SIGNALING AND SEX IN ACALYPTRATE FLIES

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"It is curious that these little flies (Sepsidae) seem to need so many aids to success in copulation—spotted wings and male display, aphrodisiac odour by the females, special male clasping organs—when other flies manage without any of these."

"A male of the Mediterranean fruit-fly, *Ceratitis capitata*. . . . The elaborate patterns and vivid colour of this fly seem to go far beyond the demands of mimicry or mutual recognition."

(Oldroyd 1964)

INTRODUCTION

The study of animal communication has always been one of the cornerstones of ethology. The pioneers of ethology, Lorenz, Tinbergen, and von Frisch, demonstrated that many of the unusual actions of animals have communicative functions, and that these behaviors have evolved in the same manner as morphological characters (Tinbergen 1951, Lorenz 1958). The behavioral ecology "revolution" that Lloyd (1980) described has given new impetus to studies of animal communication. Behavioral ecologists have built on classical ethological studies by looking in detail at the environmental and social factors that shape and constrain animal communication systems. Some behavioral ecologists have examined the ways in which animal signals are adapted to aspects of the physical environment (Cullen 1957, Morton 1975, Bennet-Clark 1970, Lall et al. 1980, Paul and Walker 1979). Another approach has been to look at the selection pressures on animal signals deriving from the types of social interactions taking place between signalers and receivers (Dawkins and Krebs 1978). In this paper I will consider a particular problem, that of why signaling is relatively simple in some species, but exceedingly complex in others. To get at this problem, I will look at signaling and mating behavior in a particular group of insects, the acalyptrate flies.

The acalyptrates are a large and diverse group of fly families which, with the bristly calyptrate flies such as the common housefly, constitute the "higher flies" (Oldroyd 1964), in contrast to "lower flies" such as mosquitoes and gnats. The best known acalyptrate flies are probably the fruit flies of the families Drosophilidae and Tephritidae. We know more about the communication of these two families than the dozens of other acalyptrate families combined. But in demonstrating the diversity of acalyptrate signals and the evolutionary factors which shape them, I will give a variety of examples. I have been studying the behavior of the tephritid Caribbean fruit fly,

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Anastrepha suspensa, so it will be the feature example. The "caribfly" excellently demonstrates many of the points I wish to make.

Acalyptrate Signals

Flies probably produce a greater variety of signals than any other insect order. Ewing (1977) has reviewed dipteran signals, so I will not attempt a comprehensive listing. Instead, a few examples will be given which demonstrate this variety. Then I will look at some ways that ecology, via the type of mating system present, influences this signal variety.

Signals may be defined as particular morphological characters or behavioral actions which have been naturally selected because of the modifying effects they have on the behavior of conspecific individuals (Dawkins and Krebs 1978). This definition excludes such phenomena as mimicry or the perception of host or prey cues by parasites and predators. Signals are probably best viewed as advertisements by individuals, which were selected because they induced specific effects. Acalyptrate flies use many different channels in their signaling, as the following representative examples show.

Visual Signals

The body of the caribfly is colored shiny gold; its clear wings are marked with distinctive brown patterns. When alert to interactions with other caribflies, it stands stiffly up on its legs; when facing another fly it holds its wings perpendicular to its body, sometimes waving them slowly back and forth, either synchronously or in alternating fashion (Dodson 1978). An early German student of the tephritid fruit flies, of which the caribfly is one, spoke of their "delicate markings" and "graceful behavior" (H. Loew 1862, quoted in Zwolfer 1974a). The visual signals of acalyptrates as a group live up to these descriptions.

In many families of acalyptrates, individuals have bright body colors, usually glossy blacks or purples or metallic greens, golds, or browns. Patterned wings are also widespread, as are distinct markings on other body parts such as head and tarsi. In many cases these visual markings are displayed and emphasized by particular movements. Most other tephritids, like the caribfly, wave their wings back and forth or up and down during courtship or aggressive encounters (Zwolfer 1974a). Males of the platystomatid *Euprosopia subula* display their distinctive black fore tarsi by waving them in the female's face during courtship (McAlpine 1973). Not only do such movements emphasize morphological characters, but, since types of movement and rates of presentation differ among sexes and species, they constitute visual signals in themselves. Special postures in particular contexts also display visual patterns and provide information about species, sex, size, or other individual characteristics of the signaler. For example, the apple maggot fly, *Rhagoletis pomonella* adopts an "active posture" during feeding and investigation, and a "pawing posture" during aggressive displays (Biggs 1972). Whole body movements and "dances" complete the list of ways that visual signals can be produced. Hawaiian *Drosophila* males "joust" (Ringo 1976), courting pairs of the otitid *Physiphora demandata* perform a "spiral dance" (Alcock and Pyle 1979) and advertising and courting tephritids spin, circle, and weave about (Dodson 1978).

