UNIVERSITY OF CALGARY

Mating and fitness consequences of breeding aggregations

in pine engraver bark beetles, *Ips pini* (Coleoptera: Scolytidae)

by

Kyle Hodnett

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE

DEGREE OF MASTER OF SCIENCE

DEPARTMENT OF BIOLOGICAL SCIENCES

CALGARY, ALBERTA

JULY, 2001

Canada

ABSTRACT

The function of breeding aggregations in non-aggressive bark beetles (Scolytidae) is unknown. I examined whether breeding aggregations of *Ips pini* were due to increased mate attraction, at least for some individuals. Mate acquisition decreased with increasing aggregation density for both large and small males. However, pioneer males, both small and large, had slower mate attraction than males in aggregations. This apparent benefit of joining aggregations rather than pioneering disappeared when offspring competition was considered. A biologically explicit simulation model of offspring competition determined that pioneers produced more offspring than joiners, except when pioneers were small and had limited time for mate attraction. Thus, I reject the hypothesis that *Ips pini* form aggregations for the purposes of mate attraction. Male settlement patterns among aggregations were not according to the Ideal Free Distribution, indicating that aggregations were not forming due to limited habitat. I discuss alternative explanations for aggregation formation.

ACKNOWLEDGEMENTS

with more than just a strong back, his help with experimental design and his organization skills were critical in my field season's success.

Finally, I am thankful to Sherri and Noah Bouchard for making my life that much richer throughout the entire experience, as well as for the hard work they both performed for me.

DEDICATION

This work is dedicated to Noah Bouchard.

Remember to always choose your own direction.

TABLE OF CONTENTS

List of Tables

List of Figures

Chapter 1

General Introduction

The question of why animals form mating or breeding aggregations is intriguing. These aggregations appear across many taxa of animals, from insects (Prokopy and Roitberg, 2001) to mammals (Stillman et al., 1993). Traditionally, aggregations have been thought to form due to benefits gained through association with conspecifics. Proposed benefits include increased mate attraction, increased breeding success, protection of individuals from predators, a limited supply of suitable resources necessary for attracting mates or raising a brood, and cooperation among family members aiding relatives (Thornhill and Alcock, 1983; Danchin and Wagner, 1997; Prokopy and Roitberg, 2001). Recently it has been argued that the post-settlement benefit of aggregations may be only one factor responsible for selecting a habitat (Stamps, 2001). She suggests that we must also consider the cost of locating habitat when considering how individuals choose where to settle and whether they choose to join conspecifics or settle alone. This approach is in its infancy, and pre-settlement choices are difficult to evaluate. Consequently, for practical reasons it is logical to examine post-settlement consequences of aggregations before attempting to assess pre-settlement benefits. In this thesis, I examine post-settlement benefits of aggregations from an individual perspective using optimization theory (which assumes that individuals behave in a manner to maximize their fitness).

Optimal Aggregation Behaviour

Optimality theory suggests that individuals will choose behaviours that maximize expected fitness returns (Alcock, 1983). This theory can be applied to the decision of an individual to join a particular aggregation, as opposed to other available aggregations, or to settling alone (Pulliam and Caraco, 1984). However, it is important to recognize that the condition or state of an individual can determine which behaviours or choices are optimal for that individual (Alcock, 1983; Andersson, 1994; McNamara and Houston, 1996). In this case, individuals may still behave optimally but they are constrained to what behaviours are available to them and fitness returns will vary according to the condition and behaviour of the individual (Dawkins, 1980; Dominey, 1984; McNamara and Houston, 1996).

Fitness returns for a particular behaviour may also be influenced by the choices made by other conspecifics (Pulliam and Caraco, 1984). The effects of frequency dependence on the type and frequency of behaviours that are expressed in a population is determined using game theory to determine evolutionary stable strategies (ESS) (Maynard Smith, 1982). An ESS is defined as a strategy that when adopted by most members of a population cannot be invaded by any alternative strategy, thereby assuming that all strategies observed yield the same fitness returns (Maynard Smith, 1982; Parker, 1984; Andersson, 1994). This approach underlies the Ideal Free Distribution (IFD) that has been used to predict the distribution and abundance of individuals among habitat patches (Fretwell and Lucas, 1970). The IFD assumes that individuals are free to decide from all available habitat and have perfect knowledge of what habitat is available, resulting in organisms being distributed among habitat patches such that all individuals

achieve the same amount of resources. Consequently, no individual can achieve more resources by moving to another patch, consistent with an ESS.

Producer- scrounger models are also game theory models based on ESS to predict the formation of foraging aggregations (Giraldeau and Beauchamp, 1999). These models predict when an individual should join a group or settle alone (Giraldeau and Beauchamp, 1999). For these models, producers are individuals that locate a resource, and scroungers are those individuals that exploit the resources located by producers. Producer-scrounger models assume that an individual can only use a single strategy at a time. In both the IFD and producer-scrounger models, it is generally assumed that all individuals are equal and are free to adopt any strategy.

While classical ESS applications focus on strategies at the population level, the assumption that all individuals are equal can be relaxed. Thus, each individual's decision to join a group can be based on ESS even though its fitness will not be equal to all other individuals (Parker, 1983; Alcock, 1993, Andersson, 1994). In this case, the individual makes a choice where it maximizes its fitness such that no other choice can result in a higher fitness for that individual (Pulliam and Caraco, 1984). By removing the assumption that individuals are the same and acknowledging that an individual's state affects its optimal behaviour, the focus returns to assessing condition-dependent consequences of behaviour. However, remaining in the framework of ESS, an individual's behavioural will be determined not only by its condition but by what tactics other members of the population are currently employing.

Thus, for condition-dependent tactics, maximizing fitness will still be subject to frequency dependent effects and the resulting suite of tactics can be considered as

evolutionary stable strategies with unequal fitness returns (Dominey, 1984, McNamara and Houston, 1996). However, continuous individual differences make classical ESS theory difficult to apply (Parker, 1984). Regardless, a first step to understanding a behaviour such as aggregation requires an assessment of the fitness consequences of alternative choices of aggregation size, and the extent to which these choices are condition-dependent. If the choice of aggregation size cannot be explained by simple or condition-dependent optima, then other influences need to be considered. Frequency-dependence of other tactics may be one such influence. In this thesis, I begin to examine the function of aggregations in bark beetles (Coleoptera: Scolytidae) by using a condition-dependent approach to examine some potential post-settlement benefits of aggregation formation.

Bark Beetle Aggregations

Many species of bark beetles form large breeding aggregations (Raffa et al., 1993). These beetles infest live, dead or dying trees. The function of aggregations for the minority of bark beetles species that infest live trees (aggressive beetles) has been explained as a 'cooperative' effort to overcome the anti-parasite defenses of the tree (Berryman, 1976). For these beetles an aggregation helps increase breeding success (Berryman et al. 1985; Raffa and Berryman, 1987). Non-aggressive bark beetles (those that infest dead or dying trees with little anti-parasite defenses) also form large breeding aggregations on their host tree (Raffa et al., 1993), even though aggregations are unnecessary to overcome host resistance. One explanation for this behaviour could be that aggregating is evolutionary carry-over from more aggressive ancestors (Alcock,

1993). This does not appear to be the case; it is difficult to see how successful breeding in live trees could occur without an already developed aggregation response. Aggressive beetles are often observed breeding in dead wood (Rudinsky 1962, Raffa et al. 1993), suggesting that breeding in dead wood is a historic trait for aggressive bark beetles.

Thus, the question of why non-aggressive bark beetles aggregate remains unanswered. Unlike beetles that colonize live trees, non-aggressive bark beetles reproductive success declines steeply with increases in aggregation density (Beaver, 1974; Anderbrant et al., 1985; De Jong and Grijpma, 1986; Robins and Reid, 1997). However, breeding aggregations of bark beetles are also mating sites. Many of these beetles use pheromones to attract potential mates to a breeding site (Borden, 1974). Aggregations may provide a greater stimulus for mates and increase the probability that a member of the aggregation acquires a mate. The effects of group size on mate attraction has received considerable attention in a wide variety of taxa (Buck and Buck, 1978; Hoglund et al, 1993; Deutsch, 1994; Widemo and Owens, 1995; Aspi and Hoffmann, 1998). However, most of this work is done on lek mating systems, where it is often not the individual that is responsible for attracting mates but the sites as the same sites are used repeatedly by individuals that breed in successive years (Hoglund et al., 1993; Westcott, 1994). Moreover, rarely is mate attraction compared between lek members and solitary individuals (Lanctot et al., 1997). By failing to compare the cost of settling alone to settling in aggregations, one may conclude erroneously that aggregations are beneficial to participants when in fact the benefits of settling alone may be greater than settling within a group.

In this thesis, I directly examine some adaptive explanations as to why a non-aggressive bark beetle, the pine engraver, *Ips pini* (Say), forms breeding aggregations. I consider an aggregation to be when more than one male settles in suitable habitat, namely a recently dead tree, because the presence of more than one male may increase the pheromone output and attractiveness of the habitat or increase competition for resources available for larval development, or both. Throughout this study I focus on the consequences of aggregations for mate attraction and offspring production as measures of individual fitness. In Chapter 2, I examine the effects of increasing aggregation density on mate attraction, while explicitly considering condition-dependent behaviour by examining the influence of male body size on mate attraction and settlement choice. In Chapter 3, I look at the fitness returns of joining an aggregation or settling alone, again as a function of individual body size. Thus, this thesis contributes to our understanding of aggregation in bark beetles by testing some previously unexamined hypotheses, namely that these aggregations are related to mating success and subsequent reproduction at least for some individuals. In the concluding chapter, I review the success of these hypotheses and consider what additional elements of reproductive fitness are needed to understand optimal aggregation behaviour in this systems.

Chapter 2

The role of individual quality in the formation of breeding aggregations in pine engraver bark beetles, *Ips pini.*

Introduction

The formation of aggregations is common for many animal taxa (e.g. birds: Hoglund et al., 1993; reptiles: Stamps, 1987; mammals: Stillman et al., 1993; invertebrates: Prokopy and Roitberg 2001). Often it is during the breeding season when many animals aggregate. There are four main explanations as to why animals would aggregate to breed.

First, breeding aggregations may result from limited suitable breeding habitat (Kimsey, 1980; Danchin and Wagner, 1997). In this case, there are more individuals than there is available habitat, forcing individuals to join other conspecifics. One body of theory suggests that, because conspecifics are competitors, joining an aggregation is not due to benefits of being with conspecifics and will result in a decline in fitness with increasing competition (Fretwell and Lucas, 1970; Parker and Sutherland, 1986).

Second, breeding aggregations may exist to facilitate mate attraction. Combined mate signalling may increase the rate and number of mates attracted (Alexander, 1975; Shelly, 1989; Lucas et al., 1996). Signal enhancement might apply to continuously produced chemical signals (Bossert and Wilson, 1963), but Bradbury (1981) suggested that for most signals, the addition of more signallers does not proportionately increase the range of the signal or the number of females that receive the signal, resulting in fewer

females receiving the signal on a per male basis. However, even if there is no per capita increase in the effective attraction radius, females may actively choose to go to a larger group in order to compare males more easily. In this case, a larger signal may result in more females responding to the signal than to the signal of a single male, increasing the number of females drawn to a site on a per male basis (Thornhill and Alcock, 1983).

A third possibility is that some individuals are exploiting the signal of other individuals. This could happen through conspecific cueing, wherein new settlers use the presence of conspecifics to evaluate if a habitat is suitable, thereby reducing search costs (Stamps, 2001). Individuals could also parasitize the signals of others, reducing their own costs of signalling while benefiting from mate attraction by others (Cade, 1980; Fairchild, 1984; Muller et al., 1997).

