this binding was not saturable). Erythrosin B could be blocking this nonsaturable binding by altering membrane fluidity and thereby decreasing the stability of the dopamine-synaptosome complex (*14*). Contrary to this speculation, increasing dopamine accumulation occurs in the absence of sodium at high erythrosin B concentrations (Fig. 3A). But this apparent increase in nonsaturable binding is likely to be artifactual since erythrosin B is present as a disodium salt, and at increasing erythrosin B concentrations sodium levels are also increased, thereby stimulating sodium-dependent dopamine uptake.

We can conclude that erythrosin B is acting as a significant dopamine uptake inhibitor when present with brain tissue in vitro. Compared with amphetamine, another known inhibitor of dopamine uptake in rat striatum (*15*), erythrosin B is about one-hundredth as potent in inhibiting dopamine uptake. It cannot be assumed that erythrosin B can inhibit dopamine uptake in vivo, since it is not known whether erythrosin B penetrates the blood-brain barrier or is present in brains of animals after peripheral administration or oral ingestion. Nor can it be assumed that erythrosin B is a specific inhibitor of dopamine uptake since a wide scope of effects by erythrosin B has been demonstrated by previous studies (*3-5*). However, it has been shown (*16*) that sodium-dependent glutamate uptake in synaptosomes prepared from rat cortex is not inhibited by erythrosin B. In fact, it has been found that low concentrations of erythrosin B (50 n*M*) actually increase sodium-dependent glutamate uptake. These recent observations suggest that erythrosin B is acting specifically on the dopaminergic system in inhibiting uptake. This is consistent with increased dopaminergic activity in vivo, which has been suggested to be involved with the hyperkinetic syndrome.

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Adaptive Female-Mimicking Behavior in a Scorpionfly

Abstract. *This study provides a clear example of female-mimicking behavior by males in insects and evaluates quantitatively the adaptive significance of this behavior, which is poorly understood in many other organisms. Males of* Hylobittacus apicalis *provide females with a prey arthropod during copulation. Some males mimic female behavior when interacting with males that have captured nuptial prey, resulting in males stealing prey which they will use for copulation. Males that pirate prey copulate more frequently and probably incur fewer predation-related risks.*

Natural selection theory predicts that intraspecific deception will be common between potential and actual mates, parents and offspring, relatives in general, and indeed between all socially interacting individuals of all animal species. According to theory, selection will favor individuals that can deceive other individuals because the deceiver may gain time or resources, both of which can be used for reproductive activities, or the deceived may be used to enhance directly the reproductive success of the deceiver (*1*). Theory predicts that small lies will be prevalent over gross lies because selection would favor individuals that can detect deception (*2*). Transvestism is "the practice of adopting the dress, the manner, and frequently the sexual role of the opposite sex" (*3*). It may be a common form of deception in animals. Apparent transvestism has been reported in humans (*4*) and a few other primates (*5*), hyenas (*6*), mountain sheep (*7*), birds (*8*), salamanders (*9*), and several fishes (*10, 11*). Speculative adaptive explanations for mimicry of the opposite sex have been provided for most of these cases. The suggested reproductive advantage incurred by transvestite males in fish species with external fertilization is the least equivocal. Males without territories adopt or retain female coloration and are observed to "sneak" into other male territories and release sperm while a female is spawning. Presumably the transvestite steals fertilizations from the territorial male (*11*); however, sneaking may be merely a complex courtship tactic in some fish (*12*).

Transvestism has not been reported in insects (*13*). I report here female-mimicking behavior of adult males of the scorpionfly *Hylobittacus apicalis* (Mecoptera: Bittacidae) (*14*) that clearly enhances the copulatory success and probably the survival of these males. *Hylobittacus apicalis* preys on arthropods. Males exhibit nuptial feeding; that is, a prey arthropod is fed to the female during courtship and copulation (Fig. 1). In hunting for prey, males expend time and are exposed to web-building spider predators. Transvestites rob males of their prey, reducing their own hunting time and risks. The reduction in hunting time allows transvestites to copulate more frequently (*15*).

The sequence of sexual behavior in *H. apicalis* begins when a male acquires a prey arthropod—through his own predatory activites or by stealing—and begins feeding on it. After feeding briefly he either discards the prey and obtains anoth-

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er if the prey is undesirable (unpalatable or too small) or, while still holding the prey in his hind legs, he initiates short flights among the herbs. After each flight, the male hangs by his forelegs from a leaf or twig and exposes his pheromone-dispersing vesicles ("calling" behavior). Females exhibit olfactory responses to males over distances up to 13 m. The prey is not important in distance attraction of females and becomes important only when courtship is initiated. Females evaluate the prey offered by a male by feeding upon it during courtship, as evidenced by the fact that females discriminate against males with unpalatable or small nuptial prey by flying away and responding to another male's pheromone or by copulating for a short duration. The female feeds throughout copulation. At copulation termination the male and female struggle for the prey; the male retains the prey 64 percent of the time ($N = 73$), the female gets it 8 percent of the time ($N = 9$), and it is dropped and lost in the leaf litter 28 percent of the time ($N = 32$). After pair separation the male again feeds briefly on the prey, and if it still contains adequate nourishment repeats the sequence. If the prey is not suitable, it is discarded by the male and he begins hunting for another prey before calling. Depending on prey size, the male may use it in as many as three successive copulations (*15-17*).

