

COURTSHIP PHEROMONES: EVOLUTION BY NATURAL  
AND SEXUAL SELECTION

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*Courtship pheromones are defined as chemical signals that are transmitted between sexual partners during courtship. Male courtship pheromones are found in a surprisingly diverse array of animals, but are most common among species of arthropods and salamanders. Methods of delivering the courtship pheromone to the female vary; there are male butterflies that dust the pheromone directly on the female's antennae, scorpionflies and crickets that produce a gustatory offering which the female ingests during copulation, and salamanders that apply a glandular secretion to the female's nares or introduce it directly into her circulatory system before sperm transfer.*

*Sexual selection is strongly implicated in the evolution of courtship pheromones since, in most instances, these chemicals probably affect male mating success. Natural selection may also affect pheromone evolution to the extent that these pheromones influence the fertility of females and the mortality of both sexes. The evolutionary elaboration of courtship pheromones is affected differently by sexual selection than by natural selection. The nature of this difference can be approached by experimental studies that assay the effects of courtship pheromones on fitness components of both males and females, and by comparative studies that document the actual course of evolution.*

*"...like the birds and beasts which,  
attracted by the gaudy appurtenances of sex,  
unwittingly perpetuate their species..."*

*Jan Morris, Farewell the Trumpets*

## INTRODUCTION

In a diverse group of animals, including insects, pseudo-scorpions, fish, mammals and salamanders, the gaudy appurtenances of sex include chemicals that do more than simply attract sexual partners. The chemicals that concern us here have sometimes been called "aphrodisiacs" but, since sexual persuasion is only one of many possible effects, we use the less loaded term "courtship pheromones." These chemicals appear to be distinct from sex pheromones that act at a distance and merely attract one sex to the other. Common denominators among the various animal groups employing male courtship pheromones are: (1) pheromones are produced from sexually dimorphic, male glands that appear to be used only in courtship, (2) the male delivers the chemical to the female after their initial encounter but before sperm transfer, and (3) the pheromone is delivered directly to the female, sometimes by active application on female chemoreceptors or by injection into the female's circulatory system. Unlike sex pheromones or attractants, which have profound economic consequences in agricultural pest control, courtship pheromones have received relatively little biochemical scrutiny. In this paper, we briefly review some diverse instances of male courtship pheromone delivery and present a conceptual framework for organizing comparative and experimental studies of pheromone evolution. We also review some recent experimental work with particular emphasis on our own study organisms, salamanders.

Our principal concern will be with the selection process that affects the evolution of courtship pheromones rather than with the immediate physiological effects of chemicals on the female. The reason for this focus is that we can expect both extremely rapid evolution of pheromones and delivery systems, as well as a great diversity of evolutionary outcomes, if variation in courtship pheromones affects male mating success. In contrast, if other components of fitness are affected by pheromones, theoretical results lead us to expect a much less dramatic evolutionary process (Fisher 1930; O'Donald 1980; Lande 1980, 1981; Kirkpatrick 1982). Our aim in this paper is to illustrate how a focus on modes of selection can be used to organize existing information and how it can inspire new experimental and comparative studies of courtship pheromones.

## SEXUAL VERSUS NATURAL SELECTION

As Ghiselin (1974:130) has remarked, very few modern authors use the term "sexual selection" as Darwin used it. Most contemporary authors incorrectly treat sexual selection as a subcategory of natural selection. Darwin (1859, 1871), however, repeatedly contrasted the two forms of selection and clearly viewed them as separate, often opposing processes. For example, "In regard to structures acquired through ordinary or natural selection, there is in most cases ... a limit to the amount of advantageous modification in relation to certain special ends; but in regard to structures adapted to make one male victorious over another either in fighting or in charming the female, there is no definite limit to the amount of advantageous modification; so long as the proper variations arise, the work of sexual selection will go on" (Darwin 1871:278). The two agents of sexual selection, females and rival males, will exert their

effects by influencing the number of mates that bear the progeny of each male, *i.e.*, by affecting male mating success.

Regardless of whether one adheres to Darwin's terminology, it is critical to ask which component of fitness is affected by the pheromone, since this can have a major effect on the evolutionary process. Four major possibilities, outlined below, are that chemical delivery during courtship affects (1) mating success (the number of mates that bear progeny sired by the male), (2) the fertility of mates (the overall number of progeny or rate of production), (3) the survivorship of the mate(s) until the production of progeny, and (4) the survivorship of the pheromone-producing male. Variation in the first component, mating success, constitutes sexual selection while variation in the other aspects, fertility and survivorship, constitutes natural selection (Darwin 1859, 1871; Ghiselin 1974; Lande 1980, 1981; Wade and Arnold 1980). Of course, a courtship pheromone may affect more than one component of fitness.

We first consider how male chemical delivery during courtship might affect these four components of fitness, and then examine the different evolutionary consequences expected under sexual versus natural selection.

*Male mating success.* A chemical produced by males during the mating season might have one or more of the following effects on mating success: (1) The chemical might enhance discovery of, or encounter with, females. Although female-produced sex attractants are common, especially among insect species, many examples are known in which males broadcast pheromones that attract females (*e.g.*, Jacobson 1965:39-48; Shorey 1973). Such male chemicals might evolve by sexual selection but would not be courtship pheromones if they merely

attract the female. (2) The male's pheromone might exert its effect after the initial encounter with the female by promoting the probability of insemination. Thus the effect may be to persuade the female to court. Such chemicals are sometimes called "aphrodisiacs." [Birch (1974) cautions against the anthropomorphic implications of this term, and we use it here only in a restricted sense, not implying guaranteed courtship success.] We later discuss a number of experimental studies of putative aphrodisiacs in butterflies, mammals and salamanders. Alternatively, the pheromone may promote insemination by enhancing coordination of partners during sperm transfer. (3) A final possibility is that the male's chemical delivery promotes paternity after the act of insemination. For example, the male's pheromone could promote sperm transport by inducing a quiescent state in the female. Paternity also may be enhanced by so called "anti-aphrodisiacs" that either induce a sexually nonreceptive state in the female (Barth and Lester 1973; Swailes 1971; Gwadz 1972; Leopold, *et al.*, 1971; Riemann, *et al.*, 1967) or repel rival males from the inseminated female (Happ 1969; Gilbert 1976; Hirai, *et al.*, 1978).

*Fertility and survivorship of mates.* It is possible that the male chemical will affect mate fertility or survivorship rather than, or in addition to, mating success. This is most likely in instances where the female actually ingests the chemical (gustatory transmission) since a considerable energetic transfer is conceivable. Thus, in many cockroaches, crickets and katydids, the female feeds on products from a specialized male gland and, apparently because she is feeding, the male is able to copulate with her (Roth and Dateo 1966, Alexander and Brown 1963, Thornhill 1976a). One effect of this chemical transfer could be promotion of male mating

success if males that produce gustatory secretions are more likely to complete insemination (Alexander 1964). Males with substantial glandular offerings also might increase the fertility or survivorship of their mates. The semen or spermatophore itself may transfer materials and energy as well as gametes to the female (Thornhill 1976a, Gwynne, 1981). Transfer of nutrients via the spermatophore has been demonstrated in three species of nymphalid butterflies where male-derived substances were later found in the developing ova of inseminated females (Boggs and Gilbert 1979). In many species of caddisflies (Trichoptera), the male transfers a protein-rich secretion to the female during copulation (Svensson 1972), and the protein source is used by the female as an energy supply. Similarly, some scorpionflies offer a salivary secretion to a potential mate (Thornhill 1976a).