Fourth, breeding aggregations may form to decrease predation risk, a common explanation for colonially breeding birds (Danchin and Wagner, 1997). Here, I examine the first three explanations for breeding aggregation formation, returning to the role of non-mating benefits in the Discussion.

The benefits of breeding aggregations are likely to depend on the density of the aggregation. When searching for breeding sites, individuals may encounter several suitable aggregations or uninhabited suitable habitat before deciding where to settle. Suitable breeding locations can be ranked by searching individuals with regards to habitat quality such as available resources and current aggregation density. Current theory assumes that all individuals rank habitat in the same manner (Stamps, 2001). Therefore, 'low quality' habitat is avoided by all individuals in the population, while 'high quality' habitat is sought by all individuals (Stamps, 2001). Stamps (2001) suggests that

researchers need to examine how different individuals may vary their ranking of habitat. It is possible that habitat ranking may vary with individual condition and ability. Therefore, it is important to examine how individuals choose a breeding habitat to understand the function of breeding aggregations, and to determine if the function of the aggregation is the same for all members of the population.

We need to examine the three hypotheses for aggregation formation from the perspective of an individual's fitness returns, as well as note how individual characteristics affects those fitness returns. If aggregation formation is due to limited resources, individuals should choose habitat based on the ideal free distribution, joining an aggregation with the lowest competitive costs compared to what other habitat is available (Fretwell and Lucas, 1970). Competitive interactions result in a decline of fitness for all individuals within the aggregation as aggregation size increases, regardless of individual quality. The hypothesis of increased mate attraction due to aggregation formation (cooperation hypothesis) suggests that as aggregation size increases, members of the aggregation experience increased fitness, also regardless of individual quality.

In contrast, the signal exploitation hypothesis suggests that some individuals will benefit at the expense of others within an aggregation. Signal parasitization can occur due to the inability (or unwillingness) of some individuals to produce an attractive signal (Fairchild, 1984; Forester and Lykens, 1986). These individuals will use the signals of conspecifics in order to encounter mates (Cade, 1980). Since signals are generally expensive to produce (Forester and Lykens, 1986; Krupa, 1989), low quality individuals may be less able to produce their own signals and therefore may parasitize the signalling by higher quality individuals. In this case, low quality individuals will benefit from

joining an aggregation to the detriment of high quality signallers (who will settle at low

density aggregations to avoid competition). Differences in individual quality may also

affect the propensity of an individual to use conspecific cueing as a suitable habitat

indicator, especially if finding unoccupied habitat increases the fitness of the searching

individual. Under these conditions, individuals with poor dispersal ability would be more

prone to use conspecific cues than more able dispersers would.

Breeding aggregations are a common phenomenon in bark beetles (Scolytidae)

(Raffa et al., 1993). Several bark beetle species, known as aggressive bark beetles,

require breeding aggregations to overcome a tree's antiparasite defences (Berryman,

1976; Filip and Schowalter, 1993). However, most members of the Scolytidae are non-

aggressive and infest dead or dying trees that possess no active defence mechanisms

(Raffa et al., 1993). Despite the lack of tree defences, many non-aggressive species still

form breeding aggregations (Raffa et al., 1993). The adaptive benefits of these

aggregations remain unclear. Here I examine whether there are mating advantages of

breeding aggregations in pine engravers, *Ips pini*, a non-aggressive bark beetle.

Each male pine engraver locates and creates a nuptial chamber in the bole of a

dead or dying tree (Wood, 1982). From this nuptial chamber, he releases a pheromone

that attracts both males and females. A male attracts an average of three females, with a

range of 0 - 5 females (Swaby and Rudinsky, 1967; Reid and Roitberg, 1994; pers. obs.)

with whom he breeds under the bark. Females create egg galleries radiating from the

male's nuptial chamber. Along these galleries females lay eggs that develop into larvae

that consume the phloem layer, and subsequently pupate under the bark. Larval

competition within this phloem layer can be intense and increases with increasing

aggregation size (Saarenmaa, 1983; DeJong and Grijpma, 1986; Robins and Reid, 1997). Consequently, there are strong competitive costs of aggregating.

Male bark beetles differ in their ability to find habitat and attract mates. Large males have better flight abilities (Robertson and Roitberg, 1998), greater fat reserves (Anderbrant, 1988) and greater pheromone production ability (Anderbrant et al., 1985; Gries et al. 1990) than do small males. Therefore, I used male body size as my measure of male quality.

Here I examine whether male pine engraver aggregation formation was based on a limited amount of available suitable habitat or if males settled in aggregations where they acted cooperatively or as parasites of other males' signals. I predicted that if resources are limited, males should settle according to the ideal free distribution. If aggregations form due to 'cooperation', I predict all males will choose to join dense aggregations and mating success will increase with increasing aggregation density. If signal parasitization is the cause of aggregation formation, I predict that small males will join dense aggregations and large males will avoid dense aggregations due to increased competition. If the parasitism hypothesis is correct, small males should increase their mating success with increasing aggregation density.

Methods

I studied pine engraver aggregations in May and June 1999 at the Kananaskis Field Station at Barrier Lake, Alberta, Canada (latitude 51° 2' N, longitude 115° 3' W). Potential aggregation sites were established in the forest in late April before the beetles began to fly and colonize logs. I selected sites by searching the forest for all newly (over

the past winter) fallen lodgepole pine trees (*Pinus contorta* var. *latifolia*), the host tree species of pine engravers in the area. On these trees I marked a 2 m long section that was observed for beetle colonization. Other sites were set up using 3 freshly cut 1 m logs placed end to end in a shaded area of the forest at least 20 m away from the next closest site. I selected four sites to monitor colonization and subsequently determine male body size and mating success. Sites 1, 2, and 3 consisted of a fallen section of tree ranging from 3.5 m to 15 m long. Site 4 was a constructed site that had 8 male beetles implanted 20 cm apart from each of their neighbours, on each 1 m section of log. These males were included in density determinations but excluded from all other analysis. I implanted males by confining a male beetle under a centrifuge tube that had its tip cut off to allow beetle access to the tree. The centrifuge tube was attached to the tree with window putty. The tube was removed once the male had established a nuptial chamber, after 24 hours. Four other sites (constructed of three 1 m logs) had their densities monitored but were not studied further.

I checked each site twice a day (in the morning and the afternoon) for new beetle attacks. Attacks were determined by the evidence of boring dust (frass) found at the opening of a newly constructed nuptial chamber. Each new attack was marked with a coloured pin representing the day and time of gallery initiation. The sites were attacked by beetles for 11 days (site 1), 21 days (site 2), 23 days (site 3) and 19 days (site 4). After colonization was complete, I mapped the 2 m observed section for each site by giving each beetle attack an x and y coordinate. I calculated the aggregation density for each site twice a day, as number of attacks per 100 cm^2. The four focal sites were then excavated using a knife to remove the bark, exposing the beetles and galleries

underneath. All exposed beetles were collected and immediately killed. I measured

body size as pronotum width (anterior to their procoxa to the nearest 0.02 mm using a

dissecting scope and an ocular micrometer) and fresh weight (to the nearest 0.1 mg using

an AND ER-120A electronic balance). I determined sex using sexually dimorphic elytra

spines (Lanier and Cameron, 1969). I tallied the number of females associated with each

male.

Data analysis

Body size measurements

For each male I measured pronotum width and fresh weight (Fig 2.1). These

body size measurements were highly correlated (Pearson $r = 0.87$, $n = 392$, $P < 0.0001$)

and result in identical conclusions when used in the following models. Due to pronotum

width being consistent throughout a male's adult life, it is presented for the following

models. All analyses were done using the statistical package JMP 3.1 (SAS, 1996)

Ideal Free Distribution

To determine if male beetles chose breeding sites according to the ideal free

distribution, I created a general linear model to examine if aggregation densities

increased evenly across all sites over time. The model examined the effects of site, date

of beetle arrival and their interaction on aggregation density.

This use of the ideal free distribution assumes that intrinsic habitat quality is the

same across all sites. One method of determining habitat quality is to examine the

distance apart that a female lays her eggs (Haack et al., 1987). The higher quality the

habitat, the closer together eggs can be placed because it requires less high quality

habitat to successfully produce an offspring than low quality habitat (Popp et al. 1989).

Sites 1 - 4 had their egg density determined for every female gallery over 15 mm in

length, due to an initial egg-free portion of each gallery of approximately 10 mm (Reid

and Robb, 1999; pers. obs.). A one-way ANOVA and a Tukey-Kramer comparison were

used to detect if there were differences in site quality (egg density).

Body size and settlement choice

To examine how body size affected settlement choice, I first calculated the mean

pronotum width of all individuals settling at a given aggregation density for each site. A

general linear model was created to examine how the body size of settlers varied with

aggregation density. To control for any influence of male size changing throughout the

flight period, the date of the males' arrival was included in the model. Site was also

included as a confounding variable, as were two-way interactions between all

independent variables. To reduce heteroscadacity, only body size means comprised of 5

or more individuals were used. Variables and their interactions were removed from the

model if the calculated Variable Inflation Factor (VIF) was greater than 10 or if they

were not significant (P > 0.10).

To determine if large and small males responded differently to increasing

aggregation densities, individual male size was regressed with aggregation density using

10 and 90 % quantile regressions. This analysis was performed using Blossom software

(United States Geological Survey, 2000). By examining the slopes of the 10 % and 90 %

quantiles, using least absolute deviations (Cade and Richards, 1996), the shape of the

relationship between body size and aggregation density can be more accurately determined. For example, there are a number of distribution patterns that can create a negative slope: a reduction in the number of large individuals settling at high aggregation densities, few small individuals settling at low densities, or, as the parasitism hypothesis predicts, large males settling first followed by small males. The quantile regression approach helps elucidate which of the possibilities is responsible for the slope.

Mating Success and Aggregation Density

The consequences of settlement choice on mate acquisition are important for determining why an individual would be choosy about aggregation size. It is also important to determine if there is an interaction between individual quality and aggregation density on mate acquisition. I used a general linear model to determine how the number of females acquired varied with aggregation density at time of a male's arrival and with male pronotum size. Site and date of arrival as well as all two-way interactions between independent variables were included in the initial model. Terms were subsequently removed based on VIF > 10 and lack of significant effect in the model (P > 0.10). To ensure that all males had sufficient time to attract a full complement of females, only males that had settled at least 4 days before excavation were included in the analysis (Swaby and Rudinsky, 1976; Reid and Roitberg, 1994; pers. obs.).

Results

Ideal Free Distribution

Throughout the flight period there were a total of 8 sites that were apparently suitable habitat for aggregation formation, as determined by the presence of male attacks. Each of these sites developed an aggregation over the 27 days that beetle attacks were examined. Aggregation densities did not increase uniformly at all sites through this time period (Fig. 2.2), indicated by a significant interaction between date and site with regards to aggregation density ($F_{8, 587} = 138.3$, $P < 0.001$). Final aggregation densities ranged from 0.95 attacks / 100 cm^2 to 6.7 attacks / 100 cm^2.

