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Female Mate Choice and Male Parental Care in a Bark Beetle
(*Ips pini*, Coleoptera: Scolytidae)

by

Mary L. Reid
B.Sc. (Hons.), Queen's University, 1983
M.Sc., Carleton University, 1986

THESIS SUBMITTED IN PARTIAL FULFILLMENT OF
THE REQUIREMENTS FOR THE DEGREE OF
DOCTOR OF PHILOSOPHY
in the Department
of
Biological Sciences

SIMON FRASER UNIVERSITY
December 1991

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ISBN 0-315-78230-7

APPROVAL

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Degree: **Doctor of Philosophy**

Title of Thesis:

FEMALE MATE CHOICE AND MALE PARENTAL CARE IN A BARK BEETLE
(*IPS PINI*, COLEOPTERA: SCOLYTIDAE)

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Female mate choice and male parental care in a bark

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Abstract

Animals choosing mates usually incur time and energy costs and predation risk to achieve a reproductive benefit from a preferred mate. These costs and benefits will influence the degree of choosiness and the mate choice tactics employed. This perspective of mate choice has been absent from mating system and sexual selection theories, although mate choice is pivotal to these theories. I investigated the mate choice tactics of female pine engraver bark beetles, Ips pini (Coleoptera: Scolytidae) to test assumptions and predictions of mate choice models. In nature, pine engravers experience a high risk of parasitism while searching for mates. Search behaviour varies with risk, but costs did not detectably affect the number of males visited or the quality of males chosen. Slightly over half of females accept the first males they encounter, mating randomly. These females mate with less preferred males than females that sample before mating. Sampling females do not revisit males, in accordance with prediction when search costs are high. However, sampling females appear to adjust their mating expectations with experience, by lowering their expectations with successive encounters with less preferred males. Evidence for learning about the availability of mate qualities was also found in a lab experiment. This tactic may be appropriate when search costs preclude revisits but mate availability is too unpredictable to have fixed preferences. These results do not support assumptions of female preferences in sexual selection models. The fitness benefits of mating preferences were also examined. Male pine engravers remain with their mates for several weeks, and a male removal experiment demonstrated that males help their mates reproduce more quickly and defend the galleries against predators. However, a model of male residence time showed that male residence time is not determined by how much males help, but rather by the availability of other mating opportunities. A rearing experiment showed that large males (preferred by females) tend to produce more offspring and larger ones, despite remaining with the brood for less time than small males did. In sum, female pine engravers appear to have adaptive mate preferences and flexible mate choice tactics.

Acknowledgements

I am grateful to my supervisor Bernie Roitberg for his constant support of my research, both financially and intellectually. I value the independence he encouraged in his students, and the example he sets in his science and his enthusiasm. I was also fortunate to have a supervisory committee that complemented (and complimented?) each other so well. John Borden's expertise and lab resources in bark beetles were essential to this project, and his editing of thesis drafts were exceptionally thorough. Les Safranyik greatly facilitated my field studies, provided useful discussions about bark beetles, and caught several important errors in the presentation of my results that eluded everyone else. Ron Ydenberg ensured that the theory I addressed was reasonable, and in particular looked carefully at the model. I thank public examiner Mark Winston for his comments, and my external examiner Marlene Zuk for reviewing the thesis in detail and improving the logic in many places.

Helpful comments on drafts of chapters 3 and 4 were provided by Fredrik Schlyter, Olle Anderbrant, Fran Lissemore, and on chapter 2 by Ann Hedrick, in addition to my committee members. Ralf Cartar read almost everything in the critical early stages and made it all more coherent.

I am indebted to Ed Senger for his utterly reliable assistance over two years; he set an example for me in data collection and organization. Preet Aujla also ably assisted, and Lena Gill, Sue Senger, Brent Zaharia, Bob/Todd Lalonde, and Chao Li all filled in at various times. The Borden lab was unfailing in their helpfulness in any matter, making this project feasible for a bark beetle novice. Very special thanks to Dan Miller for convincing me at the start of this degree that bark beetles really were the perfect study beast, and for his generosity in providing logs, beetles, and advice ever after. Darryl Devlin also helped tremendously in providing logs and beetles, and the fire crews at Williams Lake killed some trees on my and the beetles' behalf as well. Bruce Lyon's field assistants collected emerging beetles for me one year. The B6226 inhabitants provided congeniality and birthday cakes, and Pam Krannitz provided moral support.

My opportunity to write up down under was successful because of several people in addition to Ralf and Bernie. In particular, Annabelle Rahme appeared faithfully in Sydney in electronic form through the marvels of email, solved my numerous administrative queries 'back home', and also kept us in touch with SFU gossip. She and Rob Houtman also gave me a home to return to; Guy Martel provided a quiet spot for final revisions. Rob McGregor came through with some antipodal data transfer, and Rick Shine of Sydney Uni made many facilities available to me.

This research was supported primarily by Bernie Roitberg's NSERC grant, and also by two Sigma-Xi grants-in-aid to me. The Pacific Forestry Centre through Gorden Miller provided field facilities and equipment. Personal support was provided by NSERC postgraduate scholarships, B.C. Science Council GREAT awards, and SFU.

Every moment of this thesis, and of non-thesis, was better because of the support, companionship and inspiration of Ralf Cartar, my optimal mate.

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Foreward

It is paradoxical that the concept of female mate choice is simultaneously championed and neglected. The importance of female mate choice as an evolutionary force was recognized by Darwin (1871), but not generally considered until relatively recently. In the past two decades, however, female mate choice has been at the core of two active areas of inquiry: mating systems and sexual selection. The polygyny threshold model (Orians 1969) was proposed to explain why some males in territorial species had more mates than other males did. This model proposes that females would choose to be a secondary mate on a high quality territory rather than to be a primary mate on a poor quality territory, because their reproductive success would be higher. Sexual selection models, on the other hand, aim to explain the evolution of extravagant male traits (such as the archetypal peacock's tail) by female choice. The pervasiveness of these sexual selection models is such that sexual selection now implicitly means evolution by female mate choice (Arnold 1985, Bradbury and Andersson 1987), though competition among males is an alternative and less problematical mechanism (Bradbury and Davies 1987).

Given that female choice is central to these areas of research, it is remarkable that almost nothing is known about how females choose mates. Attention has been focussed almost exclusively on the features of males or their resources that make them attractive, and the fitness consequences of mate preferences to males and their mates. The polygyny threshold model explicitly assumes that females are making adaptive decisions, but only in their ranking of alternative breeding sites (Garson et al. 1981). Costs of mate searching, which will also have fitness consequences, are rarely seriously considered. Sexual selection models also have typically ignored costs of mate choice (but see Pomiankowski 1987), and the nature of the benefits females receive from choosing is subject to dispute. Handicap models of sexual selection propose that females choose mates on the basis of traits indicating heritable genetic quality (Kirkpatrick and Ryan 1991), but other models do not incorporate any survival benefits for offspring. For example, one of the more popular (though controversial) models of sexual selection has been Fisher's runaway model, in which female preferences evolve solely through their genetic linkage with male traits that confer greater male reproductive success (Arnold 1985). In this scenario, how or why females choose mates is not particularly interesting, because the preference is arbitrary and of no consequence to females. A new model of sexual selection, the sensory exploitation hypothesis, also proposes that the evolution of preferences is independent of reproductive consequences (Kirkpatrick and Ryan 1991).

The success of these research programs has been mixed. The polygyny threshold model is extremely attractive conceptually, but has received little empirical support (Oring 1982). Sexual selection models have revealed powerful mechanisms for the evolution of non-adaptive traits (female preferences), but the outcomes are sensitive to assumptions about the nature of female preferences and the benefits they receive from choice (Kirkpatrick 1987a). The simple assumptions of the main models, that female choice is free of costs or benefits, are unlikely to be general. It is time to put the female into female choice models.

The process of choosing a mate is not likely to be trivial. Male quality may be more or less variable, the distribution of males of different quality may be uneven and unpredictable (Vehrencamp and Bradbury 1984), and there may be multiple relevant criteria on which to choose (Burley 1981). There are numerous possible costs inherent in searching, such as predation risk, and time, energy and opportunity costs (Pomiankowski 1987, Reynolds and Gross 1990). Thus, searching for mates is an economic problem like optimal foraging, with the added feature that the search is for conspecifics, often with mutually beneficial outcomes. Explicit economic models of optimal mate choice tactics, initiated by Janetos (1980), have recently been revived by Real (1990). Further development of economic models, in conjunction with empirical studies, promises new insights into the expression of mating preferences in nature.

Because empirical knowledge of mate choice tactics is scarce but critical, a goal of this thesis is to investigate the choice behaviour of females in one species, the pine engraver Ips pini (Coleoptera: Scolytidae). In Chapter 1, I examine the mate choice process in nature, where the costs of choice become evident. This enables me to test many assumptions and predictions of mate choice models To my knowledge, these are the first observations of the entire mate choice process for a species with a resource-based mating system. I also examine a specific aspect of mate evaluation in a controlled laboratory experiment (Chapter 2), where I ask whether females have fixed preferences, or whether their preference for a particular quality of male is influenced by the quality of other available males. This question has implications for the outcome of sexual selection models, as well as for the distributions of males seeking mates.

An economic perspective of female choice must consider the benefits females gain from their preferences. The nature of benefits has also been a controversial issue in models of mating systems (Searcy 1982) and sexual selection (Kirkpatrick 1987b). In pine engravers, males stay with their mates through most of the oviposition period. One might therefore expect that males provide some benefit to females. In a field study, I examined possible benefits of males by determining the consequences of removing males (Chapter 3)

I approached the question from the male's perspective, because it is his decision to stay and therefore benefits should reflect his interests and not necessarily his mates'. In addition, I examined in a model the premise that the duration of male residence with his mates or brood reflects the amount of help he provides (Chapter 4). Male help is not sufficient to warrant choice, however, if males do not differ predictably in the help they provide. I therefore conducted a rearing experiment to determine the fitness consequences of mating with males bearing a preferred trait (Chapter 5).

In sum, this thesis addresses how and why female pine engravers choose mates, in an effort to further our understanding of mating patterns in nature.

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Chapter 1

Mate Choice Tactics of a Bark Beetle in the Wild

Abstract

I examined the mate choice tactics of female pine engravers, Ips pini (Coleoptera: Scolytidae) in nature. This polygynous species has a resource-based mating system in which males initiate breeding sites in dense aggregations, and provide assistance to their mates throughout their oviposition period. Choosing females can roam freely without male interference, but experience significant risks of predation and parasitism and female competition. Half of females mated with the first male they encountered, and appeared to mate randomly. The number of visits that females made did not vary with availability of males, predation risk, or female competition, but some components of searching behaviour did vary with predation and competition risks. Females that visited more than one male usually mated with males that had established chambers more recently, had fewer mates, shorter egg galleries, and were smaller than males she had rejected. There was no detectable effect of any of the search costs on the type of male that was chosen. Females did not revisit males, and therefore did not use a comparison mate choice tactic. This result is expected when search costs are high. There was evidence that female preferences were not fixed, however, and were instead affected by experience. Females mated with less preferred males when they had encountered (and rejected) even less preferred males, and when they had made more unsuccessful visits. When females (rarely) mated with a male who was much less preferable than one she had previously rejected, the better male tended to have been visited many encounters previously, suggesting females base their decisions on more recent encounters. Search costs appear to favour a threshold-preference mating tactic, but if the threshold is sensitive to experience then females can have both the opportunity to be very selective and the certainty of mating. These mate choice tactics differ from those commonly used in models of sexual selection, and may influence their outcomes.

Introduction

Interest in the evolution of sexually selected traits has prompted a wealth of theoretical and empirical studies on the nature of the benefits that accrue from preferring certain traits in mates. This approach has largely neglected the process of mate choice, yet the context in which mates are chosen will likely determine the expression of mating preferences. Recent models suggest that costs of searching for mates should influence the degree of choosiness expressed (Crowley et al. 1991), optimal mate search tactics (Real 1990), and the outcome of sexual selection (Parker 1983, Kirkpatrick 1987, Pomiankowski 1987, Reynolds and Gross 1991). Empirical studies of the process of mate choice have lagged far behind the development of theory, however (Moore and Moore 1988). We know little about how real animals make their mating decisions, and less about how ecological circumstances and individual quality might alter choice behaviour.

A diversity of mate choice tactics have been discussed following the initial work by Janetos (1980). In a fixed-threshold tactic, females accept the first male that exceeds some minimum quality. Janetos' one-step decision tactic is another tactic in which acceptance criteria change according to the amount of time females have left for searching (a dynamic decision; Mangel and Clark 1988). Copying other females' choices is another possible tactic that some (not all) females could use (Losey et al. 1986). With these three tactics, females usually do not return to mate with previously sampled males. In contrast, revisits are characteristic of comparison tactics. In a best-of-n or pool comparison tactic (Janetos 1980, Wittenberger 1983), females sample many males and mate with the best of her sample. A sequential comparison tactic involves sampling until a male that is worse than the previous one is encountered, at which point the female returns to the previous male to mate (Brown 1981, Wittenberger 1983).

In the absence of search costs, the best-of-n tactic gives females the greatest fitness (Janetos 1980). However, when search costs are considered, the dynamic one-step decision process is superior to a best-on-n (Real 1990). One key assumption to Real's (1990) conclusion is that females have accurate knowledge of the distribution of male qualities. If females begin to search without this knowledge, the optimal tactic may depend on the the nature and size of search costs as well as benefits, as discussed by Wittenberger (1983). A pool comparison tactic assures that the best male in the sample is chosen, but a variety of costs might select against revisiting males. Possible costs may be the time and energy it takes to find and assess males, predation risks, and the risk that the best male will be taken by another female while a searching females continues to assess more males. Thus comparison tactics are expected when the availability of preferred males is unknown, when males are densely distributed and easy to assess, and when predation and pre-emption risks are low (Wittenberger 1983).

If search costs preclude revisits, females could copy other females, use a fixed threshold, or adjust their acceptance threshold according to experience (i.e. learning; Real 1990). Copying will be inappropriate if female reproductive success is reduced by sharing a male. Learning permits greater accommodation to local distributions of mate qualities, but it presumably requires greater neuronal sophistication as well. A recent model by Roitberg et al. (in press) suggests that the evolution of learning may be inhibited when decisions are few but have major fitness consequences, such as mate choice decisions. However, if mate qualities are very patchily distributed, learning may be the best way to get the best mate without requiring revisits.

Although models of mate choice tactics have been developed, empirical studies are rare. Most observations of mate sampling have been done on lek-breeding animals (Reynolds and Gross 1990), for two main reasons. First, the close proximity of males, often in open areas, makes it easier for researchers to discreetly observe females encountering several males. Second and more important, it is intriguing that sexually selected traits tend to be more developed in this mating system than in resource-based mating systems, although there would seem to be less value to choice as lekking males provide only genes. Taylor and Williams (1982) suggest that mate choice is more developed in lek mating systems, perhaps because of lower search costs (Reynolds and Gross 1990). However, without empirical data on mate choice tactics in resource-based mating systems as well as lek mating systems, the basis of the comparison between mating systems is tenuous.

Here I examine the process of mate choice in nature by female pine engravers Ips pini (Say) (Coleoptera: Scolytidae), a bark beetle with a resource-based mating system. I first consider possible search costs experienced by females. I then describe patterns of visits to males and the time budgets involved in search, and determine how search costs influence these behaviours. These data allow me to test some models of mate choice tactics. I also identify characteristics of preferred males, and I investigate how preferences vary according to search costs, and vary among and even within females.

Breeding Biology of Pine Engravers

The breeding biology of pine engravers has been described by Thomas (1961), Schenk and Benjamin (1969), Schmitz (1972) and Swaby and Rudinsky (1976). Adults are ca. 4 mm long, with male ca. 10% larger than females. They breed in the phloem of weakened or recently dead trees which males colonize en masse, reaching densities of 1 to 2 per 10 cm^2. Each male constructs a nuptial chamber that he does not leave until oviposition by his mates is nearly complete two or three weeks later. Male-produced pheromones attract females to infested host trees, but it is not known whether short-range pheromones also reveals an individual male's location to females. My observations indicate that walking females do not visibly orient towards a male from much more than 2 cm away. A model of mate finding behaviour for another bark beetle indicates that under the high densities typical of pine engravers, females could encounter many males simply by random movement (Byers 1990). Pheromone constituents change with male mating status (Swaby and Rudinsky 1976), so females can assess mating situations without actually entering the nuptial chamber.

Pheromones also attract predators and parasitoids (Bedard 1965, Miller and Borden 1990). At my sites, predators were mainly clerid beetles (Coleoptera: Cleridae, mostly *Enoclerus sphegeus*, some *Thanasimus undatulus*). Also observed was the parasitoid *Tomicobia tibialis* (Hymenoptera: Pteromalidae) which causes immobility in adult beetles within about a week of parasitization (Bedard 1965).

Typically, three females will mate with a given male. This polygyny appears to be due to a biassed sex ratio at the breeding site, because virtually all males attract at least one mate (pers. obs). Females enter a male's chamber at the rate of about one per day. This rate is limited by how quickly space becomes available after each female enters the nuptial chamber. Females chew egg galleries which radiate away from the nuptial chamber, and will lay 20-50 eggs over the next two to three weeks. Eggs hatch after 5 days, and larvae mine through the phloem perpendicular to their egg gallery. By mining in this way larvae usually avoid their full siblings, but larvae from adjacent galleries may meet, usually resulting in combat and the death of the smaller larvae (Schmitz 1972,pers. obs.). It is therefore to the advantage of females to mate first rather than last with a male to provide their larvae a headstart over larvae of the later arriving females (Kirkendall 1989).

The male in the gallery system in which a female oviposits is likely to sire most of her offspring. Females rarely leave a viable male without reproducing (pers. obs.), which is ensured in part by the degeneration of flight muscles which, in a similar congener, begins as soon as a female enters the nuptial chamber (Borden and Slater 1969). Also, copulations are frequent with the breeding gallery (pers. obs.), and it seems likely that sperm of the most recent matings have precedence in fertilizations (Kirkendall 1983).

Males remain with their mates over much of the egg-laying period, during which time they clear the galleries of frass (allowing females to lay eggs more quickly) and guard against predators that might enter the gallery (Chapter 3). This investment may favour male choice as well (Gwynne 1991), and there is some evidence that male *Ips* spp. may sometimes actively prevent females from entering their nuptial chambers (Borden 1967, pers. obs.). However, the reproductive consequences of mate choice will probably be larger for females than males, because females are choosing their only mate (for that reproductive bout, and possibly their lifetime) while male fitness is derives from several mates. Male choice may influence female choice, but because it is impossible to see what males are doing in their chambers under natural conditions, I do not consider it here.

In sum, female mate choice is expected in this species because: 1) males provide economic as well as genetic resources, and 2) males are densely distributed but unable to interfere with each other. Potential costs to choice are competition among females (lost opportunities) and predation risks.

Methods

I observed colonization and female mate searchng behaviour during the first spring dispersal flight of pine engravers in three successive years. This first flight consists of overwintered adults. In two years, I worked near Riske Creek in the central interior of British Columbia, Canada, and in the third year I worked near Princeton in south central B.C. The colonization patterns in each year differed (Fig. 1.1) due primarily to the timing of warm weather suitable for beetle flight. In Princeton in 1990, very few predators or parasitoids were observed, but in the previous fall this area had the highest density of T. tibialis I have seen (1-2 per 10 cm^2), so the low densities of parasitoids observed in this study are not necessarily typical for this population.

In each year, I established 3-5 potential breeding sites within 2 km of each other. Each site consisted of 4-12 bolts 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 which was a 150 cm long remnant of one of the felled trees. Beetle activity was largely confined to the upper surface of logs under these conditions. Bolts varied in size between sites, from 60 cm long and 10 cm diameter, to 100 cm long and 27 cm in diameter, and log number ranged from 4 (for the largest logs) to 12 (for the smaller logs) at each site. Individual bark beetles visited only a small fraction of the available area, virtually always within a single bolt. However, for the purposes of analysis I combined bolts within a site to avoid possible pseudo-replication. This was because bolts within sites had generally similar colonization patterns, and the site as a whole may produce a common blend of pheromones and kairomones (log-produced) which determines the expectations of incoming females (Swaby and Rudinsky 1976). I considered each site on each day to be an independent observation.

Colonization of sites occurred naturally in most cases. At some sites I established one or two live males to produce pheromone and induce colonization when cool temperatures were reducing the number of flying beetles. Bolts were gridded into 10 cm^2 areas using thin string stretched between nails around the edge of the log's upper surface. Each new male nuptial chamber was marked daily with tacks of a day-specific colour (to keep track of

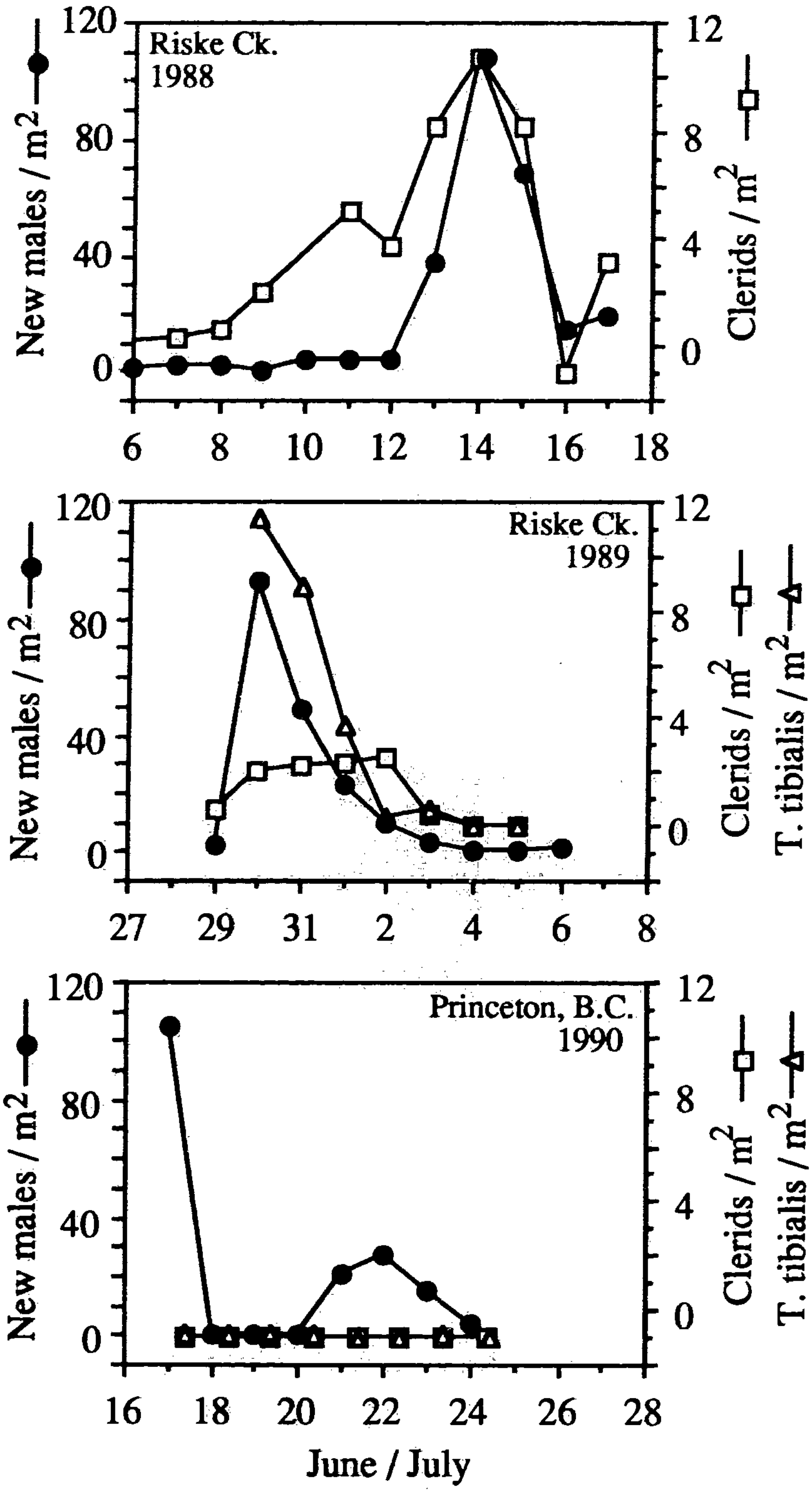

Figure 1.1. Phenologies of settling male pine engravers, predators (clerids), and parasitoids (T. tibialis). One representative site shown for each year.

chamber age), and plotted on a scale map. Predators and parasitoids were surveyed daily by scanning the gridded areas of each bolt systematically. In 1988, only clerid beetles were counted because these were thought to be the major cause of mortality for pine engravers (Schenk and Benjamin 1969), but later it became clear that the parasitoid T. tibialis was more common and more effective at attacking pine engravers.

