

FEMALE MATE CHOICE TACTICS IN A RESOURCE-BASED MATING SYSTEM: FIELD TESTS OF ALTERNATIVE MODELS

MARY L. REID^{1,*} AND JUDY A. STAMPS^{2,†}

¹Department of Biological Sciences and Kananaskis Field Stations, University of Calgary, Calgary, Alberta T2N 1N4, Canada; ²Section of Evolution and Ecology, University of California, Davis, California 95616-8755

Submitted April 5, 1996; Revised November 7, 1996; Accepted November 11, 1996

Abstract.—In this study we test theoretical models of female mate choice tactics in natural populations of pine engravers, *Ips pini* (Say) (Coleoptera: Scolytidae), a species with a resource-based mating system and high search costs. We first develop distinguishing predictions for each of four models of mate choice: random, comparison tactics, and fixed and adjustable thresholds. These predictions relate to commonly collected field data that include the visiting behavior of females and the quality of accepted and rejected mates. Using these types of data, we conclude that pine engravers use an adjustable threshold mate choice tactic because females often accepted the first male encountered, rarely revisited males, visited similar numbers of males in patches of different quality, accepted higher-quality males than those they rejected even on their first encounter with a male in a patch, and had higher acceptance thresholds in high-quality patches than in low-quality patches. This adjustable threshold tactic is consistent with a one-step decision rule and is predicted to occur in species such as pine engravers in which search costs are high and females have information about patch quality before beginning a search in a patch.

Interest in sexual selection and mating systems has prompted a recent spate of theoretical studies on the process by which females choose mates (Janetos 1980; Wittenberger 1983; Real 1990, 1991; Crowley et al. 1991; Dombrowsky and Perrin 1994; Mazalov et al. 1996). However, the proliferation of theoretical studies on mate search tactics has not yet generated a corresponding body of field studies of mate search behavior. One possible reason for the lack of information on mate choice tactics in nature is that theoreticians often neglect to frame their assumptions and predictions in terms of the types of data that field workers can readily collect. For instance, observers may be able to estimate the quality of males accepted and rejected as females first encounter prospective mates, but few models explicitly predict the quality distribution of accepted and rejected males in different search environments (but see Wiegmann et al. 1996).

The ultimate goal of this study is to test current models of female mate search tactics in pine engraver bark beetles, *Ips pini* (Coleoptera: Scolytidae). This species has a resource-based mating system (see below) that provides a needed contrast to lek-mating systems that have dominated field studies to date (Reynolds

* To whom correspondence should be addressed; E-mail: mreid@acs.ucalgary.ca.

† E-mail: jastamps@ucdavis.edu.

and Gross 1990). However, to address the problem of mate search, we first needed to identify tests that are capable of discriminating among alternative models under field conditions. Thus, we first consider four distinct types of tactics that might be employed by females searching for males. Next, we develop a number of tests that can be used to determine which, if any, of these mate search tactics occurs in a species, using types of data that can be collected in field studies of mate search behavior. Then, we briefly consider how search costs and information might affect the optimal mate search tactic for a particular species and situation. Finally, we apply this framework to pine engravers.

MATE SEARCH MODELS

The mate search models most relevant to pine engravers share several basic assumptions: mobile females visit sedentary males, each female searches for a single acceptable mate, females encounter potential mates sequentially rather than simultaneously, and potential mates are encountered randomly with respect to quality. Our use of females as the searching sex reflects the fact that females are generally not attempting to maximize the rate of obtaining items (mates), in contrast to the case for males searching for mates that more closely resembles foraging models (e.g., Parker 1978).

Four major classes of mate search tactics satisfy these assumptions: random mate choice, comparison tactics, fixed thresholds tactics, and adjustable threshold tactics (table 1). Other models of mate search tactics can be viewed as variants or combinations of these four major tactics (e.g., Brown 1981; Real 1990; Dombrovsky and Perrin 1994), and therefore we exclude them for the sake of clarity and brevity. Each of the four tactics makes certain assumptions about the information gathered by females as they search for mates and yields particular predictions about the visitation pattern of females and the quality of accepted and rejected males (table 1).

Comparisons of the quality of accepted and rejected males can be conducted on two spatial scales: within a patch and among patches that differ with respect to male quality. Within a patch, one can focus on the first male visited by each female and compare the quality of males accepted and rejected on these first visits (table 1). A more complete picture of male acceptance and rejection as a function of male quality is provided by a graph in which the quality of accepted males is indicated on the ordinate and the quality of rejected males on the abscissa (fig. 1). This type of graph can be used to compare the quality of accepted and rejected males within a patch, in which case each female provides a single datum based on the mean quality of the males she rejected and accepted during her search. A similar graph can be used to compare the quality of accepted and rejected males in different patches, in which case each datum indicates the mean quality of the accepted and rejected males at one locality.

For the sake of clarity and brevity, we have made several simplifying assumptions in this article. First, we equate patch quality with the mean quality of males within a patch, while acknowledging that variance in male quality might also affect mate search tactics (see, e.g., Real 1990; Wiegmann et al. 1996).

TABLE 1
PREDICTIONS OF FOUR MODELS OF MATE SEARCH TACTICS

MODEL	VISITING BEHAVIOR OF INDIVIDUAL FEMALES			ACCEPTED VERSUS REJECTED MATES		
	INFORMATION*	Single Visits:†	Revisits	Number of Visits Related to Patch Quality?		AMONG PATCHES OF DIFFERENT QUALITY
				First Visit‡	Graph of Pattern§	
Random Comparison	None	Yes	No	No difference	Fig. 1A	Fig. 1A
	Previous visits in patch	No	Yes	No difference	Fig. 1B	Fig. 1B
Fixed threshold	None	Yes	No	Accepted >rejected	Fig. 1C	Fig. 1C
Adjustable threshold	Patch estimate	Yes	No	Accepted >rejected	Fig. 1D	Fig. 1D

* Information about the male quality distribution in a given patch.

† A sizable proportion of females accept the first male they visit.

‡ Quality of males accepted on the first visit versus quality of males rejected on the first visit.

§ Pattern of accepted versus rejected male quality, as in figure 1.

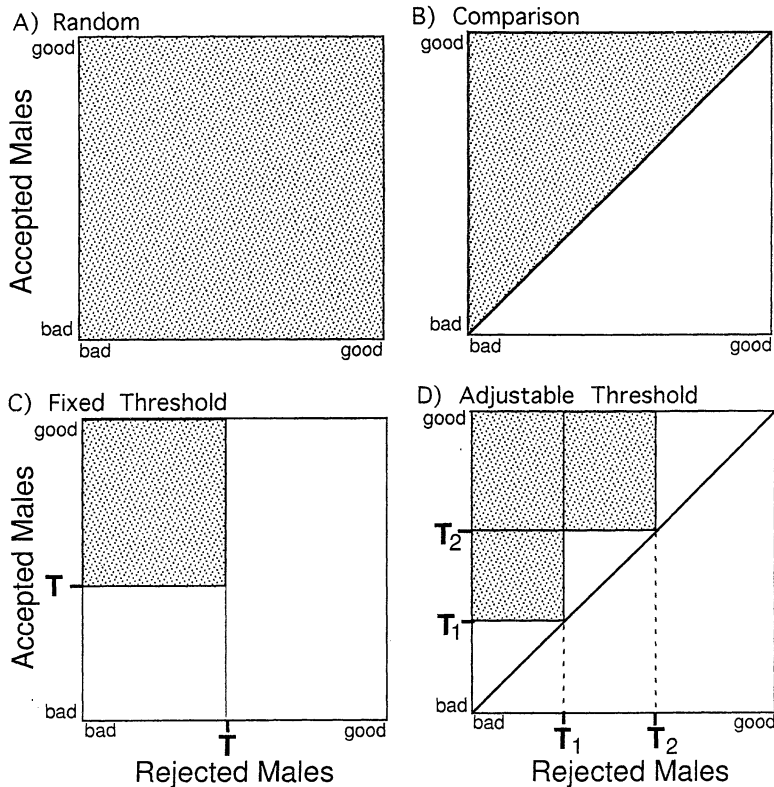


FIG. 1.—Predicted distributions for observations of accepted and rejected male quality, indicated by shaded areas for each of four major models of mate search tactics. Observations for these graphs could be contributed by individual females, or they could reflect the average quality of accepted and rejected males in patches differing in male quality. *A*, Random choice: accepted and rejected males can be of any quality. *B*, Comparison tactics: selected males are better than rejected males for each observation (diagonal line indicates equality of accepted and rejected males); observations for both accepted and rejected males cover the entire range of male quality. *C*, Fixed threshold: there is one threshold (T) for acceptance such that all accepted males fall above this threshold, and all rejected males fall below it. *D*, Adjustable threshold: there are different thresholds for acceptance. When observations are combined for different thresholds (e.g., T_1 and T_2), the pattern converges on the pattern shown in *B*).