*Survivorship of males.* Finally, chemical delivery could have negative as well as positive effects on individual male fitness. These negative effects may constitute the opposing selective forces that eventually halt the evolutionary elaboration of the delivery system. For example, the system may actually reduce the survivorship component of male fitness due to costs of manufacture and maintenance or because predators as well as mates are attracted. In analogous examples, parasitoid flies orient to cricket songs (Cade 1975), predatory bats locate male frogs from their mating calls (Tuttle and Ryan 1981) and predatory female fireflies attract and consume the males of other species by mimicking the flash responses of the prey's own females (Lloyd 1975). These examples suggest that predators could cue on sex attractants or courtship pheromones. Furthermore, the chemical may attract rival males as well as potential mates. This apparently is a common

liability associated with pheromone broadcasting. In many insects, males as well as females are attracted by pheromones produced by conspecific males (see examples in Jacobson 1965).

#### EVOLUTIONARY CONSEQUENCES

A pheromone that exclusively affects mating success is analogous to frog vocalization or to the peacock's fabulous display. Such a pheromone will have very different evolutionary consequences than one that affects mate fertility or survivorship. As Darwin (1859, 1871) pointed out, such male attributes may evolve under the force of a purely sexual advantage. Theoretical models of sexual selection show that the male's tail or his pheromone can be elaborated during evolution even though the female receives no direct or immediate advantage from mate choice (Lande 1980, 1981; O'Donald 1977, 1980; Fisher 1930; Kirkpatrick 1982). As Fisher (1930) first showed, there can be an accelerating coevolution of a male trait and the female response to this trait. Using pheromones as an example, both the male pheromone and the female reaction to this pheromone can increase during evolution since, in each generation, the males with the most effective pheromone are more likely to inseminate both the most resistant and the most responsive females. If there is heritable variation in male pheromones and in female response to the pheromone, the mate selection process can create and maintain a genetic correlation between the two attributes (Lande 1981, Kirkpatrick 1982). The evolution of female responsiveness thus can occur purely as a genetic corollary of sexual selection on male pheromone, not because the females benefit or suffer in any direct way from the pheromone.

Lande (1980, 1981) and Kirkpatrick (1982) have shown that the evolutionary outcome of this sexual selection process is

indeterminate. The equilibrium values of average male pheromone production and average female resistance will vary according to the initial conditions in the population: there is no unique evolutionary outcome. Consequently, in any radiation in which pheromonal evolution by sexual selection is a recurrent happening, we can expect a tremendous variety of evolutionary outcomes. Furthermore, the variety will be largely historical and nonadaptive.

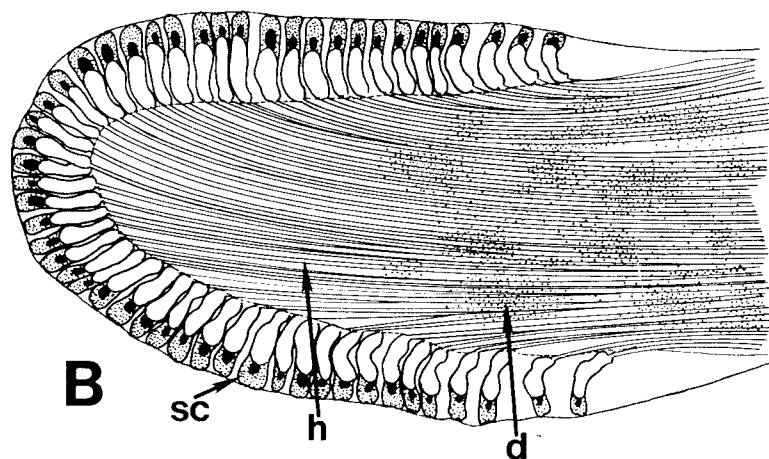
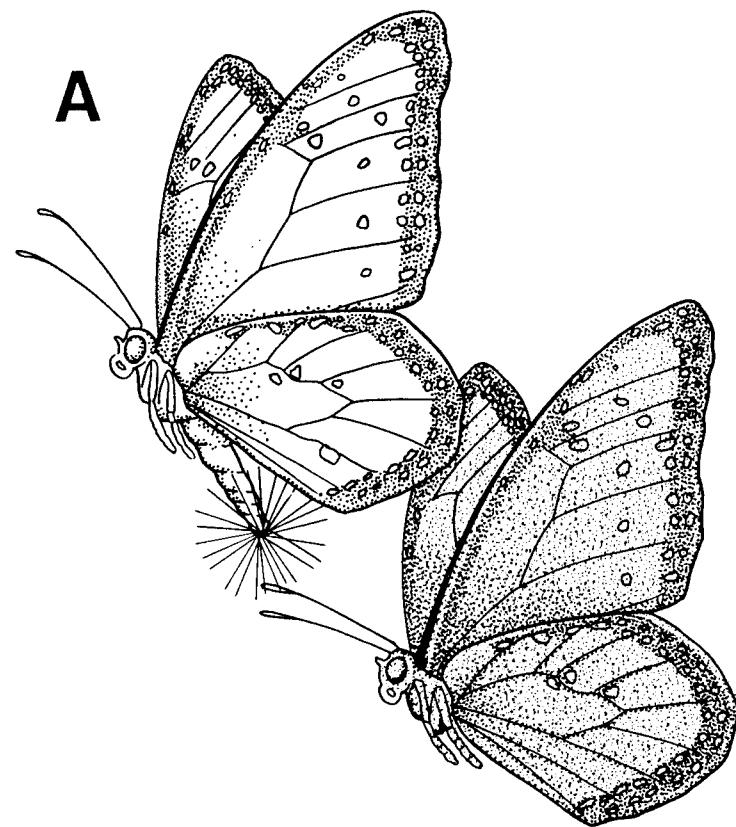
The evolutionary expectation is quite different if the male's pheromone affects the fertility or survivorship of his mates (Lande 1981). In this case there will be a unique equilibrium of male pheromone production and average female reaction. Differences between species and among higher taxa may be less extensive than differences produced purely by sexual selection.

#### SURVEY OF MALE CHEMICAL DELIVERY DURING COURTSHIP

In the following sections we consider a variety of examples in which males deliver chemicals during courtship. Male courtship pheromones are found in a diverse group of animal species, but are especially common in many orders of insects, including species of scorpionflies (Thornhill 1976a, 1976b), caddisflies (Svensson 1972), butterflies and moths, cockroaches and crickets, water bugs, bees, flies, and lacewings (see reviews by Jacobson 1965, Birch 1974, and Shorey 1973). Male chemical delivery during courtship also is known for pseudoscorpions, some fish and mammals, and for most species of salamanders. It is not our goal to present an exhaustive survey of all known examples of chemical persuasion during courtship. Instead, we focus primarily on studies that experimentally test for effects of male pheromones

on different components of fitness. Such experimental studies can indicate whether the pheromone delivery system is affected purely by sexual selection or whether natural selection on males and females also affects pheromonal evolution. Unfortunately, no species has been completely analyzed from this point of view. Nevertheless, the available studies indicate how one might address the problem of partitioning the effects of selection into the categories of natural and sexual selection.

