age (*8*, *9*). The additional data on ultrasound production by infant rats during appetitive learning and extinction make this experiment especially interesting.

If one accepts the hypothesis that ultrasounds reflect arousal (*6*), the increase in ultrasounds in extinction, particularly over the fixed 30-second interval of goalbox detention, argues against an arousal-decrement interpretation of extinction in infant rats. Informal observation of the pups provides additional evidence that extinction entails not decreasing but increasing arousal in 11-day-old pups as it does in adults. During extinction, the pups moved down the alley, hesitated, retraced, and attempted to climb out of the apparatus. Even when they were not ambulating they made curious chewing movements, sneezed vigorously, and groomed. Often they oriented toward the goalbox and moved the front limbs forward and backward while their hind limbs remained planted. Such activities, which never occurred on late acquisition trials, seemed to demonstrate conflict and suggest that the pups actually learned not to approach the goalbox.

Our findings of increased ultrasounds and other indicants of arousal in the appetitive extinction of infant rats do not support the hypothesis that the infant rat lacks inhibitory mechanisms nor that it is similar to the adult with a nonfunctioning hippocampus (*10*). Active suppression of behavior is intrinsic to extinction in these pups as it is in adults; if extinction can be said to reflect inhibition in adult rats, it would be difficult not to attribute extinction to inhibitory mechanisms in infants as well.

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13. Our ultrasound rate measure (ultrasound per second) provided data consistent with those of Fig. 2. These data, however, seemed to us less meaningful than mean ultrasounds because (i) correlations of the number of ultrasounds and response times were not consistent from one trial to the next and (ii) ultrasounds were not distributed evenly over the corresponding interval (time) scores but tended to occur in bursts, making rate measures somewhat misleading.
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Sociobiology of Rape in Mallards (*Anas platyrhynchos*): Responses of the Mated Male

Abstract. *Male mallards respond to rapes of their mate by intervening aggressively against the rapist or rapists, by attempting to force a copulation with the rape victim, or both. Aggressive intervention is more likely against a solitary male than against a group, and forced copulations are more likely immediately after a rape and especially when the rape appears to have been successful. This behavior pattern reflects strategies consistent with maximizing individual male fitness.*

Rape may be defined as forced copulation. Among animals, this designation seems reasonable when the victim shows obvious resistance, copulation being preceded by vigorous struggle and escape behavior, and without the precopulatory courtship displays characteristic of "normal" mating between members of an established pair. Rape has been well described for the surface-feeding ducks, Anatini (*1*). Recently, McKinney (*2*) has pioneered the use of natural selection at the level of individuals to interpret duck reproductive behavior, an approach that will be pursued in this report. In particular, I shall present data on male responses to the rape of their mates, and show how such responses are consistent with the sociobiologic theorem that animals should behave in ways consistent with maximizing their inclusive fitness (*3*).

These data were gathered between 1 January and 1 June in the years 1974 through 1976, at the University of Washington Arboretum, a seminatural, suburban environment with approximately 15 breeding pairs annually; 558 observation hours were conducted from 0800 to 1600 hours. I obtained an index of females present by censusing them at 15-minute intervals and found a mean of 5.6 and a standard deviation of 3.1. During this time, I observed 89 rapes, for a mean of .03 rape per female per observation hour. (Unless otherwise specified, "rapes" will be used to designate any rape attempt in which mounting occurred, without regard to presumed success in transferring sperm.) The monthly occurrence of rapes, per female per observation hour, was: January, 0.007; February, 0.01; March, 0.05; April, 0.05; and May 0.02. Males whose mates are being raped have two basic options, not mutually exclusive. (i) They can intervene aggressively, defending their mates and attempting to prevent or terminate the rape by dislodging the attacker or attackers. (ii) After the rape, they can introduce their sperm into their female as quickly as possible, so as to compete with those of the rapists.

Of the 89 observed rapes, 31 precipitated vigorous intervention by the mated male, whose response was usually grabbing the assailant by the neck and beating with the wings. In 30 of these 31 cases, this behavior was apparently successful in preventing sperm transfer by the rapist (that is, neither "bridling" nor "nod-swimming" occurred). Mated males failed to respond in the remaining 58 cases; this may be attributed to ignorance of the rape attempt, perceived female ability to defend herself, or unwillingness to incur the costs of such defense. In this regard, mated males never engaged aggressively against rapists when the female flew away to avoid rape (20 times), and did so in only 5 of 15 occasions when females responded to rape attempts by "repulsion" behavior, a characteristic, hunched posture, combined with loud and distinctive calls (*1*) which females give when approached by strange males during incubation. Such behavior apparently indicates that she is unlikely to be carrying fertilizable eggs (*2*). Finally, defense against multiple rapists is likely to be more costly in terms of physical injury to the defending male than is defense against a single rapist. Of the 89 observed rapes, 64 involved multiple males (range, 2 to 9; mean, 3.8; standard deviation, 2.1); mated males intervened aggressively during 14 of the 25 singleton rapes (.56) and 17 of the 64 multiple rapes (.27) [$\chi^2 = 5.63$, $\alpha = .05$, $P < .025$ (one-tailed test)].