Female pine engravers can be visually distinguished from males by the absence of an enlarged elytral spine (Lanier and Cameron 1969). Because females are small and cryptic, they were marked upon discovery with fluorescent powder gently applied with a fine paint brush to the posterior end of their elytra. Their behaviour was timed with a stopwatch and recorded continuously from discovery until they had entered a hole or were lost. Behaviours noted were: 1) running, 2) hiding in crevices or under bark flakes, 3) pausing (exposed) for more than a few seconds, and 4) at male entrance holes (either waiting or pushing against male). A male was considered accepted as a mate when the female had fully disappeared into his entrance hole or when she had persisted at the entrance hole for more than 30 min by the time observations ceased. A male was rejected when the female departed from the frass pile around his entrance hole. Visits to males that did not meet the acceptance or rejection criteria were excluded from analyses of mate choice criteria The age of the nuptial chamber visited, as indicated by tack colour, was noted. Most observations occurred on one or two adjacent bolts at each site, but females on other bolts were watched if possible. Females were observed mainly in midday (1100 h to 1700 h) when temperatures permitted beetle flight and hence arrival of females to breeding sites.

The galleries of some males that were visited (and rejected or accepted) were excavated to determine the mating status of males (number of mates and the length of each mate's egg gallery). In 1988 and 1989, males were collected and their body size (pronotal width) was measured later to the nearest 0.04 mm using a stereomicroscope at 25x magnification.

Where relevant, I looked for differences among years in female behaviour because mate choice may be inconsistent (Reid and Weatherhead 1990). I used analysis of variance (ANOVA) or covariance (ANCOVA) if possible, but where there was insufficient data for each of the years to warrant these analyses, I visually inspected graphical plots. When differences among years were not detectable, I combined data from all years. All statistical analyses were done using Systat 5.0 for Macintosh computers (Wilkinson 1989). Normality was checked for all variables; logarithmic transformations rectified any non-normal variables.

Results

Search Costs

The most apparent risk to bark beetles roaming on the bark surface is that of being parasitized by *T. tibialis*. This parasitoid was observed to attack only moving beetles which responded by running very rapidly and erratically, and then either dropping off the log or hiding in a crevice to dislodge the parasitoid. The beetle was usually safe when hiding, but the parasitoid often waited nearby for the beetle to come out. Sometimes the parasitoid attempted to attack the hiding beetle and pull it out, but this rarely seemed successful. *T. tibialis* attacked 8.0% of 88 females in 1988, and 15.7% of 102 females in 1989. No attacks on females were observed in 1990. I observed only one male pine engraver attacked by a clerid beetle in all three years, though clerids are considered to be a primary predator of bark beetles (Schenk and Benjamin 1969). However, I use clerid density as my measure of predation/parasitism risk because I did not count *T. tibialis* in 1988 and because numbers of *T. tibialis* and clerids were highly correlated in 1989 (r=0.748, N=10, P<0.05; Fig. 1.1).

Another cost of searching could be lost opportunities when other females are competing for access for male entrance holes. When a female arrived at a male entrance hole and discovered another female already waiting there, the arriving female usually did not persist. This observation eliminates copying as a possible mate choice tactic in pine engravers. Occasionally the arriving female attempted to push the waiting female away. Visits observed in which a female was already waiting comprised 10.3% of 97 visits in 1988, 7.7% of 196 visits in 1989, and 2.1% of 48 visits in 1990. Because it is likely that these "taken" males were most preferable, these figures represent a conservative estimate of competition for desirable mates. For each day and site combination, I used the proportion of observed visits that had another female already there as a measure of female competition.

The density of males is likely another influence on search costs. Total density increases as colonization progresses, but the density or proportion of recently arrived (new) males may be more relevant to searching females (see mate preferences below). The proportion of males that are new was positively correlated with the density of new males (*r*=0.597, N=31, P<0.01) and diminished as total density increases (*r*= - 0.437, N=31, P<0.05). The densities of new males and of all males were not correlated (*r*=0.209, N=31, P>0.1).

Predation risk and female competition were also correlated with each other and the distribution of males. The proportion of visits involving waiting females was positively correlated with the density of clerids (*r*=0.620, N=19, P<0.01) and with the proportion of males which were newly arrived (r=0.385, N=27, P<0.05). Clerid density was correlated with the density of new males (r=0.674, N=21, P<0.01) and with total male density (r=0.368, N=21, P=0.06). These correlations are to be expected because it is in the interests of both females and predators (for different reasons) to be present when many males are arriving and establishing themselves. Thus females faced the greatest competition and predation risk when recently arrived males were most common.

Visiting Behaviour

Females appeared to visit males at only one site before choosing a mate. Of the 205 females observed on logs over 3 years, only 10 flew away. None of these was seen visiting a male before flying. Therefore my observations of females who were observed both landing and mating covers the entire mate assessment period.

Of the females whose entire visiting sequence (from landing to choice) was observed, 57.5% accepted the first encountered male (Fig. 1.2). The other females did reject at least one male before choosing (one rejected 13 males), indicating active choice. The frequency distribution of number of males visited did not differ among years (χ^2=5.75, df=6, P>0.25). The sample of females observed from landing until choice was probably biassed towards short sequences because of the risk of losing sight of individuals. However, the inclusion of females with incomplete sequences did not alter the frequency distribution of visits when sequences without visits (10.7%) were excluded (χ^2=1.20, df=4, P>0.75), suggesting that those females who were not watched throughout their search were not behaving differently.

Females rarely revisited males. Only twelve females revisited males, and 9 of these returned to a male that they had just left. Only one female mated with the revisited male. Clearly, females were not using a best-of-n search tactic.

The number of visits by females did not vary significantly with any single measure of cost (Table 1.1, first column). Lack of significance could be due to having too small a sample size to detect small but real effects. However, the strongest correlation was a positive one between visit number and clerid density (P<0.1), which is opposite to what would be expected if females were attempting to minimize predation risk while searching for mates.

Time Budgets

The total time females were watched (before they arrived at the male they would accept or were lost) averaged (±SD) 426.5 s ±723.1 (N=60) in 1988, 344 .3 ±533.4 s (N=98) in 1989, and 139.3 ±209.7 s (N=32) in 1990. Differences between years correspond to differences in the time it took for females to choose mates. In 1989 and 1990 (for which

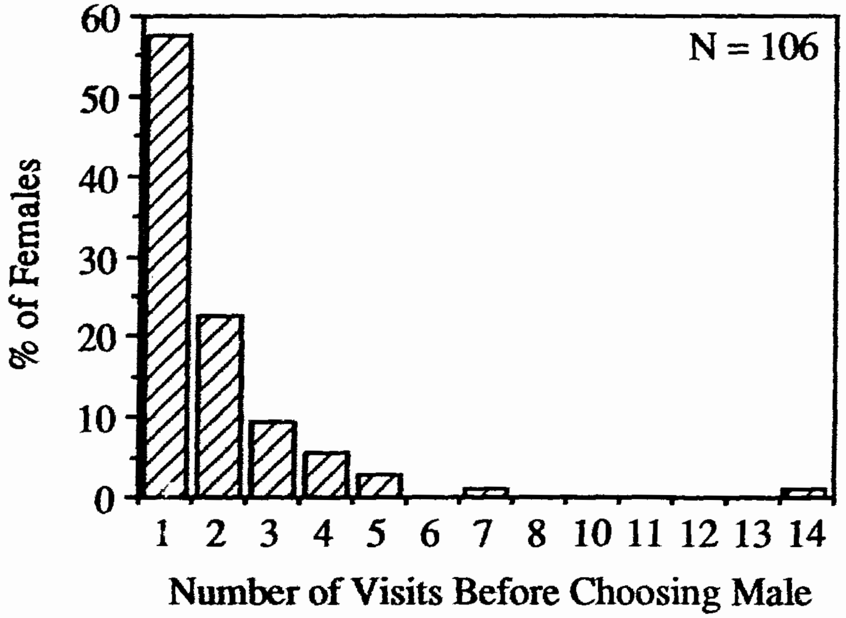

Figure 1.2. Frequency distribution of the number of males visited by female pine engravers before choosing a mate, for females observed landing.

Table 1.1. Pearson correlation coefficients between female visiting behaviours and the characteristics of the site visited. Observations from all years combined except where noted.

Site characteristic	Number of visits	Bout duration (min) At entrance	Hide	Run
Total male density	0.253	0.053	0.299	-0.061
N	22	25	25	31
New male density	0.318	0.154	0.378	-0.169
N	22	25	25	31
Proportion new male	0.144	-0.027	0.124	-0.188
N	25	25	25	31
Predator density	0.399	0.015 (0.743**)†	0.671**	0.362
N	19	18 (13)	17	21
Female competition	0.245	0.008	0.434*	-0.085
	21	24	23	28

* P<0.05, ** P<0.01

† Correlation for 1988 and 1989 only

there was a reasonable sample size), search time from landing to choice was 333.8 s ± 503.7 (N=54) and 112.5 ± 195.3 s (N=15), respectively, a significant difference between years (t-test, $P<0.05$).

Female time budgets differed among years quantitatively but not substantially (for all females observed; differences between complete and incomplete sequences were not significantly different for all behaviours). Females spent most of their time running on the log, spending a mean of 58.4 ±34.2% of their time in this activity in 1989 and 74.4 ±28.2% in 1990. Brief pauses accounted for about 3% of the time budget in both years. Females hid 8.0 ±18.5% of the time in 1989 and 13.7 ±22.2% in 1990. The rest of their time was mainly spent at entrance holes to nuptial chambers of males (25.4 ±30.6% and 9.1 ±21.9% of time for 1989 and 1990 respectively). These time budgets are similar to those observed for a congener Ips typographus (Paynter et al. 1990).

Because these time budgets include females who never rejected a male, the proportional time does not provide an accurate indication of how long females spent at an entrance hole before rejecting the resident male. For all rejections, this amounted to a mean of 98.0 ±280.0 s (N=122) in 1989 and 67.1 ±229.6 s (N=15) in 1990. Females spent much more time at the entrances of males they eventually accepted than at those they rejected. These timings are imprecise because it was often difficult to see exactly when the female had fully entered the nuptial chamber. Minimum times were 671.4 ±857.7 s (N=57) in 1989 and 537.1 ±1012.2 s (N=26) in 1990. Mate assessment can therefore be a time-consuming activity relative to the average time searching.

I examined whether the time that females spent at entrance holes, hiding and running was affected by search costs. I used mean bout length of each behaviour, to control for differences in observation time among females. A bout is the amount of time a female engages in a single behaviour before changing to another behaviour. I took the mean of bout lengths for each female, and then used the mean of all females observed on each day/site combination. Females that were not observed performing a behaviour were excluded from the calculation of means for that behaviour, as were bouts that occurred during or after a parasitoid attack.

Female search behaviour varied with predator density (Table 1.1; last 3 columns). Females hid for longer bouts and, considering just 1988 and 1989, spent more time at male entrance holes when predators were more numerous. Observations of entrance hole bouts in 1990 differed from the pattern shared by 1988 and 1989 data (Table 1.1), with females spending longer at entrance holes than expected for the other years. There is no obvious reason for this difference in 1990, except that there may have been more males who did not yet have enough room for additional females, causing females to eventually give up waiting to get in.

The significant correlation between hiding and female competition (Table 1.1) suggests the non-intuitive result that females hid more when there was greater competition. However, this correlation resulted from the correlation between female competition and predator density. When the effect of predator density was removed using partial correlation, female competition had no significant effect on hiding (r= - 0.021, N=16, P>0.5). Conversely, the relationship between hiding and predator density remained when female competition was statistically removed using partial correlation (r=0.567, N=16, P<0.05).

Effects of other search costs could also be obscured by the effect of predator density because of correlations between them. When I statistically removed the effect of predator density, the partial correlations revealed that females remained at male entrance holes significantly longer when female competition was higher (for 1988 and 1989 data, r=0.735, N=17, P<0.01). Also, for all years combined, females ran for longer bouts when recently arrived males were least abundant (new male density r= - 0.518, N=19, P<0.05, proportion new males r= - 0.504, N=19, P<0.05). In sum, components of female mate search behaviour were influenced by search costs, particularly predation risk.

Mating Preferences

As expected from the breeding biology, galleries that had been established longer (older galleries) contained more females (r=0.328, N=88, P<0.01) and were longer (r=0.614, N=85, P<0.001). Older galleries also belonged to larger males (r=0.373, N=51, P<0.01), reflecting a general pattern of large males colonizing a breeding site first (unpubl. data). These correlations make it difficult to determine whether any one of these characters is the main criterion of choice without manipulations to make them independent (Mitchell-Olds and Shaw 1987). However, if these characteristics are always correlated, females will tend to get them as a package regardless of which component is actually assessed. In support of this idea, the relationships between chamber age and each of female number, gallery length and male body size did not vary among the three years (ANCOVA: all interactions between year and age as main effects non-significant, P>0.4).

Females tended to accept recently established males, especially those that had been settled less than 2 days (Fig. 1.3). This preference was consistent among years: the chamber age of accepted males did not differ among the three years (ANOVA, F(2,110)=0.72, P>0.4), though the chamber ages of rejected males did vary (F(2,215)=5.71, P<0.01). (Hereafter, I use male age to refer to age of a male's nuptial

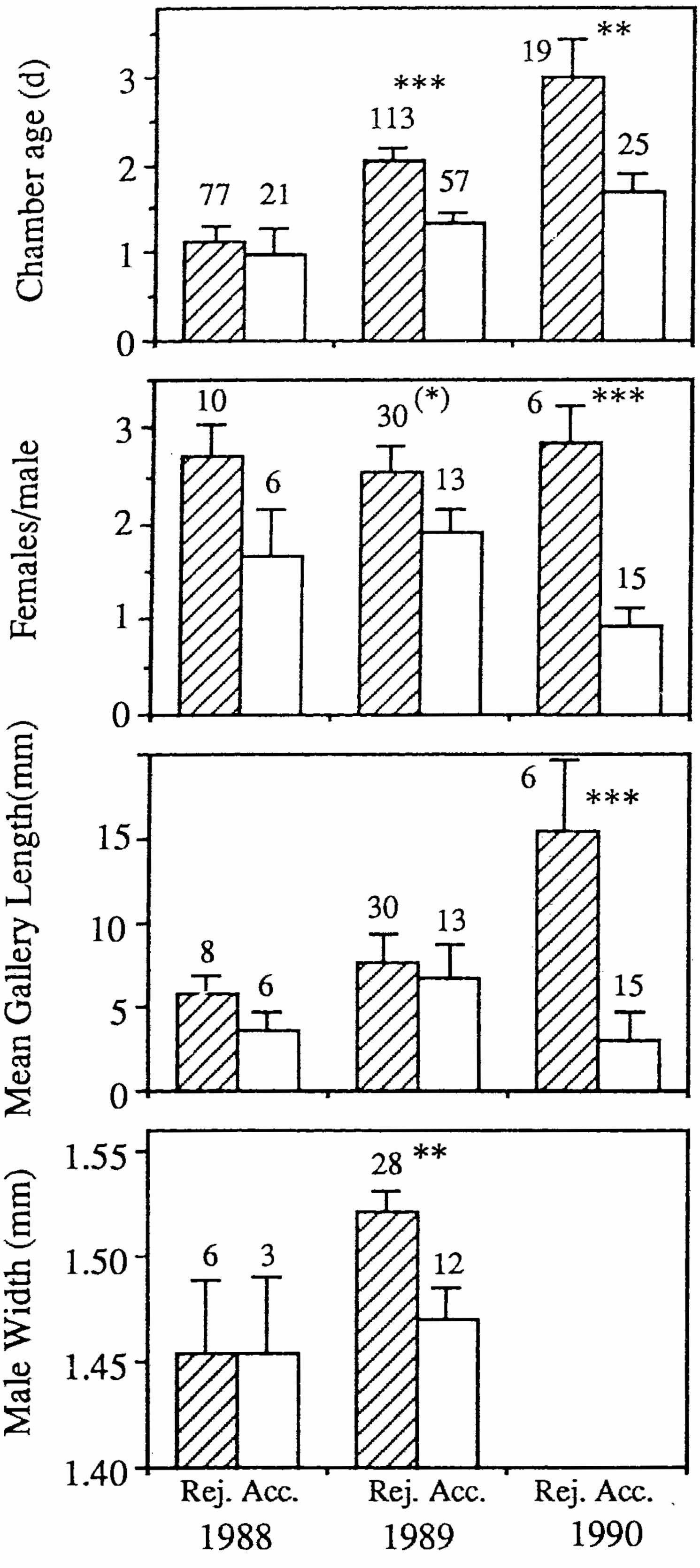

Figure 1.3. Characteristics (mean + SE) of rejected and accepted male pine engravers. Number above bars indicate sample sizes. (*) $P < 0.1$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

chamber, for simplicity.) Rejected males were on average oldest in 1990 (Fig. 1.3) when there was a gap of several days in the colonization process (Fig. 1.1) due to bad weather. To determine how the ages of accepted and rejected males compared with what was available, I examined these distributions for each day/site combination that had enough visits observed. The age distribution of visited males tended to be similar to the age distribution of all males available, suggesting random encounters, except when accepted males were included, as accepted males tended to be significantly younger than those available (Table 1.2).

As expected from the correlations among male and gallery characteristics, preference for recently established males corresponded to a tendency for females to mate with males with fewer mates, those with shorter egg galleries, and with smaller males (Fig. 1.3). Accepted males differed among years in the number of mates they already had (F(2,31)=4.10, P<0.03), but rejected males did not (F(2,44)=0.16, P>0.8). Average gallery lengths were similar among all years for accepted males (F(2,31)=2.79, P>0.05) and rejected males (F(2,41)=2.22, P>0.1).

The apparent preference for smaller males (Fig. 1.3) is likely attributable to the tendency for smaller males to be more recently arrived. In a lab study in which everything but male body size was experimentally controlled, females preferred larger males (Chapter 2). However, in the field data, the preference for small males remained when the effect of age was removed. To see this, I did an ANCOVA of male body size with acceptance as the main effect and age as the covariate. Male body size differed among accepted and rejected males (F(1,47)=4.982, P=0.031), with accepted males being smaller. Age also had a significant on body size (F(1,47)=4.975, P=0.031), and there was no interaction between age and acceptance.

As another measure of female preferences, I examined whether the length of time females persisted at male entrance holes was correlated with male characteristics. These analyses include only rejected males, when female departure could be observed. Correlations between persistence and male characteristics did not vary among years (ANCOVA, year effects and interactions non-significant (P>0.15) in all cases) so data from all years were combined. Females persisted significantly longer at the entrances of more recent males (r= - 0.280, N=180, P<0.01). The correlations between persistence and number of mates (r= - 0.029, N=42), mean gallery length (r= - 0.201, N=40), and male body size (r= - 0.269, N=31) were not significant, but in the same direction as the differences between accepted and rejected males.

Table 1.2. Goodness-of-fit tests of the chamber ages of visited, accepted and rejected males by female pine engravers compared to ages available for a given day and site.

				Visited			Rejected			Accepted		
Year	Site	Date	df[a]	N[b]	$\chi2$	P	N	$\chi2$	P	N	$\chi2$	P
88	1	12Jn	2	18	0.90	ns	6	6.32	*	9	5.62	ns
88	1	14Jn	4	23	0.90	ns	18	1.67	ns	1		
88	1	15Jn	3	25	5.91	ns	20	2.35	ns	1		
88	1	16Jn	4	12	5.76	ns	9	5.93	ns	1		
89	1	31M	1	20	3.57	ns	9	0.99	ns	6	0.28	ns
89	1	1Jn	2	25	11.30	*	19	5.00	ns	6	11.24	**
90	1	21Jn	1	7	13.28	***	2			5	7.77	**
90	2	22Jn	2	24	8.31	*	8	3.00	ns	14	15.64	***

a degrees of freedom for $\chi2$ statistic

b N=number of visits

* P<0.05, ** P<0.01, *** P<0.001, ns not significant

Effect of Costs on Choosiness

It has already been noted that for females which sampled, the age of accepted males did not vary with the abundance of new males . For these females, accepted male age also did not vary significantly with predator density (r= - 0.122, N=11, P>0.5), nor with female competition (r= - 0.214, N=13, P>0.2). There is therefore no evidence that female preferences vary with costs.

Female Differences

Females who visited more than one male mated with more recently arrived (preferred) males than females who chose their first encountered male (comparison of females observed at the same site on the same day: paired t-test, t=2.215, df=12, P=0.047). Females that did not sample may have been mating randomly. For these females, the age of accepted males was highly correlated with the availability of recently arrived males (with new male density r= - 0.653, N=17, P<0.01; with proportion of males that were new r= - 0.733, N=17, P<0.01). For females that sampled before mating, the relationship between the ages of available and accepted males was not significant (new male density r= - 0.304, N=13, P>0.2; new male proportion r= - 0.312, N=13, P>0.2). Thus, it appears that there were differences among females in their mating preferences. Moreover, by visiting more than one male, females were able to mate with males that were more preferable than the average available.

Experience and Female Choosiness

I compared the mean characteristics of rejected males with those of the accepted male for individual females with paired t-tests. Preferences for smaller, more recently arrived males with fewer mates and shorter galleries were again found at this level of analysis (Table 1.3). In fact, this paired comparison of rejected and accepted males showed even more significant patterns than at the population level because the characteristics of accepted males were positively correlated with those of the males a female previously rejected (Table 1.3, Fig. 1.4). In other words, if a female had visited only less preferred males, she tended to choose a less preferred male.

Correlations between rejected and accepted males for individual females could arise in two ways. Females could reduce their expectations after a sequence of encounters with less preferred males. Or, they could arrive with lowered expectations at sites with a large proportion of less preferred males (perhaps because of the blend of pheromones emanating from the site). To distinguish these, I examined female behaviour as a function of her sequence of encounters. I did this two ways. First, for each character, the quality of the

Table 1.3. Differences and correlations between rejected and accepted males by individual female pine engravers.

		Paired *t*-test			Pearson correlation	
Male Character	N	Mean Diff†.	*t*	*P*	*r*	*P*
Chamber age (d)	48	1.152	3.274	0.002	0.451	<0.001
Mates/male	18	0.903	3.586	0.002	0.401	<0.1
Mean gallery length (mm)	17	2.789	1.961	0.067	0.378	>0.1
Total gallery length (mm)	17	12.559	2.197	0.001	0.500	<0.05
Male width (mm)	12	0.058	3.771	0.003	0.505	<0.1

† average of all rejected males minus chosen male

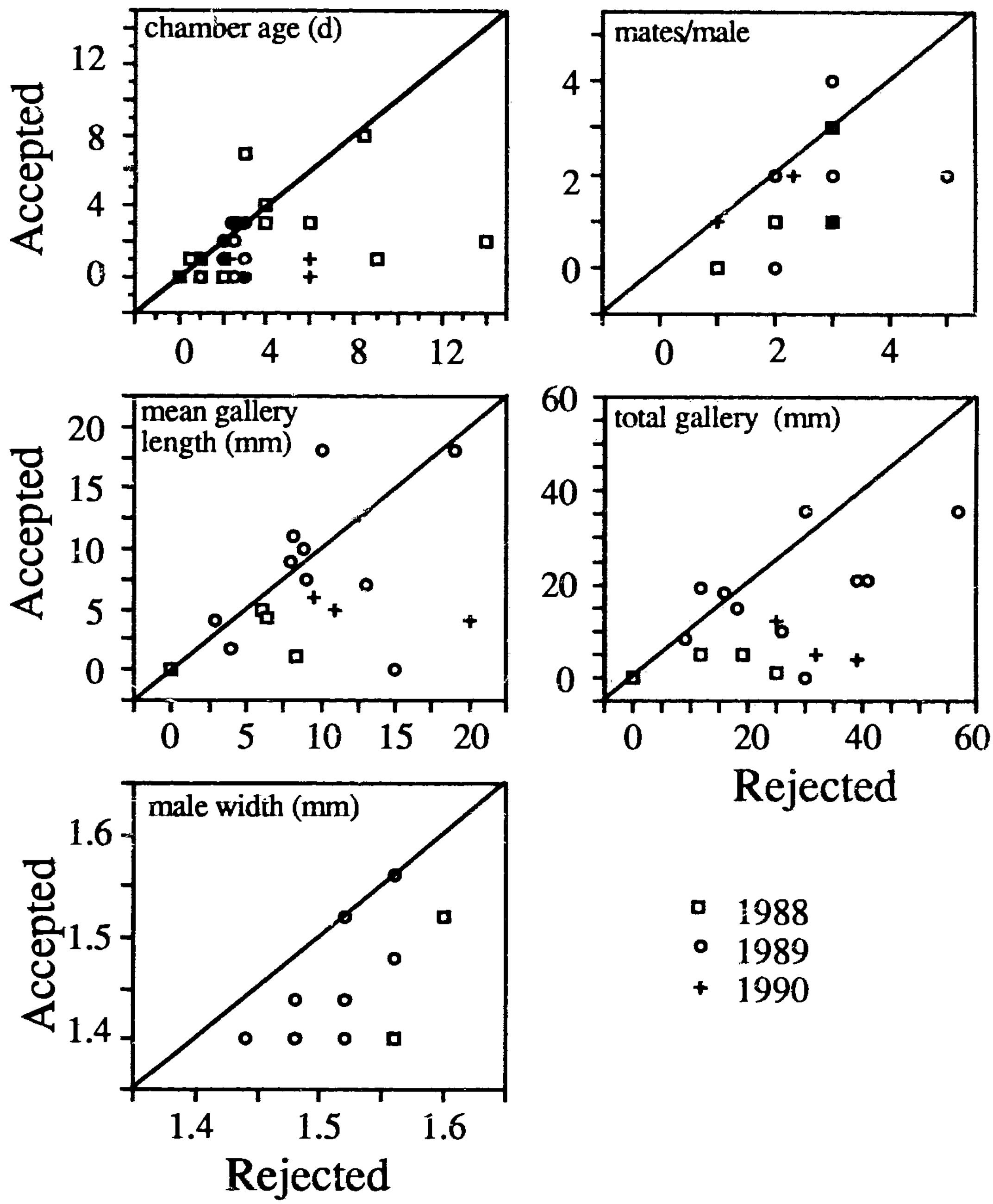

Figure 1.4. Characteristics of accepted male pine engravers compared with the means for rejected males. Each point corresponds to values for an individual female. Diagonal line indicates equality of accepted and rejected males.

accepted and rejected males was compared to see if females eventually accepted a male of the same quality as ones she had earlier rejected. I consider preferable characters to be those indicated by the population as a whole (Fig. 1.3) rather than individuals' preferences. Some females accepted males that were less preferable than the mean of males they had rejected (points above the diagonal in Fig. 1.4), but using the mean of rejected males obscures variation. I therefore compared the accepted male to each of the rejected males for each female, and found that about half of all females mated with a male who was the most preferable of any she had visited (Table 1.4). The other females mated with males who were either less preferable or the same as previously rejected males. A few females that mated with a less preferable male did so immediately after rejecting a more preferable male. This occurred in 3 of 6 cases for chamber age, one of four cases for number of mates, four of six cases for mean gallery length and one of four cases for total gallery length. However, in these cases the differences between males tended to be small. Larger differences tended to occur when the better male had been visited more visits ago, as can be seen for male mating status (the only character with sufficient variation for this analysis). Rejected males that had much fewer mates than the accepted male tended to be encountered much earlier in a female's visiting sequence (sequence difference vs mate difference $\underline{r}=0.852$, $N=9$, $P<0.01$; mate difference equals zero included). This result suggests that females may lower their standards as searching progresses, such that male characteristics that were earlier rejected eventually become acceptable.