Similarly, we join most other workers in assuming that most, if not all, of the females in a given population employ the same mate search tactics (but see Wiegmann et al. 1996). For instance, if threshold tactics are employed, we assume that all of the females searching for mates in a given patch use comparable threshold criteria when selecting a mate.

RANDOM MATE CHOICE

In contrast to the other mate search tactics, the key element for random mate choice is that the probability of accepting a male is unrelated to male quality.

Since female choice is unrelated to male quality, this tactic does not require females to assess male quality before seeking or choosing a mate (table 1). Hence, random choice implies that females will often accept the first male they encounter and that females will not revisit individual males, except by chance, before selecting one of them. In addition, random choice implies that females searching in patches of different quality would visit similar numbers of males before choosing one of them.

Random choice also predicts that there will be no significant difference between the quality of males accepted and rejected on first visits (or any visits) within a patch. Consequently, data from individual females within a patch could fall at any location within the graph of accepted versus rejected male quality (fig. 1A). The same pattern should hold across patches.

COMPARISON MATE SEARCH TACTICS

If a female is seeking the best available male, an obvious tactic is for her to investigate a number of males and then choose the best from within her sample. This has become known as the best-of- n tactic (Janetos 1980). Subsequently, other versions of comparison tactics have been proposed (e.g., Wittenberger 1983; see also Wiegmann et al. 1996). When using a comparison tactic, females assess the quality of available males in their sample as they visit the males in that patch so females need not have a prior estimate of mean patch quality before they begin to search (Real 1990).

Within patches, comparison tactics make two unique predictions that distinguish this type of tactic from the other three classes of tactics under discussion. First, females should not accept the first male they encounter (but see Wiegmann et al. 1996). Second, many females should revisit males, returning to the best male in their sample after investigating other males in the patch. Across patches, comparison tactics predict that the number of visits per female will be similar in patches with different mean male quality, provided that the variance in male quality is comparable in each patch (Real 1990; Wiegmann et al. 1996).

Comparison tactics make no prediction about differences between the quality of males accepted and rejected on first visits, since females using comparison tactics would rarely (if ever) accept the first male they encountered (see above). However, comparison tactics do make specific predictions about the quality of accepted and rejected males within and among patches (table 1). First, for any given female, the quality of the male she accepts should be higher than the quality of the males she rejects. Hence, within any given patch, observations for individual females should fall above the line of equality on the male quality graph (fig. 1B). However, different females would be likely to encounter different subsets of males within a patch. Since females are assumed to encounter males randomly with respect to quality, some females might encounter mostly low-quality males, while other females in the same patch might encounter mostly high-quality males. Thus, within a patch, observations from individual females could fall anywhere above the line of equality.

Following the same logic, a similar pattern is expected when comparing the

quality of accepted and rejected males in patches with males of different quality. In this situation, the mean quality of accepted males should be higher than the mean quality of rejected males within any given patch. However, observations for patches of different quality could fall anywhere above the line of equality (table 1), because in low-quality patches females would accept and reject males of low quality, while in high-quality patches females would accept and reject males of high quality.

THRESHOLD TACTICS

In contrast to random or comparison tactics, threshold tactics assume that females possess information about male quality distributions before they begin to search for mates within a given patch. Based on this information, females establish a threshold criterion for male acceptance. Thereafter, the first male that exceeds this threshold is accepted as a mate. Some recent models consider the situation in which thresholds can be altered during search within a patch (e.g., Dombrovsky and Perrin 1994; Mazalov et al. 1996), but for the sake of brevity we focus on thresholds set before a search (see also the Discussion).

Thresholds can be of two types: fixed and adjustable, depending on whether the threshold for acceptance varies as a function of the quality of males available to a given female. A fixed threshold mating tactic can be viewed as one in which each female uses the same threshold acceptance criteria, regardless of the mating opportunities that are available to her (e.g., Moore and Moore 1988; Zuk et al. 1990). Conversely, adjustable thresholds occur when females adjust their criteria for acceptance based on the quality of males that are available to them. Although the term *adjustable threshold* is newly coined, this concept is implicit in several influential models of mate search behavior. For instance, models of the optimal one-step decision strategy (Janetos 1980; Real 1990; Wiegmann et al. 1996) assume that females assess the quality distribution of males within a given patch so as to set the acceptance threshold that yields the highest expected fitness when searching in that patch.

Both fixed and adjustable threshold tactics predict that females will sometimes accept the first male they encounter (table 1). This follows from the assumptions that a female sets her acceptance threshold before entering a patch and that the first male will be accepted if he exceeds this threshold. Threshold tactics do not predict revisits of particular males, except by chance. These two sets of predictions can be used to distinguish threshold tactics from comparison tactics (see above; table 1).

Fixed and adjustable threshold tactics differ from each other with respect to the number of visits females should make when searching in patches of different quality (table 1). If thresholds are fixed, then the mean number of visits per female should vary as a function of patch quality, with fewer visits required to find an acceptable male in high-quality patches than in low-quality patches. In contrast, if females are able to assess patch quality before they begin to search, then females using adjustable thresholds should make a similar number of visits in all patches.

Within a patch, fixed and adjustable threshold tactics make the same prediction about the quality of accepted and rejected males: males accepted on first visits should be of higher quality than males rejected on first visits (table 1). Similarly, in both cases, a graph of accepted versus rejected male quality should produce a series of observations lying within a rectangular space, bounded by the threshold value on each axis (fig. 1C). That is, for each female, the quality of the accepted male should lie anywhere above the threshold, and the quality of rejected males should lie anywhere below the threshold.

In contrast, between-patch comparisons of accepted and rejected males yield different patterns for fixed and adjusted threshold mate search tactics. If females use a fixed threshold, then observations for all patches should fall into the same rectangle (fig. 1C). However, an adjustable threshold predicts a different pattern of observations, because the optimal threshold will vary among patches of different quality (Real 1990). In this case, the observations for each patch would be confined to a different rectangle on the graph (fig. 1D). Now the permissible area for observations across patches would have indistinct boundaries, and at the extreme, observations for different patches could lie anywhere above the line of equality (similar to fig. 1B). Hence, one way to distinguish between fixed and adjustable thresholds is to compare the mean quality of accepted and rejected males across patches that differ with respect to male quality.

OPTIMAL MATE SEARCH BEHAVIOR

The optimal search tactic in a given environment is expected to depend on two factors: search costs and information about male quality distributions. The importance of search costs is illustrated by theoretical studies comparing the fitness payoffs of best-of- n tactics with the fitness payoffs from using threshold tactics. These studies suggest that if search costs are negligible, a best-of- n tactic yields higher fitness than does a threshold tactic (Janetos 1980). However, if search costs are appreciable, the optimal one-step decision strategy (an adjustable threshold tactic) yields higher fitness than does the best-of- n tactic (Real 1990). The latter results are especially germane to the present study, because females in resource-based mating systems are likely to experience higher search costs than are the females in a lek mating systems, although quantitative estimates of search costs are lacking for many species (Reynolds and Gross 1990).

