MATING BEHAVIOR AND NATURAL SELECTION

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Laymen get the impression that biologists have an inordinate preoccupation with sex. We are immoderate, and it is excusable: sexual behavior is the key to understanding biological species. Only when he turns his attention to mating behavior does the biologist begin to use more than inferential evidence for species “boundaries.” Most basic and applied investigations ultimately depend upon a knowledge of species, whether for acquiring species pure samples, or for identifying and manipulating vulnerable points in the ecology of some competing organism. Questions that are addressed to the way species found their origin, got to be the way they are, and exist today, begin and end with a discussion of biological species.

Gene flow is the phenomenon at the center of understanding and definition of biological species. In the final analysis, when reduced to its smallest moment of flux, to its irreducible whiff of displacement, genes flow down an aedeagus and into another individual, and the genes of 2 parents flow together. (Sometimes the actual mechanics are not exactly like this—genes are handed over in sacks, left on posts, or squirted into the surrounding medium.) Mating behavior arranges for and accomplishes gene flow. It comprises the activities and events that take place as the animals seek, identify, win over and appraise, and finally accept partners in reproduction. Thus sexual behavior, in all its intimate and diverse detail in the animal kingdom, becomes a necessitous obsession with biologists. Further, because the biologies of most organisms are constructed around sexual success, there is more at stake in understanding mating behavior than “merely” straightening out species. This knowledge is fundamental to understanding biology at all, and its most important principles.

Natural selection is the choreographer, composer, and lyricist of the entire sexual performance. It brings about change in gene (allele) frequencies, and this, in a reasonable working definition, is evolution. Natural selection occurs when certain genetic sorts of individuals in a population leave a greater number of progeny than do others. As simple and old-hat as it sounds, this elementary fact can be used with considerable reward and success when one addresses mating behavior studies. Surprisingly, many

2In Shakespeare's The Merchant Of Venice copulation is “the deed of kind” (Shipley 1977).
published studies, speculations, and conclusions, indicate that not all biologists understand, use, or profit from this simple, old but fresh biological verity. One practical application or approach-plan is the one-gene-analysis-model (OGAM) that Richard Dawkins (1976) presented at a popular level in his book *The Selfish Gene*, as did David Barash (1977) in his highly readable *Sociobiology and Behavior*. This technique has been used by some biologists for more than a decade (e.g. Williams 1966). The OGAM pits 2 opposing phenotypes against each other in the reproductive game. For purposes of simplification, the competing phenotypes are based on 2 allelic forms of a gene (or as more commonly expressed, upon the 2 “genes” that are competing for a locus). Simple genetic logic is followed, or rather is pushed through to its seeming endpoint. The conclusion, as to what should or should not be, is not final or binding on nature: it merely provides a guide and prevents certain kinds of errors, raises suspicions of certain explanations or observations, suggests lines of research to be followed, and provides a sound criterion for recognizing significant observations on natural phenomena. The OGAM places in proper probability perspective some erroneous explanations that otherwise seem credible or plausible (such as the heart-warming story of the mutualistic yucca-moth, that appears in ecology texts).

To begin with a simple example, consider a species of beetle in which the female emits a pheromone that males smell at a distance and approach. Males with long antennae (gene L+) are more successful in getting to females than males with shorter ones (gene L−)—the former detect lower levels of the pheromone and are able to track it better. It is obvious that unless the disadvantages of the longer antennae outweigh the advantages, as measured in reproductive success, L+ will gradually replace L−. (We really don’t need the OGAM to come to this plain, straightforward conclusion.)