*Insects.* Pheromonal communication among insect species is widespread and diverse. Even restricting our consideration to male courtship pheromones (those produced only after the male and his potential mate have been brought together), there still are numerous examples from a variety of insect species (see Jacobson 1965, Birch 1974, and Shorey 1973). Some of the most thorough work that demonstrates the nature and effects of male courtship pheromones was conducted with the day-flying Queen butterfly, *Danaus gilippus* (Brower and Jones 1965; Brower, et al., 1965; Pliske and Eisner 1969). During the courtship season, the male is visually attracted to the female as she flutters through the air (males are not discriminatory and also may approach other males or even falling leaves; Myers 1972). The male hovers above the female and extrudes a pair of specialized glands called "hairpencils" (fig. 1). When the secretions from the hairpencils are delivered in the vicinity of the female's antennae, she tends to alight on the ground or on nearby vegetation. The male follows the female and continues to release secretions until he achieves a copulatory position. In an experimental study of the Queen butterfly conducted in a natural habitat, Myers and Brower (1969) showed that interference with male chemical delivery (either by removing the male's hairpencils or by blocking the



female's antennal receptors) resulted in substantially reduced courtship success. Thus the pheromone released from the hairpencils affects the mating success component of male fitness, so it is extremely likely that this courtship pheromone evolved by sexual selection. Male *D. gilippus* have other specialized glands, wing pockets, which also may affect male courtship success; the function of these glands, however, has not been conclusively demonstrated (Myers 1972).

In another example of chemical use during courtship, Tinbergen *et al.* (1943) showed that a male satyriid moth, *Eumensis semele*, actually moves the female's antennae between his forewings so that her antennae directly contact the specialized scales that constitute his scent patches. This direct application of courtship pheromones is exceptional since most lepidopterans apparently rely on airborne chemical delivery.

Some insect aphrodisiacs are gustatory in that chemical secretions produced by the male are ingested by the female. While the female feeds on the secretions, she usually assumes

FIGURE 1. The male Queen butterfly (*Danaus gilippus*) releases courtship pheromone from glandular hairpencils at the tip of his abdomen. (A) The male hovers and bobs in front of the female (stippled) and his fully everted hairpencils dust pheromone (a ketone) directly on the female's antennae. (B) Diagrammatic longitudinal section through the glandular base of the male's retracted hairpencil. The individual hairs (h) of the hairpencil are hollow, perforated processes from trichogen secretory cells (sc.) Globular secretions called "dust" (d) accumulate on the hairs. During courtship the glandular base everts and the hairs splay out. A retractor muscle (not shown) attaches to the proximal end of the bundle (on the left). (After Brower *et al.*, 1965).

a copulatory position and the male may inseminate her at this time. Examples of gustatory aphrodisiacs are reviewed by Birch (1974), and are found in at least one species of tephritid fly, 25 species of crickets and cockroaches, and probably in many species of coleopterans. Although some gustatory pheromones are known to promote male mating success, so that sexual selection is implicated in their evolution, they may have positive effects on other aspects of fitness as well. When there is extensive feeding on a male gland, as in many crickets, the female's clutch size might be increased.

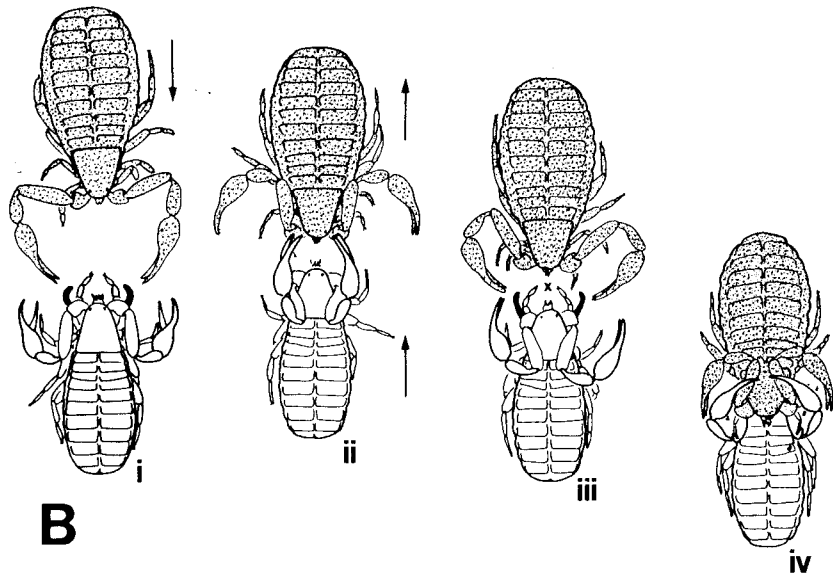
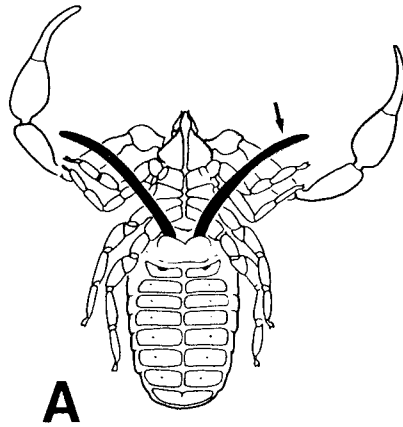
*Pseudoscorpions.* In cheliferid pseudoscorpions, females appear to orient to pheromones emanating from the male's "ram's-horn" organs (Weygoldt 1966, 1969). These organs are evaginated just before sperm transfer (fig. 2). The ram's-horn organs are not glandular, but they probably are coated with pheromones from glands that empty into the genital chamber. The female contacts these organs with her pedipalps prior to sperm transfer, and this is probably when chemoreception takes place.

*Vertebrates.* Although pheromonal communication between the male and female is common during vertebrate reproduction, most studies focus on the nature and effect of chemical signals produced by the estrous female. Instances of chemical communication directed from the male to the female are less widely studied and so the extent of precopulatory, male-to-female pheromonal communication is not known. Except for most species of salamanders, there are relatively few examples among vertebrates, especially for male chemical delivery that occurs only during courtship. Male courtship pheromones are known for some species of fish and mammals, however, and

further studies may show the phenomenon to be more widespread than previously realized.

In glandulocaudine fish of the family Characidae, males of different species show a variety of glandular pockets and scales at the base of the tail (Nelson 1964). The behavior of the male during courtship suggests that the male wafts pheromones from these caudal glands to the female (fig. 3). Compared with other characid fish, the glandulocaudines have undergone an explosive radiation in courtship glands and other sexually dimorphic structures (Eigenmann and Myers 1929), a radiation undoubtedly promoted by sexual selection.