A second test of experience is whether the quality of accepted males varied with how many males were sampled. If females were becoming less choosy the longer they searched, then males that were accepted after more visits should be of a less preferred type. For females that visited more than one male, I correlated chamber age with the minimum number of males that females had visited. (To obtain an acceptable sample size, I included females who were not seen landing and may have visited more males than I saw. This source of variation should make analyses conservative.) For all years combined, there was no relationship between the number of males visited and the age of accepted males ($\underline{r}=0.157$, $N=48$, $P>0.1$). However, the predicted relationship was observed in 1989 ($\underline{r}=0.710$, $N=14$, $P<0.01$), and was in the same direction in the other years (1988: $\underline{r}=0.308$, $N=5$, $P>0.5$; 1990: $\underline{r}=0.266$, $N=29$, $P<0.2$). The fact that visit frequency was not detectably correlated with any measure of search costs (Table 1.1) suggests these factors, at least, are not producing a spurious result here. Females may indeed become less choosy the longer they search.

Table 1.4. Number of females who chose a male that was better than, worse than, or the same as the best of the males she had rejected, for each male trait.

Trait	N	Better*	Same	Worse
Chamber Age	47	17	24	6
Mates/male	20	10	6	4
Mean gallery length	18	10	2	6
Total gallery length	18	12	2	4
Male width	13	8	5	0

* as indicated by characteristics of successful males (Fig. 1.3): more recent, fewer mates, shorter galleries, smaller body size

Discussion

Mate choice tactics are expected to vary according to the costs and benefits incurred by searching for mates (Real 1990), which in turn are expected to be related to the dispersion of males and the type of mating system (Wittenberger 1983). The value of these ideas has so far been limited by a dearth of empirical observations of either mate search behaviour or search costs in nature, and by an emphasis on one relatively rare mating system (leks) among the few field studies that have been reported (Reynolds and Gross 1990). In the present study, I examined the search costs and mate choice tactics of a species with a resource-based mating system, and I found general support for the proposed influences of costs on tactics. Also importantly, specific features of mate choice in pine engravers provide empirical justification for some assumptions in mate choice models (e.g. random encounter) and evidence for a mate choice tactic (learning) which has not yet been considered in detail (Real 1990).

The mate choice process of female pine engravers can be described as follows. Females encounter males more or less randomly. Some females mate with the first male they encounter, and these females apparently mate randomly. The remaining females sample more than one male before mating and invest significant amounts of time in each visit to a male. These females prefer recently-arrived males that have few mates and short egg galleries, and which also tend to be small. They rarely revisit males, and therefore do not use a best-of-n or pool comparison mate choice tactic (as defined by Janetos 1980). There is some evidence that choosy females also do not have a fixed acceptance threshold, but instead reduce their expectations the longer they search. This tactic is consistent with high search costs (mainly parasitism risk and female competition). Search costs also affect components of female search behaviour, especially how long females persist at male entrance holes and how much they hide. Overall, however, search costs had little effect on how much females sampled and the quality of males they accepted. This description of the choice behaviour and factors which influence choice in pine engravers seems robust because most of the relationships discussed were consistent among the three years and between the two populations of this study.

The absence of revisits (or a best-of-n tactic) in pine engravers has also been observed for mate-searching females in natterjack toads Bufo calamita (Arak 1988) and pied flycatchers Ficedula hypoleuca (Dale et al 1990). Fixed-threshold preferences, which do not require revisits, have been experimentally determined in female cockroaches Nauphoeta cinerea (Moore and Moore 1988) and jungle fowl Gallus gallus (Zuk et al. 1990). In contrast, in species with lek mating systems, pool or sequential comparisons appear to be typical (Beuchner and Schloeth 1965, Trail and Adams 1989, Pruett-Jones and Pruett-

Jones, 1990, Petrie et al. 1991; but see Gibson et al. 1991). The difference in tactics may be attributable to the costs of choice (Reynolds and Gross 1990). In the studies of lekking birds just mentioned, predation is apparently low at the lek, female competition is non-existent because males provide only brief copulations, and females appear to know the locations of most or all males. Pine engravers (and natterjack toads; Arak 1988) differ from lekking birds on all these counts. Female pine engravers face significant risk of parasitism by T. tibialis, female competition causes males to be continually and permanently removed from the pool of preferable males (which precludes copying as a tactic), and females arrive at a site naive about the spatial distribution of males. Assessment of males is also reasonably time consuming, relative to total search time. Therefore, mate searching is costly in pine engravers. This difference in search costs and mate choice tactics between pine engravers and lekking species matches well with predictions by Wittenberger (1983), Reynolds and Gross (1990) and Real (1990). A best-of-n mate choice tactic is superior when there are no costs to choice (Janetos 1980), but when there are costs, a tactic without revisits is better (Real 1990).

Although female pine engravers did not revisit males, their preferences did appear to depend on experience. There were three lines of evidence for changing preferences. First, females who encountered less preferred (less recent) males accepted a less preferred male, and this was independent of availability of preferred males. The significant relationships between characteristics of accepted and rejected males were not tight, nor should they be expected to be. Females should choose a highly preferred male if he is encountered even if the other males she has encountered are undesirable, but not vice versa. Therefore one would expect a lot of scatter below the diagonal when accepted males are plotted against rejected males, as can be seen in Fig. 1.4. Second, females who visited more males ended up mating with a less preferred males, and again visit number was not correlated with availability of preferred males. A potential problem with these two arguments is that I measured availability for the whole site and this may not be the scale at which females are assessing availability. A scenario could be imagined in which female preferences were fixed upon arrival by a local blend of pheromones. However, the third line of evidence does not depend on this. The third observation concerns those few females who chose a male that was less preferable than one she had rejected. The better the rejected male was relative to the one she accepted, the longer ago he was in her sequence of visits. Learned mate preferences in pine engravers have also been documented in a laboratory study (Chapter 2); females that had experienced large males were less attracted to a mid-sized male than females who had only visited small males previously.

There are two possible explanations for these changing preferences. One is that females should become less choosy as the time available for choosing diminishes (a dynamic one-step process; Janetos 1980). This seems unlikely in this case because the time scale over which an individual female is searching (usually less than half an hour) is small relative to the colonization period of males (several days, Fig. 1.1). The second explanation is that females are learning about the distribution of males, and their encounters with less preferred males reduces their expectations. To explain the third line of evidence, females may weight recently encountered males more heavily in their expectations.

Memory of past encounters is not necessarily expected in either Real's (1990) or Roitberg et al's (in press) models of mate choice. Both models assume random encounters with potential mates, an assumption met in pine engravers. They also both assume that females with no memory have innate expectations that are accurate. This assumption may not be valid for pine engravers. The spatial distribution of males within a log is slightly clumped for early arriving males, but then becomes increasingly regular (unpubl. obs.). Consequently there may be patches of similarly aged males. On a slightly larger scale, logs may differ in their proportions of different aged males (but not tremendously, which is partly why I considered site rather than log characteristics). This patchiness coupled with local searching may be sufficient to favour learned rather than innate expectations.

Female behaviour varies with search costs, but in a somewhat limited fashion. I have already argued that search costs may be responsible for females not using a pool comparison mating tactic, on a species level. But components of female search behaviour vary with search costs in ecological time as well. Females persist longer at entrance holes when there are more predators and female competitors around, and hide more in response to more predators. These seem like adaptive behaviours. Females behave appropriately even if they have never actually encountered a parasitoid or predator. They can predict the abundance of predators on the basis of male pheromones, since predators respond to these pheromones as females do (Bedard 1965, Miller and Borden 1990). Female competition is also correlated with the availability of new males. However, although effects of search costs could be detected for individual behaviours, there was no apparent effect of costs on either the amount of sampling females did or the age of accepted males. Real's (1990) model of threshold preferences predicts that females should reduce their acceptance thresholds in response to increased costs, which would also have the effect of reducing the number of visits a female would make. It is not clear why female pine engravers did not behave this way. It may be that correlations between costs effectively cancelled each other out. For example, both increased predator abundance and travel costs (as indexed by the inverse of male density) should reduce sampling by females, but these two costs were negatively correlated and are likely to always be in nature

Females chose males on the basis of characteristics (number of mates, length of galleries) that contribute directly to female fitness. Competition occurs between the larvae of females whose egg galleries originate from the same nuptial chamber (Kirkendall 1989). Larvae from first laid eggs not only get access to better phloem (which is degraded by their passage), but also have a size advantage which allows them to win direct encounters with later-hatching larvae. These encounters usually end in the death and consumption of smaller larvae (Schmitz 1972, Beaver 1974, pers. obs.). Thus it is clearly to the advantage of a prospecting female to select mating situations where there are few previously established females or the egg galleries have not progressed far, or preferably both. Mate number and gallery length were both correlated with how recently the male had arrived at the site. Male size was correlated with arrival time as well, with smaller males arriving later. Consequently, I believe, females tended to mate with smaller males. The success of small males remained even when arrival time effects were removed statistically, but I think that this is an artifact of these particular data because in a controlled laboratory experiment females persisted significantly longer at larger males (Chapter 2). There are no obvious advantages to mating with a small male, while larger male pine engravers tend to produce more offspring and larger ones (Chapter 5).

If females gain fitness advantages from choosing recently arrived males, it is puzzling why half of females in three successive years appear to mate randomly with the first male they encounter. Genetic differences among females in their mating preferences, commonly required in sexual selection models (Arnold 1985), are only reasonable when preferences have no fitness consequences (Kirkpatrick 1987). The possibility that females had sampled elsewhere can be excluded because I never observed a female fly away after visiting a male. The most likely reason is that these females differed in some phenotypic feature, such as body size or condition. In general, bark beetles become increasingly responsive to host trees and pheromones of the opposite sex as their fat reserves are depleted (Borden 1985). There are several possible reasons for this change in responsiveness. First, the act of searching could increase the risk of starvation. Second, low fat reserves probably means that initial egg production, and therefore hatching, would be slowed (Reid 1962). In this case, females may not realize as much of a competitive advantage from being the first mate, so there would be less benefit from searching for a preferred, recently-established male. Another possibility, related to the second, is that weakened females may be less preferred by males, if there is some male mate choice, so females reaching that state become less choosy. Unfortunately, I did not measure the size of searching females so this remains speculative.

Much of the interest in female mate choice is currently due to its importance to sexual selection (Arnold 1985, Bradbury and Andersson 1987). This study does not address sexual selection directly, because most traits that female pine engravers are choosing are definitely not genetic. Male (chamber) age, number of mates, and gallery length are all transitory states that virtually all males pass through. Only male body size may be heritable (Chapter 5), but there is also a large environmental component to body size in bark beetles (Anderbrant et al. 1985). However, the nature of mate preferences and mate choice tactics do influence the outcome of sexual selection models, particularly the likelihood of runaway selection occurring (Arnold 1985, Seger 1985, Wade and Pruett-Jones 1990). Many models assume that female preferences are constant regardless of the availability of preferred males, or that the preference is genetically fixed and not subject to experience (Maynard Smith 1987); these assumptions are clearly not tenable for pine engravers. Relative preferences, typical of comparison tactics and learning, may increase the rate at which male traits are exaggerated (O'Donald 1983), or they may slow the process (Zuk et al. 1990). This depends upon how the male trait distribution varies over time (Zuk et al. 1990). However, fixed preferences may require low acceptance thresholds, not extreme ones, to ensure that at least one acceptable male is encountered, and this will reduce the selective pressure on male traits. Dynamic thresholds that are sensitive to experience, such as pine engravers exhibit, are an intermediate tactic. Females may initially set high acceptance thresholds to favour getting a very good mating situation, but if she does not encounter many of these, her expectations are lowered. This seems a good solution when search costs are high.

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Chapter 2

Innate and Learned Mate Preferences in Pine Engravers

Abstract

The nature of female mating preferences for large male body size in pine engravers Ips pini (Coleoptera: Scolytidae) was investigated in the laboratory, in particular with respect to whether females had innate or learned preferences or both. The experimental set-up consisted of three arenas on a log, one arena containing large males, another containing small males, and a third arena with a single average-sized male. Single naive females were first allowed to visit either the large males or the small males, to determine innate preferences, and then all females were tested on the average-sized male, to determine learned preferences. This was repeated with increasing numbers of mates already present with the male, and replicated on three logs. Females innately preferred large males and males with few mates, as measured by the amount of time naive females spent at the entrance of male nuptial chambers and by the proportion of females who visited only one male during a trial. Preferences were not influenced by a female's own body size, even when the female was much larger than the males Female preference for large males was also altered by experience, as females who had experienced large males were less attracted to the same average-size male than females which had only experienced small males. This is one of the first observations of learned mate preferences, and has implications for the outcome of sexual selection.

Introduction

Interest in sexual selection and mating systems has prompted research into many facets of female choice, especially what male traits are chosen and how females benefit from choice (Bradbury and Andersson 1987, Kirkpatrick and Ryan 1991). One poorly understood aspect is how females choose one male from among those available. Although there are many possible tactics, an initial distinction among tactics is whether mating decisions are based on fixed (absolute) preferences or whether they vary with adult experience (relative or learned preferences). Most genetic models of sexual selection by female choice consider fixed female mating preferences (Arnold 1985). Lande (1981) proposed three formulations of fixed mating preferences; all three result in qualitatively similar outcomes in sexual selection models but the propensity for exaggeration of male traits by Fisher's runaway process varies among them (Arnold 1985). Other formulations of fixed preferences involve a threshold preference (Janetos 1980, Real 1990), in which any male better than some minimum quality is acceptable. Fixed preferences contrast with preferences that are altered by experience. A commonly considered relative tactic is one in which a female chooses the best of a sample of n males (Janetos 1980, Wittenberger 1983, Real 1990). This type of preference alters the rate of evolution of male traits and the stability of equilibria relative to fixed preferences in genetic models of sexual selection (O'Donald 1980, Seger 1985). Thus, the specific form of female preferences can determine the outcome of sexual selection.

Ecological circumstances will determine the costs and benefits of different mate choice tactics. If search costs are negligible, a best-of-n tactic is a superior tactic (Janetos 1980). When search costs are significant, a fixed threshold tactic yields higher fitness (Real 1990), but this conclusion is based on the assumption that females have an accurate knowledge of the distribution of male quality before they start to search (Real 1990). Recently, Stephens (1991) showed that only a small degree of unpredictability in a resource is sufficient to favour the evolution of learning. Learned preferences have been demonstrated in three-spined stickleback, Gasterosteus aculeatus, wherein female attraction to a given male depended on the attractiveness of the preceding male (Bakker and Milinski 1991).

In pine engravers, Ips pini (Coleoptera: Scolytidae), females exhibit active mate choice (Chapter 1). The biology of this species favours mate choice for several reasons. First, males provide resources. Males stay with their mates (usually three) during most of the two to three week oviposition period . They defend the galleries against egg predators and help females reproduce more quickly by clearing frass from the galleries (Chapter 3). Second, a female can visit many males within a small area. Males mass-attack weakened or recently dead trees, reaching densities of 200 to 300 per m^2 (pers. obs.). Each male chews a nuptial chamber under the bark in which he stays until the end of oviposition some weeks later; this precludes direct competition among males. Female assessment of individual breeding situations is also facilitated by male pheromones that provide information about the number of mates he has (Swaby and Rudinsky 1976) and possibly his body size (Anderbrant et al. 1985). Therefore females need not actually enter nuptial chambers to assess males. Finally, mate choice is potentially important because a female commits a large portion of her lifetime reproductive success to a one male, as she may acquire only one or two mates during her life (Pope et al. 1980).

The availability of preferred male pine engravers may vary considerably. The average body size of males colonizing breeding sites varies among sites, during the colonization of a given site, and through the season (unpubl. data). Such unpredictability may favour learning about the local availability of males (Stephens 1991). However, females also experience significant costs of searching, including risk of parasitization by parasitoids and competition with other females (Chapter 1), and these costs may reduce the value of assessment (Real 1990). Nonetheless, field observations of pine engravers suggested that females may update their mating expectations as they encounter new males. In this chapter, I examine in controlled experiments whether female pine engravers have innate, fixed preferences or learned preferences, or both.

Methods

Experimental Design

I conducted this laboratory experiment at Simon Fraser University in Burnaby, British Columbia. On a single log, I established two arenas ("patches") each containing either 5 large or 5 small males, and a third smaller arena between them with a single average-sized "test" male (Fig. 2.1). This design was replicated on 3 different logs, each approximately 50 cm long and 22 cm in diameter. Experiments began on 21 July and 8 August 1988 for logs 1 and 2 respectively, and on 4 July 1989 for log 3. All logs were cut from living lodgepole pine (Pinus contorta var. latifolia Engelmann) within a few weeks prior to use, and their ends were sealed with paraffin within a day of cutting to prevent desiccation. Arenas were made from plexiglass. Paper was placed on the outer surfaces to obstruct the beetle's view beyond the arena. The base of the arena walls were joined with the log using fresh plasticene. While an experiment was in progress in an arena, the arena was covered with sheet of plexiglass to minimize drafts and to concentrate male pheromones within the arenas.

All beetles used in this study were collected daily as they emerged in cages from naturally colonized logs collected near Riske Creek, B.C. To ensure that most (if not all) individuals were virgin adults (rather than re-emerging parents), beetles were collected during peak emergence when most individuals were obviously teneral. Females and males were separated immediately, and stored in glass jars containing tissue paper. After emerging, bark beetles typically require a period of flight or starvation before switching from dispersal to reproductive behaviour (Borden 1985). Therefore most beetles were collected the day before they were used in an experiment and kept at room temperature, which was sufficient to minimize flight tendencies. For log 1, males were collected 9 days prior to use, and females tested with males with no mates were collected 6 days prior to use. In both of these cases, beetles were stored at 4°C before use. For each experimental log, males and females came from the same source logs.

Males were selected on the basis of pronotal width, measured at 25x magnification

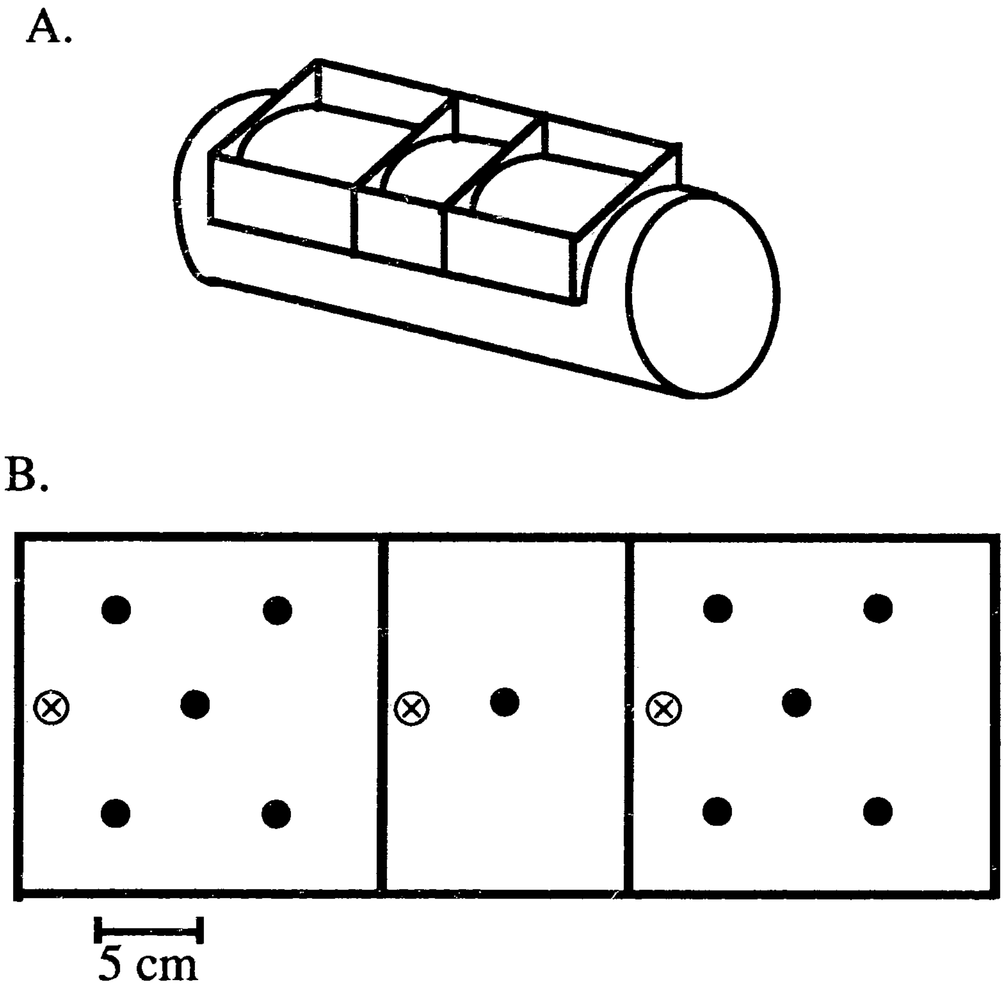

Figure 2.1. Experimental arenas. A. arrangement on log. B. distributions of males within arenas, to scale. Solid circles show male entrance holes, crossed circles are where experimental females were released.

using a stereomicroscope fitted with an ocular micrometer. I defined large and small males to be one standard deviation greater or less than the mean pronotal width, respectively; test males had pronotal widths close to the mean (Table 2.1). In the afternoon prior to the first female trials, males were 'implanted' on the log in the arrangement shown in Fig. 2.1 by confining each male within an inverted half gel capsule over a pre-made puncture in the bark. All males began their nuptial chambers within a few hours of confinement. During trials, each entrance hole to male nuptial chambers was blocked with an insect pin placed across the centre of the hole so that pheromones could be released but females could not enter. However, females and males could not physically contact one another, which may prevent another means of mate assessment.

To examine innate and learned preferences of females for male body size, individual females were tested first in an arena containing either large or small males, and then in the arena containing a single average-sized male ("trials"). I consider the behaviour of naive females in patches of large and small males to reflect innate preference, and their behaviour with the test male as reflecting learned preference. Multiple males (5) were provided in patches of large and small males to create the impression in females that the "world" contained an abundance of one type of male. Most females in nature visit fewer than 5 males (Chapter 1), but they potentially could assess the availability of preferred males by a blend of pheromones from many males. A single test male was used to provide a standard comparison among females with different experiences.