I tested the assumption of equal site quality by examining egg spacing in galleries on the four focal sites. Significant differences existed in egg spacing between sites (ANOVA: $F_{3,779} = 90.0$, $P < 0.0001$). The Tukey-Kramer test indicated that Site 3 had significantly higher egg densities (mean $\pm$ SE: 3.0 $\pm$ 0.045 eggs / cm) than any of the other three sites (Site 1: 1.9 $\pm$ 0.070 eggs / cm; Site 2: 2.1 $\pm$ 0.094 eggs / cm; Site 4: 2.1 $\pm$ 0.064 eggs / cm). The other three sites did not significantly differ from each other in egg densities. The site with the highest egg density (presumably the highest quality site) did not reach the highest aggregation density, and was not heavily settled (aggregation density < 1 male / 100 cm^2) until Sites 1 and 2 had reached densities greater than 2 males per 100 cm^2 (Fig. 2.2).

Body Size and Settlement Decisions

The mean male quality (measured as pronotum width) declined with increasing aggregation density (Fig. 2.3; body size vs. aggregation density: $R^2 = 0.55$, $F_{1,21} = 15.8$, P

< 0.001). All two-way interactions were removed from the model due to high VIF (> 10). Site and date of arrival did not significantly predict the mean male quality ($F_{3,21}$ = 1.37, P > 0.2 and $F_{1,21}$ = 0.06, P > 0.5, respectively).

To determine whether a decline in body size with increasing aggregation density was due to a reduction in the number of large males settling at high densities, or an increase in the number of small males settling at high densities, or due to the parasitization hypothesis, two quantile regressions were performed (Fig. 2.4). The 90% quantile regression revealed that there was a significant decrease in the number of large males that settled at high densities (Multiresponse Permutation Procedure (Blossom software), 10000 permutations, P < 0.05). The 10% quantile regression did not have a slope that was significantly different than zero, indicating that small males settled at all densities (Multiresponse Permutation Procedure (Blossom software), 10000 permutations, P > 0.1).

Mating Success and Aggregation Density

Males acquired more mates when they settled at lower aggregation densities (R^2 = 0.26, $F_{1,247}$ = 8.52, P < 0.01). Large males also acquired more mates than did small males ($F_{1,247}$ = 8.87, P < 0.01). A possible interaction between density and male size on mate attraction could not be examined because of high VIF. Site and arrival date also significantly affected mate attraction ($F_{3,247}$ = 6.12, P < 0.001, and $F_{1,247}$ = 15.5, P < 0.001 respectively). Site 1 and 2, which were at higher aggregation densities than Site 3 and 4 for most of the flight, obtained fewer mates per male on average (mean number of mates ± SE: Site 1: 1.85 ± 0.16 females; Site 2: 2.10 ± 0.26 females; Site 3: 2.95 ± 0.10

females; Site 4: 2.40 $\pm$ 0.13 females). The overall model with these four independent

variables explained 26% of the variation in mating success ($F_{6,247}$ = 14.4, P < 0.0001).

The number of mates declined with increasing aggregation density, but the size of

the effect for large and small males may differ. Since an interaction between density and

body size could not be reliably assessed in the previous model, I divided males into two

size classes (large males pronotum width > 1.56 mm; small males pronotum width < 1.43

mm). Mate attraction for both size classes and aggregation density was analyzed using an

ANCOVA. There was no interaction between size class and density (R^2 = 0.22; size and

density interaction $F_{1,270}$ = .0008, P > 0.9) indicating that aggregation density affected the

mating success of beetles of different sizes equally (Fig. 2.5).

Discussion

Both aggressive and non-aggressive bark beetles establish breeding aggregations

(Raffa et al., 1993). Due to the known cost of larval competition within an aggregation

(Beaver, 1974; Robins and Reid, 1997 and reference therein), it is unexpected that non-

aggressive bark beetles, that are not required to overcome a trees defense system,

aggregate. In this study I tested three reasons for aggregations, rejecting all three.

Ideal free distribution

The study area had eight concurrently available sites that were suitable habitat, as

indicated by the presence of reproducing males and females at the site. However, beetles

were settling at sites with high aggregation densities (> 3 attacks / 100 cm^2) while

relatively uncrowded sites were available (< 1 attack / 100 cm^2) (Fig. 2.2). Using egg

density as a measure of site quality (Haack et al., 1987; Popp et al., 1989), I demonstrated that males were not selecting the highest quality sites first and filling those sites before moving to lower quality sites. Two of the first sites colonized with high aggregation densities were of lower quality than an available site that had a lower aggregation density. However, because females have been observed to lower egg density in response to increasing aggregation density (Popp et al., 1989), it is important to compare sites with similar aggregation densities when using egg density as a measure of site quality. Site 3 and site 4 had similar aggregation densities but significantly different egg densities, suggesting that site quality differed between the two sites. However, males settled at equal rates at both sites (Fig. 2.2). Additionally, the number of mates obtained per male can also be used as a measure of site quality. Mate acquisition was also lower at high aggregation densities, further validating that high aggregation densities are poor habitat that should not be settled if other habitat is available.

Previous studies support the conclusion that site quality differences are not suitable justification for the settlement patterns observed. Studies performed on effects of tree quality on reproductive success have shown that growth rates in the last ten years has the greatest effect on reproductive success in pine engravers (Reid and Robb, 1999). No aspect of tree quality demonstrated in their study reduced the number of offspring produced as much as an increase in aggregation density did (Robins and Reid, 1997). Furthermore, a large range of tree quality was examined by Reid and Robb (1999), where a difference of 1 cm growth over the last ten years is considered a considerable difference in growth rates (Heath and Alfaro, 1990), In contrast, the change in female density examined by Robins and Reid (1997), from 1-5 females per 100 cm^2, is a relatively small

change in aggregation density (from 1 to 2 males / 100 cm^2, cf. Fig. 2.2). Therefore,

larval density has a greater effect on the number of surviving offspring than does tree

quality. These data in combination with my data suggest that my results are not in

accordance with the hypothesis that males settle 'ideally' with regard to habitat

availability or habitat quality.

'Cooperation' Hypothesis

If all males benefit from the presence of conspecifics or from the increased signal

produced by an aggregation, all should opt to join an aggregation. Males should also

acquire more mates as aggregation density increased. However, there was a decrease in

mean body size as aggregation density increased. This decrease in body size was due in

part to large males being less likely to settle at higher densities. The decrease in size was

not due to a change in male size over the flight period, as date did not contribute

significantly to the size of settlers. More importantly, mate acquisition also declined with

increasing aggregation density. Thus, tests for settlement choice and mate attraction both

provide strong evidence against males benefiting from cooperation.

Increasing aggregation size has been shown in a number of studies of various

animals to increase the number of females encountered per male or the number of

matings per male (Buck and Buck, 1978; Lank and Smith, 1992; Hoglund et al., 1993;

Widemo and Owens, 1995; Aspi and Hoffmann, 1998). This increase has been attributed

to two main processes. First, an increase of signaling males may increase the strength of

the signal which can then reach more females (Doolan, 1981; Lucas et al., 1996).

Second, if the strength of the signal does not reach exponentially more females (see

below), the increased signal strength can still attract more females to an aggregation by having a higher percentage of females that receive it responding than would for a smaller signal (Thornhill and Alcock, 1983). Female preference for groups can cause males to aggregate (Gibson and Jefferson, 1990; Hoglund and Robertson, 1990). In this case females are believed to prefer grouped males in order to be able to compare several potential mates with reduced search and travel time (Janetos, 1980).

There have also been other, albeit fewer, studies that have demonstrated that increased aggregation size reduces the number of females acquired per male (Bradbury, 1981; Deutsch, 1994). As well, theoretical arguments about signal propagation with increasing number of signalers have been developed that suggest the signal size does not increase exponentially with number of aggregation joiners as would be required to increase the number of females per male (Bradbury, 1981).

Bark beetle signal propagation is through a chemical signal, which unlike Bradbury's (1981) conclusion, is expected to increase its attraction area exponentially with increasing number of signalers (Bossert and Wilson, 1963). Female pine engravers exhibit mate choice despite search costs (Reid and Stamps, 1997), so could prefer to search in male aggregations. However, my results clearly demonstrate that male pine engravers are not benefiting in terms of mate attraction with increasing aggregation density.

Signal Parasitization

Large males performed as predicted by the signal parasitization hypothesis. They settled mainly at lower densities, as expected by their high pheromone output and ability

to attract females. However, contrary to the signal parasitization hypothesis, small males settled at all aggregation densities. Due to their presumably lower pheromone production ability (Anderbrant et al., 1985; Gries et al., 1990), I predicted that small males would not settle at low aggregation densities and that by parasitizing other males' signals their mate acquisition would increase with increasing aggregation density. However, small males suffered a reduction in mate acquisition in large aggregations. Both large and small males suffered similarly in terms of mate acquisition with increasing aggregation densities (Fig. 2.5). Consequently, the signal parasitization hypothesis is rejected for pine engraver aggregations.

Alternative Hypotheses

In summary, none of the three hypotheses were supported. An alternative explanation may be that aggregations protect individuals from predation (Thornhill and Alcock, 1983). The commonly cited advantages of being in a group include faster predator detection, predator confusion, and the dilution of risk (Pulliam and Caraco, 1984; Alcock, 1993). None of these factors are applicable in a bark beetle system. Beetles are confined within their nuptial chambers and so are unable to warn conspecifics of approaching predators (and they are unable to do much when the predator arrives) nor will multiple conspecifics cause confusion. There is no center of the group, so predators have equal access to all beetles' nuptial chambers equally. Finally, dilution is only effective if attack rate is independent of group size and if the predator only kills a single prey when successful (Pulliam and Caraco, 1984). Many of the pine engraver's predators and parasitoids (Coleoptera: Cleridae and Hymenoptera: Pteromalidae) are drawn to

aggregation sites through chemical signals (Raffa and Dahlsten, 1995) which may not be independent of aggregation size (Bossert and Wilson, 1963). In addition, these predators will attack multiple prey at any site. The parasitoids Pteromlaidae attack mainly searching beetles, including females (Reid, 1991) and therefore would not be a selective agent for males to aggregate. Furthermore, predation was rarely observed in the field (pers. obs). It is therefore unlikely that predation is the explanation for aggregation formation, especially given the clear cost of competition (Robins and Reid, 1997) and mate acquisition (this study).

My study is instead consistent with the idea that pine engraver aggregations result from the high cost of search for habitat rather than post-settlement benefits (Stamps 2001). Danchin and Wagner (1997) suggest that if individuals do not have perfect knowledge of their environment they may not settle in an ideal manner. Imperfect knowledge of resource distribution will increase the costs associated with finding habitat, which may limit habitat selection and result in aggregation formation. Dispersal costs have been demonstrated by Robertson and Roitberg (1998), who demonstrated that larger pine engravers could fly farther than small males, and that males found at breeding galleries are on average larger than the emerging population. This suggests that mortality occurs during dispersal and that mortality is greater for small beetles. Several other researchers have demonstrated elevated flight costs for low quality or small males (Cole, 1973; Safranyik, 1976; Gries, 1985 as referenced in Reid and Roitberg, 1995). The results obtained from my experiment suggest a hypothesis that dispersal is energetically expensive. Only large beetles, that can fly farther (Anderbrant, 1988; Robertson and Roitberg, 1998), are able to avoid settling in poor quality, high-density habitats. Small

males on the other hand, are accepting high aggregation densities, which is relatively poor habitat, or using conspecific cueing to find available habitat and reduce search costs. The difference of beetle size and settlement density, while significant, was not large (see Fig 2.4). This may suggest that while other studies demonstrate that large males are better dispersers, it is still a significant cost for large males to find good habitat and they may also rely on conspecific cueing to find suitable habitat.