Among some species of mammals, odors from sexually mature males are known to affect female behavior during courtship. In the domestic pig, an estrous female responds to pressure on her dorsum by exhibiting a copulatory stance called the "standing reaction." This reaction terminates the precopulatory phases of sexual behavior since a male can attempt intromission with a female that assumes a "standing" (braced and motionless) posture. Signoret (1976) reports that, among estrous sows, the standing reaction can be induced in 48% of females that are touched on the back by a human experimenter (no boar is present). In comparison, this response can be induced in 100% of estrous females if there is a boar present. This increase is largely attributable to male odor since the standing reaction occurs in 90% of estrous sows even when they cannot see or touch the boar. Of 90 estrous sows that originally failed to exhibit a standing reaction in response to a human experimenter, 56 (62%) of these females gave a positive standing reaction when placed in a boar's pen even though the boar was absent (Signoret and du Mesnil du Buisson 1961). Odors from fluid collected from the preputial pouch of the male were just as effective as total male odor in eliciting the female standing response (*Ibid*). Because effects on male mating success have been experimentally verified, this is the best mammalian example

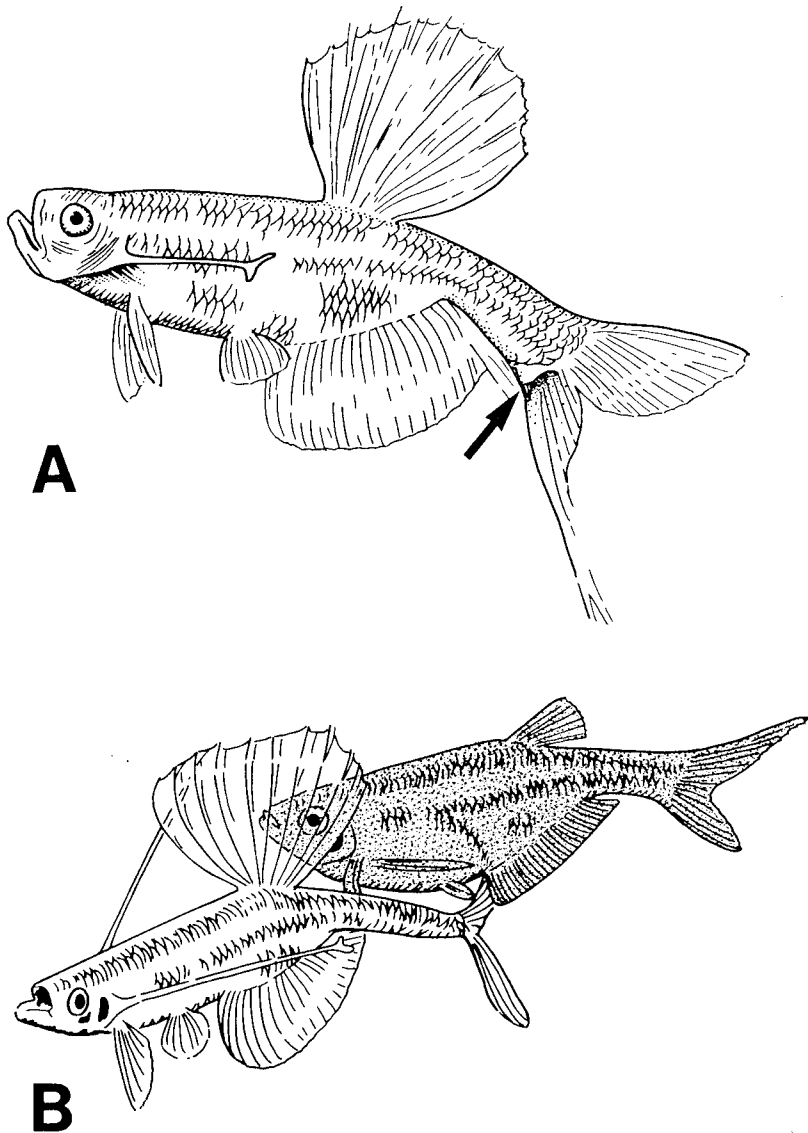


of a sexually selected courtship pheromone.

The effects of chemical delivery by other mammalian males have not been as clearly demonstrated as the effects of boar odor on estrous sows. One conspicuous example of chemical delivery is urine spraying, a behavior that is relatively common among lagomorphs and among some histricomorph rodents (porcupines, guinea pigs, agoutis and their allies). Odors in general are significant among these social species, and groups of individuals commonly share odors by marking each other and themselves. In a review of studies on the European wild rabbit, *Oryctolagus cuniculus*, Bell (1980) reports that, in 15 cases where urine spraying actually was observed in the

FIGURE 2. Delivery of a putative courtship pheromone during courtship and sperm transfer in the pseudoscorpion *Dactylochelifer latreillei*. (A) Ventral view of a male showing his everted ram's-horn organs (black). These organs are lateral diverticulae of the male's genital atrium. The ram's horn organs are not glandular and consist of a thin epithelium bounded by a cuticle. They apparently are coated with a courtship pheromone produced by one of the many glands emptying into the genital atrium. (After Weygoldt 1969). (B) The sperm transfer process: (i) The female (stippled) approaches the male as he displays his ram's-horn organs (black) and vibrates his entire body. The tips of her pedipalps (large, pincher-like appendages) are studded with setae that are thought to be chemosensory. (ii) The male stops vibrating and the pair moves backward. This activity alternates with the vibratory male display and female approach shown in (i). (iii) The male has deposited his spermatophore (x) on the substrate and has stepped back from it. The female is approaching the male and his spermatophore, apparently orienting to his ram's-horn organs. (iv) The male grasps the female's pedipalps as she settles on top of the spermatophore. (After Weygoldt 1966).





field, the spraying was performed by sexually active, dominant males and was directed toward conspecifics. In only two of the 15 cases, however, did urine spraying occur during courtship. Kleiman (1974) suggests that urine spraying during histricomorph courtship may be a method of reducing agonistic behavior in the female by clearly identifying the male as a familiar member of her social group. Although the male's use of urine may have a positive influence on female receptivity, other contexts of urine delivery preclude its consideration strictly as a courtship pheromone.

The evolution of male odors that result in female behavior conducive to copulation can be explained in terms of sexual selection since these odors apparently promote the mating success of the individual male. Although Signoret (1976) reports experimental demonstration of the effects of male odors in the domestic pig, a direct field test to evaluate the effect of odor production on male mating success would be desirable. Evaluations in field situations unfortunately can be difficult since they require quantification of natural variation in odor produced among males and since other factors, such as natural variability in female receptivity, might be difficult to measure. Although field tests are desirable,

FIGURE 3. Male *Corynopoma riisei*, like many other glandulo-caudine fish, appear to release a courtship pheromone from their caudal glands. (A) The male has highly modified fins and the extraordinary operculum is shaped like a paddle. The site of the glandular pouch that constitutes the caudal gland is indicated with an arrow. Lateral movements of the tail apparently flush pheromone out of the pouch and waft it toward the female. (B) During courtship the male swims in a figure-of-eight pattern in front of the female (stippled), a movement that probably wafts courtship pheromone to her. (After Nelson 1964).

laboratory tests of odor-related mating success in males also can be informative. Male odor could be artificially enhanced or eliminated, for example, or the receptivity of anosmic females could be compared with that of intact females. In the following section, we discuss experimental data of this sort for salamanders.