Search costs may also influence the expression of a particular mate search tactic. For instance, if females use a best-of- n comparison tactic, the number of males sampled per female is expected to decline as search costs increase (Wittenberger 1983; Real 1990). Similarly, if females use an adjustable threshold tactic, both the acceptance threshold and the number of males sampled by each female are expected to decline as search costs increase (Real 1990). Indeed, if search costs are very high, theory suggests that females should accept the first male they meet, in which case females would be mating randomly with respect to male quality.

Optimal mate search tactics are also likely to vary as a function of the information that females have about their mating options. Thus far, however, infor-

mation about male quality has played little role in evaluating optimal search tactics. For instance, Real (1990) assumed that females have perfect knowledge of quality distribution of males in a given patch. In contrast, the foraging literature views information about quality distribution as a central problem (Stephens and Krebs 1986). We suggest that the mate search literature might also benefit from an explicit consideration of the information available to searching individuals (e.g., Mazalov et al. 1996).

The four classes of mate search tactics differ in the information that females require (see above; table 1). Consequently, the types of information available to searching females are likely to affect the optimal mate search tactics. For instance, if male quality varies among patches but females have no way to assess the quality of males in a patch before a search, then adjustable thresholds are not an option. In this situation, females might use comparison tactics to acquire information about the quality of the males in a given patch. Alternatively, comparison tactics might not be optimal if high search costs discourage visits to many males before selecting a mate. In that case, females might employ a fixed threshold tactic, setting a threshold based on a global expectation of male quality, before visiting any males. If nothing else, these scenarios illustrate the importance of considering both information and search costs when trying to predict the optimal mate search tactics for a species.

METHODS

Pine Engraver Breeding Biology

The pine engraver is a small (4-mm long) polygynous species in which males provide resources to their mates and offspring (fig. 2; Reid and Roitberg 1994). Each male pine engraver establishes a mating site (nuptial chamber) beneath the bark of a tree (Swaby and Rudinsky 1976). After settling, males remain within their nuptial chambers, where they are visited by prospecting females. After landing on a tree, females walk from one mating site to another while searching for a mate. However, once a female has accepted a male by entering his nuptial chamber, she remains with him for most, if not all, of her reproductive life span. Over the next several weeks, she constructs an egg gallery radiating from the nuptial chamber and lays several eggs each day within her gallery. Males assist their mates by keeping their egg galleries clear of particles produced during gallery construction and by defending the galleries against predators of offspring (Reid and Roitberg 1994). After oviposition ceases, parents often reemerge to seek other breeding sites, but their prospects of breeding again are thought to be limited (Cameron and Borden 1967; Garraway and Freeman 1981; Amman and Bartos 1991). Thus, mate choice is likely to be important for female pine engravers, because females commit most of their fitness to one male and because males provide resources and genes to their offspring.

Male pine engravers colonize susceptible trees en masse, usually reaching high densities (two to three males per 100 cm²) within a week. Males obtain an average of three females within 3 d of arriving at a tree, after which mate at-

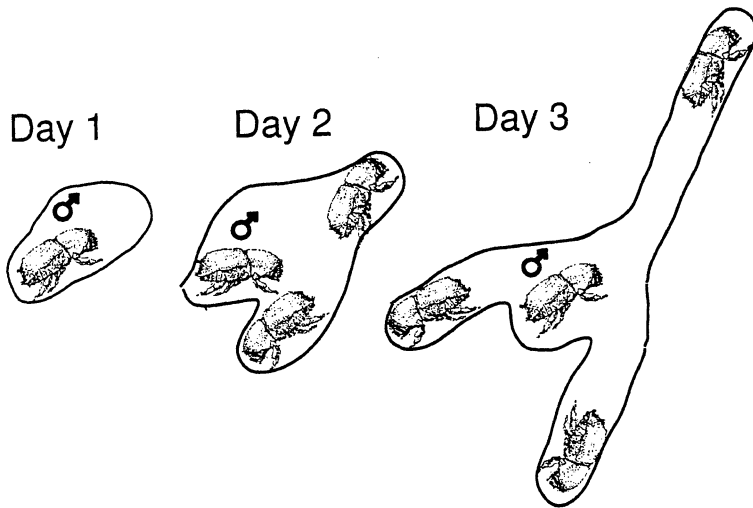


FIG. 2.—A typical mating phenology of a male pine engraver, as would be observed by exposing the tree's phloem on three successive days. The male is indicated; the other individuals are females. During day 1, the male completes his nuptial chamber. Females begin to accept him once the chamber is complete and begin to extend egg galleries, and by day 3 he has his full complement of mates.

traction virtually ceases (Reid and Roitberg 1994). Polygyny in this species appears to be due to a biased sex ratio (Anderson 1948), as few males remain unmated at a breeding site (Reid 1992). In this type of mating system, the first female to mate with a male has higher reproductive success than does the second or later mate of that same male (Schmitz 1972; Kirkendall 1989; M. L. Reid, personal observation). Hence, it is not surprising that females prefer unmated males to already mated males (Swaby and Rudinsky 1976; Reid 1992). The relatively synchronous arrival of males means that the availability of unmated males changes dramatically as colonization proceeds, typically from an abundance of unmated males at the beginning of colonization to a scarcity of unmated males a few days later.

Female pine engravers encounter two search costs when looking for a mate. The first of these is preemption by other females (an opportunity cost; Real 1990), since many females simultaneously search for potential mates. In pine engravers preemption occurs when a female arrives at a male's entrance to find another female already waiting there; when this happens, the second female usually moves off to look for another mate (Reid 1992). Overall, females encounter waiting females on 8% of their visits to males (Reid 1992). Second, pine engravers walking on the bark's surface are vulnerable to attack by a parasitoid, *Tomicobia tibialis* (Hymenoptera: Pteromalidae); this parasitoid reduces female reproductive potential by at least 50% (Senger and Roitberg 1992). However, a female's chances of being parasitized while searching for a mate varied widely within and between years, ranging from a low of 0% for all sites in 1990 to a

maximum of 30.8% at one site sampled early in the colonization period in 1988 (Reid 1992; see also below).

Information about male quality is potentially available to female pine engravers from male pheromones. In many species of bark beetles, including pine engravers, males begin to produce attractive pheromones as they dig their nuptial chamber. Pheromone production changes as a function of male mating status, and beetles can detect these pheromones before they land at a breeding colony (Swaby and Rudinsky 1976; Byers 1981; Birgersson et al. 1984). Thus, searching females might have information about the male quality distribution at a site before they begin to visit males at that site.

Field Studies

Pine engravers were observed during the first spring dispersal flight, which is composed of overwintered adults, in 1988, 1989, and 1990. The beetles were studied in 1988 and 1989 at a site near Riske Creek in the central interior of British Columbia, Canada, and in 1990 near Princeton in south-central British Columbia. Each year, three to five breeding sites were established within 2 km of each other. Each site consisted of four to 12 logs from freshly felled lodgepole pine trees (*Pinus contorta* var. *latifolia* Engelmann) placed end to end on the ground in shaded but open areas, except for one site that consisted of a 150-cm long remnant of a felled tree. Logs varied in size between sites, from 60-cm long and 10 cm in diameter, to 100-cm long and 27 cm in diameter, and the number of logs per site varied from four (for the largest logs) to 12 (for the smaller logs).

Beetles naturally colonized the upper surfaces of these logs, and the phenologies of arriving males and predators were quantified to describe the search environment for females. Daily counts of males and predators for the entire site (all logs combined) were used because logs within any given site were quite similar. Each day in 1989 and 1990, parasitoids were surveyed by instantaneous scan samples between observations of searching females.

Each morning, logs were searched for new nuptial chambers, which were apparent from the accumulation of phloem particles around each entrance, and each new chamber was marked with a color-coded tack. Males associated with the new chambers, which we call "new males," were assumed to have arrived the previous day (i.e., their galleries were 1 d old). Females sometimes visited chambers that we had not detected because of the small accumulation of phloem particles; these males were assigned a gallery age of 0 d.

