

Mating strategies based on foraging ability: an experiment with grasshoppers

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Female mate choice and the benefits of this behavior are critical aspects of Darwinian sexual selection, but they are seldom documented because it is difficult to identify the male trait(s) that females may be seeking. We conducted experiments with grasshoppers (*Melanoplus sanguinipes*: Orthoptera, Acrididae) to examine this behavior. Males that feed more intensively and select a diet mix that permits greater food intake (food intake per body mass per time) in laboratory trials were preferentially selected by females. These better foraging males on average provide greater paternal investment (greater spermatophore mass) to the female, which increases her reproductive rate (eggs produced per body mass per time). However, paternal investment may not entirely explain female choice of better foraging males, because these males were still selected even if they had their food intake restricted or had been allowed to recently mate, which reduces spermatophore production. Furthermore, males change their mating strategy in response to female choice and the foraging abilities of surrounding males. Poorer foraging males attempt forcible copulation rather than displaying and allowing female choice. A male will facultatively switch between these strategies depending on the foraging abilities of the surrounding males. While females attempt to reject forcible copulation, forcible copulation reduces the frequency with which females successfully copulate with better foraging males. Therefore, males that are less “attractive” to females adopt alternative mating strategies to counter female choice which would exclude them from mating. **Key words:** female choice, mating strategies, foraging, grasshoppers. [*Behav Ecol* 7:438–444 (1996)]

Intersexual selection usually relies on a female choosing to mate with a male that increases her reproductive success (number of offspring produced and their survival), whether through paternal investment or paternal traits that may be heritable (Darwin, 1859, 1871; Trivers, 1972). Males often advertise the traits that make them “attractive” to females in courtship displays. The displays enable a female to choose to mate with a male with traits that will increase her reproductive success. However, conflicts between female mate choice and male reproductive success (Dominey, 1980; Gross, 1982, 1984, 1991; Thornhill, 1980, 1981; Thornhill and Alcock, 1983; Thornhill and Thornhill, 1983) can lead to alternate male mating strategies, where males that are attractive to females behave in a manner that fosters female choice (e.g., displaying) and males that are unattractive attempt to circumvent female choice (e.g., forced copulation). How females evaluate male attractiveness and how unattractive males may attempt to subvert female choice are not well understood.

Male attractiveness is often related to paternal investment in a female’s offspring, which is frequently related to the male’s ability to contribute nutrients to the female for offspring production (Thornhill, 1980, 1981; Thornhill and Thornhill, 1983). A critical element of foraging theory is that better foraging individuals will have greater reproductive output (Stephens and Krebs, 1986). Therefore, a link may exist between male foraging ability, a male’s paternal investment (attractiveness), and adoption of alternative mating strategies. One common alternative mating strategy adopted by unattractive males is forcible copulation (Thornhill, 1980, 1981; Thornhill and Thornhill, 1983).

A number of studies with Orthoptera indicate that males provide substantial nutritional investment in a female’s reproduction through spermatophores and males often exhibit alternate mating strategies (Eggert and Sakaluk, 1994; Green-

field and Shelly, 1985; Greenfield et al., 1987; Gwynne, 1982, 1993; Gwynne and Morris, 1983; Sakaluk and Smith, 1988; Shelly and Greenfield, 1985; Shelly et al., 1987; Simmons et al., 1994; Wedell, 1994; Zuk, 1987a,b). Furthermore, tettigoniid orthopteran males provide females with spermatophores that vary in protein content depending on diet (Wedell, 1994). Females of many Orthoptera are able to assess a male’s potential investment prior to copulation because she consumes the spermatophore, and spermatophore size may determine male attractiveness. However, many Orthoptera, like other species, copulate prior to the female receiving paternal investment, and this poses difficulties in understanding what cues are used by a female in assessing male attractiveness.

We experimentally examined female choice and the alternate male mating strategies of courtship displays and forced copulation using the grasshopper (*Melanoplus sanguinipes*: Orthoptera, Acrididae), a species that copulates prior to provisioning spermatophores. Individuals were found to differ in their foraging ability in a common laboratory environment. Females were observed to select better foraging males and to produce more eggs when paired with better foraging males, because better foraging males on average provided greater paternal investment (greater spermatophore mass). However, a female’s selection of better foraging males was not a “fool-proof” strategy for increasing reproductive success, because food deprivation of better foraging males or a recent copulation with another female reduced the male’s ability to provide spermatophores. Therefore, a male’s foraging ability may reflect his potential paternal investment, not actual investment.