Chemical Signals

Flies cannot match the Lepidoptera in the sophistication of their chemical communication (Greenfield, this symposium), but pheromones are important in several groups of acalyptrates. Chemical communication in flies has been reviewed by Fletcher (1977) and Chambers (1977).

Sexually active male caribflies distend pouches at the end of their abdomen; at this time a clear droplet can be seen protruding from the anus. Such males wave their wings, occasionally vibrating them rapidly (see next section). Between bursts of wing fanning they often spin around, touching the tip of their abdomen where the droplet is hanging to the substrate on which they are resting (Nation 1972). What these males are doing is dispersing a pheromone which attracts receptive females (and also other males —see below). Such long-distance attractants are found in several tephritids (Chambers 1977, Pritchard 1967), in Hawaiian species of *Drosophila* (Spieth 1968), and in the otitid *Physiphora demandata* (Alcock and Pyle 1979). With only one known exception, these long-distance attractants are produced by males (Haniotakis 1974). Males of the fruit flies *Dacus orientalis* and *D. cucurbitae* even release "smoke"—along with sex pheromone, sodium and potassium phosphate particles are expelled from males, probably acting as carriers of the pheromone molecules (Ohinata et al. 1981).

Contact, or short-range, pheromones are important signals in many calyptrate flies (Ewing 1977, Fletcher 1977)—males are stimulated to mount by the "taste" of females. Contact pheromones are also present in some acalyptrates. In *Drosophila* they have been shown to be involved in recognition of species, mating status, and strain, including the "rare male effect", which females prefer to mate with males of rare types in a population (reviewed by Ewing 1977).

Females of fruit-infesting tephritids of several genera mark host fruit in which chemicals which deter other females from further egg-laying in the same fruit (Prokopy et al. 1978), thus preventing competition between the offspring of the marking female and the younger larvae of newcomers. Males of some species "eavesdrop" on these signals, remaining in marked areas and searching for the females whose proximity is thereby indicated (Katsoyannos 1975).

Acoustic Signals

Although most people think of crickets and cicadas as the only "singing insects," males of several groups of acalyptrate flies also produce complicated, stereotyped acoustic signals as part of their sexual displays.

The best studied of these signals are those of *Drosophila* (Bennet-Clark and Ewing 1970). Courting males within a few cm of a female extend one wing and vibrate it, producing species-typical acoustic signals. Because several different *Drosophila* species may be present at the same place and time, these signals are important in species recognition. Other effects are to stimulate sexual motivation in females, inhibit locomotion by females, and to increase activity and sexual behavior in nearby males (von Schilcher 1976a and b). Females of the drosophilids *Drosophila* and *Zaprionus* also produce acoustic signals when rejecting or accepting males (Bennet-Clark et al.

1980). These female songs lack the regularity and species-specificity of male songs.

In the last section, I mentioned that pheromone-calling male caribflies produce bursts of rapid wing vibration. When males fight, they also vibrate their wings rapidly, although more continuously. Also, after mounting females, both before copulation and when females become restless, males produce long sequences of rapid wing vibration (Webb et al. 1976). During these rapid wing vibrations, characteristic acoustic signals are produced: calling, aggressive, and pre-copulatory songs, each with a distinct pulse pattern. Other tephritid species also produce species-specific sound signals (Monro 1953, Rolli 1976). The behavioral effects of tephritid songs are currently being investigated, especially by a group led by Dr. D. L. Chambers and Dr. J. C. Webb in the USDA Insect Attractants, Behavior and Basic Biology Laboratory in Gainesville. In caribflies, the calling song increases female activity (Burk unpublished) and, in conjunction with the pheromone, attracts females (Webb 1973). The pre-copulatory song prolongs copulations (Burk unpublished) and probably increases female sexual motivation.

An unusual method of acoustic signaling is found in the chloropid genus *Lipara* (Mook and Bruggemann 1968, Chvala et al. 1974). Females oviposit in reed stems and males must move about from stem to stem searching for them. Males vibrate reed stems, different species vibrating in different patterns. Receptive females reply with "good vibes" of their own (female signals lacking species-specificity), and males move up the stem to mate. The system works over distances up to 2 m. This system is a marvelous example of the naturally selected fit between a species' environment and its signaling system.