We used two methods to assess the quality of males available to newly arriving females. In most cases, we used the age of male galleries as our estimate of male quality, because this character could be observed nondestructively. We also excavated the breeding sites of some males to determine their mating status (number of mates) and gallery length. For each of these males, we used both total gallery length (summed for all mates) and average gallery length (total length/number of mates) to estimate the extent of gallery development. Given the breeding biology of pine engravers, we expected females to prefer males with fewer mates and short galleries. Consequently, we plotted mating status

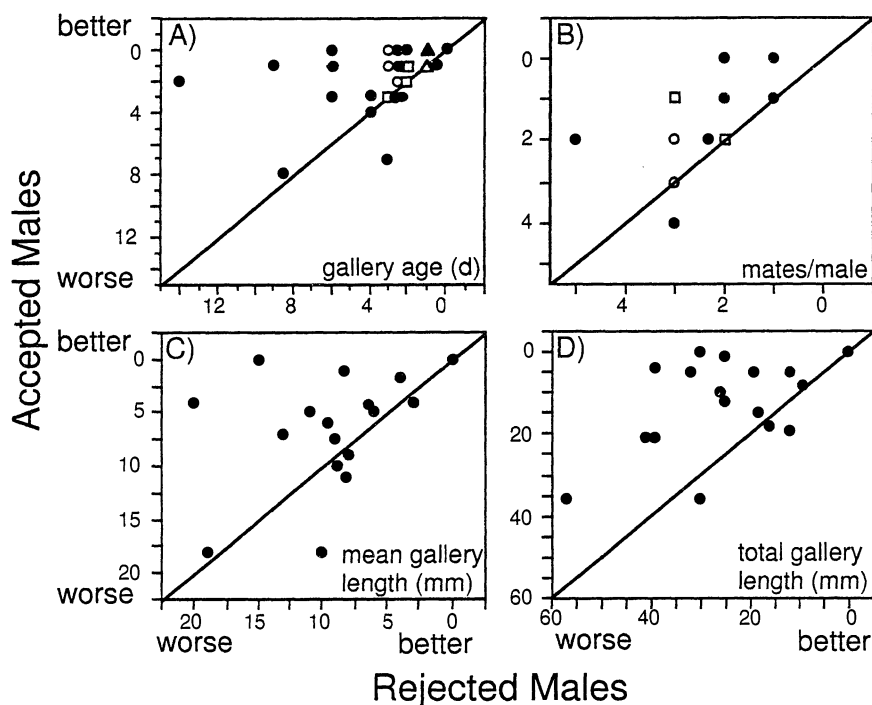


FIG. 3.—For individual females, a comparison of the characteristics of the accepted male versus the average characteristics of the rejected male(s). Symbols indicate the number of females indicated by each point: solid circles = 1; open circles = 2; open squares = 3; solid triangle = 6; open triangle = 12. Diagonal lines indicate line of equality of chosen and rejected males (see fig. 1).

and gallery characteristics with the axes reversed, such that 0 values (best) were at the right side of the abscissa and at the top of the ordinate (e.g., fig. 3).

A patch of males is defined as those males present at a breeding site on a given day. Although this meant that some males were counted on more than one day, from the perspective of a newly arrived female, a log in which most of the males were new with short galleries would differ in quality from the same log several days later, when those same males had several mates and longer galleries. We used the proportion of males that were new to estimate patch quality and assumed that the proportion of new males in a patch was positively related to male quality for that patch.

To follow individual females after they landed at a site, we marked them with fluorescent powder gently applied with a fine paintbrush to the posterior end of the elytra. Females can be visually distinguished from males by the absence of an enlarged elytral spine (Lanier and Cameron 1969). Female search behavior (visits to males) was timed with a stopwatch and recorded continuously from the time that females were discovered, preferably landing at the site, until they had

entered a nuptial chamber or were lost from view. In all, 205 females were observed in 36 patches at 11 sites, with one to 21 females observed per site.

RESULTS

General Patterns of Female Search Behavior

Female pine engravers confined their search to a single patch when looking for a mate. Of the 205 females observed on logs over 3 yr, only 10 flew away from the log, and none of the 10 females who flew away visited any males before leaving. Hence, after landing on a log, females seemed committed to search for a mate on that log.

Complete records of search behavior were available for 92 females that were observed from the time they landed on a log until they entered a male's nuptial chamber. On average, these females chose a mate in less than 2 min, but there was considerable variation among females in search time (mean search time = 1.70 min, 95% confidence interval [CI] = 1.28–2.25, maximum = 71 min, $n = 92$; all durations were ln-transformed for analysis). Search duration was positively related to the number of males visited ($r = 0.577$, $n = 92$, $P < .001$; both duration and visits were ln-transformed).

After locating a male, a female spent some time at his gallery entrance before accepting him or walking off to find another male. Females spent more time at the entrances of males that they eventually accepted (mean = 3.10 min, 95% CI = 1.91–4.91 min, $n = 65$) than at the entrances of males that they eventually rejected (mean 0.30 min, CI = 0.23–0.38 min, $n = 178$; $t = 7.06$, $P < .0001$). In only one visit of 178 rejections did a female reject a male after spending more than 17 min at his entrance (this female spent 21.6 min at the male's entrance before rejecting him). Therefore, in subsequent analyses we used a persistence of 17 min as our criterion of mate choice for females that we did not see fully enter a male's chamber during our behavioral observations. These females accounted for 8.6% of all of the choices observed in this study.

Testing Assumptions of Mate Search Tactics Models

Female pine engravers clearly satisfy the first two assumptions of the mate search tactics outlined earlier. That is, each female mates with one male, and females sequentially visit males before choosing one of them. The third assumption, that females encounter males at random with respect to male quality, needs to be examined explicitly. This assumption predicts that the relationship between the proportion of high-quality males encountered and the proportion of high-quality males available should have a slope of 1 and an intercept of 0. Conversely, the ability to encounter high-quality males preferentially implies that there would be no relationship between the quality of encountered males and their availability in the patch. For each patch, we noted the proportion of female first visits that were made to new males and the proportion of new males that were available in that patch. This analysis was confined to patches in which at least five females were observed as they visited their first male.

TABLE 2

PEARSON CORRELATION COEFFICIENTS AMONG DIFFERENT INDEXES OF MALE QUALITY FOR 75 MALES WHOSE GALLERIES WERE EXCAVATED IN THE FIELD

	Gallery Age	Mates/Male	Mean Gallery Length ^a
Mates/male	.368**		
Gallery length: ^a			
Length/mate	.575***	.648***	
Total length	.603***	.817***	.955***

^a ln-transformed.

** $P < .01$.

*** $P < .001$.

TABLE 3

DIFFERENCES BETWEEN MALES ACCEPTED AND REJECTED BY INDIVIDUAL FEMALE PINE ENGRAVERS FOR FOUR INDEXES OF MALE QUALITY

Male Character	Number of Females	Mean Difference*	t †	P
Chamber age (d)	48	1.15	3.274	.002
Number of mates/male	17	.98	3.653	.002
Gallery length/mate (mm)	17	4.15	2.347	.031
Total gallery length (mm)	17	16.09	3.627	.002

* Difference is average of all rejected males minus chosen male.

† Paired t -test.

The regression of proportion of new males encountered on first visits versus the proportion of new males available in the patch largely conformed to the predictions of random encounter. The slope of the linear relationship was not significantly different from 1 (0.82, 95% CI = 0.52–1.13, $n = 18$ patches) but was significantly >0 ($t = 5.78$, $P < .0005$). However, the intercept was slightly >0 ($0.16 \pm .07$, $t = 2.45$, $P = .03$), indicating that new males were encountered somewhat disproportionately. On the other hand, females clearly did not limit their first visits to new males, so even if visits were not absolutely random with respect to male quality, the problem of mate search tactics remains.