In a more complicated case, males of S.E. Asian *Pteropteryx* fireflies congregate in great numbers in trees and flash in synchrony. Males and females are attracted to the pulsing trees, and it has been speculated that by synchronizing their flashes these males are providing a huge beacon-tree to help (proposed context of selection) other members of their species get to a gathering place quickly and thereby avoid predation by bats. In other words, the synchrony is said to be a group adaptation (biotic as opposed to organic, Williams 1966), evolved and maintained in the context of group benefit. Let L+ result in synchronous flashing, and its competitor for that locus on the chromosome (L−) not produce such behavior. By devoting more of their activity (energy, attention) to their own reproductive success, males with L+ will find and inseminate more females, and leave more L+ progeny than their rivals leave L+, in each generation. In fact, we would predict that the synchronizing behavior should be lost; indeed, it should never have evolved. But we observe that males do flash in synchrony, and, therefore, conclude that selection producing this behavior must be acting in some context other than that proposed. Synchrony must be doing something for the competing, L−-bearing and perpetuating male. The assisted individuals, those using the beacon-effect to reach the tree, are in cueing in on a conspicuous and highly relevant marker for locating available eggs to fertilize. As a working hypothesis the benevolent-beacon theory is certainly worse than none at all—

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2Entomologists often speak of aggregation pheromones without ascertaining actual function, or even being aware that such an explanation is not simple and demands special formal support.
it flies in the face of simple genetics—and we are guided by the OGAM to seek other explanations before setting out across the Pacific to study beacontrees.

Bedbugs and kin are reproductively eccentric. Males inject sperm through the female body wall and into the hemocoeol, where evolutionarily new structures within (paragenital system) conduct as well as store sperm prior to fertilization. Males of the genus *Afrocinex* have external paragenital structures like, in fact in some respects, more developed than those of conspecific females. Males are found with copulation scars where other males have jabbed them, and with spermatozoa within. Males of *Xylocoris* mount mounted males and inject them with sperm, some of which finds its way into the sperm ducts of the prime-positioned males and hence into the females with their ejaculate. These developments were not recognized as belonging to male competition (Fig. 1)—the latter circumstance might correctly be called autocuckoldry—but instead it was even imagined that male bedbugs would evolve helper ducts to assist the alien sperm (uplifting larceny from pilferage to grand theft!) (Anon. 1974). Let D+ build the helper duct and D- not do so. D+ cannot gain. Although it may sometimes help other D-, it will on occasion, to one extent or another, contribute to the success of D-, thereby reducing its own proliferation. Because D-, on the other hand, will selfishly keep all possible fertilizations, it will always deny passage to D+. It is ironic that such a theory could be preferred when it appears that male competition probably was a major selective force resulting in the evolution of internal fertilization (Parker 1970; Fig. 2) and of the extra genital, traumatic insemination of these bugs.

In these examples the underlying assumption that permitted and led to the originally speculated “adaptations” was that behavior occurs for the benefit of the population or species. One of the greatest values of the OGAM is that it will often uncover this unlikely, if not completely erroneous, assumption. It forces one to focus on the selfish gene, its fate, and its consequences. Selfish genes instruct their gene machines, to use Dawkin’s metaphor, to be competitive in every aspect of their mating behavior, from the beginning search to final fertilization—to yield nothing without a net reproductive gain. Consider these insectan examples: sperm put into a dung fly female by a male is largely pushed aside by sperm from the next male (Parker 1970). A male heliconid butterfly puts a chemical on the female that deters other males (Gilbert 1976). After copulating, males of many insects, including flies and Lepidoptera, put plugs behind their sperm which prevent the entrance of sperm from subsequent males (Parker 1970; Leopold 1970). Male walkingsticks remain with and ride their females, as living chastity belts, for days or weeks (Sivinski 1977), and a *Parnassius* butterfly glues his genitalia to those of a female (Wigglesworth 1965). In some Diptera, males inject accessory secretions (matrone) that inhibit the mating behavior of the female by affecting components in the central nervous system (Leopold 1976 and refs.). Males of a flye fly inject flashes into the coded patterns of rivals, possibly making them appear to be those of a different species (Lloyd 1978). The external “superfemale” genitalia on *Afrocinex*