Trials of successive females were alternated between patches of large and small males. For each trial, a female was taken from the holding jar of females using cover-slip forceps and placed in half of a gel capsule. The capsule was then placed at a slight vertical angle with the opening at the release spot (Fig. 2.1) in the appropriate patch of large or small males. The female was allowed to exit the capsule by herself, and when she was on her feet on the bark, the trial began. Trials in the arenas with large or small males were 5 min long. I recorded, using a stopwatch, the time of contacts with a male's frass pile, with the entrance hole itself, and the time of departure from the frass pile.

After the 5 min trial in a patch was finished, the female was gently removed and placed into half a gel capsule. She was then promptly released into the test male arena (in the same manner as for the patch trial), to minimize the opportunity for intervening experiences. Test male trials were 3 min long because of the smaller arena size and number of males, and all visits to the test male were recorded as before. The number of females of all treatments tested on a given day was determined by the number available.

To determine if female preference for body size was affected by male mating status, I increased the number of mates per male each day for 4 or 5 successive days. A new cohort

Table 2.1 . Body sizes of beetles used in experiments. Male sample refers to the groups of males from which large, small, and test males were chosen. Females are those whose behaviour was observed in the experiments.

				Pronotal width (mm)			
Log	Sex	Group	N	Mean	SD	Min	Max
1	Males	Sample	29	1.568	0.060	1.48	1.64
		Large	5	1.656	0.036	1.64	1.72
		Small	5	1.496	0.022	1.48	1.52
		Test	1	1.56			
	Females	Expt.	45[a]	1.552	0.059	1.44	1.64
2	Males	Sample	30	1.515	0.072	1.40	1.64
		Large	5	1.608	0.018	1.60	1.64
		Small	5	1.408	0.018	1.40	1.44
		Test	1	1.52			
	Females	Expt.	83	1.518	0.069	1.32	1.64
3	Males	Sample		[b]			
		Large	5	1.648	0.044	1.60	1.68
		Small	5	1.480	0.028	1.44	1.52
		Test	1	1.56			
	Females	Expt.	125	1.501	0.080	1.32	1.76

[a] Only a subset of females measured.

[b] No representative sample was measured.

of experimental females was tested every day. After a day's trials were completed, one additional female was added to each male's nuptial chamber by confining her in a gel capsule over a male's entrance hole. The gain of one female per day is comparable to the rate of mate acquisition by males in nature (Chapter 3). Thus, for all logs there were trials with 0 to 4 mates per male on successive days. For logs 1 and 2, males were given a maximum of 3 mates per male (thus there were 4 days of trials per log), while for log 3, a maximum of 4 mates were given to each male (5 days of trials). This design does not permit distinguishing age effects of a breeding sites from number of mates per male, but here I use mates per male to refer to this treatment. Swaby and Rudinsky (1976) found that attractiveness depended more on the number of mates than on age of nuptial chamber in pine engravers.

To examine the effect of female body size on mating preferences, I measured the pronotal width (as per males) of individually identified females after their trials were completed for logs 2 and 3. Subsets of non-individually identified females were measured for log 1 to obtain average body sizes of each day's cohort.

Analyses

Data from a female were removed from analysis if the female was noted to be feeble, if she flew during a trial, or if she was disturbed during a trial or during the transition from patch to test male. For consistency among logs in analyses, I excluded trials in which males had 4 mates (in log 3 only).

Female preference was measured as the duration of a trial that a female persisted at an entrance hole of a male's nuptial chamber, and the number of separate visits to males that she made. In a field study in which entrance holes were not blocked, female persistence indicated the same preferences as actual mating patterns, though not as clearly (Chapter 1). Analysis of variance (ANOVA) on untransformed data was used to analyze the duration the trial females spent at entrance holes, with patch type (large or small males) and mates per male considered as fixed effects and log as a random effect. Data points that were significant outliers were checked for unusual attributes, and several analyses were re-run with extreme outliers removed. Removal of outliers never altered the conclusions, indicating that the results are reasonably robust, and outliers were retained in final analyses.

I used loglinear analysis (Fienberg 1980) to test whether the frequency of visits made by females was influenced by male body size and male mating status. To avoid zero observations of some frequencies, I pooled visit frequencies into only two categories for both patch and test male analyses. For patch trials, the categories were a) one visit or b) more than one visit, and I interpreted more than one visit as indicating female dissatisfaction with any individual male (i.e. short giving-up time for any given male). For test male trials, I considered a) zero visits and b) at least one visit, where lack of interest by females was inferred when females failed to visit the test male at all. I used Systat 5.0 statistical software for Macintosh computers (Wilkenson 1989) for all analyses.

Results

Innate Preferences

The total time that females spent trying to enter nuptial chambers during the 5 min test period differed significantly among logs (Table 2.2). In particular, patch type and mating status did not have the same effect in all logs, as indicated by the significant interaction terms (Table 2.2). Therefore, I analyzed each log separately for time spent at entrance holes. Naive females spent significantly more time at entrance holes of large males than at small males' entrances for logs 1 and 2, but not for log 3 (Fig. 2.2, Table 2.3). In log 3, the similarity in behaviour towards large and small males was consistent across all days.

Frequency of visits, my other measure of preference, also varied significantly among logs, but the effect of patch type and mating status did not differ among logs, as indicated by the non-significant two-way interactions, and so I combined all logs for analysis of visit frequency (Table 2.4). The tendency for females to visit only one male was not significantly influenced by male body size (Table 2.4). The trend was in the predicted direction however, with a larger percentage of single visits occurring in the patch of large males in 9 of 13 comparisons (Table 2.5; Wilcoxon matched pairs test T=21, P=0.1).

Male mating status also significantly influenced the time females spent at male entrance hole in logs 1 and 2 (Table 2.3), with females preferring males with few mates (Fig. 2.2). There was no significant effect of male mating status in log 3, but persistence was greatest at unmated males and least at males with four mates (Fig. 2.2), which is consistent with the trend. Number of mates per male also significantly influenced the number of visits females made (Table 2.4), with the general trend that females tended to make more visits when males had more mates (Table 2.5). There was no significant interaction between preferences for male body size and mating status (Tables 2.3, 2.4).

Learned Preferences

If female preferences were influenced by experience, I expected that females who had experienced only large males would be less attracted to the mid-sized test male than would females which had only experienced small males. I found that the time females spent at the test male's entrance hole differed significantly among logs, with the effect of previous patch

Table 2.2. Analysis of variance of total time that females spent at males' entrance holes as a function of patch type (large or small males), number of mates per male and log.

Source	MS	df	F-ratio	P
Patch	38672.2	1	1.34	> 0.1
Mates	24933.3	3	0.70	> 0.1
Log	72221.2	2	16.82	<0.001
Patch x Mates	4096.4	3	0.64	>0.1
Patch x Log	28801.4	2	6.71	0.001
Mates x Log	35592.7	6	8.29	< 0.001
Patch x Mates x Log	6434.7	6	1.50	>0.1
Error	4295.2	218		

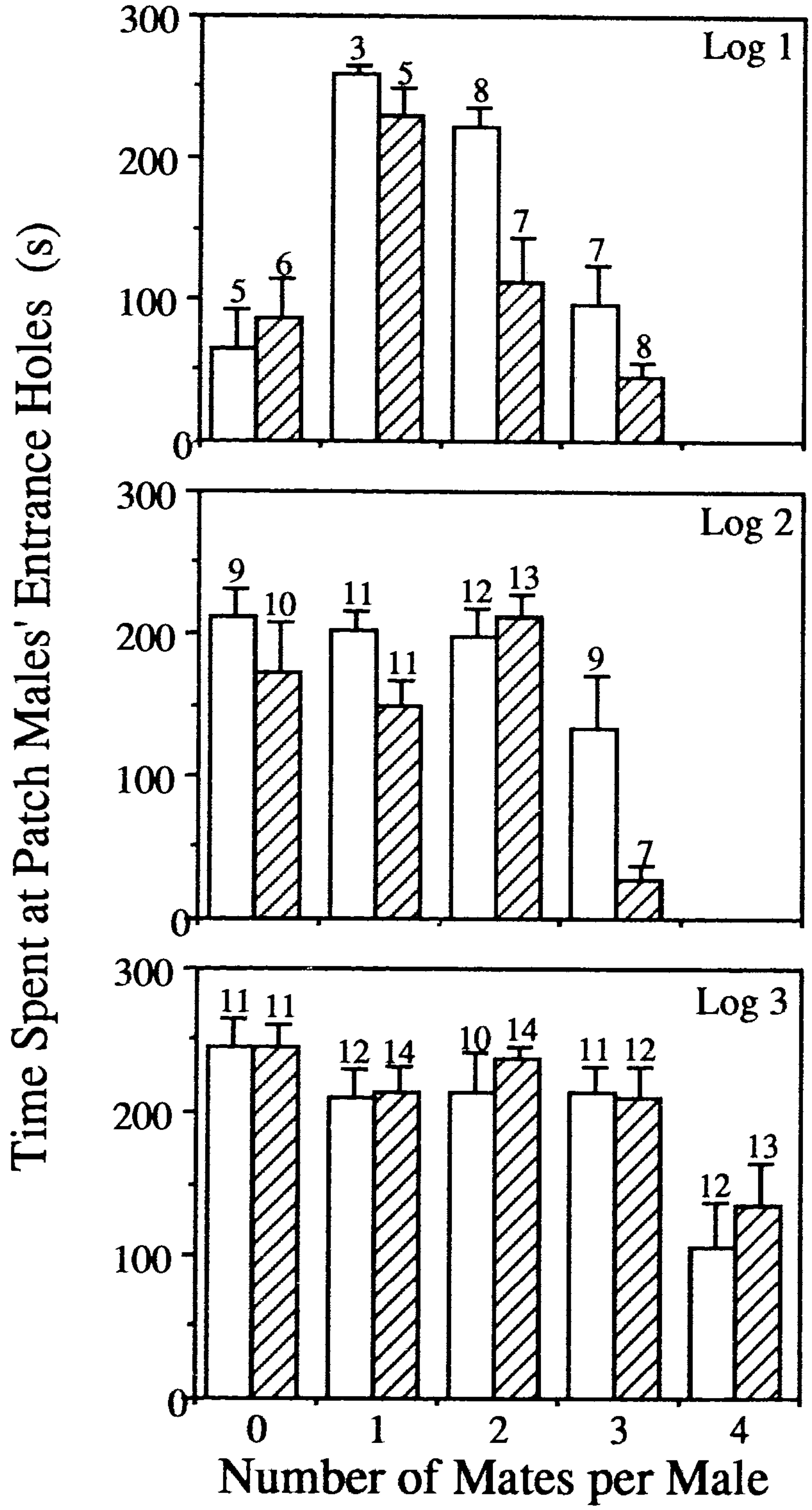

Figure 2.2. Time that females spent at the entrance of a male's nuptial chamber in patches of large males (open bars) and small males (hatched bars) with varying number of mates. Standard error and sample sizes indicated.

Table 2.3. Analysis of variance of time spent by females at males' entrance holes as a function of patch type (large or small males) and number of mates per male, for each log separately.

Log	Source	MS	df	F-ratio	P
1	Patch	29861.2	1	11.96	0.001
	Mates	103993.9	3	41.73	<0.001
	Patch x Mates	3705.3	3	1.49	>0.1
	Error	2492.3	43		
2	Patch	42861.5	1	8.24	0.005
	Mates	54720.1	3	10.53	<0.001
	Patch x Mates	12070.4	3	2.32	>0.1
	Error	5199.2	75		
3	Patch	6071.7	1	1.38	>0.1
	Mates	3928.6	3	0.89	>0.1
	Patch x Mates	2389.3	3	0.54	>0.1
	Error	4392.4	100		

Table 2.4. Loglinear analyses of the number of visits (1 or >1) that females made in patches of large or small males as a function of patch type, mates per male, and log.

Source	G^2	df	P
Visits	9.22	1	<0.005
Patch	2.72	1	0.05<P<0.1
Mates	13.97	3	<0.005
Log	31.00	2	<0.001
Patch x Mates	3.40	3	ns
Patch x Log	3.13	2	ns
Mates x Log	8.96	6	ns
Patch x Mates x Log	13.89	6	<0.05

Table 2.5. Frequency of visits to males by females in patches of large or small males, as indicated by the percentage of females making a single visit and the maximum number of visits observed.

		Large Male Visits			Small Male Visits		
Log	Mates	%Single	Max	N	%Single	Max	N
1	0	60.0	2	5	83.3	2	6
	1	100.0	1	5	66.6	2	6
	2	66.6	2	9	16.6	3	6
	3	42.8	6	7	12.5	4	8
2	0	50.0	3	14	72.7	3	11
	1	45.4	3	11	18.1	4	11
	2	50.0	3	12	46.1	3	13
	3	44.4	4	9	0	5	8
3	0	100.0	1	11	81.8	2	11
	1	76.9	2	13	78.5	5	14
	2	75.0	2	12	71.4	2	14
	3	63.6	2	11	78.5	3	14
	4	66.7	2	12	53.9	4	13

experience being marginally non-significant for all logs combined (Table 2.6). When each log was examined separately, previous patch experience did significantly influence the time females persisted at the test male for logs 1 and 3, but not for log 2 (Table 2.7). As predicted, females who had experienced large males tended to spend less time at the test male than did females which had experienced small males (Fig. 2.3). This trend was also evident for log 2 on three of the four days of trials; the conflicting result when males had one mate may account for the overall lack of significance on this log.

There was also a significant effect of previous experience on the proportion of females that visited the test male within the allotted 3 min (Table 2.8). Females who had previously experienced small males were more likely to visit the average-sized test male than females which had experienced large males (Table 2.9; Wilcoxon T=11, P<0.05). This was consistent across logs.

The effect of male mating status was again evident with the test males as it was for large and small males (Fig. 2.3). Females spent significantly less time at males with more mates in logs 1 and 2. (Table 2.7). Although male mating status was not significant for log 3, the same trend was evident (Fig. 2.3). Visit frequency differed significantly among mating status treatments (Table 2.8), but there was no consistent trend with number of mates per male (Table 2.9).

Effect of Female Body Size

Experimental females varied considerably in body size, and many were much larger than the small males (Table 2.1). Female preference for large males might be because of simple physical limitations of large females fitting through the entrance holes of small males. To see whether preference for large males varied with female body size, I did analyses of covariance with female body size as the covariate. I did this for logs 2 and 3 for which I measured individually identified females, and I analyzed these two logs separately because of previously noted differences between them.

For log 2, the effect of female body size did not differ between patches of large and small males (interaction F(1,62)=0.321, P>0.5) or with male mating status (interaction: F(3,62)=0.99, P>0.4). Overall, female body size explained little in an analysis of covariance (pronotal width, F(1,69)=0.03, P>0.8)

For log 3, the effect of female body size did differ significantly between patches of large and small males (width x patch: F(1,84)=7.38, P<0.01). There was no interaction between female body size and male mating status (F(4,84)=0.48, P>0.7). I analyzed the effect of female body size separately for each patch to see how the effect differed with large and small males. For both patches, there was no further effect of male mating status either

Table 2.6. Analysis of variance of female visit duration at test male entrance hole as a function of patch experience (with large or small males), number of mates with test male and log.

Source	MS	df	F-ratio	P
Patch	31363.7	1	6.08	0.05<P<0.1
Mates	8214.2	3	1.69	> 0.1
Log	8478.5	3	3.64	0.028
Patch x Mates	443.8	3	0.22	>0.1
Patch x Log	5157.0	2	2.22	0.112
Mates x Log	4859.5	6	2.09	0.056
Patch x Mates x Log	2014.3	6	0.87	> 0.1
Error	2328.4	223		

Table 2.7. Analysis of variance of time spent by females at test male's entrance hole as a function of previous patch experience (large or small males) and of number of mates that test male has, for each log separately.

Log	Source	MS	df	F-ratio	P
1	Patch	23397.7	1	12.39	0.001
	Mates	8075.8	3	4.27	<0.01
	Patch x Mates	1526.1	3	0.81	>0.1
	Error	1887.8	47		
2	Patch	659.6	1	0.41	>0.1
	Mates	7434.4	3	4.65	<0.01
	Patch x Mates	2146.6	3	1.34	>0.1
	Error	1597.8	72		
3	Patch	15779.4	1	5.20	<0.05
	Mates	1096.7	3	0.36	>0.1
	Patch x Mates	907.3	3	0.30	>0.1
	Error	3033.3	104		

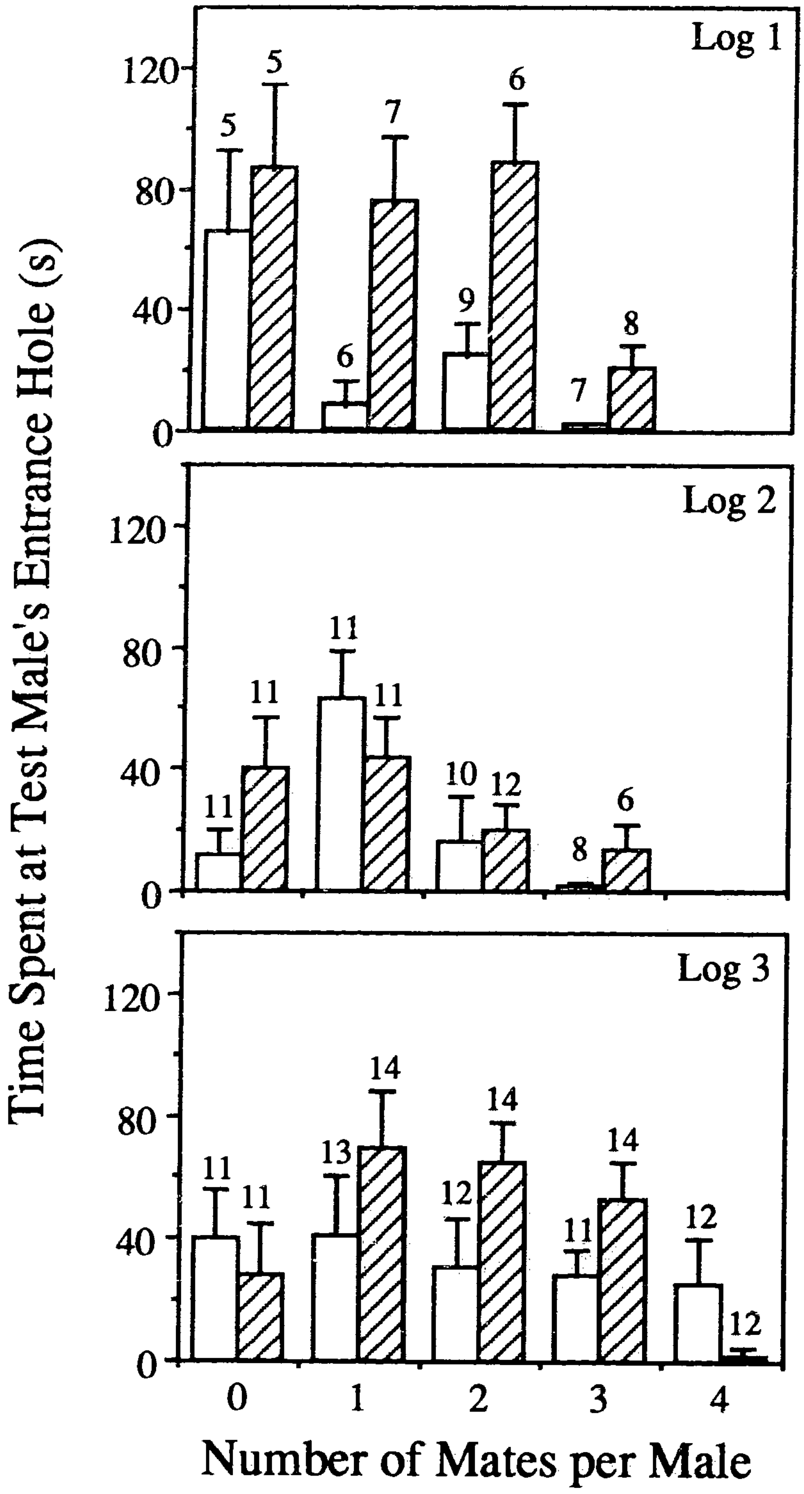

Figure 2.3. Time that females spent at the entrance of the test (mid-sized) male's nuptial chamber. Opens bars indicate females large males, hatched bars indicate female who had experienced small males. Standard errors and sample sizes indicated.

Table 2.8. Results of loglinear analyses on the number of visits (0 or ≥1) females made to test male as a function of patch type previously experienced, mates per male, and log.

Source	G^2	df	P
Visits	7.39	1	<0.025
Patch	7.84	1	<0.01
Mates	8.90	3	<0.05
Log	0.16	2	ns
Patch x Mates	4.10	3	ns
Patch x Log	4.56	2	ns
Mates x Log	8.58	6	ns
Patch x Mates x Log	5.27	6	ns

Table 2.9. Frequency of visits to test (intermediate-sized) male with respect to previous experience with either large or small males. Visit frequency is described by the percent of females who visited the test male at least once, and by the maximum number of visits made.

		Large Males			Small Males		
Log	Mates	% Visit	Max	N	% visit	Max	N
1	0	60.0	3	5	80.0	1	5
	1	16.7	1	6	85.8	2	7
	2	44.5	1	9	85.8	1	7
	3	42.9	1	7	75.0	2	8
2	0	30.8	1	13	45.5	3	11
	1	81.9	3	11	63.7	2	11
	2	45.5	2	11	77.0	2	13
	3	62.5	2	8	62.5	2	8
3	0	45.5	1	11	27.3	1	11
	1	38.5	2	13	57.2	2	14
	2	50.0	2	12	85.8	3	14
	3	72.8	2	11	78.6	3	14
	4	50.0	3	12	41.7	2	12

directly or through interactions with female body size, so I combined the data for all days of the experiment and regressed time persisting at entrance holes against female body size. In patches of large males, there was no significant relationship between persistence and body size ($y=536.4 - 8.9x$, $R^2 = -0.042$, $N=45$, $P=0.17$). Of greater interest is size-related behaviour in the patch of small males, because here many females were much larger than the males. With small males, there was a marginally non-significant effect of female size on persistence time ($y=-195.8 + 10.8x$, $R^2 = 0.064$, $N=55$, $P=0.063$), with the tendency for larger females to spend more time at the entrance holes of small males than small females did, contrary to the physical constraint hypothesis.

Female body size did not affect female behaviour at the test male in either log 2 or 3, as indicated by non-significant interactions between body size and treatments (all $P>0.2$), and by the overall lack of significance of body size as a covariate (both, $P>0.6$).

Discussion

Female pine engravers exhibited innate preferences for large males that were modified by experience. This is the first demonstration of both innate and learned mating preferences in one species. Experience-dependent preferences have recently been observed in three-spine stickleback in a similar experiment to mine, but innate preferences could not be determined in their study because females were wild-caught (Bakker and Milinski 1991). . The mating patterns of female sculpin Cottus bairdii are consistent with a tactic in which females compare consecutively encountered males, but this was not directly observed (Brown 1981). Fixed mating preferences (i.e. uninfluenced by the quality of other available males) occur in cockroaches Nauphoeta cinerea (Moore and Moore 1988) and jungle fowl Gallus gallus (Zuk et al. 1990).

These studies on the nature of mating preferences, though limited in number, indicate that preferences are not taxonomically determined, and may instead be determined by ecology. Search costs, such as predation risk or female competition for mates, are thought to be important in determining mate choice tactics (Wittenberger 1983, Real 1990). In the absence of search costs, choosing the best of a sample of n males (a form of learning) is the best tactic, while a fixed threshold mating criteria is better when search costs discourage returning to previously visited males (Real 1990). Updating mating expectations during sequential visits is an alternative tactic in which preferences can adjust to local conditions without requiring revisits to previously sampled males (a Bayesian process; Real 1990). Such updating was demonstrated in stickleback (Bakker and Milinski 1990) and is likely the tactic used by pine engravers as well. The study reported here could not distinguish a best-of-n tactic from one involving updating, but field observations of pine engravers indicate that females rarely revisit males, contrary to a best-of-n tactic (Chapter 1).

All else being equal, learning should be favoured when inherited knowledge cannot accurately describe an individual's environment. In pine engravers, body size distributions vary among breeding sites (unpubl. data) and over the course of colonization at a given site (unpubl. data). The choice females have in choosing sites or stage of colonization is probably limited because of the rarity of breeding sites. Consequently, the probability of a female finding a male of a particular size upon arrival at a breeding site may vary considerably, so that any fixed, inherited preference could sometimes result in a female either searching indefinitely or missing opportunities to breed with even larger males. However, a naive female must begin her search with some preference, and she will mate with a better male if she begins with high expectations that can be revised downwards. Such a tactic would be consistent with the innate and learned preferences exhibited by female pine engravers.