We also experimentally assessed the conditions under which males adopt a mating strategy based upon displaying to females versus forced copulation, and the reproductive success of each. Finally, we examined another popular hypothesis that females do not select males based upon their paternal investment, but select males based upon their resistance to parasites, a trait that may be inherited by offspring (Hamilton and Zuk, 1982; Kirkpatrick and Ryan, 1991; Zuk, 1987a,b).

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STUDY SYSTEM

Melanoplus sanguinipes is the most common North American rangeland grasshopper. Studies of male mating behavior have not explicitly identified alternate mating strategies for this species. However, in descriptions of mating behavior, either the male displays to a female (Cantrall, 1943; Pickford and Gillott, 1972a,b; Riegert, 1965) or the male stalks her without displaying (Otte, 1970, 1981). When displaying, a male orients his antennae toward a female and vibrates his femora, while swaying his body, and after a period of display, the male leaps onto her and attempts to copulate. When stalking a female, a male does not display, but stealthily approaches her, moving only when she moves; when the male gets close enough to her, he leaps onto her and then vibrates his femora. We interpret these distinct behaviors as possible alternate male mating strategies. Female mating behavior has been described as passive, because females do not exhibit any overt displaying or search for males, and this has been interpreted as an absence of female mate choice (Pickford and Gillott, 1972a,b; Riegert, 1965).

Copulation involves the "locking" of male and female genitalia and the insertion of one or more spermatophores over an extended period (up to 4.5 h); females will copulate repeatedly with the same or different males (Pickford and Gillott, 1972a,b; Riegert, 1965). A single spermatophore can fertilize several egg pods, since sperm can be stored by the female (Friedel and Gillott, 1977). Females that receive multiple spermatophores either during an extended copulation with one male or from copulations with several males produce more eggs and a greater proportion of the eggs hatch (Pickford and Gillott, 1972a,b; Riegert, 1965). This reproductive increase is a result of the female using nutrients in additional spermatophores to produce more and larger eggs (Friedel and Gillott, 1977). Therefore, a female can benefit by assessing a male's potential spermatophore investment and choosing males that can invest more; however, male investment is not apparent until copulation.

Our pilot observations were based on 82 copulation attempts observed over 3 days between 20 males and 10 females that were held in a uniformly lit arena (25 cm × 50 cm). First, alternate male mating strategies were indicated. In 58% of the copulation attempts, the male displayed to the female prior to leaping onto her from a distance of 2–5 cm. In the remaining 42% of the attempts, the male did not first display, but stalked the female prior to leaping onto her from a distance of 10–20 cm, and then he displayed. Second, females were not passive. When a male displayed prior to attempting copulation, females responded with femoral vibrations and body swaying. When a male stalked a female and tried to copulate without first displaying, the female reacted by leaping, flipping over, and prying at the male with her hind legs. The female's behavior was presumably a response to an unwanted forced copulation and an attempt to dislodge the male rather than a startle response, because she continued to resist after the male began to display, which gave her an opportunity to determine that the disturbance was a male grasshopper, not a predator. Even though females might refuse to copulate with males that displayed prior to attempting copulation, females only responded violently to forced copulation attempts, and forced attempts were less successful than those following displays (28% versus 51%; $\chi^2 = 4.18$, $df = 1$, $p < .03$).

Questions to be experimentally addressed are listed below and are based on the above observations.

(1) Do females choose between males based on their spermatophore investment? This is expected because females are not passive in mating and they receive paternal investment

(spermatophores). As cited earlier, this form of mate choice is not uncommon for orthoptera.

(2) How well can females identify the paternal investment that a male will provide? This depends on the cues that the female employs. If a female assesses a male trait that generally leads to greater spermatophore production, such as body size, feeding ability, etc., the female is responding to the male's potential investment, but may acquire less than this amount. Potential investment is diminished if the male has recently mated, which reduces his "stock" of spermatophores, or has recently fed poorly, which leaves him with a reduced ability to provide nutrients in spermatophores. On the other hand, a female may be able to account for recent matings and feeding to assess a male's actual paternal investment. If a female selects males based on their actual investment, she will occasionally mate with a male that has a lower potential investment than other available males, when these other males have recently mated or fed poorly. If a female selects males based on their potential investment, she may not be able to assess male history to determine actual investment, or she may be selecting for the trait (genes) that enables him to have high potential investment, because these increase her offspring's fitness.