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1*Competitive mimicry: In a competitive situation, the presentation of false information, permitting an individual to gain an advantage over a rival: 1) by making another individual of the interaction (competing male, or female) appear to belong to another class of objects (a different species), or 2) by emitting signals appropriate to the female (contested resource), and diverting the rival’s approach from the correct object.*
males may also perpetrate sexual dirty tricks, directing the copulatory thrusts of rivals to the wrong spot, more or less masturbating them as they compete to fertilize the eggs of the contested females. Males of a New Guinea longhorned grasshopper insert raspberries (i.e. Bronx cheers) into the rhythmic, "nasal" bellowing songs of nearby males (Fig. 3). Male armyworm moths emit a pheromone that inhibits the responses of rivals to available females (Hirai et al. 1978). Males of the horseshoe crab pry and shove each other as they gather around and press up against the female of a tandem-pair at the oviposition site, perhaps stealing fertilizations from the consort by releasing sperm when the eggs are laid (Fig. 4). Finally, in more straightforward competition, males of other species, such as scarabae (Fig. 5) and phengodid beetles, bite, horn, pinch, shove, kick, and maim each other in the presence of females (Otto and Stayman 1978; Eberhard 1978; Tiemann 1967).

If, in the analysis of any behavior, one finds that success in the competition doesn't seem to correlate with reproductive success, (i.e. that certain males seem to be fighting while others are doing the mating), understanding G A M, he will not conclude that they were simply "naturally aggressive" (a meaningless expression), but pause in coming to a conclusion, and give the behavior closer scrutiny. When a particular mating strategy is observed in males, a rival counter-strategy will be sought, as will ecological imperatives that make certain other strategies potent. For example, a male fly that makes the pattern of a rival appear to be that of a sympatric species has his strategy safely anchored in reproductive isolation. When it was found that the male heliconiid put a deterrent chemical on the female, Gilbert (1976) addressed himself to the question of why males continued to be deterred by the chemical and did not evolve out of the trap. The ethologist that is trying to construct an ethogram, or the sociobiologist making a sociogram, should also notice that unless competitive situations simulating possible natural events and triggers are arranged, a critical part of the catalogue is being omitted. Similarly, if mating analyses are always made under unnatural, crowded conditions in the laboratory, one cannot expect to see the entire repertory of behavior.

The mating behavior discussed so far has been rather simple. To round out this overview, I should mention insects with different ecologies and phylogenetic backgrounds. In insects that require resources that are spatially limited such as carrion, bracket fungi, dung, stream oviposition sites, or perhaps even certain insects themselves (Fig. 6), male success may depend upon the ability to fight, to take over and defend these locations or territories on them or nearby. When resources are not limiting, and populations dense, males may easily reach females, presenting each female with many suitors and the opportunity to exercise choice. If such ecological circumstances exist for some time, females may force males into leks where they must compete by singing, flashing, strutting, or butting heads for hours (Lloyd 1978). Under other circumstances, no better understood, males may bring resources or tokens to females, such as seeds, dead flies, and empty balloons (Thornhill 1976 and refs.) and the nature of the associated male rivalry is different, as

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"The discoverers of this suggested that its "biological significance... might be the increased (species) reproductive efficiency that results". Molecularly marvelous studies in chemical ecology often seem to lack biological sophistication.

"lek = mating aggregation or assembly" (Alexander 1976, p. 67).
is its theoretical interest and application. Other phylogenetic and ecological circumstances have resulted in females dispensing with males and sex, seasonally or completely, as in certain aphids, weevils, and flies, the Surinam roach in Florida, and an Australian grasshopper, to mention a few. There is even a coccid that is a self-fertilizing hermaphrodite (Britton et al. 1970). Sexual parasitism, in which females of a parthenogenic species copulate with males of another, such as the obligate, sexually parasitic spider beetle *Pterus malhis* (Woodroffe 1958), may be based on the purloining of nutritional ejaculate. Other explanations, that the egg requires a sperm trigger for development (easily corrected through evolutionary time), or that the female is preventing the mating of a potential mother of the ecological competitors of her progeny, are by themselves inadequate and unsatisfying.

To the naturalist and the theorist, each should have some of the other in him (Fig. 7), among the more interesting behaviors are those in which he sees an evolutionary tracking and one-ups-man-ship, or evidence that this has taken place. In male-male contests it is obvious that for every new strategy or ploy that evolves, a counter move may be expected sooner or later. As observers we never know when we have tuned in, in evolutionary time: is it sooner or later? Going from insect to insect is like being in a time machine in which one remains stationary as coevolutionary phylogeny moves past. Theorists and observers alike, but not the animals themselves though they may reach the point, are pursuing the so-called evolutionarily stable strategy (ESS) (Maynard Smith 1976). This is the space-time-genome coordinate at which no new mutant strategy can displace the existing strategies.