In conclusion, the absence of detectable post-settlement benefits of breeding aggregations of bark beetles suggests that the explanations for aggregations may be better found in the process of searching for habitats or from the potential costs of being solitary.
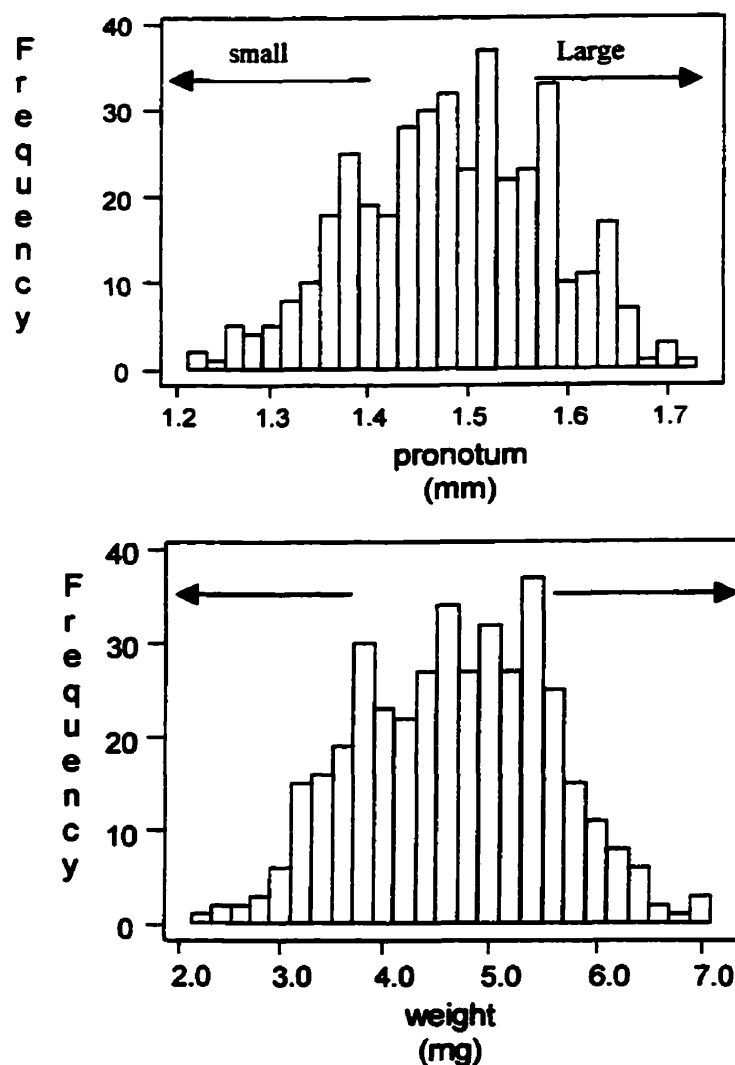
Fig. 2.1. Pronotum width and weight distributions for male pine engravers used in experiments. Males were divided into large and small categories for mate attraction implants (as designated by the arrows, Chapter 3). Category criteria were modified slightly for analyses performed in chapter 2 and Appendix 2. For analyses in Chapter 2, the small category was expanded to include beetles with pronotums less than 1.43 mm in width, to make large and small size categories equivalent in number of observations. For Appendix 2, size categories were increased to increase sample size by changing the criteria for weight and pronotum width; for large males, values were reduced to 1.51 mm and 5.2 mg, respectively; for small males, values were increased to 1.46 mm and 4.8 mg, respectively.
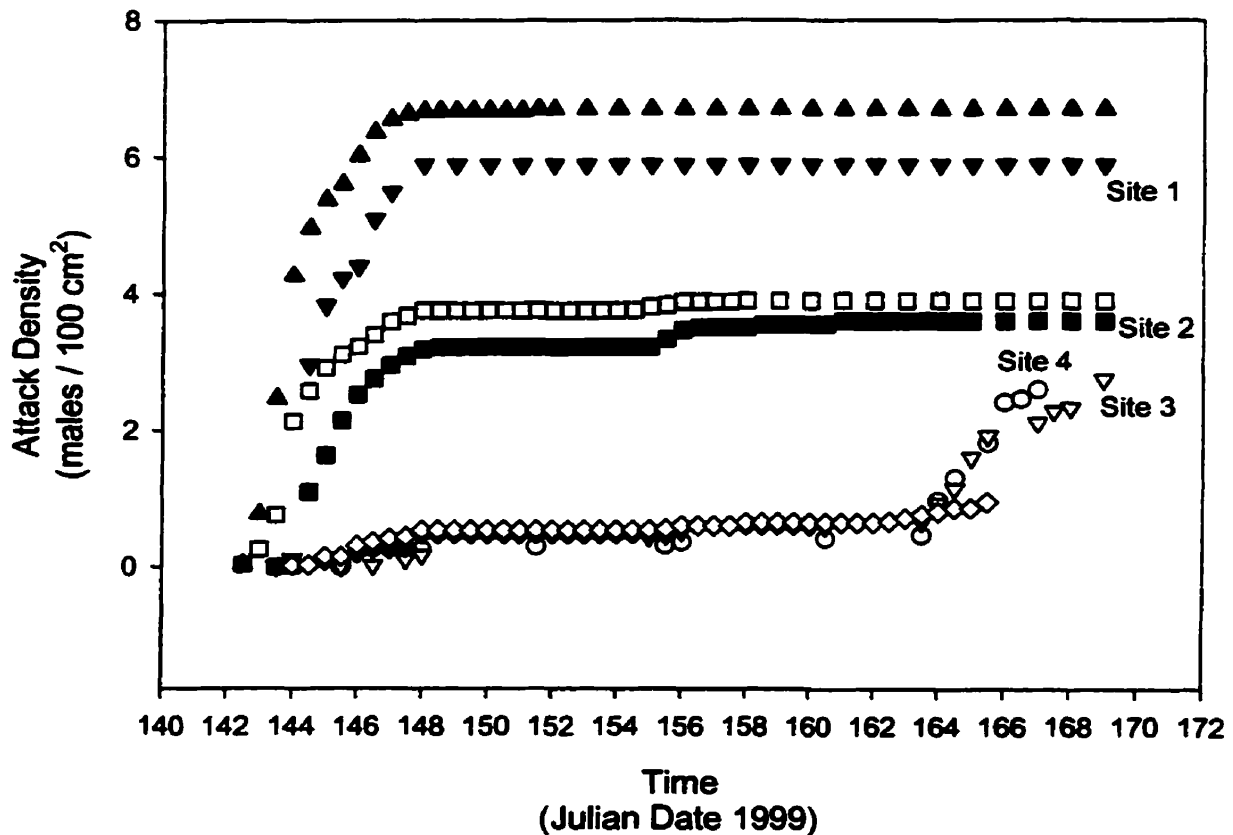
Fig 2.2. Changes of attack density over the flight period at 8 sites monitored twice daily for newly arrived males. Sites were either sections of fallen trees or were set up using three 1m logs placed end to end. From approximately Julian date 150 (30 May) until163 (06 June), there was a drop in temperature below the level that beetles usually fly (approx 15°C). Sites 1 - 4 were excavated and used in further analysis, the other 4 sites had their densities monitored but were not studied further.
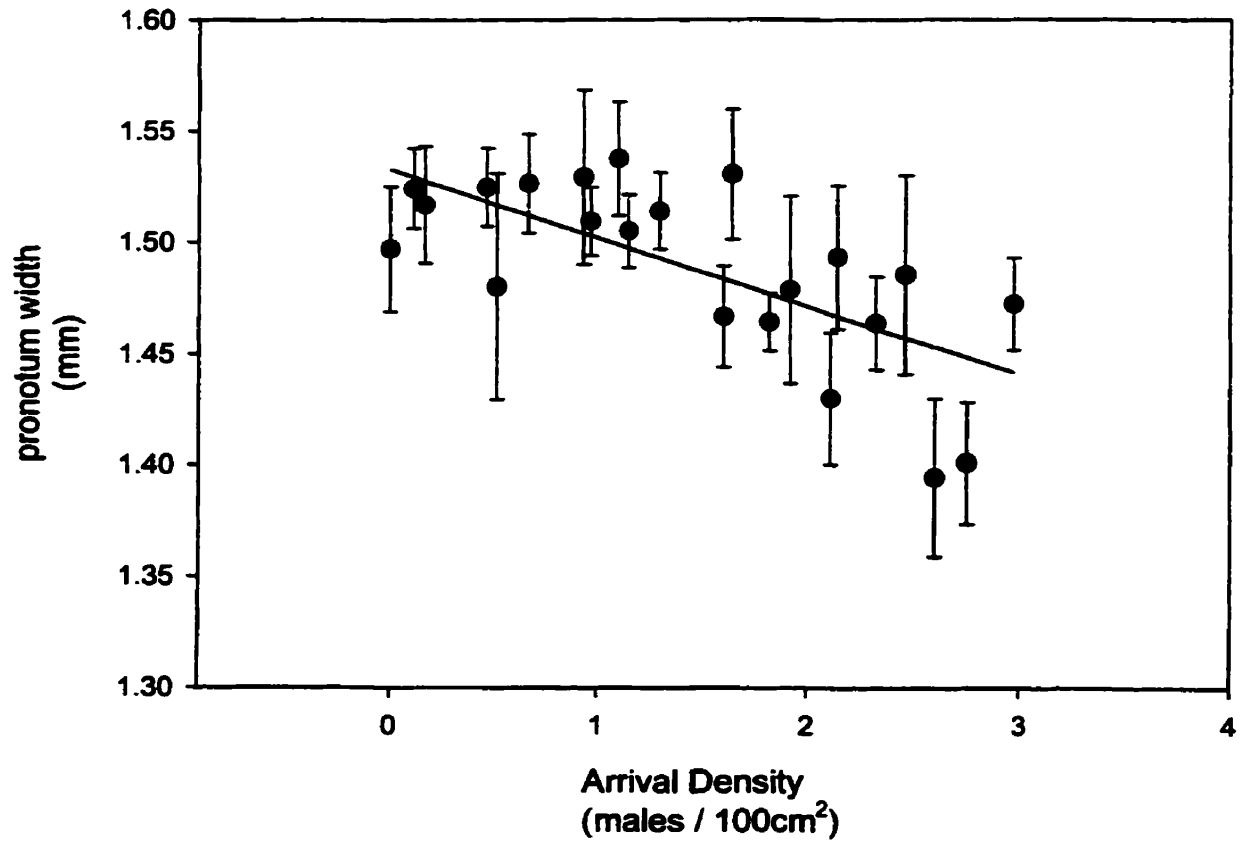
Fig. 2.3. Mean pronotum width (± SE) of males excavated from sites 1 to 4 as a function of aggregation density. Aggregation density is determined by the number of males /100 cm² at the time the male settled at the site.
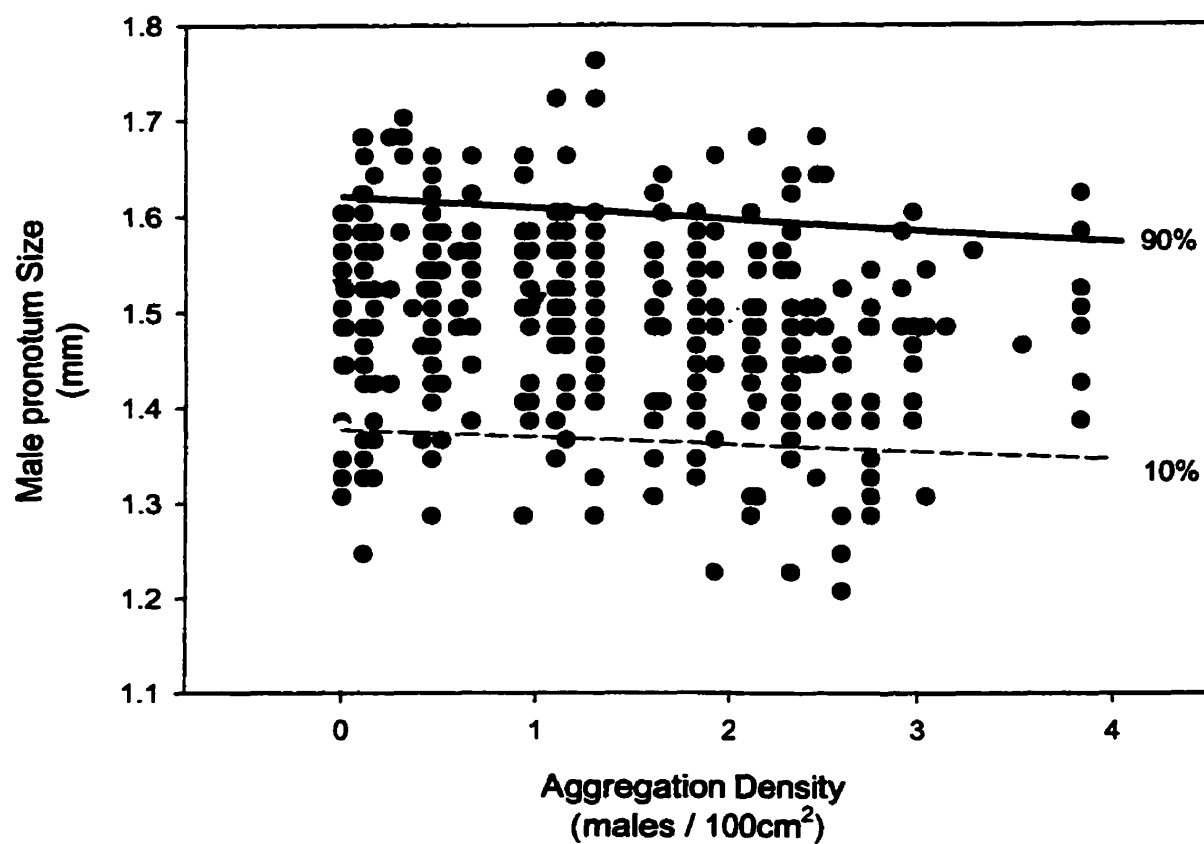
Fig 2.4. Body size of individual male settlers as a function of the aggregation density at settlement time. Indicated are quantile regressions: 90% and 10%. The continuous bold line represents a slope significantly different from 0 (P < 0.05). The dashed line represents a slope not significantly different from 0 (P > 0.1). (n = 419)
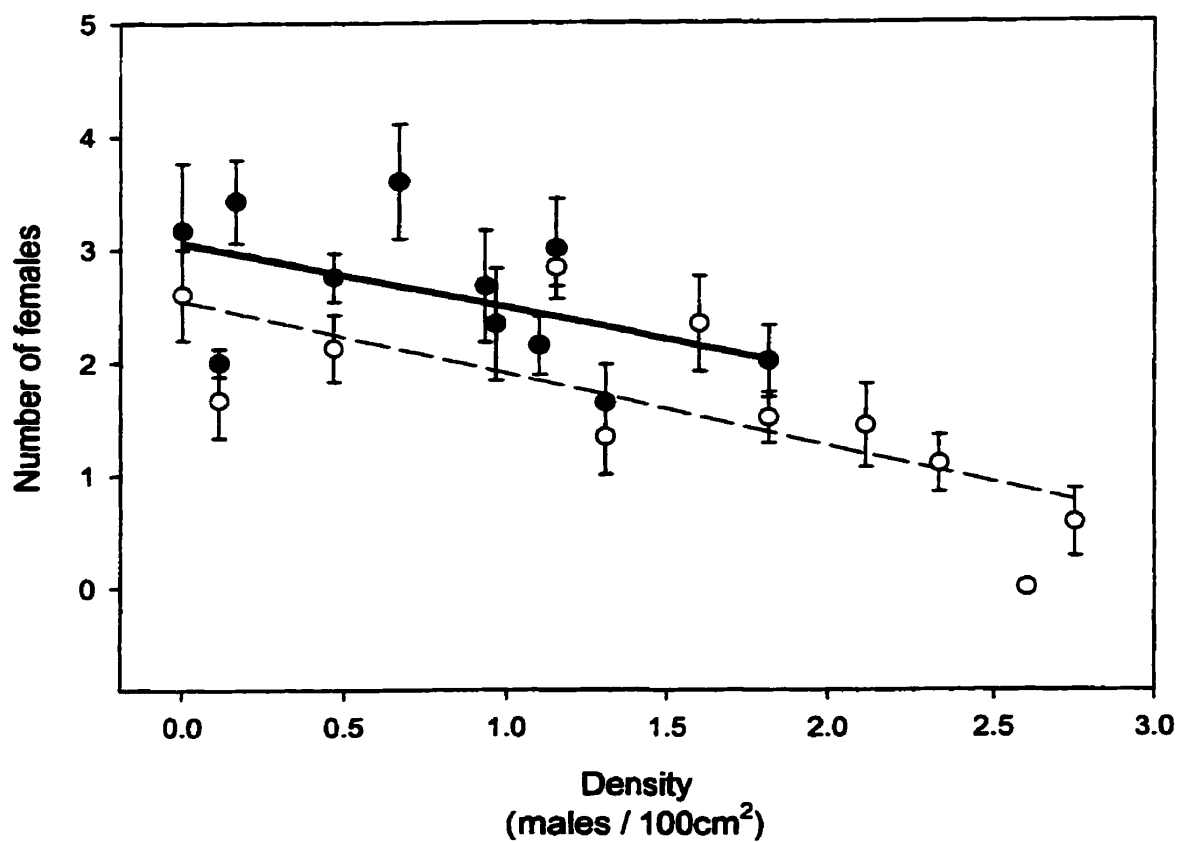
Fig 2.5. Mean number of females (± SE) acquired by large
and small males at different aggregation densities. Only means
with 5 or more observations are plotted. Solid circles and line
represent large males, open circles and dashed line represent
small males.