(3) Do females select males based upon nutritional status, if better nourished males produce a greater spermatophore mass? Nutritional differences between males might reflect potential investment, if they arise from differences in male foraging ability (ability to select a diet that provides greater nutrition), and actual investment, if they arise from a male's recent feeding history. Alternatively, a male's investment may be determined by parasites. How females might identify better nourished males can be addressed. One possibility is that nutritional status is exhibited by male body mass, if large size results from an ability to acquire better nutrition.

(4) Does a male adopt alternate mating strategies that reduce a female's ability to choose between males when he cannot invest as great a spermatophore mass as other males? This may occur when a male chases other males away from a female or attempts forced copulations. If large body size is not related to foraging ability then large males might obtain more copulations if they are better able to chase off other males by fighting or are better at subduing females, which are generally larger than males, when attempting forced copulations.

(5) How effective are male alternate mating strategies at reducing female mate choice?

METHODS

Male and female foraging abilities

We measured male and female foraging abilities in outdoor feeding trials (air temperature 24°C–27°C and diffuse sunlight) at the National Bison Range, Montana. Fifth instar nymphs were caught on the same day to minimize individual differences due to age, and they were reared to adulthood on ad libitum quantities of two readily consumed plants (*Dactylis glomerata*, a grass, and *Taraxacum officinale*, a forb). Individuals were reared in isolation to prevent mating and dominance interactions that could affect foraging behavior.

We weighed individual adults after depriving them of food for 3 h and then placed each in a 0.5 l jar covered with screening. The jar contained two squares (2.58 cm²) of the grass and two of the forb; each square was suspended on a pin, and the pins were arranged in a square configuration (8 cm × 8 cm) with pieces from the same plant species on the diagonal. The quantity provided of either grass or forb was greater than the individual could consume in a feeding trial; this means that diet selection was not influenced by food depletion. The trial lasted 20 min, which is a time period sufficient to enable the

forager to fill its gut, which was empty at the start because of the deprivation period before the trial; this helped to standardize feeding motivation among individuals. After a feeding trial, the individual was kept by itself in a 0.5 l jar and fed daily ad libitum quantities of the two foods used in the trial until the individual was used in one of the mating experiments described below.

Immediately after the trial, an individual's feeding was measured as the area of grass and forb consumed. The plant area consumed by an individual was converted to digestible energy intake knowing that the forb provides 1.4 times more digestible energy than the grass per unit of area (Belovsky, 1986). We also standardized area consumed and energy intake among individuals by dividing each individual's digestible energy intake by each individual's body mass, because larger individuals may ingest more food given their larger alimentary tracts (Belovsky GE and Slade JB, unpublished data) and greater total energy demand.

Males and females were ranked separately by their foraging abilities (area consumed or digestible energy per body mass) based upon each individual's performance in a single trial. One trial was considered adequate for ranking, because a pilot study where five adults were tested repeatedly in four trials (one per day) produced similar rankings ($r = .87$, Friedman test: $t = 0.18$, $df = 4$, $p < .90$), even though adults differed significantly in their feeding abilities (Friedman test: $t = 13.6$, $df = 4$, $p \leq .01$). Similar repeatability in foraging behaviors of individuals has been reported for another insect (Blanckenhorn and Perner, 1994).

These feeding trials can reveal several elements of an individual's foraging ability. We know that individuals of this grasshopper obtain the greatest intake of food (mass or digestible energy) from a diet composed of a mix of grass and forb (Belovsky, 1986). A mixed diet provides the greatest intake over an extended time period (e.g., a day or meal) because the forager must "trade off" the rapid harvesting of forbs and their greater fill of the gut per unit of dry matter intake (bulk *sensu*; Belovsky, 1986) with the slower harvesting of grasses and their lower fill of the gut per unit of dry matter. Therefore, a trial elucidates the ability of the individual to select between the two food types (diet composition), as well as the individual's gut capacity and rate of harvesting (amount consumed).