By adding yet another dimension to the mating behavior hypervolume I can indicate some behavior that I believe must exist and that may be very common, and some counter-behavior that may have evolved to subvert it. This will return to our point of departure, the species problem, and will link the biological species with all of their subtle sexual competition and complication, to those reminders of a simpler day, the morphological cabinet species of the museum taxonomist. In many animals, probably most insects, the energetic contributions made by the 2 parents to each individual offspring are quantitatively different, with females giving more. This fact has stimulated a great flurry of theoretical activity and animal inspection over what the consequences for mating behavior ought to be. Presently it is pretty generally concluded that this fundamental and ancient asymmetry should result in hot-to-trot males which have been selected to drop their sperm and dash to the next female, and choosy(oy) females that are very particular and selective with respect to their mates. The generalization seems legitimate, and to go a long way in explaining, for example, male coyness observed in species in which there are sex role reversals and the males have taken on rearing chores generally found in females (Fig. 8) (Trivers 1972 and refs.; Williams 1975 and refs.; Alexander and Borgia 1978 and refs.). With the occurrence of cannibalism in mantids and some few others (Fig. 9), these males may sometimes be coy also (Thornhill 1976 and refs.).

Selection for haste in males, and coyness in females, results in what amounts to competition between the sexes. Males may be selected to bypass any choice that the females attempt to exercise, and then females selected to maintain their options, to not be misled or to have their choices subverted. If males subdue and seduce females with true aphrodisiacs, females may be
expected to escape sooner or later in evolutionary time. And after sperm has been placed in a female, she should manipulate it: store, transfer (from chamber to chamber), use, eat, or dissolve it, as she makes additional observations on males. Females may accept and store sperm from a male for insurance that they will get a mate, and then become choosy. And if the male ejaculate contains nutritional elements which he contributes to his zygotes, females should evolve to get this from him for free (recall sexual parasitism). Then males should be selected to prevent it, and to make sure that their genes are used with their expensive, nutritional contributions. It is possible for sperm to be manipulated in the female (e.g. sex determination in Hymenoptera). Female reproductive morphology often includes sacs, valves, and tubes that could have evolved in this context. In fact, it is possible that some reported examples of sperm competition are actually cases of sperm manipulation.

Given that females, to one extent or another, subvert male interests by the internal manipulation of ejaculate, it is not inconceivable that males will have evolved little openers, snippers, levers and syringes that put sperm in the places females have evolved ("intended") for sperm with priority usage—collectively, a veritable Swiss Army Knife of gadgetry! Remember copulation in the bedbug and the male blade? Males of some scutellerid Hemiptera have large, bizarre genitalia, half the size of the female abdomen. In Hotea they are spiky and heavily sclerotized, and apparently tear their way through the vagina and body cavity to reach the spermatheca (Leston, in Hinton 1961). Also recall the diverse shapes of male genitalia that taxonomists have exploited for decades. These variations and elaborations may in many instances have evolved to bypass female resistance and sperm manipulation, and represent present or past sexual success strategies. Carrying this line of reasoning a bit farther, it may be possible to make certain inferences and predictions about sexual selection and courtship, and even ecology, on the basis of the diversity (adaptive radiation) of male and female genitalia within a group. This suggests that intraspecific variation, perhaps polymorphism, is to be expected and in many instances another source of taxonomic confusion.

Recognition that sexual conflict-coevolution occurs, and the consequent revolutionary perspective of mating and courtship behavior, followed from an appreciation of natural selection: the genteel view that assumed the individual got mated to serve the good of the species and to prevent its extinction was a conceptual desert, and a researcher’s dead end.