The Mate Search Tactics of Pine Engravers

Random choice.—To determine whether female pine engravers chose males randomly with respect to quality, we estimated the quality of the males accepted and rejected by individual females who visited at least two males before accepting one of them. For this analysis, male galleries were excavated after females made their choices, so that male age, number of mates, and gallery length could be compared for accepted and rejected males. Each of the measures of males quality were highly correlated with each other (table 2). The analyses indicated that female pine engravers preferred recently arrived males with few mates and short galleries (table 3). When accepted male quality was plotted

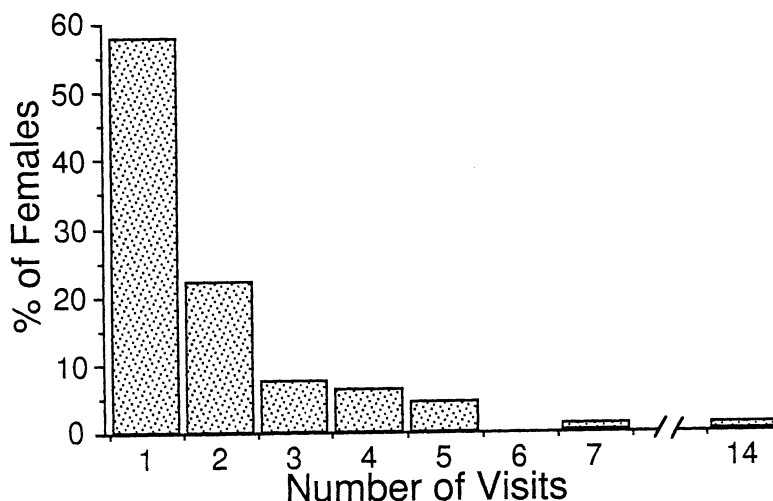


FIG. 4.—The number of visits made by 92 females that were observed throughout the search process. Most females accepted the first male they encountered.

against rejected male quality for individual females, most observations lay above the diagonal line of equality of rejected and accepted males (fig. 3). Hence, female pine engravers were not mating randomly with respect to male quality.

Note, however, that when females from different patches were plotted on the same graph, accepted and rejected males could not be distinguished by a single threshold. Instead, both sets of males had the full range of each character represented, largely filling the area above the line of equality (fig. 3). This pattern indicates that females differed in their choices, with some females accepting males that other females would have rejected.

Comparison tactics.—If female pine engravers use a comparison tactic when choosing mates, they would be expected to visit two or more males before choosing one of them (table 1). However, of the 92 females that were observed from the time they landed until they chose a mate, 57.6% chose the first male they encountered (fig. 4). The proportion of females that made single visits can also be estimated another way, by looking at the proportion of females that accepted the first male they encountered after landing. This sample of females included some individuals that disappeared from view before entering a nuptial chamber. Using this method, we estimated that 44.6% of 121 females accepted the first male they visited. This proportion is significantly smaller than the proportion of single visits observed for females whose entire search sequence was observed ($\chi^2 = 5.06$, $df = 1$, $P = .025$), suggesting that our observations of complete search sequences may have been biased in favor of females who visited fewer males before accepting a mate. However, regardless of which method we used, a sizable proportion of the females in this study accepted the first male they visited.

Comparison tactics also predict that females will revisit particular males, re-



FIG. 5.—The mean quality of the males accepted and rejected on first visits by females searching in 13 different patches. Each point represents a different patch; the diagonal line represents the line of equality for accepted and rejected males. In this analysis, age of a male's gallery was used as the index of male quality.

turning to mate with the best male in their sample (table 1). However, female pine engravers almost never revisited males. Only 12 of 205 females revisited males, and nine of these returned to a male that they had just left. Only one female mated with the revisited male. The rarity of revisits, in combination with the high proportion of females accepting the first encountered male, indicates that pine engravers do not use comparison tactics when searching for mates.

Threshold tactics.—One way to detect the use of a threshold tactic is to compare the quality of males accepted and rejected on first visits, for different females searching in the same patch (table 1). Threshold tactics predict that the males accepted on first visits should be of higher quality than the males rejected on first visits. We tested this prediction using data from 13 patches in which females accepted and rejected first-visited males, and we used male gallery age as our estimate of male quality. In nine of 13 patches, the average quality of males accepted on the first visit was higher than the average quality of the males rejected on the first visit, while another two patches had accepted and rejected males of equal quality (fig. 5; Wilcoxon ranked-pairs test, $z = -2.49$, $n = 11$, $P < .02$). When combined with the observation that roughly half of female pine engravers accepted the first male they visited in a patch, these results suggest that pine engravers used a threshold tactic when searching for a mate.

Fixed versus adjustable threshold tactics.—As noted earlier, observations

from patches of different quality can be used to determine whether individuals are using fixed or adjustable thresholds when searching for mates. The first way to distinguish between these tactics is to measure the number of visits females make in patches of different quality (table 1), recalling that the number of visits should vary inversely with patch quality for a fixed threshold tactic but remain constant for an adjustable threshold tactic. We estimated the number of female visits using two different methods: for females with complete search sequences, we computed the frequency distribution of visits for all females observed in the patch; and for those females whose first visit was observed, we estimated the proportion that accepted a male on the first visit. For these analyses, we focused on patches at the extremes with respect to male quality: high-quality patches in which $\geq 80\%$ of the males were new and low-quality patches in which $\leq 20\%$ of the males were new.

Both sets of analyses produced the same result: patch quality had no discernible effect on the number of visits per female. The frequency distributions of number of visits were comparable in high- and low-quality patches ($\chi^2 = 4.00$, $df = 2$, $P > .13$), and the proportion of females accepting the first male they visited was comparable for the two types of patches (high quality = 37.5% of 32 females, low quality = 55.6% of 36 females, $\chi^2 = 2.22$, $df = 1$, $P > .13$). Hence, the number of visits females made while searching was not affected by the quality of males in a patch, a result suggesting that females were not using a fixed threshold tactic.

Fixed and adjustable thresholds can also be distinguished by looking at the quality of males accepted and rejected in patches of different quality (table 1). Fixed thresholds predict there will be no overlap in the quality of accepted and rejected males even among patches that differ in quality, while adjustable thresholds predict that the quality of accepted and rejected males will vary as a function of patch quality. Earlier analyses have already suggested that the quality of accepted and rejected males do overlap in quality, in our comparison of accepted and rejected males of individual females (fig. 3) and in our comparison of first visits across different patches (fig. 5). The pattern of observations scattered above the diagonal line of equal male quality, seen in both figures 3 and 5, is what one would expect if females used an adjustable, but not a fixed, threshold tactic (fig. 1D, table 1).

More important, the adjustable threshold tactic predicts that female thresholds should vary as a function of the quality of the males in a patch. We tested this prediction in two ways: by examining the quality of accepted and rejected males as a function of patch quality and by examining whether the probability of accepting a male of a particular quality varied with patch quality.

We compared the quality of accepted and rejected males as a function of the percentage of new males in a patch, using gallery age as our index of male quality. We focused on three groups of males: males chosen on a female's first visit, males chosen after a female had rejected one or more other males, and males rejected on a female's first visit. Our first question was whether females changed their threshold after searching for males in a patch. However, after controlling for the proportion of new males in a patch, there was no indication that males

TABLE 4

ANCOVAs EXAMINING THE GALLERY AGE OF VISITED MALE PINE ENGRAVERS AS A FUNCTION OF THE PROPORTION OF NEW MALES IN A PATCH AND (A) VISIT ORDER FOR ACCEPTED MALES (ON FIRST VISIT OR LATER VISITS) AND (B) ACCEPTANCE STATUS (ACCEPTED OR REJECTED) OF MALE PINE ENGRAVERS

	MS	df	F	P
A. Males accepted on first visits and later visits:				
Visit type (first or later)	.14	1, 92	.56	>.4
Proportion of new males*	4.28	1, 92	19.00	<.001
B. Accepted and rejected males:				
Acceptance status (accepted/rejected)	1.66	1, 152	6.08	.015
Proportion of new males*	8.88	1, 152	32.42	<.0001

NOTE.—All slopes were homogeneous ($P > .3$).

* In-transformed covariate.