Chapter 3

Pioneer or Join? Fitness returns for large and small males using different settlement strategies in pine engraver bark beetles, *Ips pini*

Introduction

A commonly proposed benefit of mating and breeding aggregations has been the advantage of increased mate attraction and increased number of copulations for aggregation members (Buck and Buck, 1978; Hibino, 1986; Hoglund et al., 1993; Widemo and Owens, 1995; Aspi and Hoffmann, 1998; Hirschberger, 1998; however see Ehrlich and Wheye, 1986; Deutsch, 1994). Other possible functions include increased predator vigilance (Pulliam and Caraco, 1984; Parrish and Edelstein-Keshet, 1999) and increased information about resources available to participants (Clark and Mangel, 1984). Studies that have examined the mating consequences of aggregations have demonstrated that aggregations increase mate attraction, with attraction increasing with aggregation size (Buck and Buck, 1978; Shelly, 1989; Hoglund et al., 1993), at least to a point (Lank and Smith, 1992; Aspi and Hoffmann, 1998). On the other hand, a few studies have found that an increase in aggregation size decreases the number of matings that participants acquire (Doolan, 1981; Deutsch, 1994; Chapter 1).

The benefits of an aggregation do not have to increase with aggregation size in order for aggregations to be adaptive. The benefit of joining an aggregation needs only be larger than the benefits of being a solitary individual or a pioneer (Pulliam and Caraco, 1984; Parrish and Edelstein-Keshet, 1999). A high cost of being solitary has been proposed to explain aggregations that are larger than what would be considered optimal

(Aspi and Hoffmann, 1998). In the case of mating, the cost of settling alone may arise because conspecifics of both sexes are either unlikely to locate solitary individuals or choose not to join them. Consequently, deciding to pioneer an aggregation may result in settling an area that does not subsequently develop into an aggregation, which in turn favours individuals that join conspecifics rather than settling alone (Fig. 3.1a). However, few studies have directly measured mate attraction (or fitness) for pioneers or solitary individuals, and most presume the cost of being solitary is higher than that of joining an aggregation (e.g. Buck and Buck, 1978). This presumption is often made because pioneers and solitary individuals are difficult to study (Stamps, 2001).

Stamps (2001) suggests that including search costs of habitat selection can change the predictions about optimal behaviour of settling individuals. If habitat sites with existing aggregations are conspicuous and easier to find than potential aggregation sites that have yet to form an aggregation, individuals may be more likely to join an aggregation rather than pioneer their own site. The cost of finding habitat will depend on the type of site that is used for mating or breeding. Sites may be categorized as either unpredictable or traditional. Unpredictable sites are those that have either a random distribution, abundance or both. Some examples of unpredictable sites that are used for aggregations are cowpats (Aspi and Hoffmann, 1998), fallen trees (Atkins, 1966), or moose antlers (Bonduriansky and Brooks, 1999). Traditional sites are those that are used yearly or have a predictable distribution. Leks are often studied on sites that are used repeatedly (Hoglund et al., 1993; Westcott, 1994). In general, one would expect that search costs are higher for unpredictable sites than for traditional sites.

Aggregations at unpredictable sites may occur through two different processes.

The first involves an attractant that nucleates the group, in which the site itself is

responsible for the attraction of potential mates or individuals that join the aggregation

(Thornhill and Alcock, 1983; Parrish and Edelstein-Keshet, 1999). Sites such as treetops

(Svensson and Petersson, 1992), hilltops (Ehrlich and Wheye, 1986) or other

topographical features (Westcott, 1994) may provide the stimulus necessary for

individuals to find a suitable site. While these features may be somewhat permanent,

their location in the environment may be unpredictable especially when individuals are

not using past experience to return to a known site. The second type of site is one where

the individual itself (often synergistically with a weak site stimulus) is primarily

responsible for the attraction of potential mates and other conspecifics to the site

(Roseland et al., 1990; Landolt et al., 1992; see list in Alcock, 1982). In this process, the

consequences of being a pioneer with respect to individual quality may be different than

for pioneers at predictable sites or at sites that have characteristics that are responsible for

attraction of an aggregation. When individuals themselves are responsible for the

attraction of conspecifics, their ability to produce an attractive signal becomes

paramount. Low quality pioneers may be limited in their signal propagation, resulting in

a decreased chance of mate attraction and aggregation formation. Therefore, these

individuals may be required to join existing aggregations in order to have encounters with

searching mates, instead of becoming a pioneer. On the other hand high quality

individuals that are able to effectively produce attractive signals may benefit from

pioneering due to a high mate attraction and low costs of competition (Fig. 3.1b).

There may also be benefits associated with being solitary or a pioneer, due to reduced competition. Recently, pioneering has been compared to protandry (Harari et al., 2000). In this scenario, pioneering is considered advantageous because it maximizes the exposure time to potential mates (Wiklund and Fagerstrom, 1977; Thornhill and Alcock, 1983). A second suggestion is that less competitive individuals should settle alone to avoid competition with better conspecific competitors (Thornhill and Alcock, 1983; Aspi and Hoffman, 1998). The greater success of poor competitors when alone compared to when within an aggregation may mean that mating success has been underestimated for solitary individuals in lekking species (Lanctot et al., 1997). Finally, if mating aggregations also involve obtaining access to limited resources, either for the purpose of mate attraction or for post-mating breeding, then being first at a potential aggregation site may be beneficial (Fig 3.1c).