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LITERATURE CITED


Fig. 1. Wheel bugs (Reduviidae: Arilus cristatus (L.)) stacked in a sexual "encounter," with 2 males (top) competing to fertilize the eggs of the female. Probably similar interactions were significant in the evolutionary development of traumatic insemination in bed bugs. Males are touching antennae, and the upper one has his wings spread (to maintain his precarious perch?). The female may be evaluating them, or simply awaiting the victor of whatever contest is being waged. How much subtle data-processing is possible in the CNS of these animals is unknown, but male choice could involve fine-tuning to certain elements of male conduct. Little entomological attention has been paid this critical aspect of insect biology in spite of its significance for many insect management programs.

Fig. 2. Enigmatic copulation wheel in the damselfly Ischnura randi (Hagen) (male at top). In odonates the male grasps the female behind the head with terminal appendages and the female then places her terminal gonopore over the sperm, which has been placed on "accessory" genitalia beneath the basal segments of the male's abdomen. An evolution of this wheel seems as impossible as the evolution of a mechanical wheel, such as rotary wings, and for the same reason—the seeming impossibility of adaptive intermediate stages. Sexual competition or selection may have been a major factor in its evolution. Assuming an ancestral gonopore-gonopore connection (though a spermatophore placed on the ground cannot be ruled out as a starting point) the male could have pushed this connection against his ventral surface to prevent rivals from prying him loose or slipping in between, to keep the female from escaping, or to force sperm into her. Males of some species have ventro-lateral flaps (oreillote) on the second segment, which may function in these regards. Seizure of the female behind the head would have evolved later, perhaps from restraining moves by males against the delicate cervical membranes, or more plausibly, near the center of the locomotor forces females would use in escaping.
Fig. 3. The calling song of males of a New Guinea longhorned grasshopper (*Hexacentrus mundus* (Walker); *Listroscelinae*) consists of a buzz of several seconds duration followed by a series (75±) of short "quanks". S shows the end of a buzz and 7 quanks; time line at bottom, 1 sec/div. Spectrogram at upper left shows the structure of a quank, each vertical band a wing-rub: carrier frequency in kHz at left; upper time line, 0.25 sec/div. Males inject short sounds (raspberries) into the rhythmic quanking of other males. Spectrogram at upper right shows structure of a raspberry; note the slower wing-rub rate. D shows 18 sec of a sonic duel. Raspberries seem to be injected to occur in coincidence with quanks, but sometimes the quanker, seemingly detecting the raspberry, delays his quank 300-500 msec.

—Several competitive strategies occur among Orthoptera, but one of interfering with a neighbor's song to prevent females from being attracted has been suggested, discussed, discounted, and reaffirmed (Alexander 1975; Otte 1977).—The heckler's strategy may be to break the quanker's rhythm, to hide communicatively important elements at the beginning of each quank, or, like dueling banjos, to out-finesse and outscore him, while attending females keep track of each by his individually distinctive song. This dueling may have evolved from the synchrony of identical songs, and the acoustical and temporal characteristics of the raspberry may provide clues to the nature of competition in other synchronizers. Perhaps of significance to this behavior is the fact that *H. mundus* is a predaceous grasshopper.