Female preferences for larger males, both innate or learned, were not consistent among all logs in this experiment. No differences in innate preference for large and small males were detected for Log 3 (Fig. 2.2), while the effect of experience in Log 2 was insignificant mainly because of one day's observations (one mate per male; Fig. 2.3). The inconsistencies may be related to pheromone production, which was most likely the means by which females assessed male body size and mating status in this experiment. Male pheromones in Ips bark beetles change as males gain more mates (Borden 1967, Swaby and Rudinsky 1976), and in I. typographus, males reared in higher densities tend to be both smaller and have altered pheromone blends (Anderbrant et al. 1985). However, pheromone production in bark beetles can also be influenced by the quality of the phloem on which the beetle is feeding (Byers 1989). The quality of both males and phloem may have varied among the logs. Alternatively, there may have been differences in female quality among logs. For Log 3, where females apparently did not discriminate among large or small males, females were much smaller than females for the other two logs (Table 2.1). For Log 2, however, the "aberrent" females on the day that males had one mate (Fig. 2.3) did not differ in size from females tested on other days. In this case, environmental conditions, which were not controlled, may have differed on that day.

Preference for large males is clearly not governed by the physical constraints of getting through the entrance hole, because large females were at least as attracted to small males as small females were. Also, the constraint hypothesis would not predict learned preferences. Instead, the preference seems adaptive. Matings with larger male tend to produce more offspring and larger ones (Chapter 5), perhaps because of the help they provide (Chapter

3). Large body size in insects confers survival advantages through resistance to starvation (Safranyik 1976) and greater dispersal capabilities (Roff 1991). Dispersal capability is important to pine engravers because suitably weakened or recently dead trees would have been a rare and scattered resource (at least before logging was common). Superior dispersal ability may explain why larger pine engravers colonize new sites first (unpubl. data), which gives their offspring first access to fresh phloem and a competitive advantage over the offspring of later arrivals. However, body size and phloem quality were not correlated in this experiment or the one demonstrating reproductive advantages of large males (Chapter 5), because I imposed the same initiation date for large and small males, and locations on the log were arbitrary. Therefore preference and reproductive consequences are related at least in part to male size rather than simply the phloem resources he has.

Female preference for males with few mates is likely due to fitness benefits as well. In this polygynous system, a female's offspring will suffer less intra-harem larval competition (Kirkendall 1989) and less phloem deterioration if they arrive first. Further, males will actively discourage too many females from entering their nuptial chambers (Borden 1967, pers. obs), perhaps again to avoid larval offspring competition, and this should also make mated males less attractive to females. The two mate choice criteria examined here (male body size and mating status) did not influence each other, as seen by the lack of statistical interaction, and thus appear to be used simultaneously.

Fitness consequences, like search costs, may influence whether preferences are learned or fixed. When the preference is arbitrary (as assumed in most sexual selection models; Arnold 1985), the costs of mating with a less preferred male will be lower than when the preferred character determines a female's quantity and quality of offspring. Consequently, when the availability of preferred males is variable, it would be less costly for females choosing arbitrary traits to employ a fixed-threshold tactic with a lower acceptance threshold than it would be for females exhibiting adaptive choice. Females choosing on the basis of fitness-related traits may be more strongly selected to have modifiable preferences instead of a broader acceptance criterion, to allow them to mate with the best locally-available male. Interestingly, in the species in which learned preferences have been demonstrated or implicated (pine engravers, stickleback, sculpins; see above), males are associated with resources important to females (egg-laying sites), while in species with fixed preferences (cockroaches, jungle fowl), males provide mainly genes rather than resources.

The nature of mating preferences, whether fixed or modifiable, will likely influence the outcome of sexual selection. For example, relative or learned preferences may favour the evolution of exaggerated traits because females could always favour the most extreme male

(O'Donald 1980). On the other hand, the mating success of a given male phenotype may vary widely when there are learned preferences because attractiveness depends not only on a male's own phenotype but also on the phenotypes of his neighbours. Consequently, sexual selection would be inconsistent (Zuk et al. 1990). Further studies on the nature of mating preferences in species with and without strongly developed sexually-selected traits will help resolve this question empirically.

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Chapter 3

Benefits of Prolonged Male Residence with Mates and Brood in Pine Engravers

Abstract

In the pine engraver bark beetle, Ips pini (Coleoptera: Scolytidae), males stay with their mates for most or all of the oviposition period, which can last several weeks. I examined several potential benefits to males of such a prolonged association with their mates in field studies. Attraction of additional females to male breeding sites and mate-guarding of current mates did not explain the observed male residence times, because the probability of these events was negligible within a week of the male's arrival at the breeding site. Instead, a male-removal experiment showed that males significantly increased the reproductive rate of their mates, apparently by removing female-produced frass from the galleries, and males also defended the egg galleries against predators. This tended to result in increased reproductive success in galleries with males present. The breeding biology of bark beetles predisposes males to providing these types of assistance, but in many other similar species of bark beetles, males do not stay as long. I suggest that the ability to provide assistance is not sufficient to explain prolonged associations between males and their mates and brood.

Introduction

Prolonged post-copulatory associations of males with their mates or offspring (or both) are, at first glance, at odds with the general rule that males should seek additional mating opportunities to maximize reproductive success (Trivers 1972). Presumably, males that stay with their mates or offspring have higher fitness than those that desert immediately after fertilization, and several general conditions that favour staying have been proposed (Maynard Smith 1977; Ridley 1978; Gross and Sargent 1985; Zeh and Smith 1985). These conditions include: 1) attachment to a mating site (e.g. territoriality) which reduces loss of mating opportunity or may even increase opportunities, 2) the need to ensure paternity through mate-guarding, 3) lack of other mating opportunities, and 4) male parental care which significantly increases offspring survival. The first three conditions do not necessarily involve any paternal care, but care may result when the additional costs of care are low (Maynard Smith 1977), and in general more than one condition can exist simultaneously. Therefore, to understand why post-fertilization associations between mates occur in a given species, a suite of hypotheses should be examined.

Here I examine why male pine engravers *Ips pini* (Say) (Coleoptera: Scolytidae), stay with their mates for several weeks. Bark beetles, of which the pine engravers is one species, exhibit a diversity of mating associations ranging from apparent lifelong monogamy to very brief encounters between males and females (Kirkendall 1983). The breeding biology of pine engravers (Thomas 1961; Schenk and Benjamin 1969; Schmitz 1972) is representative of most *Ips* species (Bright 1976). Males synchronously colonize weakened or recently dead trees. Each male chews a nuptial chamber under the bark, and from there he attracts an average of about three females (very few males with chambers remain unmated, pers. obs.). Each female mines an egg gallery radiating from the nuptial chamber, depositing eggs in niches along its sides. All egg galleries radiating from a single male's chamber are collectively called the gallery system. Egg-laying continues for several weeks depending on temperature and density (Anderbrant 1989), during which time males tend to stay in the gallery system (especially the nuptial chamber). Males actively expel from the gallery the frass (chewed wood and feces) that females create while extending their galleries. Copulations occur throughout this period (Schmitz 1972), but females can lay fertile eggs in the absence of males (pers. obs.), as has been documented in *I. typographus* (Anderbrant and Löfqvist 1988) and other bark beetles (Kirkendall 1983). As egg-laying ceases, males and females leave the breeding site, and fly in search of another site. Overwintered adults have sufficient time to produce 2 or 3 broods in a season (Thomas 1961), but the proportion of adults that do so is unknown.

From the breeding biology of pine engravers, I can identify several possible reasons why males stay so long with their mates rather than leaving immediately after fertilization (see also Kirkendall 1983). Males may stay at the breeding site 1) to attract more females to an established mating site, 2) to guard paternity with present mates (mate-guarding), 3) to assist females to reproduce more quickly, e.g. by clearing out frass, and 4) to guard offspring against predators. Alternatively, males stay simply because it is a safe location and they have nowhere else to go. The availability of other mating opportunities may be limited by the synchrony of breeding or by the rarity of breeding sites. These possible explanations for prolonged male residence are not mutually exclusive.

Methods

I conducted field studies in 1988 and 1989 near Riske Creek in the central interior of British Columbia, Canada. To induce breeding assemblages, living lodgepole pines (*Pinus contorta* var. *latifolia* Engelmann) were felled and cut into logs less that a meter long.

These logs were laid end-to-end on the ground in a shaded area of an open stand of lodgepole pine. Several different sites were created each year, all separated by at least 50 m. Colonization by pine engravers was allowed to occur naturally. The entrance holes of newly arrived males were marked daily with coloured tacks. I conducted all studies during the season's first flight of pine engravers when overwintered adults disperse to breeding sites.

The residence times of males were observed in two ways. First, I looked for the presence of males during excavations of gallery systems of various ages at two different sites in 1988. One site was colonized early in the first flight, while the second site was colonized towards the end of the flight; together they represent the range of breeding conditions during the first flight. Second, to determine precisely the timing of male departure with respect to the oviposition period, I made observations using "phloem sandwiches" (bark, with phloem, pressed against plexiglass allowing gallery construction and egg-laying to be fully visible; Schmitz 1972). I introduced males into pre-made holes in the bark, and then added a female into each male's chamber on each of the three following days. Bark pieces were 25 by 20 cm, and two galleries systems were started 8 cm apart on each piece. I recorded gallery lengths, egg number, and the presence of males and females daily. All "sandwiches" were kept at 19-24°C, and were initiated between July and November 1990.

To examine the timing of mate attraction in pine engravers, I selected a cohort of males which had arrived on the second day (1 June) of the colonization period at one field site. Beginning on the day after arrival, I exposed 20 gallery systems each day for 5 days and 10 more on the seventh day and noted the number of mates per male. As much as possible, each day's sample was evenly divided among the six logs at the site, and between the top (sunnier) and sides (shadier) of the logs.

I conducted a male removal experiment to see if males made any contribution to reproductive success during the oviposition period. This was done at a separate site where colonization was concurrent with the previous one. Males were removed from 2 logs early in the colonization period and 2 logs late in colonization (Fig. 3.1). Pairs of established males were matched within each log according to arrival date and proximity to each other. One randomly-chosen member of each pair was removed by spearing him with an insect pin when he came to the entrance hole to expel frass, and the other male was left as the control. Gallery entrances were exposed slightly to gain access to the male for removal, and entrances of control males were similarly exposed. After removal, the logs were left *in situ* for three and four days for the late and early removal period, respectively. I then exposed the galleries of removed and control males to determine the consequences of male

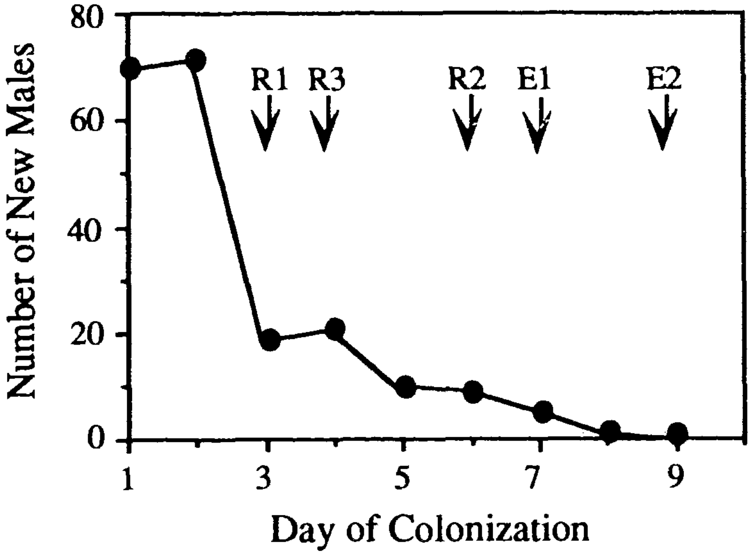

Figure 3.1. Phenology of arriving males at the male-removal site, where the first day of colonization is 1 June 1989. R1 and R2, and E1 and E2, indicate timing of early and late male removals, and subsequent gallery exposure, respectively. R3 indicates timing of male removal for fitness experiment.

removal. I recorded all male and female pine engravers in each gallery system, the length of each gallery arm and the number of eggs within it, the length of each arm beyond the last egg, the length of each gallery arm blocked by frass, and the presence of insect associates in the gallery system.

To examine the impact of removing males on the number of offspring produced I conducted another male-removal experiment in which galleries were not subsequently disturbed. I paired small, naturally colonized logs as closely as possible according to bark area (Pearson correlation $r=0.94$, $n=9$, $P < 0.01$) and number of males ($r=0.56$, $n=9$, $P < 0.05$). One log in each pair was randomly chosen for removal of all males, and the other was left as a control (entrance holes were exposed in both). Logs were left in the forest for a variable number of days to expose them to natural enemies. Each log was then placed in a separate emergence bucket (Moeck 1988), from which all emerging insects were collected for the next two months. The body size of emergent pine engravers was measured as maximum thorax width to the nearest 0.04 mm using a dissecting scope and eyepiece micrometer. This experiment was conducted in both 1988 (three pairs of logs) and 1989 (six pairs). In 1988, removals were conducted after colonization was almost completed, and the logs were left *in situ* for 8 days before being placed in emergence buckets. In 1989, I removed males in the middle of the colonization period (Fig. 3.1), and the logs were left *in situ* for 6 days before being placed in buckets. In 1989, both male removal experiments were conducted at the same site.

Results

Male Residence Time

Under natural conditions, male pine engravers were present in most active galleries initiated during the first flight, for periods of up to three weeks (Fig. 3.2). Laboratory observations indicated that males typically re-emerged after oviposition had finished, but prior to female departure (Table 3.1).

Mate Attraction

Sequential exposure of the galleries of a cohort of males over the period of 6 days revealed that males had attracted their full complement of mates (3 or 4) within 3 days of the males' arrival (Fig. 3.3), which is considerably shorter than the several weeks males have been observed to stay.

Mate-guarding

Removed males were sometimes replaced by another male, but the chance of this occurring varied with the stage of the colonization period in which the original male was

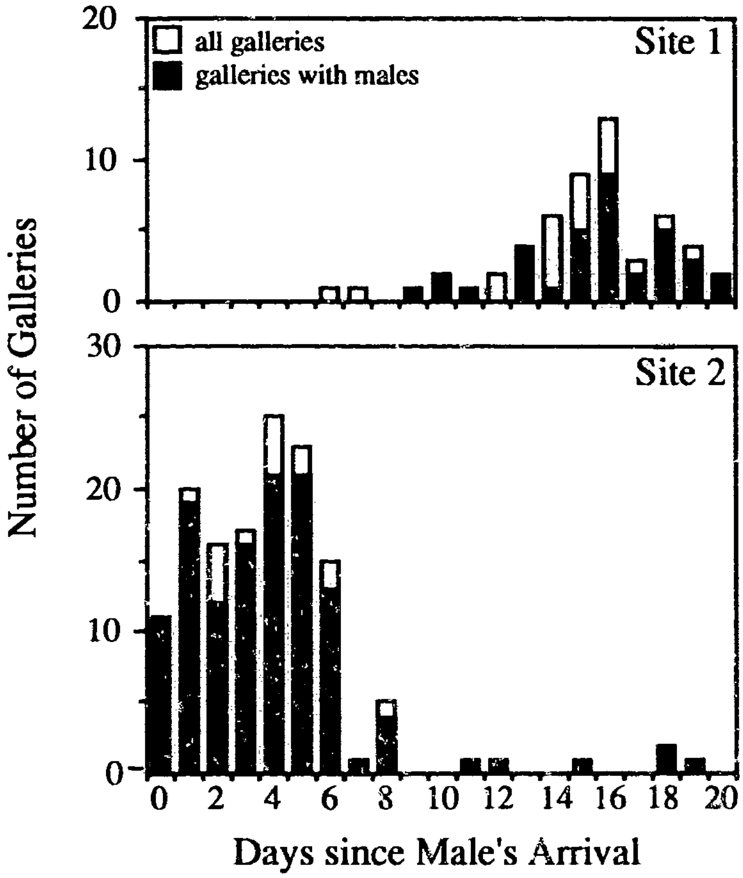

Figure 3.2. Occurrence of pine engraver galleries with males present as a function of the age of gallery system at two field sites in 1988. Colonization at sites 1 and 2 began on 19 and 31 May, respectively.

Table 3.1. Duration residence of male and female pine engravers with respect to the oviposition period for 12 gallery systems established in "phloem sandwiches".

	Total duration (d)	Duration (d) after last egg laid
	Mean ± SE	Mean ± SE
Oviposition period	11.7 ± 1.18	-
Female residence time	29.1 ± 2.58	17.4 ± 2.77
Male residence time	22.8 ± 3.07	11.1 ± 3.20

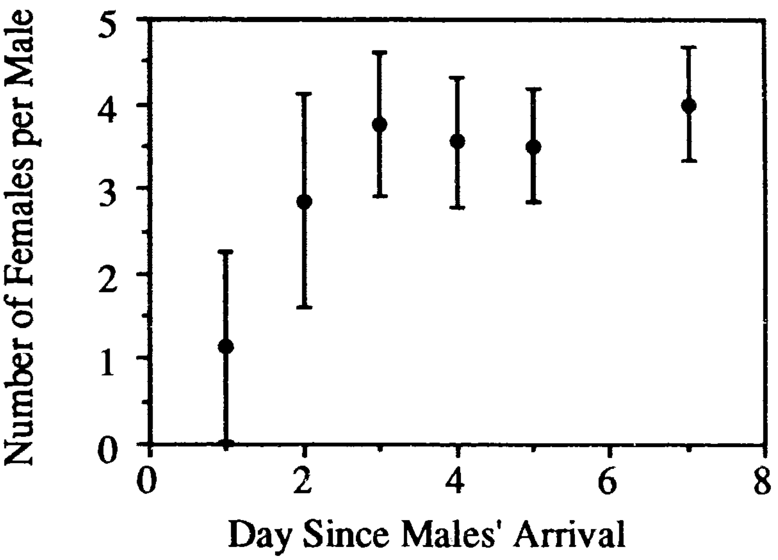

Figure 3.3. Numbers of females per male (mean ± SD) pine engraver as a function of how long a male had been established. For days 1-5, n = 20 gallery systems; for day 7, n = 10.

removed. Of the males removed at the early stage, 32.3% (10/31) were replaced, while only 4.2% (1/24) of males removed at the late stage were replaced (2-tail Fisher exact probability test P=0.015). This difference cannot be attributed to the shorter interval between male removal and gallery exposure for later removals (3 day interval) compared to early removals (4 days). If the average number of replacements per day for the late removal (1/3) is added to the total number of replacements for the late stage (to give 1.33/24 or 5.5 % over 4 days), the difference between the stages remains significant (P < 0.05).

Contribution to Reproduction

I compared characteristics of egg-galleries in which the male was removed with their matched controls to determine if reproductive rate was reduced in the absence of males. The average of all the arms of a gallery system was used for each male. Differences between matched pairs were not affected by the stage (early or late) at which males were removed (P>0.2 for all characteristics), and I therefore combined stages for analysis. Galleries without males had significantly shorter galleries and fewer eggs than their matched controls, and these eggs were distributed more densely (Table 3.2). This was accompanied by a significant increase in the amount of frass present in the galleries without males compared to galleries with males, which suggests that the removal of frass by males facilitates female construction of egg-galleries. Alternatively, the reduction in gallery construction and egg-laying could be an active decision by females to cease investing in the present reproductive attempt because of the male's absence, but the increased density of eggs and the lack of a difference in the length of the terminal egg-free gallery does not support this idea. The terminal egg-free gallery is thought to reflect the female's decision to cease reproducing and instead simply feed to regenerate flight muscles for dispersal (Haack et al. 1987). Galleries in which the removed male was replaced by another male did not differ significantly from their matched controls (Table 3.2), confirming that the observed differences between galleries with and without males was indeed caused by the male and not by some other artifact of treatment.

The effect of male removal on egg production appeared to be greater for younger galleries (Table 3.3). In galleries that were < 4 d old at time of male removal, the number of eggs laid in the absence of males was 60-80% of the number of eggs laid in galleries with males present, while the presence of males appeared to have little effect in older galleries (4-5 d old at the time of removal); however, sample sizes were small.

Defence against Intruders

The presence of insects other than pine engravers in egg galleries was examined to determine if males deter potential predators or competitors. Three different species of

Table 3.2. Comparison of pine engraver gallery systems in which males were removed or removed and replaced, with their matched controls.

	Control galleries (Mean)	Difference of removals from controls					
		No replacements			Removed male replaced		
		n	Mean ±SE		n	Mean ±SE	
gallery length (mm)	41.4	41	-7.36 ±1.51	***	10	-0.72 ±3.07	ns
egg number	13.1	41	-1.46 ±0.57	*	10	0.15 ±0.82	ns
egg density (eggs/mm)	0.31	41	0.02 ±0.01	*	10	0.02 ±0.03	ns
frass (mm of gallery)	0.07	41	3.50 ±1.13	**	10	0.0 ±0	ns
terminal egg-free gallery (mm)	3.1	33	-0.07 ±0.27	ns	9	0.83 ±0.65	ns

ns not significant, * P<0.05, ** P<0.01, ***P<0.001, paired t-test (two-tailed)

Table 3.3. Oviposition rate by pine engravers in galleries with male removed with respect to gallery age at the time of male removal.

Eggs at removal		Oviposition in 3 days after removal of males		
Gallery age (d)	Mean ± SE	Mean ± SE	n	Proportion of mean number of eggs in control galleries
1	1.58 ±0.61	7.92 ±1.50	2	0.798
2	4.10 ±0.44	7.90 ±0.87	5	0.603
3	8.60 ±0.60	6.40	1	0.719
4	12.50 ±0.79	5.10 ±1.36	5	1.000
5	17.20 ±2.25	2.13 ±1.55	9	1.014

beetles (Coleoptera) were found in the galleries of pine engravers. These were *Corticeus* sp. (Tenebrionidae), *Lasconotus* sp. (Colydiidae), and Aleocharinae (Staphylinidae). The occurrence of *Corticeus* sp. and *Lasconotus* sp. did not vary between early and late stages of removal (both: chi-square $P>0.6$, $n=109$, $df=1$), and so the stages were combined for analysis of the effect of males on the presence of intruders. Staphylinids, however, were more common in the late removals (chi-square=6.7, $df=1$, $n=109$, $P=0.01$), and therefore the two stages were analyzed separately.

Both *Corticeus* sp. and *Lasconotus* sp. were rare in galleries with males, but were found significantly more frequently in galleries without males (Table 3.4). The presence of staphylinids was not related to the presence of males. Whether males were originals or replacements did not make a difference to the presence of associates.

Reproductive Success

Low statistical power hindered my ability to detect differences in the production of beetles from logs with and without male removals. The likelihood of detecting a real effect of males in my measures of reproductive success varied between only 34% and 66% at $P=0.05$ (Zar 1984). One source of variation was the unknown number of removed males who had been replaced before the logs were placed in emergence buckets. Also, the date on which the first teneral (pale) pine engravers emerged (separately for 1988 and 1989) was taken as the dividing point between the emergence of adult and juvenile beetles, and undoubtedly there were some adults in the "juvenile" data set. On average, the production of juvenile beetles was quite low (2.5 ± 1.3 SD per gallery system on undisturbed logs) which is also a limitation in detecting differences. Therefore I looked for suggestive trends in my analyses.

Logs with undisturbed males produced significantly more juvenile males per gallery system than logs from which males were removed (mean difference = 0.36, one-tailed paired t-test, $t=1.996$, $n=9$, $P < 0.05$), and also more juvenile females, though not significantly so (mean difference = 0.50, $t=1.436$, $P = 0.095$). For the sexes combined, control logs produced 0.90 more offspring per gallery system than experimental logs did ($t=1.700$, $P=0.061$). In eight of nine pairs of logs, juvenile males were smaller in logs where males had been removed than in control logs (one-tailed Wilcoxon matched-pairs test, T=5, $P < 0.025$, mean difference between logs in mean pronotum width = 0.025 mm). There was no consistent difference in juvenile females' body size between the control-removal treatment pairs (Wilcoxon T=11, $P > 0.1$, mean difference = - 0.017 mm). Emergence times of juvenile males and females also did not detectably differ between the two treatments (males: T=21, $P>0.5$, females: T=19, $P>0.5$; two-tailed tests).

Table 3.4. The effect of the presence of males on the percentage of gallery systems with insect associates.

		Male Present						
		Original		Replacement		Male Absent		
Associate		%	(*n*)	%	(*n*)	%	(*n*)	*P*[a]
Corticeus spp.		1.89	(53)	0	(11)	33.33	(45)	< 0.001
Lasconotus spp.		5.66	(53)	0	(11)	68.89	(45)	<0.001
Staphylinidae	Early	10.34	(29)	20.00	(11)	4.55	(22)	>0.1
	Late	20.83	(24)	0	(1)	39.13	(23)	>0.1

[a] Fisher exact test (2-tailed) comparing data for male present (original and replacement males combined) with male absent.