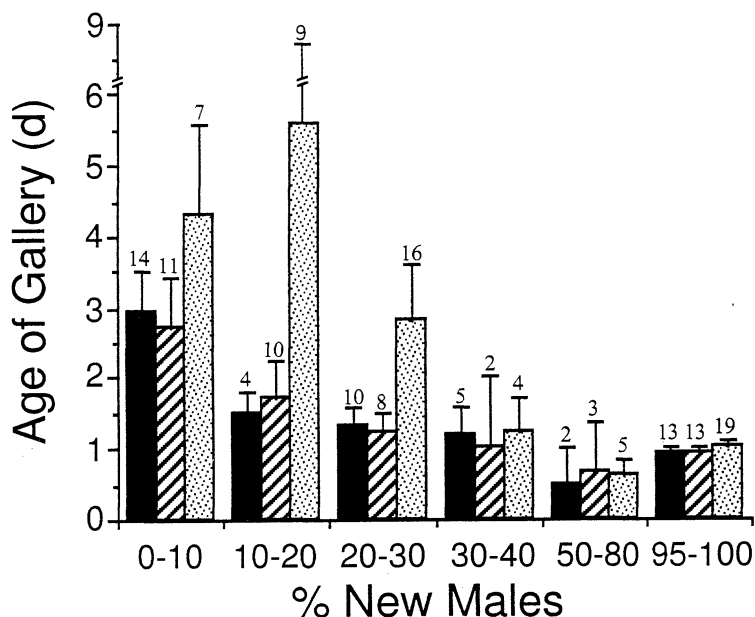


FIG. 6.—The age of male galleries (mean, SE, and sample size) as a function of the percentage of new males in a patch, for three categories of males. *Solid bars*, males accepted by a female on her first visit in a patch; *hatched bars*, males accepted by females who rejected one or more previous males; *stippled bars*, males rejected by females on the first visit in a patch. Data are combined across patches according to categories of percentage of new males.

chosen on a first visit differed in quality from males chosen by females who had previously rejected other males (table 4A; fig. 6). Hence, in a subsequent ANCOVA, we combined males accepted on first and on later visits to estimate the quality of males accepted in a patch.

The adjustable threshold tactic predicts that after controlling for patch quality,

accepted males should be better than rejected males and that the quality of accepted and rejected males should vary systematically as a function of patch quality. Both of these predictions were supported in the current study (table 4B; fig. 6). Also as predicted, females searching in high-quality patches rejected males that were better than the males accepted by females searching in low-quality patches. For example, females in patches with 0%–10% new males accepted males whose galleries were 3 d old, whereas females searching in patches with 95%–100% new males rejected males who had 1-d-old galleries (fig. 6). While this pattern of acceptance might seem similar to that expected if females accepted and rejected males at random, we emphasize that this and previous analyses clearly demonstrate that female pine engravers did not accept males randomly with respect to quality. Consequently, females must be adjusting their acceptance thresholds.

Adjustable thresholds were also evident when we examined the effect of patch quality on the probability of accepting a male of a given quality. The adjustable threshold model predicts that females will be less likely to accept a low-quality male when high-quality males are abundant than when few high-quality males are available. To test this, we examined the probability of accepting an age 2 male (a low-quality breeding situation) as a function of the proportion of new males in a patch. For this analysis, we included accepted males and males rejected by females on their first observed visit (as for the previous ANCOVA). We found that the probability of accepting an age 2 male declined as the proportion of new males increased (logistic regression with ln-transformation of proportion of new males: $\log(p/[1 - p]) = 4.78 - 1.44x$, $n = 31$ females, $\chi^2 = 4.02$, $df = 1$, $P = .045$). Thus, female pine engravers adjusted their acceptance threshold in relation to patch quality.

Search Tactics and Search Costs

Pine engraver females are likely to encounter at least two costs when searching for mates: risk of preemption by other females, and risk of parasitism by *T. tibialis* (see above). In theory, animals are expected to search less when search costs are higher (Wittenberger 1983; Real 1990). However, female pine engravers did not detectably alter their visiting behavior in response to either female competitors or parasitoids. Across patches, there was no correlation between the mean number of visits females made before mating and the proportion of visits in which females encountered other, waiting females at a male's entrance (mean number of visits per female vs. proportion of visits with female-female encounters: $r = 0.063$, $n = 22$ patches, $P > .50$; overall proportion of visits with female-female encounters was 8.0% of 374 visits; range among patches was 0%–28.0%). Similarly, there was no detectable relationship between the density of parasitoids in a given patch and the number of visits females made in that patch (mean number of visits vs. density of parasitoids: Spearman $r = 0.44$, $n = 13$ patches, $P = .13$; parasitoid densities per patch: mean \pm SD = 8.6 ± 14.2 parasitoids/m², range = 0–45.6 parasitoids/m²). Hence, although theory suggests that females should alter their search tactics in response to variation in

search costs, we were unable to find any evidence of such facultative responses in the current study.

DISCUSSION

Our results suggest that female pine engravers use an adjustable threshold tactic when choosing mates. Conversely, we were able to rule out three other possible mate search tactics for this species: random choice, comparison tactics, and fixed threshold tactics. Females appeared to adjust their acceptance threshold before visiting any males within a patch, because female thresholds varied as a function of the quality of males in a patch, and these thresholds were evident as soon as females began to encounter males in that patch. As far as we can tell, this is the first empirical evidence for a prepatch adjustable threshold, although some prominent theoretical models of optimal mate search assume that females can assess male quality distributions before they begin to search for a mate (Real 1990). Given the results of this study, it would be interesting to pursue experimental tests of prepatch adjustable thresholds in pine engravers, where prior experience is manipulated.

The results of this study also support previous suggestions that search costs affect the optimal mate search tactic for a given species. As was noted earlier, current theory suggests that comparison tactics may yield the highest fitness for females if search costs are negligible, whereas threshold tactics are favored if search costs are significant (Real 1990). Female pine engravers searching for mates are subject to two different search costs: the risk of parasitism from the parasitoid *Tomicobia tibialis* and the risk of preemption by other females. As shown in this article, both of these search costs may be appreciable. Hence, this is a system where we would expect threshold tactics, and our study supports this expectation.

In contrast, most previous studies of mate search tactics have focused on lekking species, in which potential males are clustered closely together and in which any given male can potentially mate with large numbers of females. In this situation, search costs are apt to be low (Reynolds and Gross 1990), and, in fact, search costs appear to be negligible in all of the lekking species studied thus far (Pruett-Jones and Pruett-Jones 1990; Reynolds and Gross 1990; Petrie et al. 1991; Gibson and Bachman 1992). When search costs are low, a comparison mate search tactic, such as a best-of- n tactic, can be an effective strategy (Janetos 1980; Real 1990). As expected, then, females seem to use a comparison tactic, judging by revisiting behavior, in the lekking species studied to date (Beuchner and Schloeth 1965; Gibson and Bradbury 1986; Trail and Adams 1989; Pruett-Jones and Pruett-Jones 1990; Petrie et al. 1991; but see Wiegmann et al. 1996).

Comparison tactics have also been reported for several studies of birds with resource-based mating systems where there is a risk of preemption (Bensch and Hasselquist 1992; Dale et al. 1992). In these species, females rarely accept the first male encountered and revisit males. However, in the populations studied, males were in relatively close proximity, and both travel and time costs ap-

peared to be low. In the one study that varied travel costs of search by changing the distance between males, females did not seem to use a comparison tactic when males were far apart (Alatalo et al. 1988).