Fig. 4. Horseshoe Crabs on a beach at Stiltsville, Florida. At spring high tides during March-May females (large individual at lower left-center) approach the water's edge, acquire a consort, dig in and lay their eggs. Males outnumber females at the beach, and fertilization is external. Competing males pry and push each other as they press up against the female, presumably stealing fertilizations from the consort (top center). The consort position, the best place to be, is taken first. Males have hooks for hanging onto the carapace. One wonders if the mating strategies of this living fossil (from the Paleozoic, more than 2 million centuries ago) are as unchanged as its external morphology.
Fig. 5. Sexual selection in Japanese beetles (Scarabaeidae: Popillia japonica Newman). Females are slow in acquiring mates. Although 25-200 males may gather (barr) around a female when she emerges from the ground, Fleming (1972) observed only 1 copulation in several hundred balls. Later, at feeding sites such as the raspberry bushes where these photos were taken, copulation remains uncommon. While observing dozens of pairs I found no intromission and only one instance of adegal probing. Males ride females for long periods, occasionally slipping backwards to stand on their tip toes (upper left) and rapidly rub consorts with their sterna. Female decision-making and intersexual selection is certainly involved. Male competition (introsexual selection) is common. Males kick each other with their hind legs and use their pronota for skewing and levering. They dislodge mounted males with assaults from the side, front (upper right), and rear (lower right). In the photo at lower left 3 males are jousting upon a female; the male in the consort position is being pushed from the front, and shoved and lifted from the rear. Defending males hang on, parry, and kick, the one at lower right having just kicked his tormentor in the chops. Females more than once, and sperm introduced in the last mating before oviposition are most likely to fertilize the eggs (Ladč 1956). This may explain the premium on females at feeding sites, whence they depart to oviposit. Male riding may also be chastity-guarding to ensure paternity, as found in Sivinski's (1977) walkingsticks. This beetle would seem to be a subject of choice for basic research on sexual selection, and its economic importance should facilitate cooperation and funding.
Fig. 6. The small dung flies (Sphaeroceridae: Copromyza (Borborillus) sp.) on the back of this ball-forming dung beetle (Scarabaeidae: Canthus pilularius ?) are cleptoparasites, and develop in the dung balls. A fly, apparently a mated female, will ride the beetle, appearing like the supervisor on a piece of heavy machinery, as the dung ball is rolled some distance from the cow pie. Apparently the egg is placed with the ball after its storage underground. Tumblebugs, “robot” territories that package, transport, and bury larval food, are a limited resource, and seemingly sites for the formation of resource-based leks (see Alexander 1975 for discussion) where males compete for fertilizations. During a short period of observation I found up to 11 flies on the back of a single, ball-building beetle.

Fig. 7. A pair of dung beetles (Scarabaeidae: Boreocanthon depressipennis) with a dung ball enroute from cow pie to burying place. In the pairs I observed males did the pushing (lower right) and females rode, tumbling over and over as they clutched the balls. Moments after this photo was made the female was away on whirring wings, while the male remained to push and then bury the ball. The female of another pair departed after reaching the burial site, immediately after the male had dug his way out of sight beside the ball. Upon viewing the desertion an observer wonders if the female left a permanent mate, which she will meet and recognize again at the pie, to begin another ball; or, recalling the theoretical considerations of Robert Trivers (1972) on parental investment and mate exploitation, could the female have helped and played the male along to a point where a single parent could succeed, then have run off to repeat the performance with a new male? A forsaken partner has no viable choice but to attend the ball. Might a male abscond first? What are the relative investments and their scheduling in such pairs?
Fig. 8. A male belostomatid bug (Belostomatidae: Belostoma butarium Stal.) burdened with eggs cemented on his back by the female. His investment in each offspring goes considerably beyond a dab of sperm. Unlike males of many other belostomatids, he is unable to further his total reproduction by pursuing and copulating with many females. Theory predicts that males of species such as this should be more discriminating in their choice of sexual partners, past selection having favored males that responded appropriately to certain cues emanating from females during courtship. The nature of this information is a complete mystery, as it is in virtually all other insects. One thing is obvious: males must have a way of assuring their paternity of the eggs they tend. Smith (1976) found that males keep the eggs wet, expose them frequently to atmospheric air, maintain water flow over them, and select microhabitats that promote their development. He suggested that among probable costs to males were reduced hunting efficiency, increased exposure and susceptibility to predation, reduced dispersal options, and the already-mentioned limit on total reproduction.

Fig. 9. Firefly femme fatale (female Photuris versicolor complex) eating a male she has attracted with false mating signals. Various parts of him are scattered in the foreground, as she stands over and chews on his thorax. A flight wing protrudes from between her mandibles. Males of prey species are in a bind: competition is keen and they must hurry to gain mates, but they must avoid mimics. Selection should strongly favor discrimination! Although cannibalism of conspecifics has not been observed, this mimicry probably originated with predation on mates and/or conspecific males that were attracted after insemination. Should a female fertilize her eggs with sperm from a male she has been able to catch? Getting caught is poor recommendation for a sire—his sons will presumably have a tendency to be like him, and being eaten ends prospects for gaining additional fertilizations. Food abundance, mate availability, and age should have a bearing on this behavior. In any event, in carnivorous species the last "question" on the mate examination may be the touchy.