Male-terminated copulations result in maximum insemination, inducing oviposition and sexual nonreceptivity in females. These females remain unreceptive for about 3 hours, during which they drop an average of three eggs into the ground litter while hanging from the vegetation. Females copulate and receive a nuptial feeding at the end of each 3-hour period of sexual unreceptivity. Females feeding on nuptial meals of males alone are as fecund as females that have continuous access to prey. Females seldom hunt on their own when males emerge and become abundant, and depend primarily on prey provided by males (*15-17*).

Prey piracy is an important component of male-male competition for females in *H. apicalis*. By following each of 42 individually marked males through four successive copulations in nature, I have shown (i) that search time for prey comprises about 50 percent of intercopulating time (*17*); (ii) that the number of times a male is robbed of his prey is positively correlated with intercopulatory duration (a robbed male must obtain another prey for successful copulation) resulting in a reduction in his copulatory frequency (*17*); and (iii) that males that steal rather than catch prey reduce intercopulatory time by 42 percent, obtaining more copulations per unit of time than nonprey pirates. The third finding is based on 26 intercopulatory periods for prey pirates compared to 46 intercopulatory periods for males catching prey on their own. Intercopulatory duration was reduced from a mean of 26 to 17 minutes (Mann-Whitney U test, $P = .01$) (*17*).

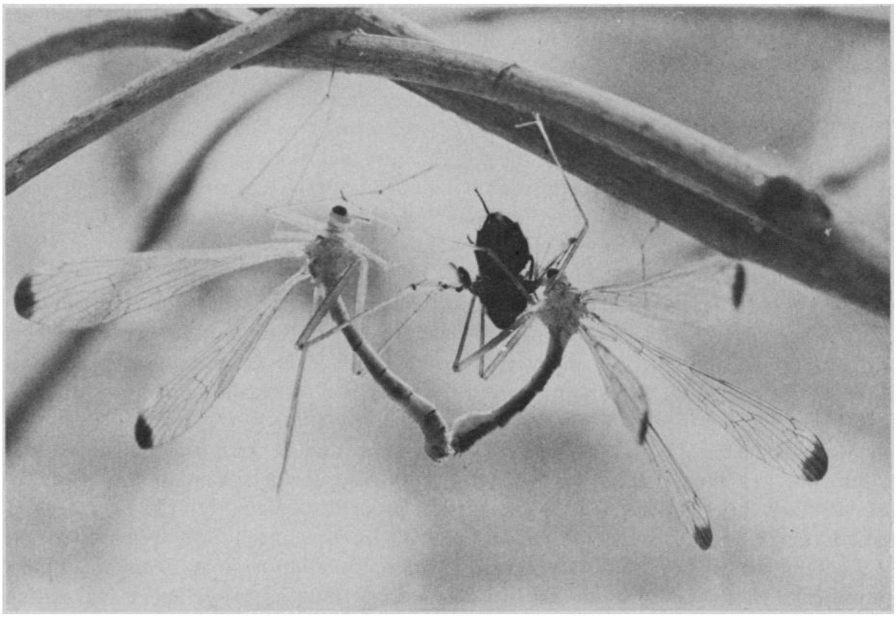

Fig. 1. Copulating pair of *H. apicalis*. The female (on right) is feeding on the nuptial prey (a blowfly) provided by the male.

Observations on marked males between copulations indicate that males display a mixed hunting strategy (*15-17*). If a male first encounters another male or copulating pair with prey, he attempts to steal the prey. However, if the same male first encounters a prey arthropod, it becomes his victim. A mixed hunting strategy has probably been selected for because the success of a male in prey theft depends on the availability of other males and population sex ratios and sizes fluctuate in time and space (*15, 17*). An individual male may employ two prey-piracy behaviors: he may fly forcefully into another male or copulating pair possessing prey, perhaps causing prey to be released, or he may fly up to a male with prey and assume the wing postures and abdominal movements of a female (that is, transvestite behavior).

Both sexes of *H. apicalis* position their wings almost perpendicular to the body axis during the day. At night during rest both sexes lower the wings and position them alongside the body. At the instant a female arrives in the immediate vicinity of a male in response to his pheromone, she lowers her wings. At this time the female is hanging directly in front of the male and usually less than 10 cm away. Wing-lowering is apparently the cue males use for presentation of the prey to the female (*18*). The male retains a grasp on the prey with both hind legs and one or both middle legs during prey presentation to the female and during feeding by the female (Fig. 1). After initiation of feeding on the prey the female may or may not raise her wings; this does not influence male behavior. The male attempts to couple his genitalia with those of the female as the female feeds on the nuptial prey. However, the female initially keeps her abdominal tip pulled away. Eventually, the male engages the female's genitalia, but only after she has evaluated the quality of his nuptial offering (*16, 17*).