Other Signals

Tactile signals are important in the courtship of many insects, and play a role in species recognition in some calyptrate flies (Tobin and Stoffolano 1973). Tactile signals might also function in evaluations of size or other qualities of interacting individuals. Various acalyptrates lick, kick, or probe with their legs during aggression and courtship (Biggs 1972, Ewing 1977, Wangberg 1978). Some of these actions probably help in the transmission of visual or chemical signals, but tactile signals are probably also involved. Examples in the caribfly include fighting males butting heads and males mounted on females probing and licking with their proboscis (Dodson 1978, Nation 1972). No detailed studies have been made of the effects of such actions.

One set of structures that may constitute visual and tactile signals are the long eyestalks of some acalyptrate flies. Such characters, with the eyes located on the end of long stalks, are found in at least 8 families (McAlpine 1979). Usually the character is sexually dimorphic, males having more highly developed eyestalks. McAlpine (1979) has shown that in several cases, males butt heads during aggressive displays and utilize the eyestalks in the shoving matches. Some interactions end without actual fighting, suggesting that the length of eyestalks might be used as a visual cue about the size of opponents.

In last year's symposium, Thornhill (1980) gave examples of courtship feeding of female insects by males. Some examples of this phenomenon can be seen in the acalyptrate flies (see review in Dodson 1978). Males may provide salivary droplets to females during copulation (Wheeler 1924) or con-

struct mounds of foam on which females feed while males copulate (Stoltzfus and Foote 1965, Pritchard 1967, Foote 1967, Novak and Foote 1975). These nutritional offerings or mating inducements qualify as signals to the extent that they act as chemical or visual attractants to females, especially in cases where males build froth masses or blow bubbles in the absence of females (Stoltzfus and Foote 1965, Novak and Foote 1975).

Generalizations

After this brief survey of acalyptrate signals, some generalizations can be drawn. First, as has been pointed out for Diptera generally by Ewing (1977), almost all signals are produced in a sexual context. In flies, it is only during sexual encounters that the kinds of social interactions occur in which signaling behavior would be beneficial. This is not surprising since, as Lloyd (1979) has emphasized, sex is the most important thing there is for most organisms. Second, most signals are male-produced. This is in line with the idea that males are generally the more sexually aggressive sex, because of the male-female dichotomy in parental roles (Trivers 1972, Thornhill 1980; see Greenfield, this symposium). Third, there are vast differences in the complexity of sexual signals exhibited by different species. Some hardly signal at all while others, such as the caribfly, bombard the environment with visual, chemical, acoustic, and other signals. This last observation is the one I want to pursue in the remainder of this paper. To do so requires a slight diversion—we must look at the mating systems of acalyptrate flies.

Acalyptrate Mating Systems

The links between patterns of parental investment, resource distribution and availability, and form of mating system have been well demonstrated in several recent papers (Trivers 1972, Emlen and Oring 1977, Alcock 1980). Mating systems can be classified in a variety of ways. For our purpose, two of the most useful are those of Alexander (1975) and Borgia (1979). The first is based on what Parker (1978) calls the "encounter site convention"—the encounter site being the place where males and females meet and mating takes place. Alexander distinguishes between encounter sites in immediate proximity to important resources needed by females for successful reproduction (food sites, refuges, oviposition sites, etc.) and encounter sites not so located ("resource-based sites" vs "nonresource-based sites"). Borgia classifies mating systems according to the interactions between males and females, particularly which sex can best be said to control the decision whether or not a mating will take place. A combination of these two approaches seems to work best in classifying acalyptrate mating systems and in providing insights into the effects of mating systems on signaling behavior.

In many acalyptrate flies, sexual encounter sites are resource-based. This occurs when female-required resources are distributed in discrete, scattered, predictable patches. In some such cases, males are able to control access to the resource, only allowing access to females in return for copulation: such matings might even be called rapes (Smith and Prokopy 1980). Sometimes males establish individual territories on the resource. Males of fruit-infesting and gall-forming tephritids establish exclusive territories on host plants, expelling other males and copulating with females who arrive to oviposit (Bush

