communication and deception: "Oh, what a tangled web." Pages 113–128 in R. W. Mitchell and N. S. Thompson, eds. *Deception: perspectives on human and nonhuman deceit*. SUNY Press, Albany, N.Y.
- Löfstedt, C., N. J. Vickers, W. L. Roelofs, and T. C. Baker. 1989. Diet related courtship success in the oriental fruit moth, *Grapholita molesta* (Tortricidae). *Oikos* 55:402–408.
- Magnus, D. 1958. Experimentelle Untersuchungen zur Bionomie und Ethologie des Aisermantels *Argynnis paphia* Girard (Lep. Nymph.). *Zeitschrift für Tierpsychologie* 15:397–426.
- Markl, H. 1985. Manipulation, modulation, information, cognition: some of the riddles of communication. Pages 163–194 in B. Hölldobler and M. Lindauer, eds. *Experimental behavioral ecology and sociobiology*. Sinauer, Sunderland, Mass.
- Maynard Smith, J. 1991. Theories of sexual selection. *Trends in Ecology & Evolution* 6:146–151.
- Nishida, R., T. C. Baker, and W. L. Roelofs. 1982. Hair pencil pheromone components of male oriental fruit moths, *Grapholita molesta*. *Journal of Chemical Ecology* 8:947–959.
- Nishida, R., H. Fukami, T. C. Baker, W. L. Roelofs, and T. E. Acree. 1985. Oriental fruit moth pheromone: attraction of females by an herbal essence. Pages 47–60 in T. E. Acree and D. M. Soderlund, eds. *Semiochemistry, flavors and pheromones*. de Gruyter, Berlin.
- O'Donald, P. 1983. Sexual selection by female choice. Pages 53–66 in P. Bateson, ed. *Mate choice*. Cambridge University Press, Cambridge.
- Pagel, M. 1993. The design of animal signals. *Nature (London)* 361:18–20.
- Pomiankowski, A. 1988. The evolution of female mate preferences for male genetic quality. *Oxford Surveys in Evolutionary Biology* 5:136–184.
- Proctor, H. C. 1991. Courtship in the water mite *Neumania papillator*: males capitalize on female adaptations for predation. *Animal Behaviour* 42:589–598.
- . 1992. Sensory exploitation and the evolution of male mating behaviour: a cladistic test using water mites (Acari: Parasitengona). *Animal Behaviour* 44:745–752.
- Rand, A. S., M. J. Ryan, and W. Wilczynski. 1992. Signal redundancy and receiver permissiveness in acoustic recognition by the Túngara frog, *Physalaemus pustulosus*. *American Zoologist* 32:81–90.
- Rowland, W. L. 1975. The effects of dummy size and color on behavioral interaction in the jewel cichlid, *Hemichromis imaculatus* Gill. *Behaviour* 53:109–125.
- . 1989. Mate choice and the supernormality effect in female sticklebacks (*Gasterosteus aculeatus*). *Behavioral Ecology and Sociobiology* 24:433–438.
- Ryan, M. J. 1990. Sexual selection, sensory systems and sensory exploitation. *Oxford Surveys in Evolutionary Biology* 7:157–195.
- Ryan, M. J., and A. Keddy-Hector. 1992. Directional patterns of female mate choice and the role of sensory biases. *American Naturalist* 139(suppl.):S4–S35.
- Ryan, M. J., and A. S. Rand. 1990. The sensory basis of sexual selection for complex calls in the túngara frog *Physalaemus pustulosus* (sexual selection for sensory exploitation). *Evolution* 44:305–314.
- . 1993. Sexual selection and signal evolution: the ghost of biases past. *Philosophical Transactions of the Royal Society of London B, Biological Sciences* 340:187–195.
- Ryan, M. J., J. H. Fox, W. Wilczynski, and A. S. Rand. 1990. Sexual selection for exploitation in the frog *Physalaemus pustulosus*. *Nature (London)* 343:66–67.
- Searcy, W. A. 1992. Song repertoire and mate choice in birds. *American Zoologist* 32:71–80.
- Smith, J. W. 1977. *The behavior of communicating*. Harvard University Press, Cambridge.
- . 1986. An "informational" perspective on manipulation. Pages 71–86 in R. W. Mitchell and N. S. Thompson, eds. *Deception: perspectives on human and nonhuman deceit*. SUNY Press, Albany, N.Y.
- Sugawara, T. 1993. Oviposition behaviour of the cricket *Teleogryllus commodus*: mechanosensory cells in the genital chamber and their role in the switch-over of steps. *Journal of Insect Physiology* 39:335–346.

- Sugawara, T., and W. Loher. 1986. Oviposition behaviour of the cricket *Teleogryllus commodus*: observation of external and internal events. *Journal of Insect Physiology* 32:179–188.
- Tinbergen, N. 1951. *The study of instinct*. Oxford University Press, Oxford.
- Weary, D. M., T. C. Guilford, and R. G. Weisman. 1993. A product of discrimination learning may lead to female preferences for elaborate males. *Evolution* 47:333–336.
- West-Eberhard, M. J. 1984. Sexual selection, competitive communication and species-specific signals in insects. Pages 283–324 in T. Lewis, ed. *Insect communication*. Academic Press, New York.
- Wickler, W. 1965. Mimicry and the evolution of animal communication. *Nature (London)* 208: 519–521.
- Wiley, R. H. 1983. The evolution of communication: information and manipulation. Pages 156–189 in T. R. Halliday and P. J. B. Slater, eds. *Animal behaviour*. Vol. 2. Communication. Freeman, New York.
- Williams, G. C. 1992. *Natural selection*. Oxford University Press, Oxford.
- Zahavi, A. 1975. Mate selection: a selection for a handicap. *Journal of Theoretical Biology* 53:205–214.
- Zucker, N. 1974. Shelter building as a means of reducing territory size in the fiddler crab, *Uca terpsichores* (Crustacea: Ocypodidae). *American Midland Naturalist* 91:224–236.

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