#### CHEMICAL DELIVERY DURING SALAMANDER COURTSHIP

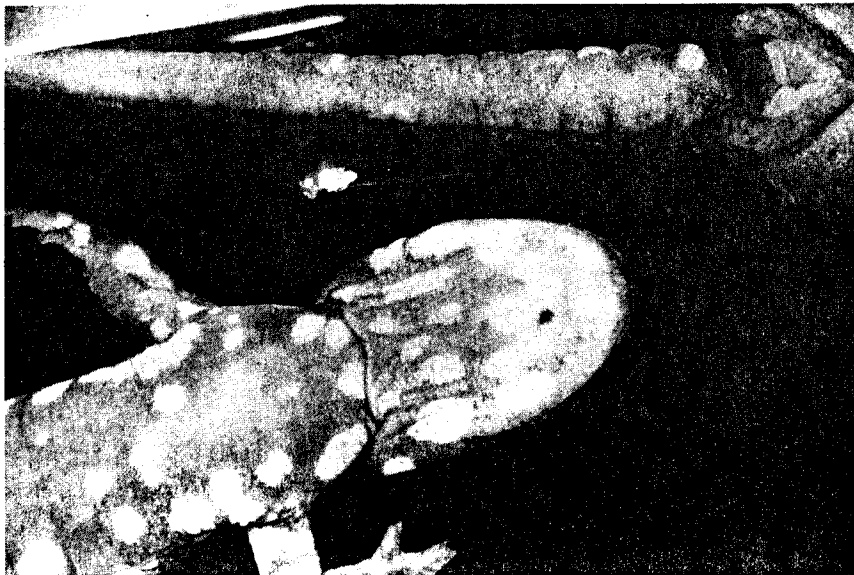
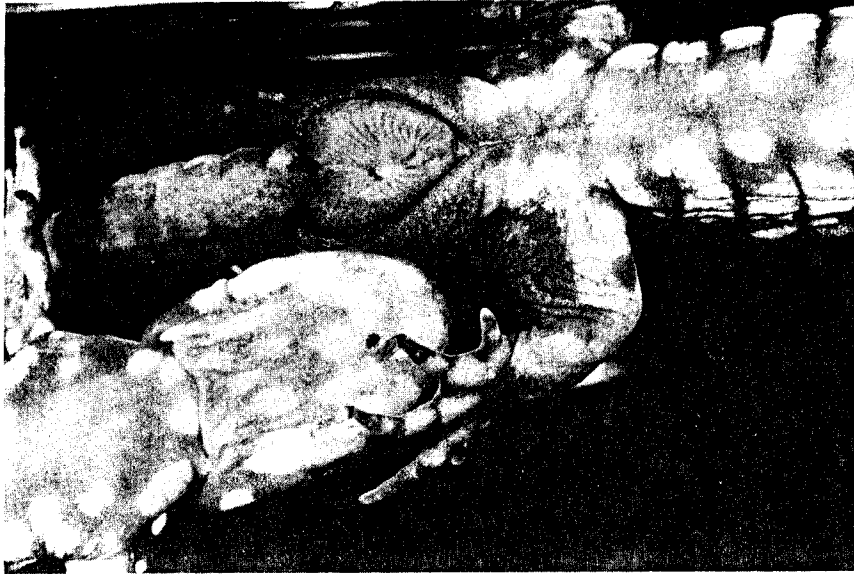
Most salamanders are nocturnal and, not surprisingly, many aspects of their sexual behavior are chemically mediated. The functions of chemical signals include mate attraction, orientation and coordination during sperm transfer, and sexual persuasion. Twitty (1955, 1961), for example, found that male newts of the genus *Taricha* can identify conspecific females even by their skin secretions alone. Male *Taricha* are attracted to sponges soaked with secretions from conspecific females, but not to sponges soaked with secretions from hetero-specific females. As in most salamanders, *Taricha* males nose the female before initiating courtship, and species and sex identification probably is accomplished at this early stage. It is not known whether the female has evolved a special sex attractant pheromone or whether the male simply responds to normal, epidermal secretions.

Chemical signals from the male play an important role during the final stage of courtship, when coordination of male-female actions is crucial during the intricate process of sperm transfer. In most salamanders, sperm is transferred via spermatophores attached to the substrate. Commonly, the female finds the spermatophore only by following the male and, among aquatic species, by orienting to pheromones released by glands in the male's cloaca. During sperm transfer in the

aquatic-breeding tiger salamander (*Ambystoma trigrinum*), for example, the male walks with his tail raised at a 45° angle and the female orients to his cloacal glands (Arnold 1976) (fig. 4). Sexual selection probably contributed to the evolution of these glands, but experimental tests for an effect on mating success have not been performed.

There is evidence in salamanders that sexual persuasion of the female is accomplished by male glands that are employed during the intermediate stage of courtship. The length of this stage varies within and among species but is defined as the time after individual identification but before attempts at sperm transfer. During this intermediate stage, males deliver secretions from specialized epidermal glands that are present only in adult males and are most highly developed during the courtship season. Commonly, these courtship glands are located on the male's head and are rubbed directly on the female's nares. In aquatic species, secretions from cloacal glands may be wafted towards the female's nose by the male's tail fanning behavior. Although courtship glands are extremely common and diverse in salamanders (Noble 1931, Arnold 1977), their persuasive effects have been experimentally studied only in two genera of newts (*Notophthalmus* and *Triturus*) and in the plethodontid genus *Desmognathus*. We review these experimental data below.

In the eastern North American newt, *Notophthalmus viridescens*, the male adjusts his courtship to the responsiveness of the female (Humphries 1955; Arnold 1972, 1977; Verrell, pers. comm.). The male's courtship display is extremely brief if the female indicates receptivity by actively approaching the male, or if she does not swim away when the male approaches her. In these situations the male gives a short display with undulating tail, and, if the female responds, he proceeds directly with spermatophore deposition. In contrast, if the female is not



immediately receptive and she swims away from the approaching male, he pursues her and attempts to capture her with his hind limbs. If he succeeds, he holds the female in amplexus and for an hour or more delivers secretions from courtship glands before attempting sperm transfer (Arnold 1977, fig. 5). Two kinds of courtship glands are employed during amplexic courtship. A sexually active *N. viridescens* male has genial glands on his cheeks (fig. 5). The development of these glands is hormonally regulated (Pool and Dent 1977), and their product is a sulfated mucin that is released in response to cholinergic stimulation of myoepithelial cells (Pool et al., 1977). Secretions from the genial glands are repeatedly rubbed over the female's nares. In addition, glands in the male's cloaca are everted during courtship. Pheromones from these cloacal glands probably are wafted to the female's nares by fanning movements of the male's recurved tail. Dye placed in the water near the male's cloaca is transported by water currents produced by the male's tail movements and the dye

FIGURE 4. The female tiger salamander (*Ambystoma tigrinum*) appears to orient to the male's cloacal glands during sperm transfer. A pair of courting salamanders was photographed from below, through the floor of a glass-bottomed aquarium. ABOVE. The female nudges the male's cloaca as he deposits a spermatophore. The whitish sperm mass, which is perched on the top of a transparent pyramidal base, is visible at the center of the male's cloaca. The papillae of his cloacal glands fringe the posterior edge of his cloaca. BELOW. The male moves forward away from his spermatophore. Only the white sperm mass at the apex of the clear spermatophore is distinctly visible. The female follows the male, apparently orienting to a courtship pheromone released from his cloaca. She will settle on top of the spermatophore and remove the sperm mass with her cloacal lips.