Finally, foraging rank may not reflect an individual's inherent foraging ability if it is weakened by parasites. Therefore, after each mating experiment or when an individual died, we immediately dissected the individual to examine for parasitic nematodes and parasitoid diptera and hymenoptera.

Male foraging ability and spermatophore production

We kept 25 adult females of similar body mass (340–360 mg) separately in 1 l jars covered with screening without food for 3 h to ensure that their guts were empty. Each female was then weighed and returned to her jar. A virgin male of known body mass and foraging ability (see above) was placed with each of 15 females. Ten control females kept without males were weighed individually every 15 min; their proportional weight loss (current mass/initial mass) was averaged. The pairs were observed to ascertain when copulation began and ended. When a copulation ended, the female was removed from the jar and weighed. The female's current body mass less her initial mass multiplied by the control's proportional lost mass at the time when copulation ended estimated the spermatophore mass contributed by the male. This mass was compared with male foraging ability, body mass, and duration of copulation.

Reproductive rate

Reproductive rate was correlated with male and female foraging ability using 32 males and 32 females whose foraging abilities as adults were known and who were virgins (see above). Individuals of each sex were randomly paired and each pair was kept in a 1 l jar covered with screening and containing 2 cm of vermiculite for ovipositing. Every day each pair was provided with equal ad libitum amounts of the two plants used in the feeding trials to ensure that feeding abilities were unchanged, which might occur if food species or abundances were modified. When one individual of a pair died, we measured the pair's total reproductive output as the number of eggs deposited in the jar plus the number of functional ovarioles in the dissected female (current egg development; Uvarov, 1966). To compute reproductive rate for a pair, the pair's total reproductive output was divided by the number of days that the pair had been together and the female's body mass. Reproductive rate controls for differences between the pairs in how long both individuals survived. The reproductive rate divided by female body mass controlled for the positive log-log correlation with female size (Joern and Gaines, 1990).

Female mate choice

We examined female mate choice without male interference by giving a female (1 of 80 females) a choice between two adult males randomly chosen from 80 of known foraging abilities. Males were tethered on 20 cm of monofilament that restricted them to opposite ends of an arena (25 cm × 50 cm) so they could not fight with each other, while females were not restricted. The arena floor was covered with sand and uniformly lit. The female was placed in the arena center, where she could see both males, and her behavior toward the males was observed for 1 h. We identified the male selected by the female by her spending more time close to and displaying to one male. Copulations were not measured because the tether impeded the male's copulatory leap, either by preventing it or by frightening the female if the tether hit her before the male could mount. Tethering does not appear to modify any other behaviors, except to prevent flight, and this grasshopper does not employ flight in its mating behavior (Belovsky et al., 1990). A number of experimental variants were employed to test possible stimuli for female choice:

1. Female choice was assessed for a randomly selected virgin female with a randomly selected pair of virgin males (27 trials). If spermatophore production is related to foraging ability, this experiment determined whether females can assess a male's potential investment, because the males have experienced the same feeding environment and have not depleted their spermatophores.

2. A randomly selected virgin female was placed with a pair of males: the better foraging male had copulated with another female within 3 h and the poorer foraging male was a virgin (24 trials). This experiment determined whether females could select males based on actual investment, because the better foraging male cannot invest his potential spermatophore production due to a recent mating.

3. A randomly selected virgin female was placed with a pair of males: the better foraging virgin male had been fed every other day ad libitum quantities of food and the poorer foraging virgin male had been fed every day ad libitum quantities of food (24 trials). This experiment determined whether females could select between males based on differences in actual investment, if spermatophore production is related to feeding.

4. Experiment 1 was repeated with females that were "blinded" using a drop of black lacquer placed over each eye (20

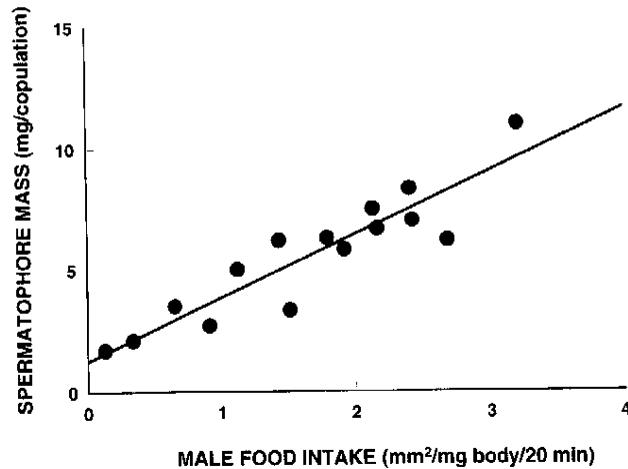


Figure 1
Spermatophore mass provided to a female during a single copulation by a male as a function of his foraging ability measured in the feeding trials described in the text.