Here I examine the consequences of being a pioneer in pine engravers, *Ips pini*. This species exhibits strong conspecific attraction that is responsible for aggregation formation (Borden, 1974 and references therein) but mating success declines with aggregation size (Chapter 2). Male pine engravers emerge from overwintering in the duff of the forest floor in the spring or early summer and search for recently fallen trees to make a nuptial chamber under the bark, where they release attractive pheromones. Fallen trees are an unpredictably distributed resource within a forest and are used for only a single year. Colonizing individuals are primarily responsible for the attraction of an aggregation, so pioneers are not guaranteed to attract an aggregation or to have female visitation. Males are also committed to their choice of habitat for a period of time. When males initiate their nuptial chambers, they begin to break down their flight muscles,

confining the male for a period of approximately 10 days at their chosen site (Robertson, 1998). Most flight periods (when females are searching for mates) last about a maximum of 15 days of good weather. Consequently, a male pine engraver may effectively be able to make only one settlement choice in his lifetime.

Individual quality of pine engravers (and other bark beetles) is linked with the number of mates acquired (Chapter 2), and signalling ability of males (Anderbrant and Schlyter, 1989; Gries et al., 1990). Large males have been demonstrated to acquire more mates than their smaller counterparts (Chapter 2). Their advantage in mate attraction may be attributable to the ability of large males (measured by body size, weight or fat concentration) to produce a greater pheromone signal compared to small males (Birgersson et al., 1988).

Pine engravers both mate and oviposit within the phloem layer of a fallen tree, which is an exhaustible resource. Intraspecific larval competition for this resource has been demonstrated to be high for pine engravers and other bark beetles (Beaver, 1974; Anderbrant et al., 1985; DeJong and Grijpma, 1986; Robins and Reid, 1997). Therefore, I expect that there will be post-mating fitness consequences of aggregations. The question I address here is whether there is a mating cost of pioneering, at least for some individuals, that exceeds the larval competition costs within aggregations, thereby accounting for aggregation formation in this species.

Methods

A) Mate Attraction

I examined the mating consequences of being a pioneer or of joining an existing aggregation for small and large males in a field experiment. The experiment took place during the 1998 and 1999 field seasons at the University of Calgary's Kananaskis Field Station (Barrier Lake), Alberta, Canada, within a mature lodgepole pine (*Pinus contorta* var. *latifolia*) dominated forest (latitude 51° 2' N, longitude 115° 3' W). Every season there are two pine engraver dispersal flights in search of breeding habitat. The first flight consists of adults that over wintered from eggs laid late the previous summer. The second flight is a combination of re-emerging first flight adults and their offspring. In the 1998 field season only the second flight was used, and in 1999 only the first flight was used.

Beetles used in this experiment were collected from Lindgren funnel traps (cleared twice a day so beetles would not deplete fat reserves) baited with the pine engraver pheromones ipsdienol and laneirone (Phero Tech Inc.), or they were collected from emergence cages that had a 1 m section of lodgepole pine tree that had been colonized the previous summer. These cages were kept in the laboratory at 20 - 25°C and 40% -60% relative humidity with a 16:8 hour light:dark schedule. They were cleared daily. The size of all collected beetles was measured as pronotum width (to the nearest 0.02 mm) using a dissecting microscope fitted with an ocular micrometer, and as weight (to the nearest 0.1 mg) using an AND ER-120A electronic balance. Males were then divided into three size classes: large, small and medium. Large beetles were defined as

those within the 4th quartile for both pronotum width (> 1.56 mm) and weight (> 5.4 mg). Small beetles belonged to the 1st quartile for both pronotum width (<1.41 mm) and weight (< 4.1 mg) (Fig 2.1). Only large and small males were used in these experiments. All trees used in this study were lodgepole pine that had been cut or had fallen during the previous winter.

To determine the effects of body size on mate attraction for pioneers or joiners, I used a 2x2 design. Large and small focal males were implanted within an aggregation and at a site with no other males present (pioneer site). In 1998 and 1999, there were 3 and 1 aggregation sites, respectively, and 6 and 2 pioneer sites, respectively. Each site consisted of three 1m sections of lodgepole pine (diameter > 15 cm) placed end to end to resemble a fallen tree. Approximately 5 fresh branches were placed at one end of the logs in order to simulate a fallen tree (Fig. 3.2).

Aggregations were initiated by implanting 5 – 10 'bait' beetles on the logs at the aggregation site. Beetles were implanted by confining them over a small predrilled hole on the log within an microcentrifuge tube with its tip cut off. These logs were placed together in the forest to allow the further development of the aggregation to happen naturally. Focal males were implanted on an area of the log that had duct tape covering a 10 cm by 10 cm area from other beetle attacks once the aggregation had reached approximately 1.2 males per 100 cm^2. At the time of the implantation, there was approximately 1 week of remaining flight time available for all sites. A single large or small beetle was implanted at each pioneer site, and both a large and small male were implanted at each aggregation site, on the central log of the three logs. The logs for the pioneer sites were placed in the forest at the same time as those for the aggregation sites,

but were placed individually and separately to prevent an aggregation forming until the aggregation sites were ready to receive their focal male implants. At this time, pioneer logs were assembled into their sites, and focal males were implanted in both pioneer and aggregation sites. Focal beetles were confined under their microcentifuge tubes for 24 hours, to allow them to complete their nuptial chambers. All implants were performed on the same day for each year.

Four days after the implanted focal males had created nuptial chambers, I excavated them and tallied the number of females attracted. Due to a small sample size the data were non-normal and therefore run through a randomization procedure (Manly, 1991) equivalent to a two way balanced design ANOVA using the male size class and situation (pioneer/joiner) as the two factors; I included the interaction as well. F-values for the two factors and the interaction term were calculated from the original data using an ANOVA. Data were then randomly re-assigned across all treatment groups and F-values re-calculated (100,000 iterations). P-values represent the proportion of times the randomised F-values exceeded or equalled the F-values from the original data.

B) Offspring Competition

Competition among offspring as a function of when a male joined an aggregation cannot be examined directly since by the time larvae pupate, it is impossible to determine the egg gallery it originated from. Therefore, I developed a simulation model of offspring performance. This model is loosely based on a model created by DeJong and Saarenmaa (1985). It determines the number of offspring that reach a minimum

emergent size for each male, for parental males that are either small or large and are either pioneers or joiners of an aggregation.

The model was programmed in StarLogo T2001 (Appendix 1; Wilensky,1997). The model is a dynamic simulation model. The model takes place on a two dimensional array that represents the phloem layer of a tree. The array is composed of individual cells that are 1 mm x 1 mm square. Males create nuptial chambers, females construct galleries, and larvae mine paths within the array. As individuals move from one cell to another, the used areas are transformed from phloem rich to phloem poor. Parameters for male, female, and larval behaviour are discussed below and listed in Table 3.1.

Both pioneer and aggregation trials were run with large and small males. Large and small pioneers differed in their probability of attracting mates as determined by my previous field experiment. For pioneer males, the number of mates acquired over the four day period for all pioneers (for each body size class) was divided by the number of sites and by eight half days, in order to calculate the half day probability of a pioneer of a given size class attracting a mate. For large and small males within an aggregation, the probability of attracting mates was determined by examining the proportion of males at naturally settled sites that had attracted 1, 2, 3,or 4 mates for each half day the aggregation was observed (22 days) (see Appendix 2a). This was a more accurate determination of mate attraction that included the effect of males having already obtained 1, 2, or 3 mates on their subsequent mate attraction probability. These data were unavailable for pioneer males due to small sample size. Therefore, the mate attraction probability of pioneers did not include the effect of already having other mates on their mate attraction probability.

The model used half-day steps and tracked the settlement of males at the site. Male settlement was based on actual settlement patterns observed in the 1999 field season. I considered an area of phloem that was 25 cm by 25 cm. Aggregation trials and pioneer trials were run separately. For aggregation trials of the model, settlement of males followed exactly the settlement pattern of a site during the 1999 field season. The first male to arrive within the 25 cm x 25 cm region for an aggregation trial was not considered a pioneer, but instead was assumed to be joining other males that were located on other areas of the log. Therefore, mate attraction probabilities for all members of an aggregation trial were the probabilities for aggregations (Appendix 2a). For pioneer trials, the male had an equal chance of attracting another male as it did attracting a female in a pioneer situation. Once the pioneer male attracted three other males, the pioneer was considered to be in an aggregation and thereafter had the same probability of female attraction as for an aggregation (Table 3.1). Once three males had been attracted by a pioneer then other males settled with the same temporal and spatial pattern as the aggregation runs (starting at the time the third male was attracted by the pioneer).

Once females had joined a male, they began creating galleries and laying eggs. As eggs hatched, the progress of the larvae through the two-dimensional array was tracked and the phloem they passed through was consumed. Larvae completed their development when they reached a certain size, which was equivalent to the consumption of a certain amount of phloem. If they did not reach this size before entering an area with no phloem for a set amount of time (Table 3.1) their energy reserves were considered to be depleted and they were considered dead. This was the competition effect of this model. The

model tracked the development of all larvae and their survival to pupation or death

belonging to the focal male (pioneer runs) or all males (aggregation runs).

I ran both aggregation and pioneer simulations with two different settlement

patterns (A and B) derived from two observed settlement patterns in which all males were

assigned to be either large or small. All males that had a pronotum width greater than

1.50 mm were considered large, while males whose pronotum was less than 1.49 mm

were considered small. Settlement pattern A (11 large males and 11 small males) had 10

replicates of aggregation simulations performed for each flight time (see below). Each

male in the aggregation had the number of offspring they produced tabulated and the

mean for the ten replicates calculated for each flight time. For pioneer runs, there were

10 replicates performed for each of 6 pioneers (3 for large and 3 for small focal males)

for each flight time. Again, means for each focal male were calculated from the ten

replicates for each flight time. Settlement pattern B (11 large males and 10 small males)

also had 10 replicates of aggregation simulations for each flight time performed, and 10

replicates of 4 pioneer simulations (2 for large and 2 for small focal males) for each flight

time. Data were dealt with in the same manner as data for Situation A.

I used four different flight times for each settlement pattern: 3 days, 5.5 days, 10.5

days and 14.5 days. Flight times were the number of days left in the flight after the

arrival of the pioneer male or the first male in aggregation runs. Flight times impacted

both female availability and male arrival. Once the number of days had passed the flight

time, no more male settlement occurred and no more females were attracted.

The data that I collected from the model were the number of females acquired and

the number of offspring that each male produced that survived to pupate; the latter was

considered the fitness returns for each male that was examined. As a means of

assessing the strength of the patterns observed in these simulations, I used standard

inferential statistics on the data I collected from the simulations. To determine the

difference in fitness for small and large males that either join an aggregation or were

pioneers, two-way ANOVAs, blocked by settlement pattern, were performed for each

flight time. Size (large and small) and situation (pioneer or joiner) and their interaction

were examined. All pioneer males were used in each of the four flight times simulated.

In aggregation runs, males used in analysis had residence times equivalent to the same

four flight times. However, for aggregations runs that were 5.5 days, 10.5 days and 14.5

days, males that settled plus or minus one half day residence time were also included in

the analysis in order to increase the number of different aggregation males included in the

analysis (this was not done for the 3 day flight time due to a large number of males that

had that residence time). All ANOVAs initially included the settlement pattern (A or B)

variable, which was removed from the model if did not contribute significantly to the

model ($P > 0.10$). I used simple linear regression analysis to examine if the number of

pupae changed with increasing flight time for all four categories of males (large pioneers,

large joiners, small pioneers, small joiners). For comparisons between pioneers and

joiners within a size category, t-tests were employed, with a decreased alpha value ($\alpha =$

0.025) due to multiple testing of the same data set.