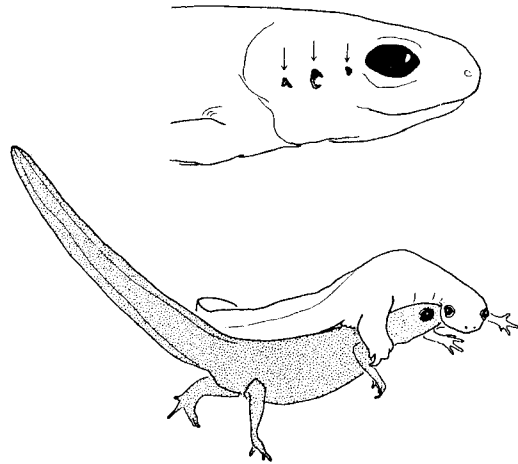


FIGURE 5. The male red-spotted newt (*Notophthalmus viridescens*) produces a courtship pheromone in glands on his cheeks. ABOVE. The male's head showing the apertures of his genial glands. BELOW. During courtship the male clasps the female (stippled) and repeatedly rubs his glands across her nares. (From Arnold 1977). Reprinted with permission, from "The Reproductive Biology of Amphibians", 1977, Plenum Publishing Corporation, New York.

gathers about the female's snout (Verrell, pers. comm.). Throughout the lengthy amplexus, direct delivery of genial gland secretions alternates with wafting delivery of cloacal secretions. The complex temporal structure of these and other activities during the amplexic courtship is described by Zeller (1890), Jordan (1891), Humphries (1955) and Arnold (1972).

Experimental and observational studies of *Notophthalmus viridescens* indicate that chemical delivery during amplexic courtship promotes sperm transfer and hence male mating success. Rogoff (1927) found that the female would not follow the male for sperm transfer after amplexus if the male's genial glands were artificially occluded or if the female's nares were

plugged. Verrell (pers. comm.) found that sperm transfer was positively correlated with two indices of genial gland application.

Experimental studies of European newts of the genus *Triturus* also suggest that chemical delivery during courtship enhances mating success. Unlike *Notophthalmus*, *Triturus* never show amplexus behavior and thus the male never restrains the female during courtship. Other aspects of courtship behavior are similar between these two genera, however, and *Triturus* may be derived from a *Notophthalmus*-like ancestor (Salthe 1967, Arnold 1972, Halliday 1977). During courtship, a male *Triturus* performs an elaborate tail fanning display in front of the female as a precursor to sperm transfer. As in *Notophthalmus*, the male's cloacal glands are everted during this display and tail fanning creates a water current that probably wafts cloacal pheromones to the female's nose (Tinbergen and Ter Pelkwijk 1938, Halliday 1975b). In the most studied species, *T. vulgaris*, the male may deposit as many as seven spermatophores when courting a female, although the average per courtship is two (Halliday 1977). After each spermatophore deposition and transfer attempt, the male reverts to his tail fanning display. Remarkably, the continuation of male courtship does not depend on whether the female picks up sperm from spermatophores. The male is just as likely to proceed with courtship after a successful transfer as he is after an unsuccessful attempt (Halliday 1975a). The male does change the timing and content of his displays in relation to the number of spermatophores already deposited. Apparently the male can manufacture only a limited number of spermatophores each day and, as the male approaches the end of his spermatophore supply, his display is slower and more elaborate (Halliday 1976). By manipulating anaesthetized females so that their "behavior" indicated

receptivity, Halliday (1975a) was able to show that temporal changes in the male's courtship displays are due to the male's state as well as the female's behavior. As the male exhausts his supply of spermatophores, he requires more tactile cues from the female before he will deposit another spermatophore. The depletion of the male's spermatophore supply apparently accounts for the change in courtship choreography.

The tail fanning aspect of the male *Triturus* display may have a cumulative chemical effect on the female. Females tend to walk past the spermatophores deposited early in courtship, and spermatophores that are missed invariably are reproductive failures. Females are more likely to retrieve sperm from spermatophores deposited late in courtship, after the male has delivered much pheromone to the female. Thus female *T. vulgaris* retrieved sperm from only 29% of the first spermatophores deposited during courtship, but they retrieved sperm from 62% of the third spermatophores (Halliday 1977). This suggests that chemical delivery during the tail fanning display may have a cumulative, aphrodisiac-like effect on the female. Alternatively, Halliday (1977) proposed that the tendency of females to miss early spermatophores represents a form of mate assessment. By missing the first spermatophores deposited by a male, females might avoid insemination by males with relatively poor spermatophore supplies.

In contrast to the aquatic courtship typical of salamandrids and ambystomatids, most plethodontid (lungless) salamanders court on land. Sexually mature males of most plethodontid species possess a submandibular or mental (*mentum* = chin) gland (fig. 6) that is maximally developed during the courtship season (see Lanza 1959 and Sever 1976a). Glandular development is hormonally controlled; Sever (1976b) showed that, in *Eurycea quadridigitata*, even females would develop a mental gland when

injected with testosterone. Sexually active males of many plethodontid species also have specialized teeth that differ from the female's teeth both in size and shape (fig. 7). The male's mental gland is the primary source of courtship pheromones and, in species where males also have specialized teeth, these teeth are an integral part of the chemical delivery system.

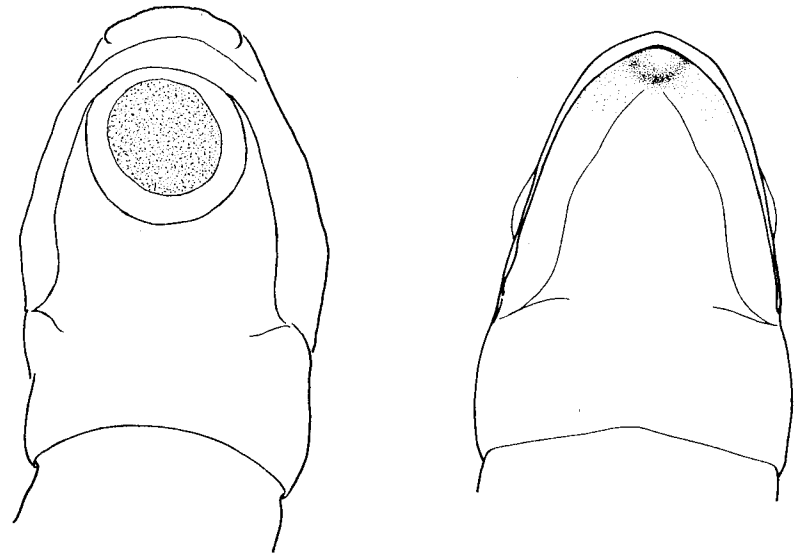


FIGURE 6. Male plethodontid salamanders have courtship glands on their chins. LEFT. *Plethodon jordani* males have large, disc-shaped mental glands. Such large glands are characteristic of species that deliver the putative courtship pheromone by slapping the gland on the female's snout, so that she inhales the secretion. (From Arnold 1972). RIGHT. Male *Desmognathus fuscus* have small mental glands, set on a platform at the tip of the chin. Small glands are found in species that introduce the putative courtship pheromone directly into the female's circulatory system by abrading her skin with protruding premaxillary teeth. (After Noble 1927).