trials). From pilot observations of “blinded” females, we did not observe any effects on their feeding behavior or willingness to mate. This assessed whether female choice depended on visual stimuli. A control with clear lacquer was not employed, because clear lacquer appeared to impair vision.

5. Experiment 1 was repeated using a pair of males that were killed by freezing for 30 min and then placing the bodies with the female (20 trials). Killing the males by freezing produced corpses whose color did not appear to change and whose biochemical characteristics should be least modified; this assessed whether the female responded to male motion or posture.

Male mating strategies

Male mating strategies were compared with a male’s relative foraging ability using four virgin males (randomly chosen from 20 individuals) with two virgin females (randomly chosen from 20) in the arena described above. Individual males were identified by painting each a different color on the pronotum. Males and females could move freely. In each trial (1–2 h), we recorded whether the male’s foraging ability and body mass were above or below the average for all males in the trial, then we observed each male’s mating behavior and recorded attempted (i.e., male mounted female) and successful copulations. We conducted 24 trials in which individuals were used more than once, but the same combination of four males or two females was not reused. Copulations were interrupted before spermatophore exchange could take place; this eliminates the effects of past matings on paternal investment.

RESULTS

Foraging ability

An individual’s energy intake in a 20 min feeding trial was related to its body mass and the proportion of its diet composed of forbs (ρ : arcsine square root transform), using multiple regression ($r^2 = .84$, $p < .0001$, $N = 63$). Energy intake increased with body mass ($p < .03$), increased with ρ ($p < .001$), and decreased with ρ^2 ($p < .003$). Given the quadratic relationship, energy intake was maximized when the diet was comprised of 68% forbs. Therefore, foraging ability reflects diet selectivity and increased consumption as body mass increases. Energy intake and total plant area consumed were

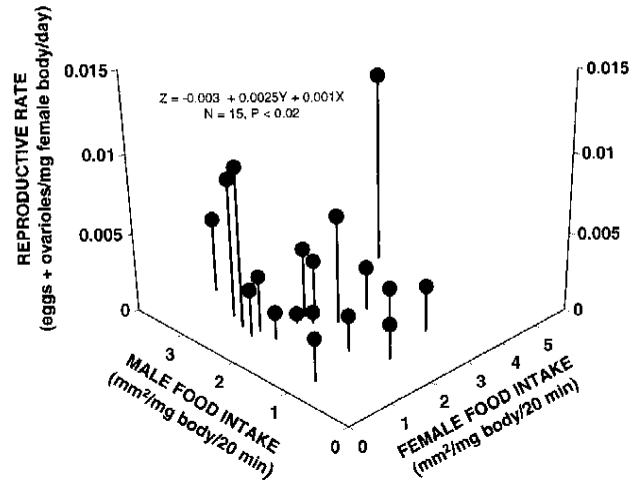


Figure 2
Female reproductive rate (eggs and functional ovarioles per female body mass per day) as a function of the foraging abilities measured in the feeding trials described in the text for both the female and male comprising a pair. The regression statistics are presented.

correlated ($r^2 = .98$, $N = 63$, $p < .0001$); likewise, total area consumed was greatest when a mix of the two foods were ingested, because more area could be consumed when the individual “balanced the trade-off” between cropping rates and bulk for the two foods. Therefore, we used the simpler area measure.

An individual’s food consumption per unit of body mass (area consumed per milligram body mass per 20 min) was used to rank grasshopper foraging abilities, because this largely eliminated the effects of body mass on food consumption ($r^2 = .03$, $N = 63$, $p < .15$). Finally, foraging ability of the individuals was not related to the presence of parasitic nematodes or parasitoid diptera and hymenoptera in an individual (ANOVA: $F = 0.02$, $df = 1,60$, $p < .88$).