Discussion

Male pine engravers remained with their mates through most of the oviposition period, which could last for several weeks. The prolonged association cannot be explained by continued mate attraction because males obtained their full complement of mates within a few days. Prompt mate attraction has also been observed in other populations of pine engravers (Swaby and Rudinsky 1976). Females prefer recently settled males (Chapter 1), probably because the offspring of a late arriving females would be greatly disadvantaged by competition with the offspring of a male's earlier mates (Kirkendall 1989). This risk of offspring competition can also adversely affect males reproductive success. I have observed male pine engravers actively reject mate-searching females after the males had been settled for a few days and presumably had a full complement of mates (see Borden (1967) for a similar observation in I. paraconfusus). Late-arriving females may have low reproductive prospects and would only reduce the local quality of the habitat for a male's earlier mates. Therefore it is in the interests of both females and males to avoid mating once males have been established for a few days.

Although some removed males were replaced by others, this occurrence was almost entirely restricted to males that were removed early in the colonization period. Colonization in pine engravers and other bark beetles (Coulson 1979) is usually very synchronous (weather permitting), and at the site of the removal experiment, colonization was almost complete at the time of the late removal (Fig. 3.1). Therefore there were few arriving males that could become replacements of removed males. The evolved avoidance of anti-aggregation pheromones in many bark beetle species (Borden 1985) also suggests that arriving males would prefer not to settle in fully established breeding aggregations whether or not galleries were protected by males. Because of this low risk of usurpation after about a week, it is unlikely that that males remain with their galleries for up to 3 weeks in order to mate-guard.

It appears instead that male pine engravers are helpful during the oviposition period. By increasing the rate of egg-laying, males provide offspring with a temporal advantage against deterioration of phloem quality at the breeding site and against offspring from other gallery systems (Beaver 1974). The lower density of eggs in galleries with males also reduces competition among siblings (Kirkendall 1989). My finding that galleries with males tended to produce more offspring and larger ones is consistent with reduced competition. The slower rate of egg-laying in the absence of males may be due to the extra effort females must expend in removing frass themselves (some galleries remained clear of frass in the absence of males), and the obstacle that frass creates when it does accumulate. The problem of frass accumulation is associated with the particular manner of egg-laying typical of bark beetles, in which females must face backwards (relative to the end of the gallery) to lay an egg (Schmitz 1972). Thus, after a female has chewed out an egg niche at the end of her gallery, she backs down her gallery to a place where there is enough room to turn around (typically the nuptial chamber in pine engravers), and returns backwards up the gallery to the egg niche in order to lay her egg. Then she must return to the nuptial chamber to again reverse direction in order to continue extending her gallery. Any obstacle, such as frass, on this route therefore impedes her rate of egg-laying. If access to the nuptial chamber is blocked, females will chew a turning niche in their gallery. In bark beetle species with brief male residence in the galleries (e.g. Dendroctonus spp.), frass is not actively expelled from the gallery, and instead becomes a packed, resinous blockage at the base of the gallery (Reid 1958). Females must then continue to make new turning niches as their galleries progress. The rate of egg-laying should therefore be relatively reduced in these species without frass removal. In D. ponderosae, egg galleries without males were shorter than galleries with males present (Amman and Cole 1983).

Male pine engravers also defend their gallery systems against intrusion by other insects. The insect associates found in galleries without males, Corticeus sp. and Lasconotus sp., are common associates of bark beetles, and are generally considered to be egg and larva predators (Parker and Davis 1971; Hackwell 1973; Goyer and Smith 1981). Staphylinid beetles within the Aleocharinae tend to feed on fungus rather than eggs or larvae (Crawson 1981), and I found no effect of males on their occurrence in egg galleries. The blockage of the egg gallery with a resinous frass plug, as occurs in Dendroctonus spp., would also seem to provide a barrier against predators. However, Dendroctonus spp. are still vulnerable to egg and larval predators (Schmid 1971; Cole 1981) including, apparently, Corticeus spp. (Parker and Davis 1971; Goyer and Smith 1981). Thus males may or may not provide greater defence of egg galleries than physical barriers, but given clear galleries in which females can lay eggs more rapidly, male defence becomes beneficial.

It seems likely that parental care evolved from a state of no care, because care is generally uncommon in insects (Tallamy and Wood 1986), and the occurrence of care among bark beetle species suggests such a transition (Kirkendall 1983). Some breeding biologies may predispose insects to providing care (Tallamy and Wood 1986) and bark beetles have two relevent features in their biology. First, feeding, mating, oviposition, and offspring development all occur at the same place. Therefore males simply need to persist longer at the mating site to provide care. Initially, mate-guarding may have prompted males to stay some time after copulation. In this study, there was a reasonable risk of replacement (for a few days) by other males when the original male was removed. Takeovers of a recently initiated nuptial chamber should be favoured because initiating a nuptial chamber exposes beetles to predation (Chapter 1). The behaviours involved in mate-guarding, namely deterring intruders, are readily transferable to defending offspring. While mate-guarding, a male bark beetle would also have to maintain access to his mates by removing the frass produced by females. Therefore it would be a small evolutionary step for males to continue these behaviours throughout the oviposition period, even after the threat of rival males became negligible. Mate-guarding appears to have preceded offspring defence in sphecid wasps in a similar manner (Brockmann and Grafen 1989). The second feature of bark beetles that favours care is that reproduction occurs in a defendable location. Bark beetles can effectively block the entrance holes to their gallery systems with their bodies. Parental defence of offspring is frequently observed in arthropods that have some sort of brood chamber (Peckham 1977, Brockmann and Grafen 1989, Wyatt and Foster 1989, Mora 1990).

The importance of male parental care, as demonstrated in experiments such as this one, is often considered to be a sufficient explanation for prolonged pair bonds (Bart and Tornes 1989). However, the amount of care that a male can contribute to a given brood may have no consequence on how long he remains with that brood, if he can provide the same help to subsequent broods. Instead, the likelihood of obtaining a second brood is the key determinant of male residence time (Chapter 4). In other bark beetle species, with similar breeding ecologies to pine engravers, males have much shorter residence times which corresponds to higher survival among breeding sites (Chapter 4). I expect that females in species without male assistance would suffer a reduction in reproductive performance, particularly slower oviposition rates and perhaps more densely distributed eggs As mentioned above, predation risk in the absence of males may be reduced by blocking the entrance with accumulated frass, but at the expense of oviposition rate. Comparable studies to ours in bark beetles with other male residence times are needed to test this idea.

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Chapter 4

On the Importance of Parenting Needs and Mating Opportunities in Determining Pair Bond Durations

Abstract

The duration of pair bonds and male parental care has been attributed to both the need for care and the availability of other mating opportunities. In this paper, I present a model which examines the relative importance of these two factors in determining optimal residence time for males. My model system is bark beetles (Coleoptera: Scolytidae), a family of ecologically-similar species exhibiting the gamut of pair bond durations. I found that the size of a male's contribution to oviposition and predator defence had little or no influence on optimal male residence times. For oviposition rate, this result is because a male's contribution is the same for present and future broods, so that any loss from a male's absence in the first brood is always balanced by a proportional gain in the second brood, no matter what the size of the loss. For offspring defence, optimal residence time is determined by maximizing the number of offspring defended, regardless of the amount of defence. The amount which a male helps does affect offspring number, and the cost of deviating from the optimal residence time, but residence time itself is largely unaffected. It is clearly not true that the need for more care necessarily results in longer pair bonds, even when all else is constant. Instead, the probability of obtaining other mating opportunities had a large influence on male residence time. I suggest that mating opportunities are the primary determinant of male residence times, and that any help males can provide will increase secondarily when mating options are limited.

Introduction

Mating systems are defined in part by the duration of pair bonds between mates (Selander 1972, Emlen and Oring 1977). Within almost all major animal groups, there are some species in which females and males join only for copulation and other species with lifelong bonds that end only with the death of one of the partners. To explain this variation, we often look to the male's reproductive options, because male reproductive success tends to be limited by the number of mates he obtains, while females are limited by the resources they can invest in reproduction (Bateman 1948, Trivers 1972). Therefore, as a general rule, it is in females' interests to have prolonged assistance from their mates, but males may realize greater fitness returns by leaving to seek additional mates.

Decisions about when to leave a mate are thought to depend on the fitness that can be gained by investing in the current reproductive attempt relative to fitness gained by leaving to seek additional mates (Orians 1969, Maynard Smith 1977). Although this view incorporates both present and future prospects, variation in one may be more critical than the other in explaining variation in mating systems within some taxa. Frequently, prolonged associations of males with their mates and broods are attributed to a greater need for parental care to successfully rear offspring (Selander 1972, Mock and Fujioka 1990, Tallamy and Wood 1986, Schneider and Lamprecht 1990). The need for parental care is defined in terms of a single breeding attempt, and is often indexed by the loss in reproductive success to the remaining parent upon the loss of this parent's mate (Mock and Fujioka 1990, Webster 1991). Many studies involving the removal of male mates have shown that pair-bonded males do increase female reproductive success (Chapter 3, Trumbo 1989, Scott 1990, Bart and Tornes 1989). In some cases, however, the contribution of males to the reproductive success of their mates has been found to be negligible (Gowaty 1983, Martin and Cooke 1987, Freed 1987), and in these cases it appears that the lack of other mating opportunities accounts for long pair bonds. Interestingly, the need for parental care and the lack of other breeding opportunities often co-occur (Shachak 1980, Kudô et al. 1989, Scott 1990, Nalepa and Jones 1991). Because there does not seem to be a necessary ecological connection between these two features, it suggests that care may evolve secondarily when breeding opportunities are rare (Maynard Smith 1977). If this is often true, then greater emphasis on mating opportunities rather than male parental care is needed to understand mating systems.

The possibility that parental care requirements or mating opportunities evolve secondarily confounds empirical analyses of the origin of prolonged pair bonds (Westneat et al. 1989). A companion approach to the problem is to build a mathematical model (G.A. Parker in West-Eberhard et al. 1987, p. 194) in which a variable can be altered independently of the other components. In this paper, I present a model which examines the importance of parenting needs (for a given brood) and breeding opportunities in determining the length of time male bark beetles (Coleoptera: Scolytidae) remain with their mates and broods. I define the need for parental care as the gain in reproductive success in a brood when the male is present, compared to when he is absent, and refer to the male's contribution to reproductive success as helpfulness.

Bark Beetle Biology

Bark beetles are an ideal model system for examining male residence time decisions because they exhibit the gamut of mating associations, from brief encounters between males and females to lifelong monogamy (Kirkendall 1983), while having similar breeding biologies (Wood 1982). They spend most of their life mining through the phloem of vulnerable trees, where feeding, oviposition and the entire developmental process occur. Individuals of one sex initiate breeding sites beneath the bark, to which the other sex is attracted. Females oviposit for several weeks in egg galleries extending from initiation sites over several weeks, during which time males may or may not remain to help. When males remain with their mates, they enhance female reproductive success by defending their egg galleries against predators and by helping their mates to reproduce more quickly by clearing the galleries of frass (Chapter 3, Amman and Cole 1983). Most parental males and females will re-emerge to search for new breeding sites, with the possibility of having two or three broods before they die. Although my model is sufficiently general to apply to most bark beetles, it is biassed towards the biology of the pine engraver Ips pini because of my familiarity with this species. Male pine engravers initiate breeding sites, and remain with their mates throughout most of the oviposition period (Chapter 3).

Model of Male Residence Time

My approach is to determine the length of a male's residence time with his first brood that maximizes his lifetime reproductive success. In the scenario described by my model, a male could have two broods in his life, and his life span (T) was set at 30 days after his arrival at the first host tree (see Table 4.1 for summary of variables). The number of mates he attracted was constant, and females were assumed to initiate breeding on the day of the male's arrival. Females remained breeding for 30 days (F), regardless of whether the male was present. Their rate of egg-laying declined exponentially with time, expressed in the form $g\exp(-at)$ (where time t is measured in days) in accordance with patterns observed in several bark beetle species (Anderbrant 1990, Amman and Cole 1983) including pine engravers (pers. obs.). When a male left his first brood at time T_S, he arrived at the second tree instantaneously, but with a probability (p) of less than one. I varied this probability to determine its impact on when a male should leave the first brood to begin a second one. The male remained with the second brood until his death. Thus, each brood could have a male present for part of the time, and absent for the rest.

The effect of male absence on egg-laying was modeled in two ways, to reflect how the impact of males might be manifested. First, the absence of males could diminish egg-laying rate by a constant proportion throughout the egg-laying period. For this I varied the initial egg-laying rate g in the negative exponential oviposition relationship, from g with males present to g' with males absent, where $g > g'$. Second, the effect of male absence could increase through time, perhaps because the consequences of accumulating frass are accentuated as galleries get longer. Here I varied the exponent or slope of the oviposition

Table 4.1. Definitions of variables used in the model of male residence time, with range of values examined.

Variable	Definition	Value(s) Examined
T_S	male residence time with first brood (days)	1-30
T	male lifespan after arriving at first brood (days)	30
F	female lifespan after arriving at first brood (days)	30
g	initial rate of egg-laying when male present	6
g'/g	relative decrease in initial rate of egg-laying when male absent	0.1-1.0
a	rate of decline in egg-laying when male present	0.1, 0.2
a'	rate of decline in egg-laying when male absent	0.2
γ	offspring mortality when male present	0.02-0.04
γ'/γ	relative increase in offspring mortality when male absent	1.001-3
D	days that offspring are vulnerable to predators	1-30
p	probability of having a second brood	0.005-0.905

relationship from a to a' where $a' > a$. (However, my limited data for pine engravers did not indicate a greater effect in galleries which were older at the time of male removal (Chapter 3, Table 3.3).)

I considered two variables which influence offspring mortality. First, the instantaneous rate of offspring mortality was greater in the absence of the male (γ') than when the male was present (γ), because predators can enter the gallery when males are absent. I varied γ' relative to γ. Second, I varied the length of time (D) an offspring was vulnerable to predators against which the male could defend. Common bark beetle predators eat eggs, larvae, and pupae to varying degrees (Reid 1957; Hackwell 1973; Cole 1981; Goyer and Smith 1981). In pine engravers, eggs hatch after 5-7 days and the larval period is usually 13-14 days (Thomas 1961, Schmitz 1972). Given that predator larvae need development time as well, I usually set the vulnerable period to 10 days (the "head start" needed to escape predator larvae) when varying other parameters in my model.

I now present the components of the model determining offspring number, beginning with the male's first brood. Offspring from this brood include those that developed from eggs laid while the male was present, and those from eggs laid after the male left. Consider first eggs laid while the male was present. If the male leaves before any of these offspring become invulnerable, the number of offspring he obtains depends on the number of eggs laid [$g\exp(-at)$] and their mortality while he was present [$\exp(-\gamma(T_S - t))$] and while he was absent [$\exp(\gamma'(t + D - T_S))$]. Thus,

$$A_1 = \int_{t=0}^{t=T_S} g \exp(-at) \exp(-\gamma(T_S - t) - \gamma'(t + D - T_S)) \, dt.$$

If, on the other hand, the male leaves after some early-laid eggs have reached the invulnerable stage, the resulting offspring will include those that were protected by males throughout their vulnerable period, and those who were not protected for some of their vulnerable period. In this case, the number of offspring resulting from eggs laid while the male was present is:

$$A_1 = \int_{t=0}^{t=T_S - D} g \exp(-at) \exp(-\gamma D) \, dt$$

$$+ \int_{t=T_S - D}^{t=T_S} g \exp(-at) \exp(-\gamma(T_S - t) - \gamma'(t + D - T_S)) \, dt$$

A male will also have offspring from eggs laid by his first mate after he leaves until she dies. These eggs may be laid at a slower rate and suffer higher mortality during their vulnerable period. These offspring are calculated as:

$$A_2 = \int_{t=T_s}^{t=F} g' \exp(-a't) \exp(-\gamma' D)\, dt$$

Thus, the offspring a male gets from his first brood is A1 + A2.

The calculation of offspring from a male's second brood follows the same logic as for the first brood, but here the male's absence occurs with his death rather than his departure. The offspring he obtains from eggs laid before he dies, if he dies before any of them become invulnerable, is:

$$B_1 = p \int_{t=T_s}^{t=T} g \exp(-a(t-T_s)) \exp(-\gamma(T-t) - \gamma'(t+D-T))\, dt$$

If the male dies after some of his offspring have become invulnerable, the number of offspring he obtains from eggs laid before he dies is:

$$B_1 = p \int_{t=Ts}^{t=T-D} g \exp(-a(t-Ts)) \exp(-\gamma D)\, dt \quad +$$

$$p \int_{t=T-D}^{t=T} g \exp(-a(t-Ts)) \exp(-\gamma(T-t) - \gamma'(t+D-T))\, dt$$

The number of second brood offspring developing from eggs laid after he dies is:

$$B_2 = p \int_{t=T}^{t=T_s+F} g' \exp(-a(t-Ts)) \exp(-\gamma D)\, dt$$

Combining offspring from both broods, a male's fitness is calculated as:

$$\omega = A_1 + A_2 + B_1 + B_2$$

To calculate optimal residence times for a given set of parameters, I integrated each equation for integer values of residence time between 1 and 30 days, and determined which residence time resulted in the highest fitness. Under the conditions I investigated, it was never optimal for a male to stay less than half his life (< 15 days) with the first brood, because the second brood was always discounted by the probability of the male successfully initiating one. Therefore a very short residence time in this model was 15 days, and the longest was 30 days.

Results

Reproductive Rate

When male absence diminished female oviposition rate by a constant proportion throughout the egg-laying period, males realized maximum fitness if they stayed with the brood for longer than the minimum time, but left before the end of the first female's oviposition period (Fig. 4.1). This is because the largest absolute effect of male presence is at the beginning of the egg-laying period (when oviposition rate is highest), and the male also benefits from being with the second brood for this period. Therefore male assistance to reproductive rate can reduce male residence time below the maximum. However, the magnitude of male reproductive assistance did not further influence how long a male should stay; the optimal leaving time was the same whether females suffered a 10% or a 90% loss in egg-laying rate in the absence of males (Fig. 4.1, filled symbols). This is because the difference in egg-laying rate with and without males is the same for both broods, and the relative difference is constant for any point during the oviposition period. A male should leave his first brood when the gain from the second brood, discounted by the probability of having one, exceeds the loss to his first brood upon his departure. Because the gain and loss are calculated from the same two egg-laying functions (with and without male) for both broods, the gain and loss will always be proportional regardless of how much the two functions differ. Therefore, the residence time that maximizes the gain relative to the loss will always be the same.

If the costs of male absence to his mate increased as the egg-laying period progressed, optimal residence time with the first brood increased relative to constant costs (Fig. 4.1; compare lines with open and filled symbols of the same type). This effect is greatest when the initial rate of egg-laying was not also depressed very much in the absence of males ($g'/g \geq 0.5$), since this tended to overwhelm the effect of increased male assistance towards the end of egg-laying period (when the absolute rate of egg-laying was small even when the male was present). The magnitude of the effect was also influenced by the probability of successfully finding a new breeding site, and reached its maximum at a relatively low probability ($p = 0.2$). At high probabilities of breeding again, the amount of help a male provided again had little influence on the optimal residence time.

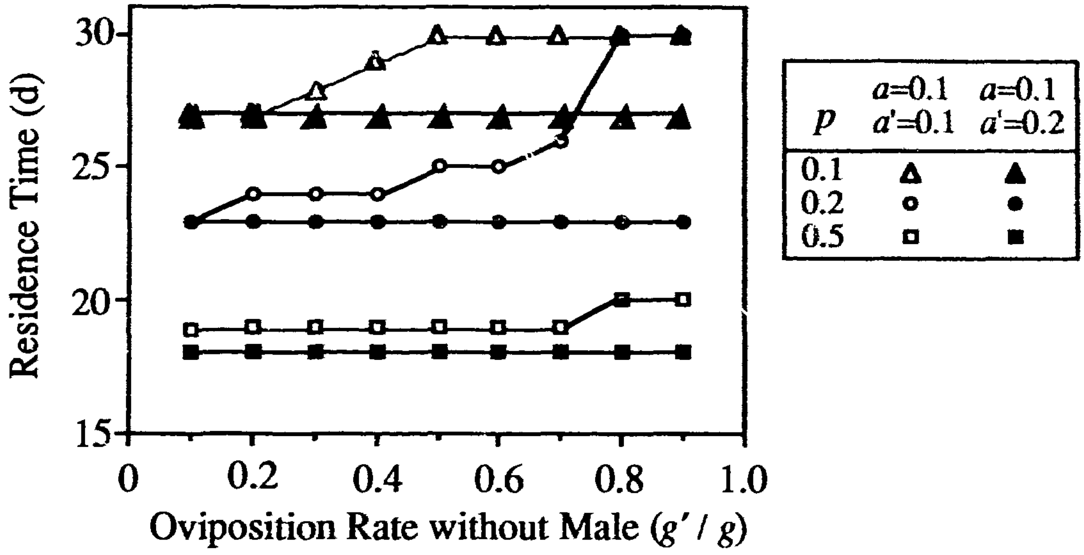

Figure 4.1. Effect of male contribution to oviposition rate on optimal male residence time. Horizontal axis is initial oviposition rate without male (*g*') relative to with male (*g*). Different symbols indicate different probabilities of having a second brood (*p*). Solid symbols indicate constant costs of male absence (*a*=*a*'), open symbols indicate increasing effects of male absence with time (*a*'>*a*).

Offspring Defence

I examined increases in the instantaneous rate of offspring mortality without males ranging from 1.001 to 3 times the mortality when males are present. Male residence was favoured whenever males diminished offspring mortality, but, similar to my results for reproductive rate, I found that the amount of defence a male contributed had no effect on optimal residence time under most conditions. Higher offspring mortality did reduce male fitness, and increase the costs of deviating from the optimal residence time, but the optimal leaving time itself was not affected. The explanation for this result is that each offspring defended in the first brood means an offspring will not be defended in the second brood, and a male will maximize his fitness by maximizing the number of defended offspring, regardless of the amount of that defence.

An effect of male defence on residence time was manifested through the length of the vulnerable period of offspring. In general, the longer the vulnerable period of each offspring, the longer was the optimal residence time with the first brood (Fig. 4.2). If the offspring's vulnerable period was longer than 15 days, it was usually optimal for males to stay with the first brood until the end (except when the likelihood of reaching a new tree was very high). Vulnerable periods of much less than 10 days, which selected for early departure from the first brood, do not seem biologically reasonable (see above).

Probability of Having a Second Brood

It is evident from Figures 4.1 and 4.2 that the greatest variation in male residence results from variation in the probability of a male having a second brood. Especially at low probabilities ($p < 0.4$), a small change in likelihood of second brood results in a relatively large reduction in optimal residence time (Fig. 4.3). The largest influence on this relationship was the rate of decline in egg-laying rate (compare two lines in Fig. 4.3); as stated above, the magnitude of male assistance to egg-laying rate or offspring defence had little influence on optimal residence times.

Discussion

I conclude from my model that the amount of help males can provide to a mate has very little effect on how long they should stay with their mate. This conclusion differs from similar models (Maynard Smith 1977, Zeh and Smith 1985) which emphasized the importance of the amount of male help on male residence time. This is because I asked when a male should desert, not if he should desert. All males in my model had two broods, so they never had to completely forfeit offspring from the second brood. The

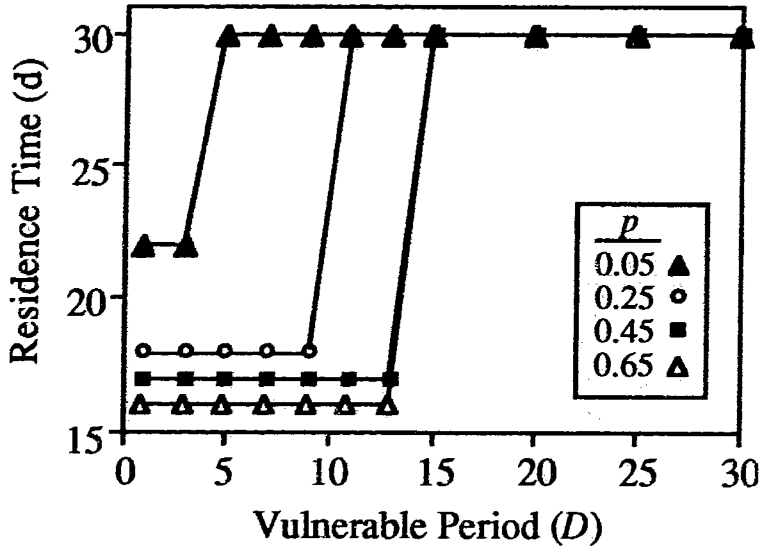

Figure 4.2. Effect of offspring vulnerable period (*D*, in days) on optimal male residence time, for varying probabilities of having a second brood (*p*). Offspring instantaneous rate of mortality with male $\gamma = 0.02$, without male $\gamma' = 2\gamma$. No effect of male on oviposition rate.