Although support for thresholds in mate search is currently sparse (but see Moore and Moore 1988; Zuk et al. 1990), it might be worthwhile to focus on species with high search costs when looking for threshold search tactics. For instance, scorpion flies (*Hylobittacus apicalis*) are well known for the nuptial gifts that males provide to females, and individuals appear to be vulnerable to predators while searching for mates (Thornhill 1980). Studies of mate choice in this species have revealed that the basic assumptions of sequential encounter and random encounter are satisfied in nature, and they have shown that the females of this species accept any male bearing a nuptial gift above a threshold size (Thornhill 1980). There are indications that the quality of males available to females varies spatially and temporally in this species, but the female threshold does not appear to vary as a function of patch quality. Hence, female *H. apicalis* may use a fixed threshold tactic when choosing mates. Natterjack toads (*Bufo calamita*) provide another example of a species with search costs, in that females risk preemption by other females when looking for mates (Arak 1988). This species satisfies the assumption that females encounter males sequentially, and females exhibit behavior reminiscent of a threshold tactic: half of females accept the first male encountered, females rarely revisit males, and accepted males are better than rejected males. The quality of male natterjack toads accepted or rejected on first visits was not reported, but for those females who visited more than one male, a threshold tactic in which females accept the first male better than the previous one (Mitchell 1975) fits the data reasonably well. Thus, the threshold tactics that we report here for pine engravers may be present in other species.

Theory suggests that search costs should also affect the level of the acceptance threshold, with higher search costs favoring a lower acceptance threshold (Real 1990). In support of this idea, several studies have recently demonstrated that in the presence of predation risk individuals show weaker mate preferences (Forsgren 1992; Berglund 1993; Godin and Briggs 1996) and show less search activity (Sih et al. 1990; Dale et al. 1992) than when risk is absent. However, there was no indication that female pine engravers altered their search tactics in response to variation in the risk of preemption or parasitism. It may be that female pine engravers were unable to assess the risk of preemption or parasitism in a patch before they began to search for males in that patch.

Information may be as important as search costs in determining the optimal mate search tactic for a given species. For instance, the one-step decision model proposed by Real (1990) may be optimal only if females are able to assess the quality of males in a patch before they begin to search, and then adjust their threshold accordingly. In pine engravers, females can probably estimate expected male quality in a patch based on the pheromones emanating from the patch. We suggest that prepatch assessment of male quality distributions may actually be quite common in species in which females travel to aggregations of males to search for mates and in which the quality of males differs among ag-

gregations (Lawrence 1987; Alatalo et al. 1992). The issue for this type of species is how females might estimate the quality of males in a patch without visiting individual males within that patch. We suggest that chemicals or acoustic signals are likely candidates for providing patch quality information in many species (e.g., Waage 1978). For instance, in many anurans and orthopterans, the frequency of male calls is correlated with male body size (Ryan and Keddy-Hector 1992). To date, most workers have emphasized that this information would allow females to choose the largest males when selecting a mate from among the array of males vying for their attention (Arak 1983). However, it is equally likely that females could use the sounds produced by a chorus to estimate the size distribution of the males within that chorus. The idea that females can home in on the best male from a distance has been refuted in at least some species, as female anurans seem unable to localize and assess individual males within a chorus until they are quite close to them (Gerhardt and Klump 1988; Bourne 1992).

The notion that searchers might assess patch quality before beginning to search in a patch is already familiar in the foraging literature (Stephens and Krebs 1986; Valone and Brown 1989), but it has been overlooked in empirical studies of mate choice. By further analogy with foraging models, females may search for mates using a hierarchy of information, using cues used to locate suitable patches, to decide which patches are worthy of closer inspection, and to determine whether a particular item will be chosen within a given patch (Hassell and Southwood 1978; Roitberg 1985). While we have highlighted the importance of patch-level information in this study, we have thus far ignored the possibility that females might also gain information during the search process within a patch. One reason for emphasizing prepatch information in pine engravers is that most females visited only one or two males before choosing a mate. Hence, most females had little opportunity to adjust their acceptance thresholds during search. In addition, recent theory suggests that a tactic in which females adjust their acceptance threshold according to the quality of individual males encountered (adaptive search) often yields lower fitness payoffs than a prepatch threshold that is not changed during search (Mazalov et al. 1996). Nevertheless, several models of female mate search now predict within-patch adjustable thresholds, such as a one-step decision model with a finite time horizon (Janetos 1980; Real 1990), Bayesian updating (Real 1990), and adaptive search (Dombrovsky and Perrin 1994; Mazalov et al. 1996). These models require empirical tests, perhaps similar to those of Bakker and Milinski (1991) and Collins (1995). The framework that we developed here for testing mate search models can be readily extended to provide predictions of these additional models.

In summary, this study supports the theoretical prediction that females should use a prepatch adjustable threshold mate search tactic when there are search costs. However, we emphasize that such a prediction should be viewed in the context of the information available to females about male quality and search costs. Female pine engravers can probably assess patch quality before landing, and therefore a prepatch adjustable threshold tactic is appropriate for this spe-

cies. Patch-level information about male quality may be available in other species as well, but species lacking this information would be expected to exhibit different search tactics. Conversely, pine engravers may not be able to assess variation in search costs before visiting prospective mates, but estimates of search costs may be more readily available to other species (Lima and Dill 1990). Our study provides encouraging support for current models of optimal mate search tactics, while highlighting the need for further empirical and theoretical studies on the consequences of information and search costs on mate search tactics.

ACKNOWLEDGMENTS

We thank E. Senger for his excellent assistance in the field. We also thank P. Aujla and S. Senger for additional field help; D. Miller, D. Devlin, and the British Columbia Ministry of Forests fire crew for generously providing logs; and the Pacific Forestry Centre (Canadian Forestry Service) and R. Reid for kindly providing field accommodation. For comments on various drafts of this study, we thank J. Borden, R. Cartar, R. Gibson, T. Halliday, J. Hutchinson, A. Kacelnik, B. Luttbeg, M. Mangel, N. Perrin, L. Real, B. Roitberg, L. Safranyik, D. Wiegmann, R. Ydenberg, and M. Zuk. A. Kacelnik was particularly generous with his thoughtful insights into mating probabilities. Fieldwork for this study was supported by a Natural Sciences and Engineering Research Council (NSERC) of Canada postgraduate scholarship and Sigma Xi grants-in-aid of research to M.L.R., Science Council of British Columbia, graduate research engineering and technology awards to M.L.R. and B. Roitberg, and NSERC operating grants to B. Roitberg. Support during manuscript preparation was provided by an NSERC postdoctoral fellowship and research grant to M.L.R.

LITERATURE CITED

- Alatalo, R. V., A. Carlson, and A. Lundberg. 1988. The search cost in mate choice of the pied flycatcher. *Animal Behaviour* 36:289–291.
- Alatalo, R. V., J. Höglund, A. Lundberg, and W. J. Sutherland. 1992. Evolution of black grouse leks: female preferences benefit males in larger leks. *Behavioral Ecology* 3:53–59.
- Amman, G. D., and D. L. Bartos. 1991. Mountain pine beetle offspring characteristics associated with females producing first and second broods, male presence, and egg gallery length. *Environmental Entomology* 20:1562–1567.
- Anderson, R. F. 1948. Host selection by the pine engraver. *Journal of Economic Entomology* 41:596–602.
- Arak, A. 1983. Male-male competition and mate choice in anuran amphibians. Pages 181–210 in P. Bateson, ed. *Mate choice*. Cambridge University Press, Cambridge.
- . 1988. Female mate selection in the natterjack toad: active choice or passive attraction? *Behavioral Ecology and Sociobiology* 22:317–327.
- Bakker, T. C. M., and M. Milinski. 1991. Sequential female choice and the previous male effect in sticklebacks. *Behavioral Ecology and Sociobiology* 29:205–210.
- Balmford, A. 1991. Mate choice on leks. *Trends in Ecology & Evolution* 6:87–92.
- Bensch, S., and D. Hasselquist. 1992. Evidence for active female choice in a polygynous warbler. *Animal Behaviour* 44:301–311.