Male foraging ability and spermatophore production

Spermatophore production (measured as mass gain by a female after mating with a male) was highly correlated with a male’s foraging ability (Figure 1: $r^2 = .83$, $N = 15$, $p < .0001$). Neither male body mass ($r^2 = .07$, $N = 15$, $p < .67$) nor copulation time ($r^2 = .03$, $N = 15$, $p < .47$) was correlated with spermatophore production. None of these males was infected by parasites or parasitoids. Therefore, foraging ability was solely correlated with a male’s ability to provide spermatophore mass to a female, suggesting a nontrivial nutrient cost to the male for spermatophore production.

Reproductive rate

Reproductive rates were obtained for 29 pairs (3 pairs were lost when an individual in each escaped). The females in all pairs survived long enough (10–45 days) for functional ovarioles to be produced or eggs laid. Female body mass determined whether any eggs or functional ovarioles were produced (discriminant analysis: $F = 2.97$, $df = 1,26$, $p < .09$), since small females were barren. For 18 pairs with reproductive output, the reproductive rate increased with greater male ($p_{\text{one-sided}} < .006$) and female ($p_{\text{one-sided}} < .06$) foraging ability (Figure 2), indicating parental investment by both sexes. Male foraging ability explained more of the variance than female ability, suggesting substantial paternal investment (Friedel and Gillott, 1977; Pickford and Gillott, 1972a,b; Riegert, 1965).

Nematode parasites in the female or male of a pair (12 of 31 pairs had at least one member parasitized) did not prevent reproduction ($F = 0.24$, $df = 1, 26$, $p < .63$) or reduce the reproductive rate (ANCOVA with foraging abilities: $F = 0.07$, $df = 1, 14$, $p < .79$). Nematodes did decrease female survival, reducing lifetime reproductive output ($F = 5.77$, $df = 1, 26$, $p < .02$). Therefore, nematodes had a limited effect on reproductive rate.

Female mate choice

When a pair of virgin males could not interfere with female mate choice, because they were tethered, females spent more time displaying to the male with the greater foraging ability in 20 of 27 trials; this is significantly greater than random expectation (binomial probability: $p < .006$). Females, when displaying, spent more than 80% of their time displaying toward the better foraging male. Therefore, because females devote more attention to the male that she selects for mating, these results indicate that females tend to choose males that are better foragers. This experiment served as the baseline for comparison with other female mate choice trials.

When a pair of males could not interfere with female mate choice and the better foraging male had mated within 3 h and the poorer forager was a virgin, females still spent more time displaying toward the better foraging male in 17 of 24 trials. This was significantly greater than random expectation (binomial probability: $p < .02$) and was not different from baseline (contingency table: $\chi^2 = 0.38$, $df = 1$, $p < .55$), indicating that recent male investment did not influence female choice or females were unable to assess it.

When a pair of virgin males could not interfere with female mate choice and the better foraging male, but not the poorer, was fed only every other day, females still spent more time displaying toward the better foraging male in 16 of 24 trials. This was significantly greater than random expectation (binomial probability: $p < .04$) and was not different from baseline (contingency table: $\chi^2 = 0.32$, $df = 1$, $p < .59$), indicating that male nutritional status did not influence female choice or females were unable to assess it.

When the initial experiment with a pair of virgin males was repeated with "blinded" females, we found that female selection of males was random (binomial probability: $p < .58$), because they selected the better forager in only 12 of 24 trials, and this was different from the baseline observations (contingency table: $\chi^2 = 3.15$, $df = 1$, $p < .07$), where they preferentially mated with better foraging males. This indicates that females appear to respond to visual stimuli to select males.

When the initial experiment with a pair of virgin males was repeated with males killed by freezing, females would not display toward them. Therefore, females may respond to male movement during the male's courtship display, even though male color might be related to nutrition (Chapman, 1982).