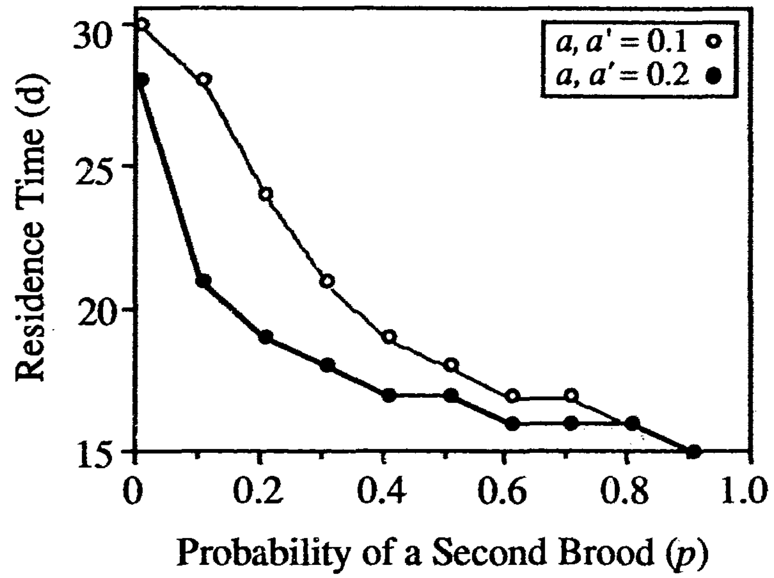

Figure 4.3. Effect of the probability of having a second brood on optimal male residence time, for two rates of decline in oviposition with time (a, a': the same with and without males). Other parameters are: vulnerable period $D = 10$ days, initial oviposition rate without males relative to with males $g' / g = 0.8$, offspring mortality rate with males $\gamma = 0.02$, without males $\gamma'=0.028$.

case where a male provided no help at all is a special one in my model, as a male would realize the same fitness for any residence time. In reality, there would undoubtedly be other features that would determine a particular residence time. One might normally expect a male to leave immediately, but in bark beetles one could imagine that the nuptial chamber would be a safe place to spend time. Because of the vagueness of the no-help case, I restrict further discussion to scenarios in which males provide some finite help, though it may be minimal.

I varied four variables relating to male assistance, and for two of these the magnitude of male assistance had no influence at all on male residence time. When male contribution to oviposition rate was constant over time, the size of the contribution is immaterial because the difference in oviposition rate with and without male help is the same in all broods. Thus, whether oviposition rate drops slightly or markedly when males leave, it is always balanced by a slight or marked gain, respectively, in subsequent broods. Analogous observations have been made regarding the importance of relatedness and certainty of paternity in determining helpful behaviour (Grafen 1980); when the payoff from investing in a future brood is identical to the payoff from the current brood, the optimal behaviour is insensitive to the size of the payoff. In the case of a male's contribution to defence, a male's departure decision depends on maximizing the number of offspring defended, regardless of how much he can defend them.

When I varied two other variables describing a male's contribution, there was some effect on optimal residence time under some conditions. These variables were the duration of the offspring vulnerable period, and the extent to the size of a male's contribution to oviposition rate increased later in the oviposition period. A common feature of these two variables is that they relate to the timing of a male's contribution. In general, the later a male's contribution is made in a reproductive bout, the longer he should stay. It is difficult to determine the relative importance of the amount of male contribution and the timing of the contribution. It seems likely that the same total contribution would result in different residence times depending on what stage of a reproductive bout the contribution was made. For example, optimal residence times were shorter when a male's contribution was substantial at the beginning of the reproductive bout (e.g. $g'/g = 0.2$, Fig. 4.1 solid symbols) than when the male's contribution was less but later in the reproductive bout (e.g. $g'/g = 0.8$, Fig. 4.1 open symbols). Thus, the amount of assistance that males can provide does not explain by itself male residence times. Regardless of this argument, there were broad ranges of offspring vulnerable periods in which optimal residence time was not affected. Therefore the conclusion remains that there is not a clear link between the need for male assistance and male residence time.

This conclusion is robust with respect to assumptions inherent in the model. First, I assumed that a male's costs of helping (other than time) did not vary with how much he helped (i.e. constant parental investment; Trivers 1972) but this is not critical because the parental care explanation for extended pair bonds is concerned with the needs of females for male assistance, not how much males must pay to provide the assistance. There is no necessary link between benefits and costs of helping to males. For example, it may cost a male bark beetle very little to block the egg gallery entrance to exclude predators, but this may be a task of great reproductive consequence which an ovipositing female could not do. Including additional costs of helping to the model does not result in a consistent effect on male residence time, as the outcome depends on the exact relationship between benefits and costs of helping. As a second assumption, I considered only two broods in my model, but the logic of my conclusions is insensitive to brood number. The optimal departure time would certainly be earlier if a male could have more broods (our minimum residence time was half the male's lifespan), but the balance between present and future broods would result in the same optimal residence time for the same number of potential broods regardless of how much males help.

In my model, the probability of finding alternative breeding opportunities had a much greater effect on optimal male residence times than their ability to help did, especially at low probabilities. Consistent with this, it has been observed that the need for male assistance does not differ between monogamous and polygynous birds, suggesting that the nature of pair bonds is determined by male mating opportunities rather than ecological emancipation from parental care (Webster 1991). Male parental care is associated with scarce breeding opportunities in many species (Atkins 1966, Gowaty 1983, Hannon 1984, Freed 1987, Scott 1990, Nalepa and Jones 1991). In a biparental cichlid fish, males deserted earlier when the proportion of females in the population increased (Keenleyside 1983). Thus there is support for the idea that mating opportunities are very important in determining how long males stay with their mates.

The probability of finding another breeding site may explain the diversity of male residence times found among bark beetle species. Two factors which may determine this probability are the availability of suitable host trees and the degree of synchrony of breeding females. The availability of breeding habitat has obvious importance in determining the probability that a male will achieve a second brood, and this availability varies widely among species of bark beetles (Atkins 1966). For species which require very weak or recently dead trees (such as *Ips* spp.), suitable trees would be transient (because of deterioration) and relatively rare before logging was common. In *I. typographus*, the probability of successfully reaching a new host tree has been estimated to be from 9 to 43%

(Anderbrant 1989; Gries et al. 1989). In my model, such low probabilities of between-brood survival favours males which stay with their first brood for much of the oviposition period, as indeed occurs in I. typographus (Anderbrant 1989). In contrast, other species of bark beetles (e.g. some Dendroctonus spp.) may have much higher probabilities of successfully initiating a second brood, since at large population sizes they can overwhelm the defences of a large proportion of living host trees. Survival of D. ponderosae between successive broods has been estimated to be 40% at constant host availabilities, and may range from 8% to 90% at low and high host availabilities respectively (Klein et al. 1978). Similarly, the estimated average between-tree survival of D. frontalis is 43%, and this fluctuates between almost 0% and 75% (Pope et al. 1980). In addition to higher mean survival probabilities, higher variance in these probabilities could select for reduced residence time in the first brood, because the fitness returns of occasionally successful additional broods can exceed the small return males realize towards the end of the oviposition period of the first brood. In other words, it may pay males to always leave early just in case there is an abundance of breeding opportunities available (or, if beetles can assess habitat availability, males may be able to alter their residence times accordingly). Indeed, male residence times of Dendroctonus spp. are typically less than Ips spp. (Kirkendall 1983).

Synchrony can be critical in determining mating opportunities in bark beetles because immediately after breeding is initiated a given female becomes unavailable for a few weeks while she oviposits. Therefore if all females begin breeding simultaneously, there would be no breeding opportunities available for a male after his first mating, and his best option is then to remain with his first brood and help (Knowlton 1979). Synchrony is determined initially by weather during the first spring flight in search of breeding sites for most temperate bark beetles, as beetles require warm, calm days for flight. In my studies of pine engravers, conducted towards the northern limit of their range, the first flight spanned from four to seven weeks (pers. obs.). In more southern areas, the flight period may be more contracted (Thomas 1961), and this latitudinal effect seems equally plausible for other species. Later in the season, synchrony breaks down as parental females and their offspring re-emerge over several weeks to search for new breeding sites. The importance of synchrony in determining male residence time could be assessed by comparative studies using latitudinal and seasonal variation as independent variables.

Once the opportunity for additional matings is small, the cost to males of helping the present brood may be quite small (Maynard Smith 1977). Bark beetles are pre-disposed to parental care because mating and oviposition occur in the same place, and the small entrance hole makes defence against intruders possible, two conditions which are relatively rare among insects (Tallamy and Wood 1986). The amount of help that males provide will depend on such ecological factors as well as investment costs to males. However, my model shows that magnitude of a male's contribution has no consistent effect how long males should stay with their mates and brood. I suggest instead that the chance of obtaining additional broods is the major factor determining the duration of pair bonds in animals.

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Chapter 5

What do female pine engravers (Coleoptera: Scolytidae) gain by preferring large males?

Abstract

Theory suggests that the preference of female pine engravers Ips pini (Say) (Coleoptera: Scolytidae) for large males may be adaptive because large males provide more help (mainly frass removal during the oviposition period), or they provide better genes. These hypotheses predict that females mated to large males have greater reproductive success. In contrast, runaway models of sexual selection or models of direct selection on females (for mate finding, for example) do not predict differences in the number of offspring in relation to the preferred trait. I investigated the reproductive consequences of male size in a laboratory experiment in which males of varying sizes were each mated with 3 females (the typical breeding arrangement in nature). Matings with large males produced more offspring (especially over two broods) and larger offspring (significant for male offspring). This was despite the fact that large males tended to leave their broods before small males did. There was no evidence that females compensated for the earlier departure of large males by investing more in their brood than mates of small males. Female preference for large males is adaptive because they gain more and larger offspring, but it is not clear whether the advantage results from paternal care or good genes.

Introduction

There is currently considerable interest in the evolution of mate choice, as evident by the diversity of recent hypotheses of sexual selection by female choice (Maynard Smith 1987, Pomiankowski 1988, Kirkpatrick and Ryan 1991). When males provide resources that increase female reproductive success, the selective advantage to choice is obvious. However, female choice in mating systems in which males provide only genes has prompted the search for other advantages of choice. Some male traits may be attractive because female neurophysiology is already sensitive to similar stimuli for other reasons (the sensory exploitation hypothesis, Ryan et al. 1990) or because the traits enable females to find mates more easily (Arak 1988). In these cases, selection operates on female survival directly rather than through the number or quality of her offspring. Other hypotheses for mate choice focus on the evolution of mate preferences through selection on offspring. According to Fisher's runaway process, female choice can evolve through linkage of genes for female preference with genes for an attractive male character (Arnold 1985). Females gain no fecundity advantage (or disadvantage) from mating with an attractive male, but their sons realize greater mating success by inheriting the attractive trait. Alternatively, "good genes" hypotheses argue that selection favours females who prefer males with traits that reliably indicate superior genetic quality for survival (Hamilton and Zuk 1982, Kodric-Brown and Brown 1984, Andersson 1986, Pomiankowski 1988). The assumption here is that viability is heritable and expressed by both daughters and sons. Although good genes hypotheses do not predict differences in female fecundity, the good genes could potentially be expressed at any stage of development after fertilization resulting in differential reproductive success.

Clearly, some of these hypotheses differ in their predictions for the effects of female choice on female reproductive success. In practice, distinguishing them by the outcome of a single reproductive bout may be difficult because individuals may alter their investment patterns in response to mate attractiveness or quality. An individual may invest more in a current reproductive bout (at the expense of future offspring; Trivers 1972) if its mate is better than it can expect in the future (Maynard Smith 1977). Consequently, if mates of more attractive males have greater reproductive success in a single reproductive bout, one cannot necessarily conclude that attractive males have provided resources or good genes; the females' survival must also be considered. This idea is the basis of Burley's (1986) differential allocation hypothesis which predicts that attractive individuals will reduce their parental investment in a particular brood, live longer, and consequently have greater lifetime reproductive success. This can occur because mates of attractive individuals will invest more in their current brood at the expense of their own survival and future reproduction. The increased reproductive success of attractive individuals through reduced parental investment is a means by which arbitrary as well as functional traits can be selected even in monogamous species.

Although theories for the evolution of mate preferences are well-developed, empirical data on the reproductive consequences of choice are needed to evaluate their relative importance. In this paper, I examine why female pine engravers Ips pini (Say) (Coleoptera: Scolytidae) prefer larger males (Chapter 2). The breeding biology of pine engravers is described by Thomas (1961), Schenk and Benjamin (1969), Schmitz (1972) and Swaby and Rudinsky (1976). Males are polygynous, with an average of three females per male. They initiate a nuptial chamber under the bark of weakened or recently dead trees, to which females are attracted. For the next two or three weeks, females mine egg galleries radiating from the nuptial chamber. Males remain with the gallery system for most of the oviposition period, guarding against predators and removing frass and boring dust created by the mining females (Chapter 3).

Because pine engravers exhibit biparental care, choosy females could gain resources, superior genes, or both from mate choice. Alternatively, because female pine engravers search for males and therefore incur search costs (Chapter 1), their preference may be because large males are easier to find (perhaps because of greater pheromone production; Anderbrant et al. 1985). In this case, there may be no reproductive consequences of mate choice once search costs are removed. To examine whether male size affects female reproductive success, I conducted a breeding experiment in which females were mated with large, medium, or small males. I also considered the effect of body condition, to see if this measure of male vigour was more important than size alone in determining reproductive outcomes. In addition to measuring the reproductive success of these matings, I examined investment patterns of males and their mates, as indicated by their survival and time spent with the brood. This was done to determine whether preferred males contribute more or, as predicted by Burley's (1986) differential allocation hypothesis, they contribute less to reproduction.

Methods

Pine engravers were obtained from lodgepole pine, Pinus contorta var. latifolia Engelmann, which had been naturally infested by overwintered adults near Princeton, British Columbia, Canada. Infested logs were placed in large screened cages at 28°C. Emerged beetles were collected daily, placed in jars with tissue paper and kept at 4°C until needed (for a maximum of two weeks).

I indexed beetle body size as pronotum width and total body length (anterior edge of pronotum to posterior edge of elytra) using a stereomicroscope fitted with an ocular micrometer at 25x magnification. Measurements were precise to the nearest 0.04 mm. To ensure a broad representation of male body sizes in my sample, I chose equal numbers of males (14) from three size categories based on pronotal width: small (≤ 1.48 mm), medium (>1.48 to 1.60 mm), and large (≥ 1.60 mm). Small and large males deviated from the mean male size by at least one standard deviation for most of the collections I have made over several years. To minimize effects of female body size, females at the extremes of the size distribution were excluded visually. The resulting mean pronotum width of females used in the experiment was 1.523 mm (SD=0.069, range 1.36 to 1.72 mm). Males, but not females, were individually weighed to the nearest 0.1 mg immediately prior to being implanted into breeding logs. I defined body condition of males to be weight per volume, and calculated it as weight / length x width^2 because bark beetle bodies are cylindrical.

All parental beetles were marked so that I could monitor the initiation of breeding and recognize re-emerging parents. The mark was a small spot of Superglue® placed at the edge of the elytral declivity to which fluorescent powder was added. All males were marked with green powder, while primary, secondary and tertiary females were marked with orange, green and pink powder, respectively. These marks were not always permanent, so only a subset of re-emerged beetles could be detected (the rest were indistinguishable from new adults). A preliminary study revealed no detectable effect of marking on mortality.

Fourteen males of each size class were "implanted" on small lodgepole pine logs (one male per log) by confining them within half a gel capsule over a pre-made small hole. Before implantation, beetles were kept at room temperature for 24 hours to ensure that they are ready to initiate breeding. On each successive day after a male was implanted (given that copious frass indicated a nuptial chamber had been completed), a single female was added to the gel capsule, for a total of three females per male. This number and rate of female introduction matches the natural breeding arrangement for an individual male (Swaby and Rudinsky 1976, Chapter 3). Females were assigned to males arbitrarily (without regard for female size). Mean female size per male did not differ among the three male size categories (ANOVA: $F=0.199$, $P>0.8$). Some males and females died, had not entered the nuptial chamber or they had escaped from the gel capsule after 24 h; these were replaced until a full complement of one male and three females was obtained (except for two cases with only two females, and one with only one female).

The logs on which males were implanted were 13 to 15 cm in diameter and 30 cm long. They were cut from 3 recently felled trees near Princeton, and their ends were sealed with hot paraffin within a day of cutting to prevent desiccation. Logs with the implanted males and females were placed in individual cages which were placed in rows of 6 on 7 shelves (42 cages). I arranged cages as four adjoining replicates of a three by three Latin square design (plus one row) so that cages of a given size category were separated vertically and horizontally by cages of each of the other two treatments. Most cages (35 of 42) were 20 cm high, 30 cm wide, and 60 cm long while the remaining seven cages were 20 by 40 by 90 cm; I detected no effect of cage type in subsequent analyses. On one end of each cage, an opaque white plastic funnel was mounted on plywood and a transparent collecting vial was placed on the end of the funnel's spout. This end of the cages faced a bank of fluorescent lights (six 120 cm tubes, 40 W each) which was the room's only light source (18L:6D photoperiod). Newly emerged beetles are phototactic, and moved from the log through the funnel into the collecting vials. The mean temperature was 26.7°C (range 21° to 33°) with 55% relative humidity.

From 6 July to 6 October, I collected beetles daily from the collecting vials. I also examined each log twice a week for any secondary gallery initiations by re-emerged parents or emerged offspring. I exposed all secondary galleries, measured their lengths , collected adults, and destroyed visible eggs or larvae to ensure that emerged offspring were from the galleries I established. To determine the original emergence/re-emergence dates of beetles in secondary galleries, I counted 1 day for every cm of gallery (Schenk and Benjamin 1969). For single males in nuptial chambers, I assumed that emergence had happened two days before discovery. I examined all collected beetles for fluorescent marks, and measured their pronotal width and total length.

Remeasurements of marked parental beetles showed that body length was a more repeatable measure (r=0.88) than pronotum width was (r=0.82). Also, paternal length was more variable than width (coefficients of variation were 5.3% and 3.9%, respectively). For these reasons, I used body length as my continuous body size variable in analyses. Length and width were correlated measures of size in paternal beetles (r=0.73, N=42). In most analyses I used Pearson correlations to examine the effects of paternal size on offspring size because I was interested in the existence of an effect rather than an exact relationship (the biological significance of a large effect compared to small but significant one is unknown). However, for offspring body size I calculated linear regressions on paternal length in order to estimate the heritability of body size (Falconer 1989).

Results

Offspring Number

Seven of the 42 cages in the experiment produced fewer than 6 beetles, including parents, over the entire collection period. These included 3 large males, 2 average-sized males, and 2 small males (as defined by pronotum width). I considered these to be breeding failures, and I excluded them from analyses of reproductive outcomes. For the remaining cages, the timing of emergences was bimodal (Fig. 5.1) and corresponds to two successive broods (Thomas 1961, Schenk and Benjamin 1969). This result was unexpected because I had attempted to remove secondary galleries, and dissection of 11 experimental logs after termination of the experiment indicated that all secondary galleries had already been uncovered. However, I may have been unsuccessful in destroying all the eggs and larvae from these galleries. I therefore consider all beetles emerging before 2 September to be from the first brood.

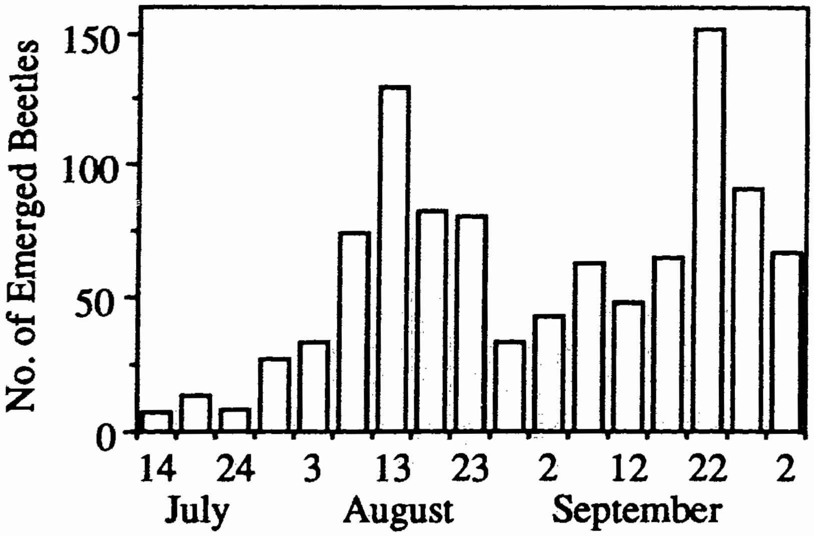

Figure 5.1. Phenology of emergence of pine engravers from all cages.

To examine the effect of paternal body size on the number of offspring produced, I excluded an additional 3 cages which did not have three females initially, to control for number of original mothers. These included one cage in each paternal size category. The remaining 33 cages produced a range of 6 to 90 beetles ($\bar{X}$= 29.4, SD= 20.0) over the entire collection period. For the first brood, beetle production ranged from 3 to 68 ($\bar{X}$=13.7, SD=12.9).

Cages with larger males tended to produce more offspring (Fig. 5.2). This was statistically significant over the entire collection period, but not for first brood beetles (although the relationship was in the same direction). The number of beetles removed from secondary galleries was positively correlated with the number of first brood beetles ($r=0.432$, $P<0.01$), and this effect would amplify the result for the first brood beetles. There was no significant effect of male body condition on offspring number; if anything, males in better condition tended to produce fewer offspring (first brood: $r= -0.217$; both broods $r= -0.113$, N=30).

Offspring Size

For the first brood, body size declined significantly as the emergence period progressed (for body length, pooling cages: females $r= -0.229$, N=260, $P<0.001$; males $r= -0.187$, N=201, $P<0.01$). Therefore I restricted my analyses of offspring body size to beetles that emerged during 10 days around the first peak of brood emergence (11 August through 20 August; Fig. 5.1). This resulted in a mean of 4.1 females per cage (range 1 to 19, N=31 cages) and 3.7 males per cage (range 1 to 17, N=27). The contribution of unmarked parental beetles to this sample is probably small, based on emergence times of marked beetles. Only one (9%) of 11 marked males and six (25%) of 24 marked females re-emerged during the peak period, so that the expectation is less than one parent per cage in the sample.

Larger males tended to produce larger offspring, as indicated by positive slopes in linear regressions of offspring body length on paternal length (Fig. 5.3). Regressions were significant for male offspring (slope $\underline{b}$ = 0.23 ± 0.11 SE, $R^2=0.162$, $P < 0.05$) but not for female offspring ($\underline{b}$ = 0.18 ± 0.12, $R^2=0.074$, $P=0.14$). Paternal body condition did not influence offspring size ($R^2<0.01$ for both males and females).

Timing of Emergence

In calculating mean emergence times, I omitted the first four beetles emerging from each cage to avoid including re-emerging parents. (All recaptured marked parental males were among the first four males emerging, and 21 of 24 recaptured marked females were

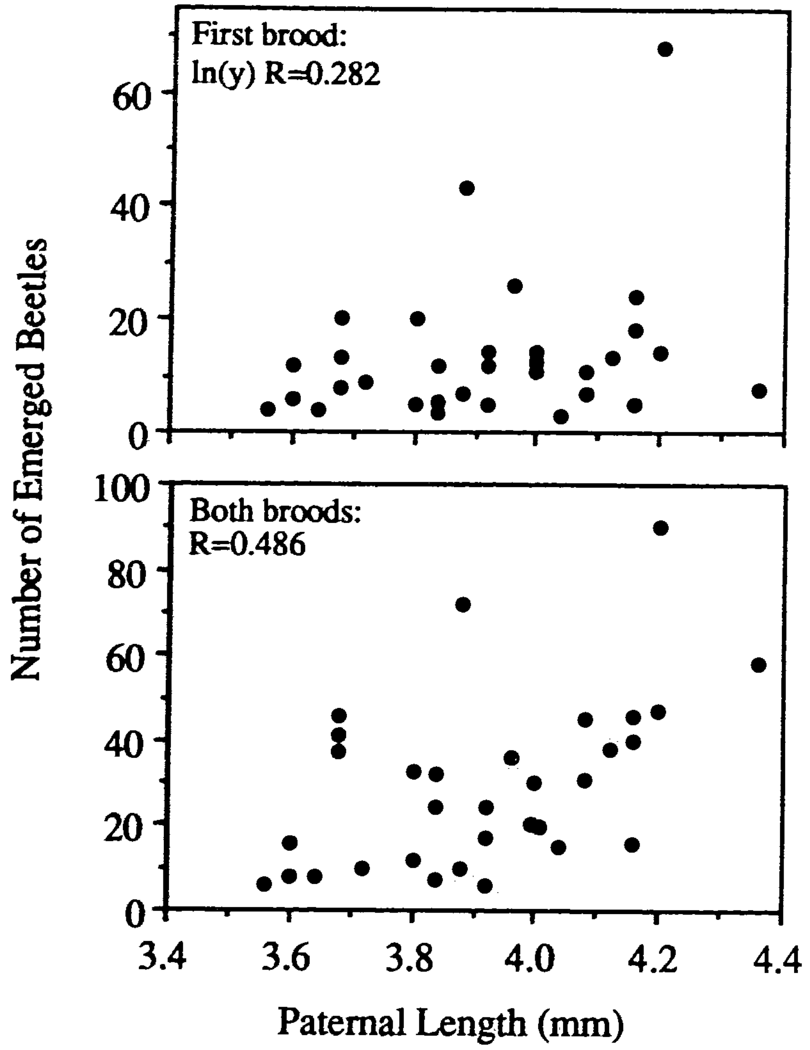

Figure 5.2. Effect of paternal size on the number of emerged beetles in the first brood (top) and in both broods combined (bottom).