Rapid sperm introduction is an additional possible strategy for the mate of a just-raped female. Among mallards, copulations between individuals of a mated pair are preceded by a variety of well-documented, mutual displays, notably "head-pumping" immediately before mounting (*4*). However, I observed 39 occasions when copulations among apparently bonded individuals were *not* preceded by head-pumping. In such cases, the male grasped the female by the nape and simply attempted to mount; in 36 of the 39 instances, the female visibly struggled, but in no case did she flee. Thus, such behavior has some, but not all, of the characteristics of rape among unpaired individuals. I call this behavior "forced pair copulations" (FPC's) after Barrett (*5*), who described the phenomenon in captive mallards. It is particularly noteworthy that of the 39 FPC's observed in the present study, 30 occurred within 10 minutes of an observed rape attempt on the female in question. An average of .03 rape per female per hour equates to one rape per female per 33 hours. This provides for an average of 198 10-minute intervals between rapes, so that if FPC's were randomly distributed during the observation periods, only 1 in 198 (.5 percent) would be expected to follow within 10 minutes of a rape. Instead, 30 of 39 did so (77 percent). Confidence that the male performing the FPC was indeed the female's mate was provided in each case by some combination of at least two of the following: (i) individual recognition—three mated pairs were recognizable by feather peculiarities; (ii) defense of the female during a preceeding rape; (iii) failure of the female to avoid the male, both before and after the FPC; and (iv) continued mutual display between the pair after the FPC.

Although a high proportion of FPC's clearly followed rapes, many rapes (.59, or .66) were not followed by FPC's. Important postcopulatory displays among mallards are "bridling" and "nod-swimming," which have been assumed to signal successful copulations (*4*). Of the 59 observed rapes not followed by FPC's within 10 minutes, I have data on 14; only one of these resulted in the postcopulatory displays indicative of successful copulation. By contrast, of the 30 rapes followed by FPC within 10 minutes, I have data on postcopulatory displays of 12; of these, five showed evidence of sperm transfer [$\chi^2 = 38.45$, $\alpha = .01$, $P < .001$ (one-tailed test)]. Hence, FPC's, when they occur, are (i) significantly more likely to follow within 10 minutes of rape and (ii) significantly more likely to follow successful rape than unsuccessful rape.

A lower proportion of FPC's result in apparent sperm transfer than do normal copulations; of the 39 FPC's observed in the present study, only 10 (.26) were followed by postcopulatory display, as opposed to 144 of 185 normal copulations among apparently mated pairs (.78) (Fisher's exact probability test, $P = .052$). Given the strong selective pressures that have doubtless favored the evolution of female insistence upon accurate, species-typical male courtship (*6*), the low success rate of FPC's is not surprising. Nevertheless, FPC's probably represent efforts by the mates of just-raped females to make the best of a bad situation. Given the usual excess of males over females in surface-feeding ducks (*7*) mates of rape victims do not have the option of an aggressive response, as reported for mates of seemingly adulterous mountain bluebirds (*8*), since replacement females are presumably unavailable. Under this circumstance, optimum male strategy is probably to stick with his mate, but also to introduce his sperm as quickly as possible—hence the forcing of a copulation.

An evolutionary perspective on behavior suggests that individuals will behave so as to maximize the difference between the benefits and costs associated with any potential act, with both benefits and costs evaluated in units of inclusive fitness. Rape of one's mate imposes a potential cost, in that it increases the likelihood of another individual's fathering her offspring. The responses available to a rape victim's mate also carry benefits and costs, and the observed pattern suggests that the mate behaves in accord with evolutionary prediction. Thus, aggressive intervention has the benefit of reducing the likelihood of the rape's being successful, but at the cost of possible injury to the male. Accordingly, such behavior occurs most often when the costs are low (a single rapist rather than several) and less often when the benefits are low (the female is unlikely to have been fertilized as indicated by her repulsion behavior). Similarly, forcing a copulation with a just-raped female conveys the benefit of introducing his sperm as quickly as possible to compete with those of the rapist, but at the possible cost of weakening the pair bond. Accordingly, FPC's occur only when their benefit is likely to outweigh their presumably high cost. Because of the close association of reproductive success with fitness, behaviors associated with reproduction should be especially susceptible to the action of natural selection. Hence, they should be especially amenable to sociobiologic analysis (*9*). The response of male mallards to rape of their females would appear to be a good example.

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Identification of the Female Japanese Beetle Sex Pheromone: Inhibition of Male Response by an Enantiomer

Abstract. *(*Z*)-5-(1-Decenyl)dihydro-2(3*H*)-furanone, isolated from virgin female Japanese beetles (*Popillia japonica*) attracted males of the species in field bioassays. However, the synthesized racemic mixture of this compound did not attract male Japanese beetles. The* Z *and* E *isomers and the saturated analog of both enantiomers of this compound were synthesized stereospecifically. Pure synthetic (*R,Z*)-5-(1-decenyl)dihydro-2(3*H*)-furanone was competitive with live females and with the pheromone isolated from live females in attracting males. Male response was strongly inhibited by small amounts of the* S,Z *isomer. Although the* E *isomer and the saturated analog of the pheromone are present in the material obtained from females, the role of these compounds in mediating the insect's behavior is unclear.*

The Japanese beetle, *Popillia japonica* Newman (Coleoptera: Scarabaeidae), was introduced to North America about 1916 and has since become well established in the eastern part of the United States (*1*). The adults are devastating pests of a variety of trees, ornamentals, and cultivated crops, and the larvae attack the roots of grasses. We report the isolation, identification, and synthesis of a sex pheromone produced by female Japanese beetles. We also report the in-