Male mating strategies

In the 24 male mating trials, we observed 82 attempted copulations and 26 attempts led to copulation. Above average-foraging males attempted more copulations than randomly expected (56 of 82; binomial probability: $p < .0005$). For the 26 successful attempts, displays preceded 18 of them and 8 were forcible, so that above average-foraging males achieved more copulations than randomly expected (18 of 26; binomial probability: $p < .025$). Seventeen of the 18 males copulating after displays were above-average foragers (median test: $\chi^2 = 14.22$, $df = 1$, $p < .001$), while males attempting forcible copulation always were below average ($\chi^2 = 8.00$, $df = 1$, $p < .005$) (Figure 3). Furthermore, males copulating after displays

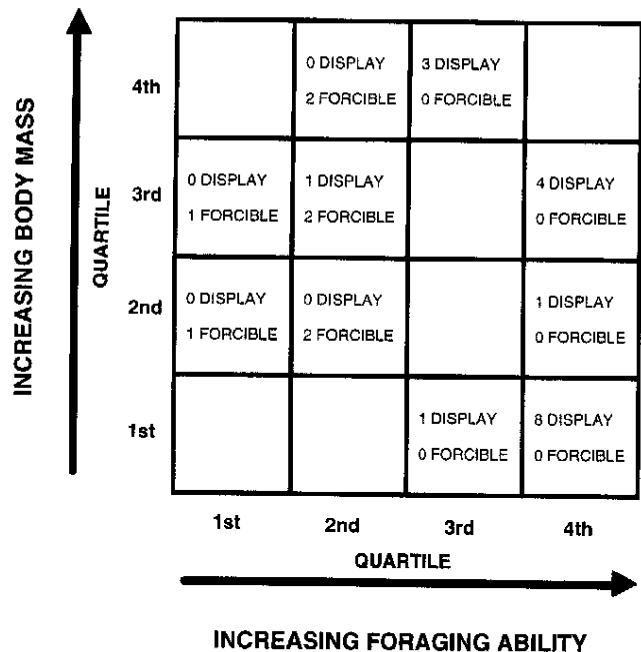


Figure 3

Copulations arising from different male mating strategies (display versus forcible) as a function of the male's ranking in quartiles for foraging ability (see text) and body mass.

(median test: $\chi^2 = 0.22$, $df = 1$, $p < .95$) or forcibly ($\chi^2 = 0.50$, $df = 1$, $p < .90$) were not smaller or larger than the average body mass of males present (Figure 3).

We used discriminant analysis to assess whether body size rank had an effect after the strong effect of foraging ability was considered. As expected, male foraging ability was significant in determining whether males copulated after displaying or attempting to mate forcibly ($F = 65.11$, $df = 1, 24$, $p < .0001$). However, there was a tendency for males copulating forcibly to be large-bodied, below-average foragers, and for males copulating after displaying to be small-bodied, above-average foragers ($F = 2.53$, $df = 1, 24$, $p < .12$). This tendency can be seen in Figure 3, where the distributions of the copulations are indicated and all quartile cells were represented by an equal number of available males.

In the 24 male mating trials, there were eight cases where the same male (four individuals) was used more than once. In some of the trials, the individuals were above-average foragers (four cases) and in others, below average (four cases). In seven of these eight trials, the same male with poorer foragers attempted to copulate after displaying, but with better foragers attempted forcible copulation (binomial probability: $p \leq .03$).

DISCUSSION

Our results indicate that females choose to mate with males that are better foragers. This can be explained in part by a better foraging male's ability to provide greater paternal investment (greater spermatophore mass), a substantial factor in egg production. However, paternal investment cannot entirely explain female mate choice, because choice was not influenced by male nutrition when some males were deprived of food or had recently mated, both of which should reduce a male's ability to provide spermatophores. This suggests that female choice may also involve the male's ability to increase offspring fitness by contributing to offspring genotype, if foraging ability is heritable. However, this cannot be documented

in our study, since the fitness of progeny was not measured. Finally, even though nematode parasitism was greater in our experiments than observed in the field (38% versus <1%), there is no evidence that females selected unparasitized males as mates, because male foraging ability was not correlated with nematode parasitism and females selected better foraging males.

This study has not been able to identify the proximate cues that females employ to ascertain better foraging males, but the ultimate factor seems to be paternal investment, which increases with male foraging ability. However, a number of points can be made to address the proximate cues. Females and males were raised separately, and no food was present during mating experiments; this prevented females from observing male foraging and gaining experience about their ability to provide paternal investment. Likewise, females were unable to observe previous matings by a male or his foraging environment. No correlation between male body mass and foraging ability was found, so females could not use male body mass as a surrogate trait; this finding was counter to results with tettigoniid Orthoptera (Gwynne, 1984). We heard no sounds when males and females vibrated their femora. Furthermore, we did not expect auditory stimuli, because species of the genus *Melanoplus* are not known to communicate by stridulation or crepitation.