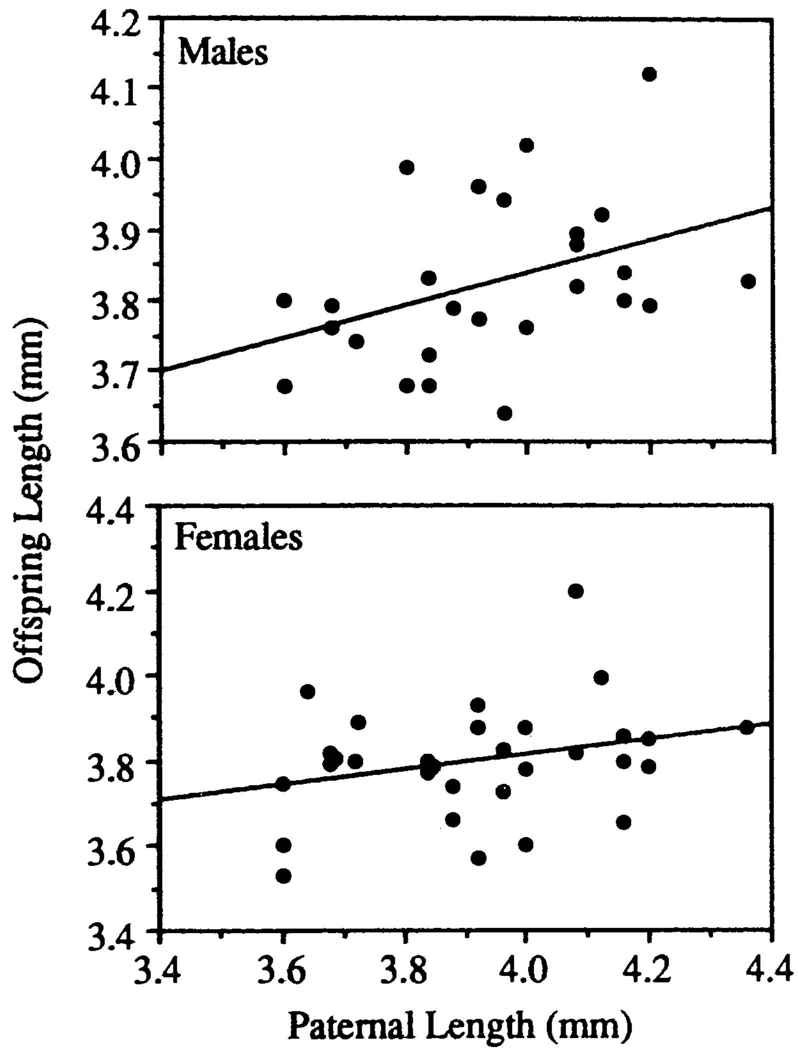

Figure 5.3 Effect of paternal body size of pine engravers on the size of sons and daughters. Least-squares regression lines indicated: for males, y=2.911+0.232x; for females, y=3.908+0.179x.

among the first four female emerging.) There was no significant correlation between paternal body length and the average emergence time for the first brood (males $r=0.213$; females $r=0.085$, $P > 0.2$ in both cases). Paternal body condition also did not detectably influence emergence dates (males $r=0.233$; females $r=0.184$; $P > 0.2$ for both). Considering the emergence times of just the fifth to the ninth emerging beetles from each cage, to prevent the number of emerging beetles from affecting the mean, still disclosed no detectable effect of paternal length or condition (length: males $r=0.233$, females $r= 0.184$; condition: males $r=0.271$, females $r=0.217$; $P > 0.2$ for all).

Parental Residence Time

Of the marked parental beetles, 11 males and 24 females were recaptured with their marks still visible. More males (6) from the large pronotum width category were recaptured than from medium or small categories (2 and 3 respectively), but the sample size was small and the difference was not significant ($\chi^2=2.36$, $P > 0.2$). I also compared re-emerged males with the rest of the males (which included both males that did not re-emerge and those that did but had lost their marks). There was no significant difference in body length between these two groups of males (re-emerged: $\bar{X}=3.95 \pm 0.07$ SE; other $\bar{X}=3.89 \pm 0.04$, t-test $P>0.4$), but re-emerged males were in poorer condition than the others (re-emerged $X=0.485 \pm 0.015$; other $\bar{X}=0.532 \pm 0.011$, $P<0.03$). Eight females from each male size category were recaptured.

The mean residence times for males and females were, respectively, 36.5 ± 6.2 SE and 32.7 ± 2.3 days. Larger males stayed with their brood for significantly less time than smaller males did (residence time vs. body length $r= -0.645$, $P<0.05$; Fig. 5.4). Male residence time was not significantly influenced by body condition, though there was a tendency for males in better condition to leave earlier ($r= -0.499$, $P<0.15$). Female residence time did not vary with female body length ($r = 0.13$; $N = 24$, $P > 0.5$), nor with the size category of their mates (ANOVA, $F(2,23) = 0.31$, $P > 0.7$).

Discussion

In this study, large male pine engravers produced larger and more numerous offspring than small males did. Although the effect on body size was not large (explaining at most 16% of the variation), consequences of body size are evident in all stages of a bark beetle's life. Larger beetles survive longer under adverse conditions (Safranyik 1976, Langor and Raske 1987), tend to have greater dispersal abilities (Slansky and Haack 1986, Roff 1991),

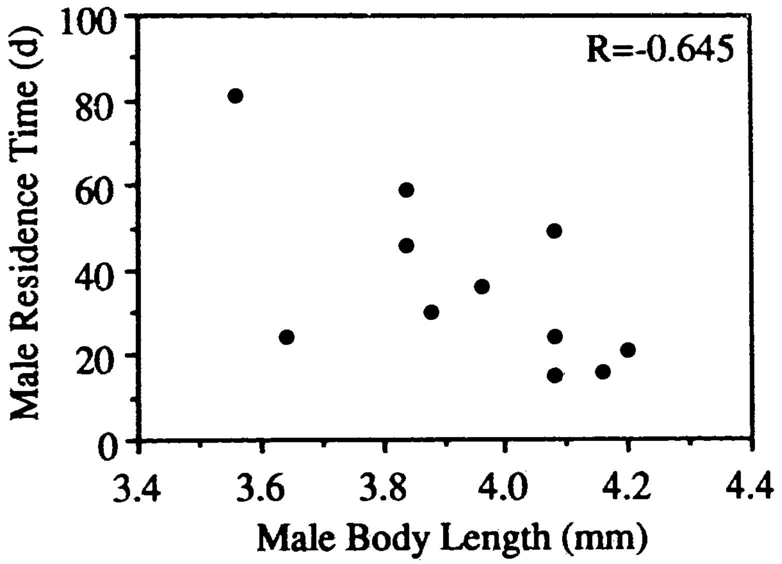

Figure 5.4 Residence times with brood of paternal male pine engravers as a function of body size.

produce more pheromones (Anderbrant et al. 1985) and may be better able to cope with host tree defences (Gries et al., ms.). Large females are also the more fecund (Amman 1972). Therefore the relationship between paternal size and offspring size that was detected in this study is likely to have biological significance.

The influence of paternal size on offspring number became most evident when both broods were considered together. The circumstances that resulted in second broods are not clear, but there is no doubt that male size played a role. Large males tended to produce more offspring in the first brood, and the number of secondary galleries was positively correlated with the number of first brood offspring. Therefore the positive effect of large males on offspring number in the first brood was amplified when both broods are combined, allowing it to be detected statistically. There could also be effects of large males on the body condition of mates and initial offspring which would favour these females to initiate secondary galleries.

Because of the effects on female reproductive success, female preference for large male pine engravers is unlikely to have resulted from a runaway selection process, from direct selection on females' sensory systems (Ryan et al. 1990), or because large males are easier to locate (Arak 1988). Three remaining mechanisms could explain the effect of large males on female reproductive success and female choice. These are: 1) greater parental investment by large males, 2) greater parental investment by mates of large males, and 3) paternal genes for large size and early survival. These possibilities are not mutually exclusive.

Male pine engravers help females to extend their galleries more quickly and lay more eggs that are more widely spaced (Chapter 3). Consequently, larvae in galleries with males should experience less competition relative to galleries without males, and therefore they would have better growth and survival. It is possible that large males may help more than small males do, perhaps by cleaning out frass more promptly and thoroughly, and this could result in more offspring and larger ones. With this help, mates of large males could be in better condition, favouring the production of second broods. Several considerations are relevant to this hypothesis. First, larger males remained with their brood for less time than small males did, which is at odds with the idea that large males help more. However, many males stayed much longer than the egg-laying period of the first brood (the period for which they help), which was probably less than 40 days. If we consider male residence time for only the first 40 days, there is still a tendency for larger males to leave earlier (R= -0.440, N=7; Fig. 5.4), though sample size prohibits meaningful statistical conclusions. If residence time is a measure of parental investment (see below), we can conclude that large males do not invest more than small males, and may actually invest less. Second, one might expect body condition to be more important than body size in determining the vigour with which males help, but condition had no detectable effect on offspring size and number. Finally, if large males helped females to reproduce faster, their offspring should emerge earlier, but paternal size did not affect emergence time in this study. While none of these points is conclusive, they do not lend support to the idea that large males provide more help than small males do. However, direct observations of large and small males inside egg galleries are needed before the paternal care hypothesis can be rejected with confidence.

The greater reproductive success of larger males may result from increased investment by their mates rather than by large males themselves. For species with biparental care, the differential allocation hypothesis predicts that preferred individuals will reduce their share of investment (and gain in survival), while the mates of preferred individuals will increase their investment (Burley 1986). In pine engravers, the reduced residence time of large males supports this idea, and the greater recapture rate of large males, although not significant, suggests that they may survive better. However, female residence time and survival (as indicated by recaptures) did not differ among the male size categories, so there is no evidence of increased parental investment by mates of large males. Increased maternal investment by mates of preferred individuals has been noted in other species however. Female sawyer beetles Monochamous scutellatus had a higher oviposition rate when mated with large males (preferred) than small males (Hughes and Hughes 1985). Similarly, female field crickets Gryllus bimaculatus who chose their mates laid a greater proportion of their available eggs than females who were not allowed to choose (Simmons 1987a). Thus, although the differential allocation hypothesis is not supported in this experiment, further investigation is warranted on the effect of mate quality on female investment.

My assumption that residence time reflects parental investment bears further examination because of its importance to the previous two hypotheses for female choice in pine engravers. Residence time is likely to depend on a beetle's readiness to disperse in addition to what it can invest in offspring, and dispersal readiness depends on fat reserves and the regeneration of flight muscles (Borden and Slater 1969). The accumulation of energy by feeding probably occurs at the expense of reproductive activities (oviposition in females, helping in males). If large and small beetles differ in the time it takes to gain sufficient energy to build muscles and fat reserves for dispersal, then residence time is not an accurate measure of parental investment. Large insects need proportionately less fat to disperse a given distance because their metabolic rate is relatively lower (Roff 1991). In this experiment, larger males began breeding in the same or better body condition as small beetles (condition vs. length r=0.218). Because they would lose weight more slowly (or gain weight more quickly) than small males, larger males may have had to spend less time feeding themselves in preparation for leaving. Therefore, large males could have helped as much as small males and still have left their galleries sooner. However, the differences in residence times between large and small males seem too large (up to several weeks; Fig. 5.4) to be explained entirely by this energetic argument. Substantial fat accumulation can occur in a week in males of another bark beetle (*Dendroctonus pseudotsugae*; Nijholt and Sahota 1974). Therefore I suggest that male residence time may indeed reflect the amount of help males provide rather than simple preparation for dispersal.

Size and number of offspring may be determined by genes rather than investment by parents. In pine engravers, the estimate of heritability of male body length is 0.46 ± 0.22 (twice the slope of the father-son regression; Falconer 1981), which is significantly different from zero. The estimate of heritability of paternal size for daughters was smaller ($h^2 = 0.36 \pm 0.24$) and while it is not significantly different from zero, it is also not significantly different from heritability in males. The statistical power of this experiment was not sufficient to detect small effects of paternal size on offspring size, though these effects may be real. In the congeneric spruce beetle, *Ips typographus*, the heritability estimate of pronotal width is lower than my estimates for pine engravers but it is statistically significant ($h^2=0.25 \pm 0.095$; F. Schlyter and O. Anderbrant, pers. comm.). These heritability estimates for *Ips* spp. must be viewed with caution, however because paternal behaviour may confound genetic effects. Also, in my study, the environments of parents and offspring were not identical. However, the estimates for pine engravers are within the range of heritabilities found for body size in field crickets (Simmons 1987b) and birds (Boag and van Noordwijk 1987, Wiggins 1989). Female preference for heritable male traits has now been observed in several studies (Carson and Lande 1984, Simmons 1987b, Hedrick 1988).

The greater production of offspring by large males may also be due to "good genes" for growth and survival. It is interesting that the effect of large males on offspring number became clearest when both broods were considered, but large males were more likely to have left before the second brood was initiated. This suggests that paternal genes may be more important than paternal help in determining offspring number. Similar conclusions have been reached in studies of animals without paternal care. In the tobacco moth, *Ephestia elutella*, females preferred large males and had more and larger offspring when mated with large than small males (Phelan and Baker 1986). In both field crickets and *Drosophila melanogaster*, females who chose their mates had offspring with greater vigour (Simmons 1987a, Partridge 1980). In *D. melangaster*, larval competitive ability was also positively correlated with paternal mating success (Taylor et al. 1987). The possibility of differential investment, raised above, remains as an alternative explanation in these studies, however. A clear example of a preference for good genes rather than differential investment can be seen in a Colias butterfly, in which females choose on the basis of a trait corresponding to a single locus which determines flight performance (Watt et al. 1986). Seaweed flies Coelopa frigida also prefer males whose genotype enhances offspring survival (Crocker and Day 1987).

Some cages in this experiment failed to produce any offspring, and others produced relatively few. Female pine engravers can produce 20 to 50 eggs in a single gallery (Schenk and Benjamin 1969), so the lack of production under these low density conditions is surprising. All beetles appeared vigorous when introduced to the breeding site. Log quality may have varied, but pine engravers have relatively broad habitat requirements (Schenk and Benjamin 1969), and all logs in this study were cut from recently felled trees of the same diameter and from the same site. One possible explanation is that beetles were not given an opportunity to choose a mate, and they withheld reproduction if the match was unsuitable. As mentioned above, field crickets showed reduced oviposition when unable to choose a mate, even if the provided mate was large (a preferred trait; Simmons 1986, 1987a). However, most females in this study readily entered the male's nuptial chamber to which they were assigned.

To summarize, female pine engravers prefer larger males, and this study showed that larger males produced more offspring and larger offspring. Runaway models and direct selection on females (through mate search costs for example) are therefore rejected. Large male pine engravers spent less time with their broods than small males did, but still had greater reproductive success. Although this result is consistent with Burley's (1986) differential allocation hypothesis, there was no indication that mates of large males were paying any cost of reduced male investment by large males. These findings are consistent with adaptive female choice for males who provide either better care or better genes, or both. However, differential investment patterns, some potentially subtle (Eberhard 1991), deserve further attention in studies of the reproductive consequences of mate choice.

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Chapter 6
Concluding Discussion

I have shown that female pine engravers compare and choose mates on the basis of male traits which appear to contribute to female reproductive success. These results are novel for several reasons. First, the mate choice process has rarely been observed in nature in a species with a resource-based mating system, and the use of a mating tactic in which males are compared has only recently been demonstrated (Bakker and Milinski 1991). Mating tactics involving comparisons have been largely neglected in mate choice theory and sexual selection models (Real 1990, Kirkpatrick and Ryan 1991). Second, the adaptiveness of mating preferences is often controversial (Borgia 1987). Finally, it is not clear why male traits reliably predict future benefits. I now discuss these issues in turn.

In pine engravers, active mate choice (defined operationally by the rejection of some potential mates) is exhibited by a large proportion of females. Females encounter males at random, but those that visit more than one male tend to mate with better males than are generally available. They achieve this by continuing to visit males until a preferred male is encountered. This is consistent with a threshold preference rather than a best-of-n tactic (Janetos 1980, Wittenberger 1983), but in pine engravers this threshold is modified as females encounter males. The effect of experience on preference was suggested by the behaviour of females in nature (Chapter 1), and confirmed in a controlled lab experiment (Chapter 2). The ability to modify preferences based on recent experience allows females to have a high acceptance threshold initially (to increase their chances of obtaining a highly preferred mate), without incurring the risk of forfeiting mating altogether if a preferred mate is not available. Such a sophisticated tactic in a small insect suggests that complex mating tactics may be much more widespread than is generally credited.

There are several factors which may favour a modifiable threshold mating tactic in pine engravers. In this species, females can exercise choice behaviour without interference from males. There are costs to searching however, especially the risk of parasitism and the probability of being pre-empted by competing females at mating sites. Costs can explain why females do not revisit males (Wittenberger 1983, Real 1990). However, the observation that females altered their preferences according to the males they encountered suggests that the local availability of preferred males is not predictable. The variability in the distribution of male pine engravers is not yet quantified, nor is it known from theory what male distributions would favour learned mating expectations. This could be profitably modeled, as begun by Stephens (1991). Female mate choice tactics may in turn influence male settlement patterns (Gibson et al. 1990), further complicating the relationship between male distributions and female tactics.

Female pine engravers chose males on the basis of traits that appeared to enhance their reproductive success. By preferring recently settled males (Chapter 1), females reduce the level of competition experienced by her offspring from both within and among harems (Kirkendall 1989). Mating preferentially with large males (Chapter 2) increases reproductive success and offspring size (Chapter 5). I cannot conclude whether the benefits of mating with a large male were genetic or the result of male helpfulness (Chapter 3), or both. The distinction is not important to organisms choosing mates (for whom the end, not the means is key), but it is of considerable interest to an understanding of evolution of mate choice and sexual selection (Borgia 1987). If benefits are solely genetic, a problem in theory is maintaining genetic variation in fitness (Fisher 1930) and the male trait, though some specific mechanisms that could ensure continued variation have been proposed (Lande 1976, Hamilton and Zuk 1982). Several recent studies have found that preferred male traits are heritable (Simmons 1987, Hedrick 1988) or have reproductive consequences in the absence of material benefits (Watt et al. 1986, von Schantz et al. 1989). However, variation in phenotypic features such as resource provisioning will usually exceed purely genetic variation (Searcy 1982), and for this reason it may be more likely that the benefits female pine engravers receive from mating with large males relate to male parental care rather than good genes. Once variation among males in the trait is sufficient to favour mating preferences, the amount of variation will further determine optimal mate search tactics (Real 1990). This could be a factor which contributes to differences in mate choice tactics between species with and without resource provisioning by males (if such differences exist). Thus, to fully understand the mate preferences and mating tactics of a species, we need to determine whether the preferred trait affects female reproductive success, how the trait affects reproductive success, and how much males vary in the trait .

The conclusion that male body size contributes to female reproductive success must be qualified because it was not clear whether large males or their mates determined the number and size of emerging offspring (Chapter 5). It is possible that females (or males) will invest more in reproductive bout when their mate is more attractive (regardless of the mate's contribution), resulting in a short-term increase in reproductive output, at the expense of later reproduction (Maynard Smith 1977, Burley 1986). I found no conclusive evidence of such an effect in pine engravers, but two observations are suggestive. First, large males remained with their brood for significantly less time than small males did, but still produced more offspring (Chapter 5). This could result if mates of large males invested more in parental care, though this was not detected in the survival of parental females. Second, large females tended to persist longer at the entrance holes of small males than small females did (Chapter 2). Perhaps large females prefer small males because these males will invest more for a large mate than large males would. This hypothesis of differential allocation of reproductive investment is obviously speculative with respect to pine engravers, but it merits further investigation because it is a potentially widespread phenomenon affecting mating tactics. Two necessary conditions for this to occur are, first, that the attractive sex contributes something other than parental investment that makes its offspring more valuable, and second, that there is a trade-off between present and future reproduction.

Female pine engravers appeared to assess and choose mates at least partly on the basis of male pheromones at the entrance to male nuptial chambers, which requires that pheromones contain reliable information about males. It is not necessarily in the male's interest to be honest. For example, my model of male residence time (Chapter 4) suggests that males help females mainly because they have low prospects of obtaining other breeding sites, and not because helping will always maximize a male's fitness. Therefore a female cannot necessarily expect a male to act in her interests. One might expect that all male pine engravers should appear most attractive by signalling large size and lack of mates. However, male Ips spp. pheromones do appear to indicate a male's true state. Male attractiveness starts to decline as soon as he has one female (Swaby and Rudinsky 1976, Chapter 2), and this change is attributable to changes in male pheromone and not to his mates (Birgersson et al. 1984). Pheromones also vary with male body size (Anderbrant et al. 1985).

One possible mechanism ensuring reliability is having a costly signal. If pheromone synthesis is metabolically demanding, it may not benefit males to broadcast false information. Some consequences of over-investment in pheromone production may be lowered survival, lowered ability to assist mates, or reduced dispersal prospects after re-emerging from the current breeding site. Thus, if the benefits of mate attraction diminish with each additional mate obtained, the optimal investment in pheromone production may also decrease. A prediction of the costly signal hypothesis is that pheromone quantity and constituents produced by an unmated male would require more energy to produce than pheromones produced by a mated male. To apply to a permanent character such as body size, the hypothesis requires that genes or development result in a suite of characters such as body size, pheromone production ability, and ability to help, perhaps through efficient energy use or disease resistance (Hamilton and Zuk 1982, Kodric-Brown and Brown 1984).

Limited availability of pheromone precursors may also ensure reliability. If precursors are obtained from the current breeding site (Borden 1985), then pheromone production may be determined by feeding rate. Small males may be unable to feed as much as large males, and mated males may feed less than unmated males because they are pre-occupied with their mates. If pheromone precursors are obtained during the larval period, then pheromone constituents may be a true indicator of larval habitat, which also determines body size (but not mating status). Consistent with this, Anderbrant et al. (1985) observed that bark beetles from crowded larval habitats are small and have altered pheromones. A similar argument regarding larval resources and pheromone production has been forwarded for moths (Conner et al. 1990). Thus there are several possible mechanisms for ensuring the reliability of male pheromones as indicators of male status, but all remain to be tested.

I have investigated female preferences for characteristics of males (body size and mating status) and not of habitat. In my lab experiments on female choice (Chapter 2) and reproductive consequences of body size (Chapter 5), breeding habitat and male traits were randomly associated, and therefore I was able to detect the importance of males traits independent of habitat. It is possible that female bark beetles also evaluate phloem quality at a male's nuptial chamber, as this will contribute greatly to a female's reproductive success (e.g. Slansky and Haack 1987). Host tree volatiles (kairomones) are probable cues. If females do assess phloem quality independent of male quality, then the criteria on which female pine engravers make their decision are multiple (at least two male traits and phloem quality). Other studies (on birds) have shown that females use multiple criteria in mate choice (e.g. Burley 1981, Reid and Weatherhead 1990), and it appears that this is true for another insect as well (Simmons 1987). Again the point is that the mate choice process can be quite complex.

In overview, this thesis has been an attempt to increase our understanding of sexual selection and mating systems through the study of the behavioural ecology of a model species, the pine engraver. This approach, which emphasizes the importance of costs and benefits in determining an organism's behaviour, has provided several novel results. I have documented the mate choice process of pine engravers in nature, which addresses assumptions and predictions of common models of mate choice and sexual selection which have been largely untested. The existence of learned mate preferences, which I have shown for pine engravers (Chapters 1 and 2), has also been largely overlooked in these models. Male pine engravers assist their mates (Chapter 3), which is relatively rare in insects (Zeh and Smith 1985). It may be that large males help more, thereby explaining female preference for larger males and the greater reproductive success resulting from mating with larger males (Chapter 5). However, my model of male residence time suggests that the helpfulness of males cannot explain why males remain with their mates as long as they do; rather, the availability of other mating opportunities appears to be the main determinant of male residence time (Chapter 4). To determine the generality of each of these findings, comparable studies are needed of species representing the range of diversity of mating systems and of intensity of sexual selection. This thesis is one contribution towards elucidating mating patterns in nature.

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