1969, Zwolfer 1974b, Batra 1979, Prokopy 1980). Males of the neriid cactus fly, *Odontoloxozus longicornis*, defend decaying patches on cacti, the female oviposition site (Mangan 1979). Males of the dryomyzid *Oedoparena glauca* defend areas of barnacle beds at low tide, seizing and copulating with females who come to the barnacle beds to deposit their barnacle-consuming larvae (Burger et al. 1980). In other cases, males search actively over resource patches for females, not defending particular areas but still interacting aggressively with other males. Searching replaces territoriality where the number of competing males is very high or where resources are short-lived, less discrete, or otherwise less economic to defend (see review by Davies 1978). Examples include the sepsid fly, *Sepsis cynipsea*, whose males search for ovipositing females on the surface of fresh cow pats (a resource only good for a few minutes) (Parker 1972), and another sepsid, *Themira putris*, whose males form vast aggregations over sewage sludge, the larval habitat (Oldroyd 1964)[1].

In some acalyptrates, sexual encounters take place on female-required resources, but control of the mating decision is maintained by females. This may be due to physical or behavioral adaptations which allow females to fend off males or because resources are more available or evenly distributed, thereby less monopolizable by males. Courtship and mating in most species of *Drosophila* occurs on food sites, where males approach and court feeding females (Spieth 1974). The searching behavior of male reed flies (*Lipara*), who vibrate reed stems hoping for a reply from a female, has already been described (Chvala et al. 1974). Even in some of the gall-infesting tephritids, territory-establishing males do not monopolize all potential oviposition sites, so that females are presented with a choice of ovipositing in sites with or without resident males.

The third basic type of acalyptrate mating system is that in which encounter sites are not found in proximity with female-required resources. Mating away from resources can be thought of as a system that males only adopt when the resource-based alternative is too costly or otherwise unavailable to them. The reasons for this high cost or unavailability vary, and in some cases are imperfectly understood. I will present some examples, trying to account for the lack of resource-based mating in each case.

One type of non-resource based system, common in other groups of flies, is the aerial swarm, so well discussed by R. Sullivan in this symposium (see also Downes 1969). Aerial swarms are uncommon in acalyptrates, but a few examples are reported from three families (McAlpine and Munroe 1968). Best studied are several species of Lonchaeidae, which form swarms that in all respects fit the patterns described for lower Diptera by Sullivan. The retention of this mating system in these acalyptrates is probably related to the usual low population densities and unpredictable distribution of larval habitats (injured plant tissues), which would tend to lower the encounter rates with females that could be expected by a male occupying a resource.

Unlike most other *Drosophila*, mating in Hawaiian *Drosophila* does not take place on food sites. Instead, males form aggregations on vegetation, where males joust with each other, perform sexual displays, and mate with incoming females (Spieth 1968, Ringo 1976). By analogy with the mating aggregations of vertebrates, these male mating aggregations have been called "leks," a name which can be applied to all aggregations of displaying

[1]Superscripts refer to notes in the appendix.

males away from female-required resources. Lekking in Hawaiian *Drosophila* may be due to predation pressure: the native insectivorous birds of Hawaii may have taken a heavy toll of flies behaving conspicuously at exposed food sites, necessitating mating away from such sites. Borgia (1979) has described a similar case. Small, dung-ovipositing flies are forced to mate away from dung pats because of the presence on dung pats of the larger, predatory dung fly, *Scatophaga stercoraria* (which does have a resource-based mating system).

The caribfly is one of a number of species of fruit-infesting tephritids which often do not mate on host fruits, but on vegetation (sometimes, but not always, in host trees) (Dodson 1978). Other, better-studied examples include the Mediterranean fruit fly, *Ceratitis capitata* (the "medfly") (Prokopy and Hendrichs 1979) and the Queensland fruit fly, *Dacus tryoni* (Tychsen 1977). In these species, aggregations of males form on vegetation, often with males establishing small territories consisting of a single leaf. From these territories, males interact with each other, perform sexual displays, and court arriving females. Lekking in these tephritids is probably related to biogeographical and ecological factors. Lekking species tend to be tropical or sub-tropical; like many such groups, they tend to have wide host ranges, unlike temperate species that tend to specialize on particular hosts. Populations persist for much or all of the year, and host fruits are not seasonally synchronized. The caribfly has been reported from over 100 fruits (Swanson and Baranowski 1972); the medfly from over 200 (Christenson and Foote 1960). Male resource monopolization in such polyphagic species is unlikely to lead to high encounter rates with females (see Prokopy 1980)[2].