Two additional points elucidate whether chemical or visual cues are used. First, experiments with "blinded" females help to elucidate whether females are able to select males on the basis of chemical or visual cues. If "blinded" females are still able to select better foraging males, a chemical cue is suggested. On the other hand, if "blinded" females are no longer able to select better foraging males, a visual cue is suggested. Our results suggest a visual cue. Other mating studies with *M. sanguinipes* males indicate that they employ visual stimuli (Friedel and Gillott, 1977; Pickford and Gillott, 1972a,b; Riegert, 1965). Second, experiments with males killed by freezing help to elucidate whether females respond to males on the basis of color, chemical, or movement cues. If a female can still select the better foraging male after he is frozen, which tends to preserve his color and chemical characteristics, the female may be responding to color or chemical cues. On the other hand, if females no longer select these males, a movement or posture cue may be indicated. While *M. sanguinipes* males attempt to copulate with "dummies" of females (Pickford and Gillot, 1972b), we found that females did not respond to male corpses, and therefore appeared to require male movement or a certain posture. While male foraging ability might be exhibited in the male's display, we could not detect any differences in male displays with foraging ability.

While not identifying how a female ascertains a male's relative foraging ability prior to copulation, our data suggest that females may select the smaller-bodied, above-average foragers. This might be advantageous in terms of paternal investment, because a small-bodied male will have a lower maintenance requirement for nutrients and therefore could allocate more resources to spermatophores. Finally, this raises the issue whether females assess a male's foraging ability by comparing male volume (mass) to length, where length would have to be assessed using a body part (e.g., pronotum) that does not change with feeding (e.g., abdomen). We did not measure length because this did not appear to be a useful measure; females selected the food-deprived, better-foraging males, which would have a reduced volume-to-length ratio.

Males adopted labile alternate mating strategies in an attempt either to reinforce female mate choice (displaying prior to copulation) or to circumvent female choice (forcible copulation) based on their foraging ability relative to other available males. Males attempted to copulate with females after

displaying when their foraging ability was greater than the average for available males, but attempted to copulate forcibly when their foraging was below average. Therefore, males, like females, can assess male foraging ability and vary their mating behavior accordingly. Finally, while all males attempted to disrupt copulations obtained by other males, and larger size may be beneficial in these fights, large size had little effect on male reproductive success, because it was not correlated with foraging ability, spermatophore production, mating strategy, or mating success.

By comparing results from the female mate choice experiments with the male mating strategy experiments, it becomes apparent that alternative male mating behaviors in part circumvented female choice. When males were tethered so they could not interfere with female choice, females chose better foraging males 74% of the time (20 of 27 trials). When males could interfere and forcibly copulate (untethered), better foraging males obtained a similar proportion of the copulation attempts (68%: 56 of 82 attempts) (contingency table: $\chi^2 = 0.20$, $df = 1$, ns). However, with the ability to interfere and to forcibly copulate, copulation attempts by displaying males were successful less than randomly expected, in part due to disruption by other males (18 copulations of 56 attempts) (32%: $\chi^2 = 7.66$, $df = 1$, $p \leq .006$), and forcible copulation accounted for 31% of copulations (8 copulations of 26 copulations). Our results also suggest that larger-bodied males are better at forcible copulation.

Conclusion

We believe our results reflect field behavior for the grasshopper (*Melanoplus sanguinipes*) at the National Bison Range, Montana. Forcible copulation and copulations after displaying were observed in the field. Females have ample opportunity to compare and select among males in the field, because 4 to 12 adult males/m² often occur (Belovsky and Slade, 1995). Finally, the paternal investment advantage for a female to select better foraging males may be enhanced in the field because populations of this grasshopper were food-limited (Belovsky and Slade, 1995).

Our results indicating that females are able to assess male foraging ability and select better foraging males for mating links theoretical studies of foraging and mating strategies. However, the study raises many issues. In particular, how much of this female strategy might be determined by paternal investment and how much by the potentially heritable male trait of foraging ability (Kirpatrick and Ryan, 1991)? These questions are particularly important, because females continued to select better foraging males that had either recently mated or had been deprived of food, which would reduce their paternal investment.

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