There are four modes of chemical delivery during plethodontid courtship. The first two modes are termed "pulling" and "snapping." "Pulling" consists of a series of rapid strokes with the male's chin pressed down on the female's body

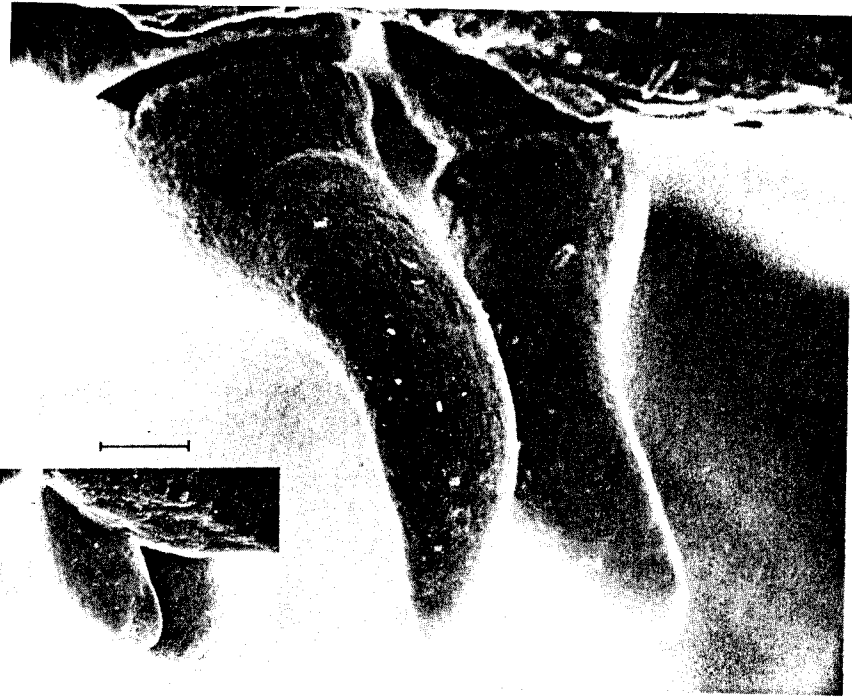


FIGURE 7. Scanning electron micrograph of the premaxillary teeth of *Desmognathus ochrophaeus*. The adult male has monocuspid premaxillary teeth that are roughly three times the size of the female's bicuspid teeth (inset). The male's teeth are used to introduce a courtship pheromone into the female's circulatory system and also in biting combat with other males. The male's and female's teeth are shown at the same scale (bar = 0.5 mm).

while "snapping" consists of a single very forceful stroke, accomplished by a sudden snapping action of the male's body which may fling the male away from the female (fig. 8). Pulling and snapping often are used alternately during courtship and occur in species with relatively small mental glands and protruding premaxillary teeth. Both actions apparently

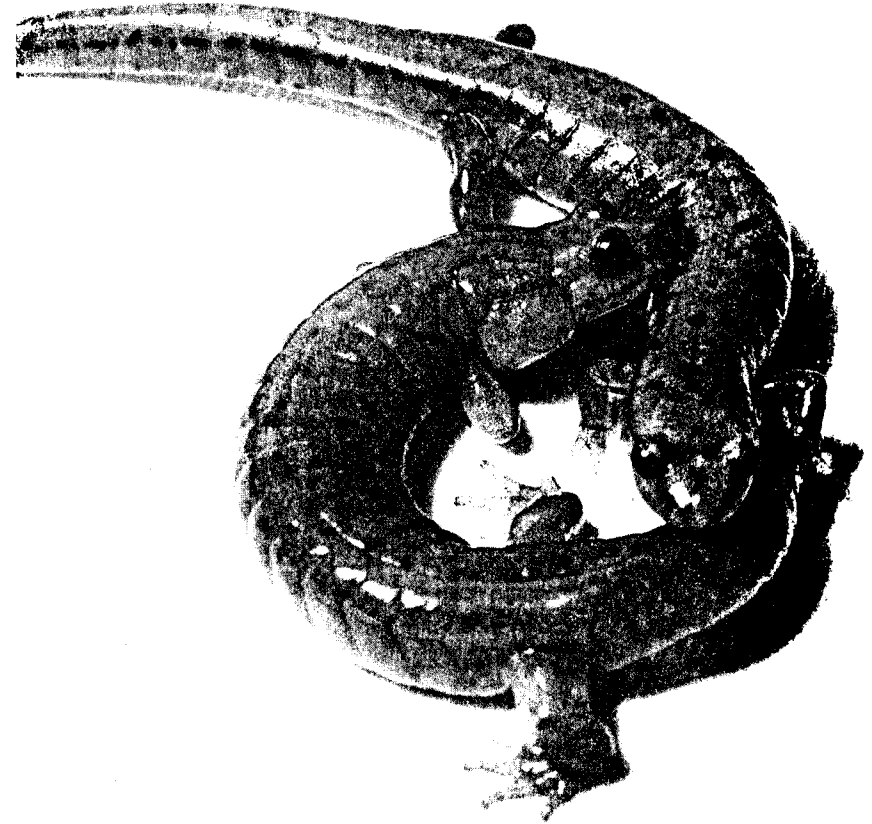


FIGURE 8. Delivery of courtship pheromone in *Desmognathus ochrophaeus*. The male presses his protruding premaxillary teeth and mental gland against the female's flank as she straddles his undulating tail. From this position the male forcefully snaps his head downward, abrading the female's skin at the site rubbed with secretion from his mental gland.

have the effect of "vaccinating" the female with mental gland secretions (Organ 1961, Arnold 1972). These two actions occur in many diverse genera and tribes of plethodontids, and probably represent the ancestral delivery modes (Arnold 1977). The third delivery mode, "slapping," occurs only in species that have relatively large mental glands but lack protruding premaxillary teeth. These species slap the mental gland on the female's snout and the female apparently inhales the secretions through her nares (Arnold 1976). The fourth delivery mode, biting, is known to occur only in one species, *Desmognathus wrighti* (Houck 1980). The male bites the female as the initial courtship action and holds on tenaciously. The males possess highly modified mandibular teeth, and the secretions from the mental gland apparently are introduced through perforations in the female's skin produced by these teeth.

The only experimental analysis of the effect of male chemical delivery during plethodontid courtship was conducted with the salamander *Desmognathus ochrophaeus*. Details of the experiment are reported elsewhere (Houck and Arnold, in preparation), but are summarized here. Since courtship and sperm transfer in *D. ochrophaeus* occur on land, aspects of chemical delivery therefore are somewhat different from those reported for the aquatic breeding newts. During the courtship season, an adult male *D. ochrophaeus* has specialized monocuspid premaxillary teeth that are about three times longer than the female's bicuspid premaxillary teeth (fig. 7; also see Noble 1931). Males of this species also have a mental gland, and secretions from this gland are applied to the female primarily during the two male behaviors termed pulling and snapping (described above). The experiment investigating chemical persuasion during *D. ochrophaeus* court-

ship was designed to test whether a male's ability to inseminate a female is affected by (1) the lack of a mental gland, (2) the lack of premaxillary teeth, or (3) lack of both the mental gland and the premaxillary teeth. The experiment involved surgical treatment of three groups of males, each with its own control group of sham-operated males (mental gland removed, premaxillary teeth removed, both mental gland and premaxillary teeth removed), as well as a control group of intact males. Surprisingly, none of the surgically treated groups of males showed any impairment in insemination success.