Mating Systems and Signaling Behavior

Behavioral ecologists look for relationships between ecological factors and the behavior patterns of animals. A clear connection exists between ecological circumstances and mating systems in the acalyptrates. This connecting thread also links up mating systems and signaling behavior.

In those species with resource-based, male-controlled mating systems, sexual signaling is usually very simple. In some cases, males do not signal at all but merely jump on and attempt to copulate with any object of approximately the correct size and shape (Berube 1978). In such mating systems, males who control resources are assured of a high encounter rate with females. Therefore, male reproductive efforts are better directed toward adaptations for locating resources quickly, defending them against other males, and seizing and retaining hold on encountered females (Parker 1970, 1974a). Where signaling is present, as in the gall-forming tephritids, it usually consists of simple repetitive actions involving a single channel, probably acting mainly as a species-identifying cue. The repetitive wing-waving of many tephritids falls into this category (Zwolfer 1974a).

When high encounter rates on resources are not so certain, or where mating decisions are made by females, sexual signaling by males is more highly developed. Female *Drosophila* must be courted and induced to mate; male *Drosophila* have evolved courtship songs that not only identify the species of the male but also have arousing effects on females. Male tephritids in some species must advertise their resource-based territories with pheromones or induce females to oviposit in their territories with nutritional

offerings (Stoltzfus and Foote 1965). Females may respond to such pheromones or offerings because they allow rapid location of suitable oviposition sites or because the nutritional offerings help them to produce more eggs: in effect, they trade a copulation for reproductive assistance by the male. (An additional benefit may be reduced risk of predation while searching for oviposition sites or food.)

The extremes in male signal complexity, represented by such species as the caribfly, are reached when mating takes place in leks, away from resources and with control of the mating decision firmly in female hands. Unlike other *Drosophila,* Hawaiian *Drosophila* are large, have patterned wings, produce elaborate sexual displays and aggressive behaviors, and disperse long-distance pheromonal attractants (Spieth 1974). The lekking tephritids retain bright colors and wing-waving, are more likely to produce long-distance pheromones, and include all the species that are now known to produce acoustic signals (Dodson 1978). The otitid *Physiphora demandata,* another lekking species, produces attractant phermones and exhibits a complicated spiral courtship dance (Alcock and Pyle 1979). It is worthwhile to consider the interactions that account for this clear connection between lek mating systems and conspicuous, elaborate sexual signals.

As Labeyrie (1971) and Zwolfer (1974b) have emphasized, mating on the larval host plant often eliminates the need for attractant signals. In lekking species mating away from host plants, males are selected to produce conspicuous, high intensity attractants. Males who call in groups may be able to attract females from greater distances, resulting in a tendency for males to aggregate (Otte 1977). This probably accounts for the high response of males to male-produced sex pheromones in such tephritids as the caribfly (Perdomo et al. 1976—male responses are typically equal to those of virgin females) : males must locate leks, either to establish their own calling stations or to become "satellites" of calling males (Cade 1980).

The proximity of competing males in leks adds other selection pressures. Males may fight to establish calling stations in favorable locations or to keep other males at a distance—aggressive interactions are common in groups of male caribflies (Dodson 1978). Parker (1974b) and Maynard Smith and Parker (1976) have shown that selection often favors the substitution of "war propaganda" signaling (Borgia 1979) in place of actual fighting, and Barnard and Burk (1979) have shown that in such a competitive situation signals may become more complex due to contrasting selection pressures on males to evolve ever more intimidating displays and ever less gullible responses to the displays of other males.

The presence of females in leks adds more complexity to the situation. To point signals at individual females, males may be selected to switch from omni-directional calling signals to more restricted courtship displays (for example to switch from long-distance pheromones to short-distance visual displays). To reduce competition from neighboring males, males may perform courtship displays less intensely than calling displays. Alexander (1975) considers the variety of signaling interactions that may occur between males in leks.

Female mate choice adds another selection pressure. Where females can not obtain parental assistance or nutrition, they are expected to sexually select males of high genetic quality (Trivers 1972), as indicated by pheno-

typic vigor[3]. The signals of individual males may differ in ways which indicate differences in male quality: females may observe the "war propaganda" signals of males (Borgia 1979); mere establishment of a calling station may indicate successful fights against other males (Burk 1979); large males may produce more intense signals (Forrest 1980); or dominant males may be more likely to signal or may produce more continuous signals (Burk 1979, Crankshaw 1979). If such signal differences exist, females will be selected to utilize them in mating decisions (Fisher 1958). However, such female choice of male signals may set up another "arms race" (Dawkins and Krebs 1979), similar to the one between fighting males. All males will be selected to produce signals which induce females to mate, thereby mimicking the signals of high-quality males. Females will be selected to become ever choosier and coyer to avoid being deceived by low-quality males. In such an arms race, signals may replace one another over evolutionary time, or signals may become "layered" (Barnard and Burk 1979, West Eberhard 1979). This may account for cases where courting males must perform a series of actions, sometimes even involving different signal channels, before females will mate.