Data were analyzed using JMPin (SAS Inc. 1996). The number of pupae were

transformed to meet parametric assumptions (ln(number of pupae + 1)). All means are

presented $\pm$ 1 SE.

Results

A) Mate Attraction by Large and Small Pioneers and Joiners

Males in aggregations acquired significantly more females within four days than did pioneer males (Fig. 3.3; randomization test, pioneer/joiner: $P = 0.051$). Large males attracted significantly more mates than did small males in both aggregations and as pioneers (Fig. 3.3; randomization test, body size: $P = 0.039$, body size-situation interaction: $P = 0.82$). These mate attraction data were used to parameterize the model's female acquisition for large and small males as described in Methods (Table 3.1).

B) Offspring Competition Model

To examine whether the fitness consequences of pioneering or joining differed for small and large males, I examined the two-way ANOVAs with their interaction for these two factors. The interaction was only significant for the 3 day flight (ANOVA: $R^2 = 0.88$, interaction: $F_{1,16} = 33.28$, $P < 0.0001$, for all other flight times, $P > 0.1$). With this short time remaining in the flight, small pioneers produced significantly fewer pupae than small joiners ($t_9 = 4.11$, $P < 0.025$), while large pioneers produced significantly more pupae than large joiners ($t_8 = -2.896$, $P < 0.025$; Fig. 3.4a). For all other flight times, both small and large males had higher fitness as pioneers than as joiners (5.5 days: $F_{1,25} = 12.3$, $P < 0.01$; 10.5 days: $F_{1,22} = 25.2$, $P < 0.0001$; 14.5 days: $F_{1,16} = 30.6$, $P < 0.0001$; Fig. 3.4b-d). Large males produced significantly more pupae than small males for 5.5 and 10.5 days (5.5 days: $F_{1,25} = 11.2$, $P < 0.01$; 10.5 days: $F_{1,22} = 5.22$, $P < 0.05$; Fig. 3.4b

and c). However, the fitness difference between large and small males disappeared with the longest flight time (14.5 days: $F_{1,16} = 0.18$, $P > 0.5$; Fig. 3.4d).

C) Effects of flight time

The fitness of small pioneer males increased as flight time increased ($R^2 = 0.61$, n = 20, $P < 0.0001$). Small pioneers produced more offspring that survived to pupation with increasing time available in the flight because small males were able to attract more females given more time (Fig. 3.4e-h). In contrast to small pioneers, large pioneers realised lower fitness as flight times increased ($R^2 = 0.34$, n = 20, $P < 0.01$; Fig. 3.4a-d). This was because large pioneers realised virtually no mating advantage to having longer flight times, because they attracted mates quickly (Fig. 3.4e-h). In addition, they suffered from the increased competition due to more beetles settling with longer flight times. The fitness of both large and small joiners was not affected by an increase in flight time available (large joiners: $R^2 = 0.026$, n = 31, $P > 0.25$; small joiners: $R^2 = 0.024$, n = 25, $P > 0.25$, Fig. 3.4a-d). This is due to a rapid asymptote of fitness with increasing aggregation density (Robins and Reid, 1997; unpublished data). Due to the increasing fitness of small pioneers and decreasing fitness of large pioneers with increasing flight time, the effects of body size disappeared with long flight times (Fig. 3.4d). Thus, limitations on mate acquisition of small pioneers was overcome by an increase in remaining flight time, thereby increasing their fitness. However, increasing flight time for either large or small males that joined an aggregation or for large pioneers resulted in an increase in competition that outweighed the benefits of increased mate attraction for these groups.

Discussion

In the field experiment, mate attraction by male pine engravers was faster for individuals that joined an aggregation than for those that settled as pioneers. This suggests that there is a cost to pioneering in terms of mate attraction. These findings are in accordance with other studies that have demonstrated that joining aggregations increased the number of encounters with potential mates as well as increased number of matings experienced per male (Buck and Buck, 1978; Hoglund et al., 1993; Widemo and Owens, 1995). In contrast, it was previously demonstrated that mate attraction in pine engravers decreased with increased aggregation size (Chapter 2). However, the decrease in mate attraction for pioneers may be greater than the decrease for joining an aggregation of any size, thereby favouring aggregation behaviour. Small pine engravers were particularly affected by reduced mate acquisition as pioneers relative to joiners. My results from the simulation model suggest that when flight times are less than 10.5 days, small pioneers will acquire fewer mates than if they settled at moderate aggregation densities (less than 3.0 males / 100 cm^2; Chapter 2). Mate attraction in my simulations were similar to that observed in the field, as expected since mate attraction probabilities were derived from field data. Simulations revealed that while mate acquisition by large males was approximately equal for pioneers and joiners after 5.5 days, small males' mate acquisition always remained lower for pioneers than for joiners. These findings suggest that small males should favour joining aggregations in order to attract mates. This is supported by the finding that there was a tendency for small males to settle at higher aggregation densities than did large males (Chapter 2).

In accord with other studies (Hibino, 1986; Aspi and Hoffman, 1998), male pine engravers in aggregations acquired more females than did solitary pioneer males. However, the cause for lower mate attraction may be different than the reasons commonly proposed in the lek literature. For pine engravers, the lower mating success of pioneers resulted from the failure of an aggregation to subsequently develop around a lone male. The relative lack of attractiveness of lone males is unlikely to be because females and other males dislike lone males, as female fitness declines greatly with competition (Robins and Reid, 1997). Instead, pioneer males may simply be hard to locate. Difficulty in finding a pioneer has two consequences. First, if individuals are responsible for attraction of the aggregation and that attraction ability is condition dependent, it is expected that only the individuals best able to produce attractive signals will be pioneers. This is in opposition to other studies that have found that the earliest settlers are often in the worst condition, and settle early to increase exposure time to searching females or to avoid better competitors (Thornhill and Alcock, 1983; Hoglund et al., 1993; Aspi and Hoffmann, 1998). For pine engravers it can be expected that males in good condition may pioneer because they acquired more mates than poor competitors and may be more conspicuous (Anderbrant and Schlyter, 1989; Gries et al., 1990). Therefore, if possible, poor condition males should avoid pioneering in the interests of mate attraction. As a second consequence of lone males being difficult to locate, all beetles may readily accept aggregations because of the difficulty of finding an unoccupied site, thereby exacerbating the risk that no other beetle will encounter a lone male.

Despite strong effects of aggregations on mate attraction, mating success may not correlate well with fitness (Lanctot et al., 1997). This is the case if females mate with

more than one male (Thornhill and Alcock, 1983), or if there is a strong post mating

breeding effect on offspring survival (Robins and Reid, 1997). Using a biologically

realistic simulation of breeding for pine engravers, I found that in most cases both large

and small males realized higher offspring production as pioneers than as joiners. The

effect of intense larval competition for a limited resource in an aggregation outweighed

any mating disadvantage of being a pioneer. The only situation in which males suffered

from being a pioneer was if the male was small and there was a short remaining flight

period (3.5 days). However, even with a short flight time, the fitness reduction from

pioneering rather than joining was small.

While pioneering was an advantageous tactic, it was due to post-mating offspring

competition and not due to a mating advantage. This is in contrast to existing hypotheses

of why males would pioneer. Protandry suggests that increased exposure time to

searching mates will result in a greater number of matings (Wiklund and Fagerstrom,

1977). This idea is rejected for my study because there was a decrease in number of

matings acquired by males that that were first at a site because males did not always

attract a subsequent aggregation. Alternatively, pioneering may be advantageous for less

competitive males (Thornhill and Alcock, 1983; Aspi and Hoffman, 1998), but this was

rejected due to an increase in mate attraction for small pine engraver males when among

conspecifics. In bark beetle aggregations, males remain within their nuptial chambers

and are therefore unable to dominate an area and force lesser competitors away from the

aggregation.

I found that when female arrival is prolonged, all males benefit from being

pioneers of a new habitat although there is a reduction in the rate of mate attraction at

these sites compared to within aggregations. This was due to the high conspecific competition costs experienced by developing larvae of males that join aggregations (Beaver, 1974, Robins and Reid, 1997). However, if the time of female availability is short, then large and small males should use different strategies to maximize their fitness. Large males should continue to pioneer, whereas small males should join an aggregation because the increased mate attraction outweighs the competition costs of joining an aggregation. Although there is a predicted fitness increase for most males to act as pioneers, pioneering is rarely observed.

Pioneers or solitary males are rarely examined in species that predominately form aggregations (but see Greenfield and Shelly 1985; Hibino, 1986; Aspi and Hoffman, 1998). Furthermore, in those studies and others that examine success within aggregations, mating success rather than fitness is usually measured (Lanctot, et al., 1997). For logistical reasons these studies have focused on predictable mating sites, or solitary males have been presented females experimentally, instead of being responsible for attracting mates (Greenfield and Shelly, 1985; Hibino, 1986; Aspi and Hoffman, 1998). However, mating aggregations commonly form on unpredictable resources or are influenced by the occurrence of the males themselves (Borden, 1974; Alcock, 1982 and references therein). I was able to observe both solitary males and males within aggregations in a species where males are primarily responsible for female attraction at unpredictable breeding sites. I demonstrated the importance of examining both mating success and fitness for pioneers as well as for joiners of aggregations, in order to determine whether or not individuals should join an aggregation or settle alone.

In my study, male fitness was measured by surviving offspring and did not correlate with male mating success. While the assumption that mating success correlates with fitness should always be made with caution, it is especially likely to be the case when mating sites are also breeding sites. Animals using unpredictable and ephemeral resources, as bark beetles do, often use these resources for both mating and breeding (Tallamy and Wood, 1986). In these animals, the fitness consequences of offspring competition may often exceed any benefits in terms of mate attraction that derive from being in an aggregation. This situation, as observed in pine engravers, indicates that ecological factors other than mating success are responsible for the occurrence of aggregations. Other factors could include limited resources (Chapter 2), unpredictability of resources (Chapter 4) and high search costs for appropriate breeding habitat (Stamps, 2001; Chapter 4).

Table 3.1. Parameters used for the simulation model.