- Berglund, A. 1993. Risky sex: male pipefishes mate at random in the presence of a predator. *Animal Behaviour* 46:169–175.
- Beuchner, H. K., and R. Schloeth. 1965. Ceremonial mating behavior in Uganda kob (*Adenota kob thomasi* Neumann). *Zeitschrift für Tierpsychologie* 22:209–225.
- Birgersson, G., F. Schlyter, J. Löfqvist, and G. Bergström. 1984. Quantitative variation of pheromone components in the spruce bark beetle *Ips typographus* from different attack phases. *Journal of Chemical Ecology* 10:1029–1055.
- Bourne, G. R. 1992. Lekking behavior in the neotropical frog *Ololygon rubra*. *Behavioral Ecology and Sociobiology* 31:173–180.
- Brown, L. 1981. Patterns of female choice in mottled sculpins (Cottidae, Teleostei). *Animal Behaviour* 29:375–382.
- Byers, J. A. 1981. Effect of mating on terminating aggregation during host colonization in the bark beetle, *Ips paraconfusus*. *Journal of Chemical Ecology* 7:1135–1147.
- Cameron, E. A., and J. H. Borden. 1967. Emergence patterns of *Ips confusus* (Coleoptera: Scolytidae) from Ponderosa pine. *Canadian Entomologist* 99:236–244.
- Collins, S. A. 1995. The effect of recent experience on female choice in zebra finches. *Animal Behaviour* 49:359–373.
- Crowley, P. H., S. E. Travers, M. C. Linton, S. L. Cohn, A. Sih, and R. C. Sargent. 1991. Mate density, predation risk, and the seasonal sequence of mate choices: a dynamic game. *American Naturalist* 137:567–596.
- Dale, S., H. Rinden, and T. Slagsvold. 1992. Competition for a mate restricts mate search of female pied flycatchers. *Behavioral Ecology and Sociobiology* 30:165–176.
- Dombrovsky, Y., and N. Perrin. 1994. On adaptive search and optimal stopping in sequential mate choice. *American Naturalist* 144:355–361.
- Forsgren, E. 1992. Predation risk affects mate choice in a gobiid fish. *American Naturalist* 140:1041–1049.
- Garraway, E., and B. E. Freeman. 1981. Population dynamics of the juniper bark beetle *Phloeosinus neotropicus* in Jamaica. *Oikos* 37:363–368.
- Gerhardt, H. C., and G. M. Klump. 1988. Masking of acoustic signals by the chorus background noise in the green treefrog: a limitation on mate choice. *Animal Behaviour* 36:1247–1249.
- Gibson, R. M., and G. C. Bachman. 1992. The costs of female choice in a lekking bird. *Behavioral Ecology* 3:300–309.
- Gibson, R. M., and J. W. Bradbury. 1986. Male and female mating strategies on sage grouse leks. Pages 379–398 in D. I. Rubenstein and R. W. Wrangham, eds. *Ecological aspects of social evolution*. Princeton University Press, Princeton, N.J.
- Godin, J.-G. J., and S. E. Briggs. 1996. Female mate choice under predation risk in the guppy. *Animal Behaviour* 51:117–130.
- Hassell, M. P., and T. R. E. Southwood. 1978. Foraging strategies of insects. *Annual Review Ecology and Systematics* 9:75–98.
- Janetos, A. C. 1980. Strategies of female mate choice: a theoretical analysis. *Behavioral Ecology and Sociobiology* 7:107–112.
- Kirkendall, L. R. 1989. Within-harem competition among *Ips* females, an overlooked component of density-dependent larval mortality. *Holarctic Ecology* 12:477–487.
- Lanier, G. N., and E. A. Cameron. 1969. Secondary sexual characters in the North American species of the genus *Ips* (Coleoptera: Scolytidae). *Canadian Entomologist* 101:862–870.
- Lawrence, W. S. 1987. Dispersal: an alternative mating tactic conditional on sex ratio and body size. *Behavioral Ecology and Sociobiology* 21:367–373.
- Lima, S. L., and L. M. Dill. 1990. Behavioral decisions under the risk of predation: a review and prospectus. *Canadian Journal of Zoology* 68:619–640.
- Mazalov, V., N. Perrin, and Y. Dombrovsky. 1996. Adaptive search and information updating in sequential mate choice. *American Naturalist* 148:123–137.
- Mitchell, R. 1975. The evolution of oviposition tactics in the bean weevil *Callosobruchus maculatus* (F.). *Ecology* 56:696–702.
- Moore, A. J., and P. J. Moore. 1988. Female strategy during mate choice: threshold assessment. *Evolution* 42:387–391.

- Parker, G. A. 1978. Evolution of competitive mate searching. *Annual Review of Entomology* 23:173–196.
- Petrie, M., T. Halliday, and C. Sanders. 1991. Peahens prefer peacocks with elaborate trains. *Animal Behaviour* 41:323–331.
- Pruett-Jones, S. G., and M. A. Pruett-Jones. 1990. Sexual selection through female choice in Lawes' parotia, a lek-mating bird of paradise. *Evolution* 44:456–471.
- Real, L. A. 1990. Search theory and mate choice. I. Models of single-sex discrimination. *American Naturalist* 136:376–404.
- . 1991. Search theory and mate choice. II. Mutual interaction, assortative mating, and equilibrium variation in male and female fitness. *American Naturalist* 138:901–917.
- Reid, M. L. 1992. Female mate choice and male parental care in a bark beetle (*Ips pini*, Coleoptera: Scolytidae). Ph.D. diss. Simon Fraser University, Burnaby, British Columbia.
- Reid, M. L., and B. D. Roitberg. 1994. Benefits of prolonged male residence with mates and brood in pine engravers (Coleoptera: Scolytidae). *Oikos* 70:140–148.
- Reynolds, J. D., and M. R. Gross. 1990. Costs and benefits of female mate choice: is there a lek paradox? *American Naturalist* 136:230–243.
- Roitberg, B. D. 1985. Search dynamics in fruit parasitic insects. *Journal of Insect Physiology* 31:865–872.
- Ryan, M. J., and A. Keddy-Hector. 1992. Directional patterns of female choice and the role of sensory biases. *American Naturalist* 139:S4–S35.
- Schmitz, R. F. 1972. Behavior of *Ips pini* during mating, oviposition, and larval development (Coleoptera: Scolytidae). *Canadian Entomologist* 104:1723–1728.
- Senger, S. E., and B. D. Roitberg. 1992. Effects of parasitism by *Tomicobia tibialis* Ashmead (Hymenoptera: Pteromalidae) on reproductive parameters of female pine engravers, *Ips pini* (Say). *Canadian Entomologist* 124:509–513.
- Sih, A., J. Krupa, and S. Travers. 1990. An experimental study of the effects of predation risk and feeding regime on the mating behavior of the water strider. *American Naturalist* 135:284–290.
- Stephens, D. W., and J. R. Krebs. 1986. Foraging theory. Princeton, Princeton University Press, N.J.
- Swaby, J. A., and J. A. Rudinsky. 1976. Acoustic and olfactory behaviour of *Ips pini* (Say) (Coleoptera: Scolytidae) during host invasion and colonization. *Zeitschrift für Angewandte Entomologie* 81:421–432.
- Thornhill, R. 1980. Mate choice in *Hylobittacus apicalis* (Insecta: Mecoptera) and its relation to some models of female choice. *Evolution* 34:519–538.
- Trail, P. W., and E. S. Adams. 1989. Active mate choice of cock-of-the-rock leks: tactics of sampling and comparison. *Behavioral Ecology and Sociobiology* 25:283–292.
- Valone, T. J., and J. S. Brown. 1989. Measuring patch assessment abilities of desert granivores. *Ecology* 70:1800–1810.
- Waage, J. K. 1978. Arrestment responses of the parasitoid, *Nemeritis canescens*, to a contact chemical produced by its host, *Plodia interpunctella*. *Physiological Entomology* 3:135–146.
- Wiegmann, D. D., L. A. Real, T. A. Capone, and S. Ellner. 1996. Some distinguishing features of models of search behavior and mate choice. *American Naturalist* 147:188–204.
- Wittenberger, J. F. 1983. Tactics of mate choice. Pages 435–447 in P. Bateson, ed. *Mate choice*. Cambridge University Press, Cambridge.
- Zuk, M., K. Johnson, R. Thornhill, and J. D. Ligon. 1990. Mechanisms of female choice in red jungle fowl. *Evolution* 44:477–485.

Associate Editors: Richard D. Howard
Alejandro Kacelnik