Thus, three types of selection pressure occur in leks which all tend to increase the elaborateness and complexity of male sexual signals: the necessity of attracting females, competition with neighboring males, and the demands of female choice. These factors account for the wealth of signals in such lekking acalyptrates as the caribfly.

Concluding Comments

Through the course of this paper, I have tried to show how ideas from behavioral ecology help one to understand some aspects of insect communication. Such understanding can have practical benefits. (1) Some predators and parasites intercept dipteran signals and use them to locate prey or hosts —for example, the hymenopteran parasite *Opius lectus* locates its apple maggot hosts by responding to the oviposition deterring pheromones of adult female apple maggot flies (Prokopy and Webster 1978). (2) Sex attractants can be used in the monitoring and control of pest populations. Field trials using the male sex pheromones of the caribfly and medfly have shown them to be at least as effective as traditional non-pheromonal attractants; pheromones have the advantage that both sexes respond in large numbers (Perdomo et al. 1976, Chambers 1977). The oviposition-deterrent pheromones of fruit-infesting female tephritids have shown great promise as a means of reducing attacks by ovipositing females (Katsoyannos and Boller 1980). (3) Because they are conspicuous and often stereotyped, and because control techniques such as the release of sterilized males rely on their effective production, sexual signals are particularly appropriate as indicators of the quality of mass-reared insects (Huettel 1976, Sharp and Webb 1977).

In a wider sense, though, the behavioral ecology approach to the study of insect communication is likely to be important to pragmatic entomologists for the same reason that it is to ethologists. Thorough understanding of an insect's behavior, whether from a theoretical or pragmatic standpoint, depends on knowledge of the total biology of the species. The behavioral ecology approach is the method best suited to give us such an understanding.

SUMMARY

Acalyptrate flies produce a great variety of visual, chemical, acoustic, tactile, and other signals. Most signals are produced by male flies as part of sexual behavior, and species differ greatly in the degree of complexity of these sexual signals. Patterns of parental behavior and resource structure lead to three basic types of mating systems in acalyptrate flies: (1) Male-controlled matings on female-required resources, (2) Female-controlled matings on female-utilized resources, and (3) Female-controlled matings in male aggregations away from resources (lek mating system). Differences between species in complexity of sexual signals are the result of these differences in mating systems. Signals are simple in male-controlled systems, intermediate in complexity in female-controlled resource-based systems, and most complex in lek systems (because of the complexity of male-male and male-female intractions in leks).

APPENDIX

[1]In cases where mating decisions are controlled by males, it is often found that females mate many times over their lifetime, as multiple visits are made to resources (Foote 1967, Berube 1978). Where mating occurs away from resources, multiple matings are rare (often only occurring when females run low on stored sperm) (Cunningham et al. 1971). However, in species where females are forced to copulate, they may still retain ultimate control, through mechanical or physiological adaptations, over whether or not insemination occurs following a particular copulation (Lloyd 1979, Walker 1980).

[2]This classification of acalyptrate mating systems is, of course, an oversimplification in some respects. One complication is the presence in a single species of alternative mating "strategies," as discussed by Cade (1980). Smith and Prokopy (1980) and Prokopy and Hendrich (1979) have given examples of alternative patterns in tephritid fruit flies. In *Rhagoletis pomonella,* female-initiated matings take place on vegetation early in the fruiting season of their hosts; later, when most females have already mated, males attempt to force copulations on fruit with ovipositing females (Smith and Prokopy 1980). A similar vegetation/host encounter site dichotomy is found in *Ceratitis capitata;* in this case male mating strategies differ according to the time of day (Prokopy and Hendrichs 1979).

[3]A controversy exists as to whether such female selection for high-quality males can really be effective. It is argued that any genetic variance in characters selected by females will be quickly eliminated (see Borgia 1979 and Thornhill 1980). A useful way of considering this problem would be the "E.S.S." method (see Cade 1980). Would such a female choice "strategy" be invadable by a strategy in which females mated randomly?

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