Males do not show an olfactory response to calling males but do exhibit a visual response to such males (*15*). Some males attempt prey piracy of calling males by adopting female behavior. The transvestite flies up to a calling male, lowers his wings and typically (67 percent of 90 field observations) is offered the nuptial gift; otherwise, the male does not present the prey to the transvestite and flies away with it (33 percent of 90 observations). Males always present their prey to females (*15, 16*). This is the only context other than rest in which males lower their wings. The male originally in sole possession of the prey attempts to couple his genitalia with those of the transvestite as the latter feeds. The transvestite keeps his abdomen beyond the reach of the other male's genitalia, as do females while initially feeding on and evaluating prey. With-in a short time [2.2 ± 0.06 minutes (mean ± standard deviation), $N = 50$] the male that presented the prey to the transvestite tries to retrieve it by wrestling it from the transvestite's grasp. About 33 percent of the time (20 of the 60 observations in which prey was presented to transvestites), the transvestite has secured a stronghold on the prey and flies off with it. The overall transvestite's success at theft is 22 percent (20 successful robberies divided by 90 attempts).

Males are subject to prey theft while feeding on prey prior to calling, during flights among the herbs while holding prey between calling bouts, during copulation, and during calling. However, transvestism has only been observed in the context of attempted theft of the prey of a calling male's prey. This is the only appropriate context for the behavior since only in this context are males "expecting" the arrival of a female. About 48 percent of attempts at pirating prey of calling males involves transvestism (80 of 165 observations); otherwise, pirating attempts involve flying forcefully into the male dispersing pheromone and struggling with him for a stronghold on the prey. The latter tactic results in only 14 percent theft success compared with an overall 22 percent theft success rate for transvestites.

Transvestism in *H. apicalis* is unrelated to conspecific predation, which has only been observed where the prey is recently emerged and thus soft and vulnerable. There apparently is no risk of cannibalism associated with transvestism. Cannibalism has never been observed in the contexts of male-male competition or male-female sexual interaction (*19, 20*).

The reduction in time for obtaining prey and the concomitant increase in copulation frequency is only part of the increased fitness incurred by transvestite male *H. apicalis*. Males that steal prey from other males rather than catch it on their own probably experience reduced predation. During the 6 years of this study, web-building spiders were the most important source of adult mortality (about 95 percent) observed for two bittacid species, *H. apicalis* and *Bittacus strigosus* (*21*). Bittacids encounter spider webs during flights through the herbs. The predation is significantly male biased in *H. apicalis* (246 males and 111 females; $P < .001$, χ^2) but not in *B. strigosus* (59 males and 41 females). The difference in the nature and extent of such predation on these species is explicable by a comparison of their mating behaviors. Female *H. apicalis* rarely hunt for food on their own because of nuptial feeding and thus are less likely to encounter a spider web than males. In order for a male to obtain nuptial prey he must move about in the habitat; more movement leads to greater chance of encountering a web and thus higher mortality for males. In *B. strigosus*, the sexes hunt similarly and nuptial feeding does not occur (*17*). This leads to similar mortality of sexes from web-building spiders. Also, *B. strigosus* moves only when disturbed during the day and primarily feeds at night in the treetops. This may explain lower predation on *B. strigosus* than on *H. apicalis*.

This comparison of predation on *H. apicalis* and *B. strigosus* suggests that male *H. apicalis* that steal prey would reduce predation-related risks associated with hunting prey. Fifty percent of the intercopulatory time of *H. apicalis* males is spent hunting prey, and transvestites reduce the time between copulations significantly by stealing prey. I marked 20 males and 20 females individually and recorded the intercopulatory movement of each in the habitat for 1 hour. This observation period represents about two intercopulatory periods for each male because an average time between copulations for males is 1/2 hour; it represents 1 hour of an average 3-hour intercopulatory period for females. Female activities between copulations are associated with egg laying, but females do not appear to be actively searching for oviposition sites and move around very little between copulations (mean, 15.8 m/hour). Males move significantly more (Mann-Whitney U test, $P = .001$) between copulations (mean, 33 m/hour). In addition, male pirates appear to move less than nonpirates. In 1 hour of observation, six of the 20 marked males pirated prey once, and two other marked males employed transvestism successfully. The six pirates moved significantly less (mean, 12.7 m) than any of the other males (41.5 m) (Mann-Whitney U test, $P = .01$). The two transvestites moved only 9.7 m and 11.2 m, respectively, the least movement recorded for any of the marked males.

Transvestism in *H. apicalis* is clearly adaptive: a transvestite experiences a greater copulatory frequency and probably reduced predation. The following features may contribute to success of transvestites: males and females are monochromatic and show no significant dimorphism, and male genitalia are not greatly enlarged, and thus conspicuous, in *Hylobittacus* compared to some bittacids. Males are observed to avoid piracy by transvestites in two ways: (i) by not offering them the nuptial prey 33 percent of the time, apparently because of unsuccessful deception, and (ii) by regaining possession of prey from the grasp of the transvestite 67 percent of the time. I hope that this report will promote further studies of transvestism in animals. Such studies may lead to an understanding of the general selective forces favoring this and other behavioral strategies used by males in their attempts to maximize reproductive success.

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