The lack of demonstrable effects of mental gland secretions is surprising since the courtship pattern in *D. ochrophaeus* fits our initial conditions for a situation where chemical persuasion is suspected: (1) the males possess specialized glands and associated structures that are well-developed only during the courtship season, (2) males deliver glandular secretions only during courtship, after the initial contact with the female, and (3) the male secretions are applied directly to the female. The experimental results, however, certainly suggest that mental gland delivery does not enhance insemination success. It is nevertheless possible that the gland and sexually dimorphic teeth evolved by sexual selection. For example, it is conceivable that the mental gland secretions promote sperm uptake from the spermatophore after insemination. This could be accomplished very simply by inducing a quiescent state in the female which promotes sperm transfer from the spermatophore to the female's spermatheca, and consequently paternity. Of course this is mere speculation and new experiments will be necessary to determine whether sexual or natural selection is the most plausible agent for the evolution of plethodontid mental glands.

## PHEROMONAL EVOLUTION

How do aphrodisiacs and other pheromones evolve? In order to answer this question we must know more than the physiological "function" of the pheromone, although this is certainly an important consideration. To answer even the simpler question of whether the pheromone evolved by sexual or by natural selection, it is desirable to marshal evidence from a variety of sources.

*Evidence from sexual dimorphism.* Darwin (1871) outlined three criteria that implicate evolution by sexual selection rather than by natural selection. Sexual selection is implicated if the character is (a) present only or most highly developed in males; (b) most highly developed at sexual maturity and (c) present in highest development during the breeding season. Even if a character meets all these criteria there still is some ambiguity about the form of sexual selection. For example, the antlers of the stag may have evolved due to advantages conferred in male combat or because females chose the best endowed stags as mates.

*Evidence from behavioral context.* Strong hints about the nature of selection can be derived from the behavioral contexts in which pheromones and other structures are used. A male pheromone that is applied directly to the female's olfactory receptors during courtship is likely to be sexually selected, either because it promotes the male's mating success directly, or indirectly if it lessens the chance that the female will mate with other males. A chemical that is applied to the female's body, rather than on her receptors, may simply repel other males and have no effect on the female herself (e.g., Gilbert 1976). Natural selection also is implicated if there

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is a considerable transfer of materials or energy, since effects on fertility or female survivorship are conceivable. Of course, these kinds of evidence are circumstantial and merely suggest possible effects on fitness. Furthermore, the situation can be more complicated if a pheromone or gland affects more than one component of fitness.

*Comparative evidence.* Only comparative studies can document the actual occurrence of evolution. The best evidence of this kind will come from studies of pheromones in groups with well-established phylogenies. Phylogenetic correlation with social system can give clues about evolutionary history. If, for example, male pheromones tend to occur in species with polygynous mating systems but not in related, monogamous species, we have a *prima facie* case for chemical evolution by sexual selection. Likewise, spectacular phylogenetic diversity may indicate rapid evolution by sexual selection. This expectation comes from theoretical predictions of rapid evolution under sexual selection (Fisher 1930) and of numerous alternative outcomes at equilibrium (Lande 1981). Thus the spectacular plumage diversity in male birds of paradise, which perform elaborate displays at traditional mating grounds and form no pair bond with the female, is almost certainly a product of rapid evolution driven by sexual selection. The rapidity and superficial nature of the divergence among these birds is indicated by the fact that even populations with striking differences in plumage are known to hybridize (Gilliard 1969). We know of no comparable studies of courtship pheromone diversity.

*Experimental evidence, genetic analysis and the measurement of selection.* Variation, inheritance and selection are necessary,



although not sufficient, conditions for pheromonal evolution; they are the key issues for analysis of the evolutionary process. There is much to be learned about each aspect. Within populations, the study of individual variation both in pheromone production and in the reaction to pheromones is pivotal since analyses of inheritance and selection are predicated on a characterization of such variation. Despite recent discoveries of optical isomers (enantiomers) and multi-component pheromones in insects (see review in Ritter 1979), for example, it still is not clear whether there are stable individual differences in kinds of pheromones within conspecific populations. Technical limitations may force a typological attitude: it is easy to assume that all individuals are identical if individuals can not be assayed. In order to characterize the structure of sex pheromones in the cockroach *Periplaneta americana*, Persoons and Ritter (1979) had to extract intestines from 32,000 insects. When this many individuals must be pooled for chemical analysis there is little margin to detect individual differences in pheromones. We may be missing the raw materials upon which selection acts.

Genetic analysis also confronts formidable obstacles. In addition to the technical problems of extraction, there are problems in characterizing individual variation if pheromones change with age, diet or social situation (e.g., see Bell 1976). Nevertheless, there are some encouraging developments. Host races of the larch bud worm, *Zeiraphera diniana*, differ in sex attractants released by females and the males show corresponding differences in electrophysiological response by antennal receptors.  $F_1$  hybrid male antennal responses include both the responses characteristic of the two parental host races and a receptor cell that shows maximal response to both parental pheromones (Priesner 1979). The potential for

screening large numbers of individuals in order to detect heritable variation in chemoreception is illustrated for garter snakes (*Thamnophis*) by Arnold (1980, 1981). Furthermore, there is evidence for coevolution of sex pheromones and responses to sex pheromones in the pine beetle, *Ips pini* (Plummer et al. 1976). This species shows geographic variation both in enantiomers that compose the pheromone and in responses to these enantiomers, making this system an outstanding candidate for genetic analysis. Because so little is known about genetic variation both in sex pheromones and the responses they elicit, we are a long way from a direct test of genetic predictions made by sexual selection theory. One prediction is that evolution of courtship pheromones by sexual selection should create gametic (or linkage) disequilibrium between the pheromones of males and the response by females (Lande 1981, O'Donald 1980). This genetic prediction could be tested by assaying for genetic correlations in natural populations (e.g., by testing for a statistical regression of daughter's response to pheromone on father's pheromone characteristic). Falconer (1980) and Bulmer (1980) discuss estimation techniques.

Experimental tests for the presence of selection on the pheromone can be arranged by ablating or occluding the glands that produce the pheromone. In order to test for sexual selection, the mating success of ablated males can be compared with an intact group. Such tests can even be performed in the field (see Brower et al. 1965 and Myers and Brower 1969). Assays of this kind measure the force or gradient of selection along an artificial character scale ranging from no pheromone to the mean pheromone characteristic of the population. In order to measure the actual force of selection acting on the spectrum of pheromone variation in nature, it would be necessary to measure both the pheromone characteristics and the mating

success of each male in a sample (Arnold and Wade, in prep.; Lande and Arnold, in prep.). With appropriate longitudinal data (individually marked males followed through time), it should be possible to determine whether pheromones are favored by sexual selection (e.g., by mate attraction or persuasion) but disfavored by natural selection (e.g., by attracting predators). The opposing forces of natural and sexual selection could act to stabilize the size of the pheromone-producing gland. Tests and evaluation of selective pressures ultimately depend on having some means of characterizing the pheromone chemistry of individuals. If this can be accomplished, then the relative success of particular pheromone phenotypes in attracting mates could be assayed. Among insect species, there are standard insect baiting assays commonly used in economic applications. Data from assays such as these could then be used to estimate the actual force of selection exerted by mate attraction on the male population.

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