Variable	Description	Assigned value	Source
Female attraction by males in aggregations	The probability that a large (L) or small (S) male in an aggregation will acquire a female each half day, depending on number of mates already attracted	1st female = 0.92 (L), 0.75 (S) 2nd female = 0.75 (L), 0.55 (S) 3rd female = 0.30 (L), 0.10 (S) 4th female = 0.05 (L), 0.01 (S)	Appendix 2a
Female attraction by pioneers	The probability that a large (L) or small (S) male that was a pioneer acquired a mate each half day	0.37 (L) 0.05 (S)	Mate attraction of pioneers in the field experiment (this chapter)
Female starting position	The direction a female begins her gallery from the male's nuptial chamber.	The females starting position is dependent on other females' positions (see Appendix 2b)	Appendix 2b
Female gallery extension	The rate at which females extended their galleries each half day	5 mm / half day	Appendix 2c
Egg laying	The probability for each female 1 mm step that an egg would be laid.	P = 0.25 (there was an equal chance that the egg was laid to the female's left or right side)	Appendix 2c
Larval hatch time	The time since the egg was laid until it hatched and began feeding	9.0 half days	Appendix 2d
Larval movement	The number of 1 mm steps a larvae made per half day.	2 mm per half day	Appendix 2d
Minimum food	The minimal distance a larvae would have to travel to reach pupation size.	40 mm	Appendix 2d
Maximum food	The farthest distance a larvae would travel before pupating	65 mm	Appendix 2d
Starvation	The number of consecutive 1 mm steps a larvae could make before starvation (death)	10 mm	DeJong and Saamerena (1985)
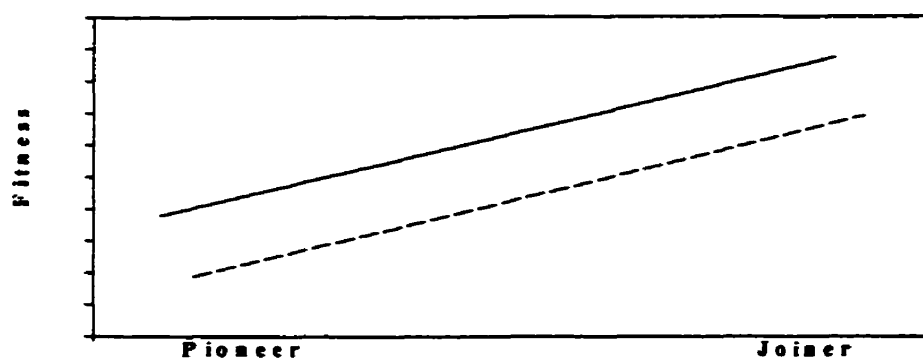
A. Mate attraction is negatively affected by pioneering
for both large and small males. Mate acquisition
varies with male size, but both size classes are
affected similarly.
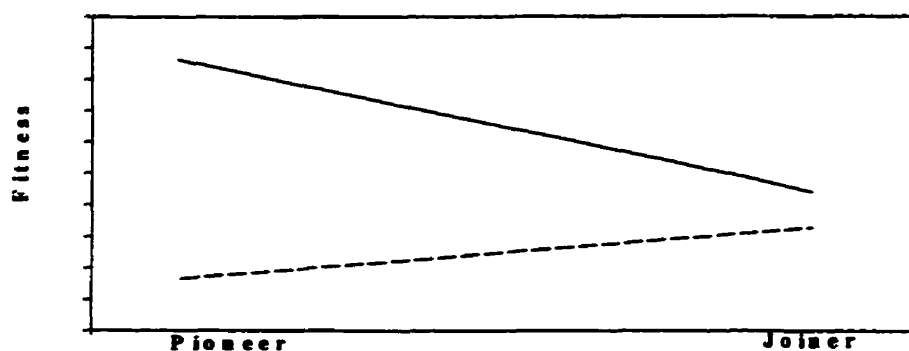
B. Large and small males differ in mate acquisition as
pioneers and as joiners. Mate acquisition is negatively
affected by pioneering for small males but not for large
males.
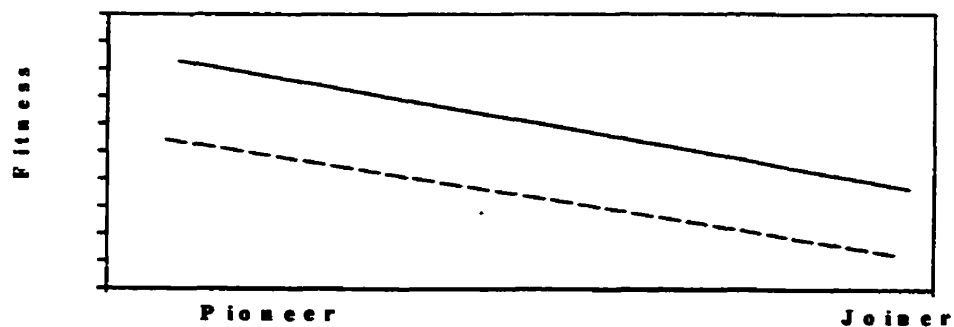
C. Mate attraction is not affected by pioneering
for both large and small males. Mate acquisition
varies with male size, but both size classes are
affected similarly.

Fig. 3.1. Predictions of fitness consequences for pioneers or aggregation joiners with different abilities to acquire mates. The solid line and short dashed line are for large and small males (respectively).
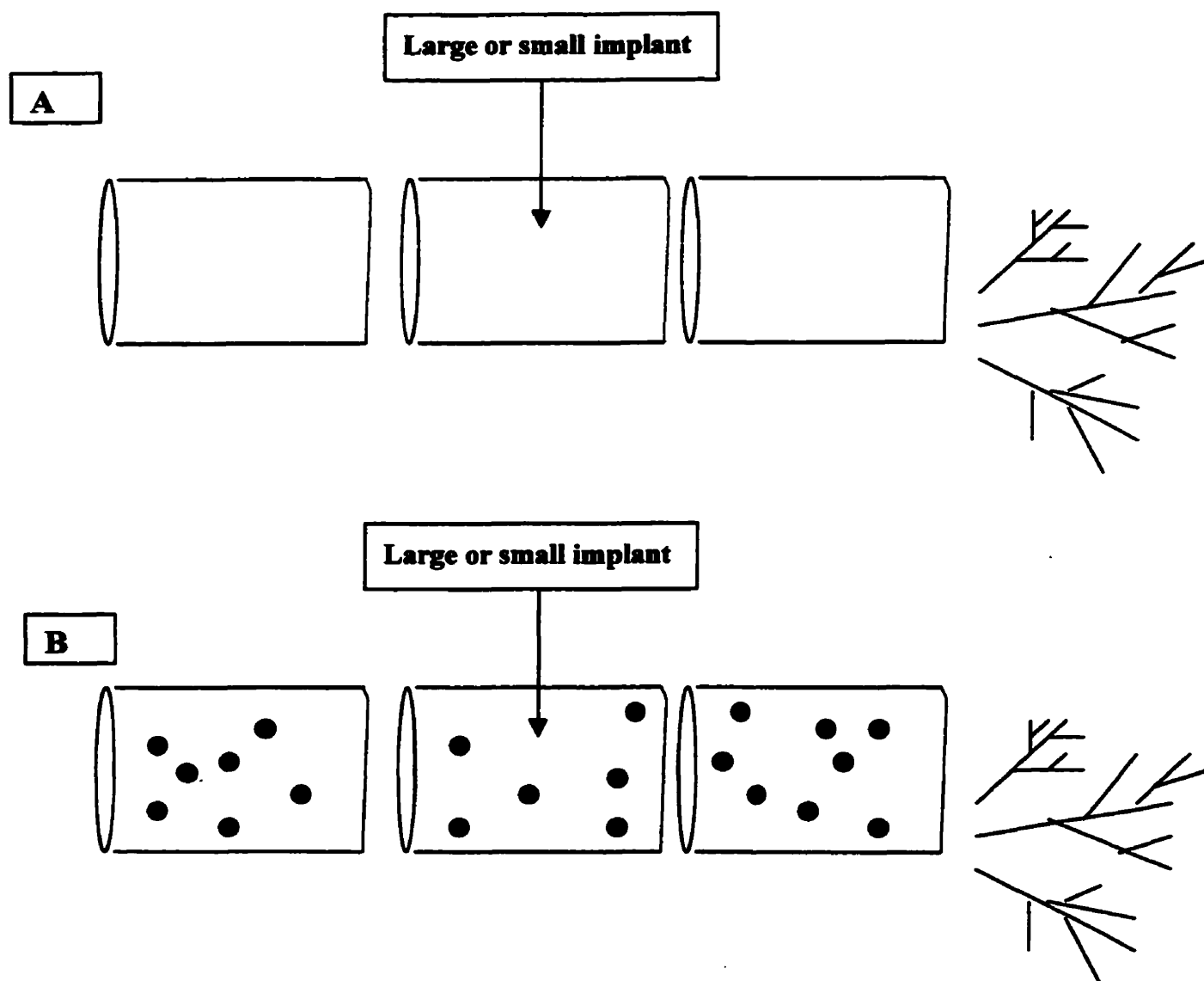
Fig. 3.2. Mate attraction experimental set up (not drawn to scale). Pioneer sites, A, had a single large or small male (depending on the treatment) implanted on the middle log of three 1 m logs. Aggregation sites, B, were assembled in the forest and implanted with a large and small male (depending on the treatment) on the middle of the three logs once the aggregation had reached approximately 1.2 males per 100 cm^2 (beetles represented by black circles). Both types of sites had several cut branches placed at one end of the logs to better simulate a fallen tree.
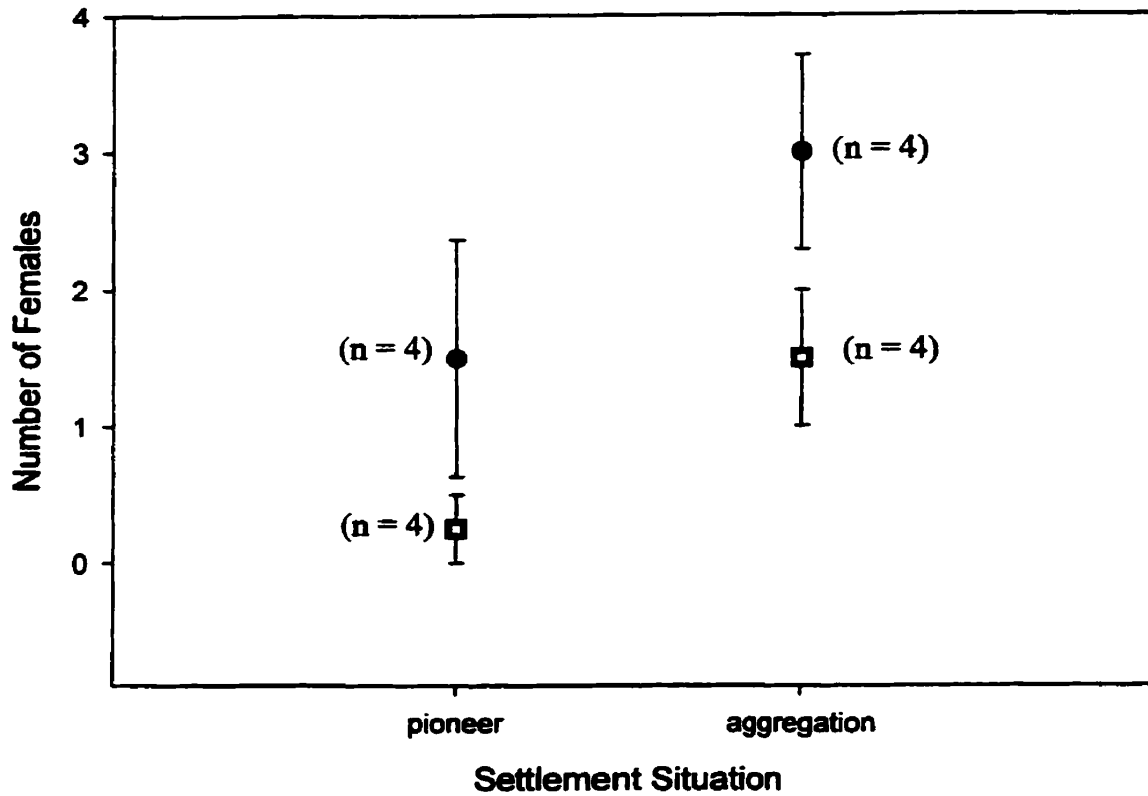
Fig. 3.3 The number of females acquired by large (circles and solid line) and small males (squares and short dashes) that were forced to settle alone (pioneer) or were placed as part of an aggregation (means ± S.E.). Males were allowed 4 days to acquire mates before their nuptial chamber was excavated and females were tallied.
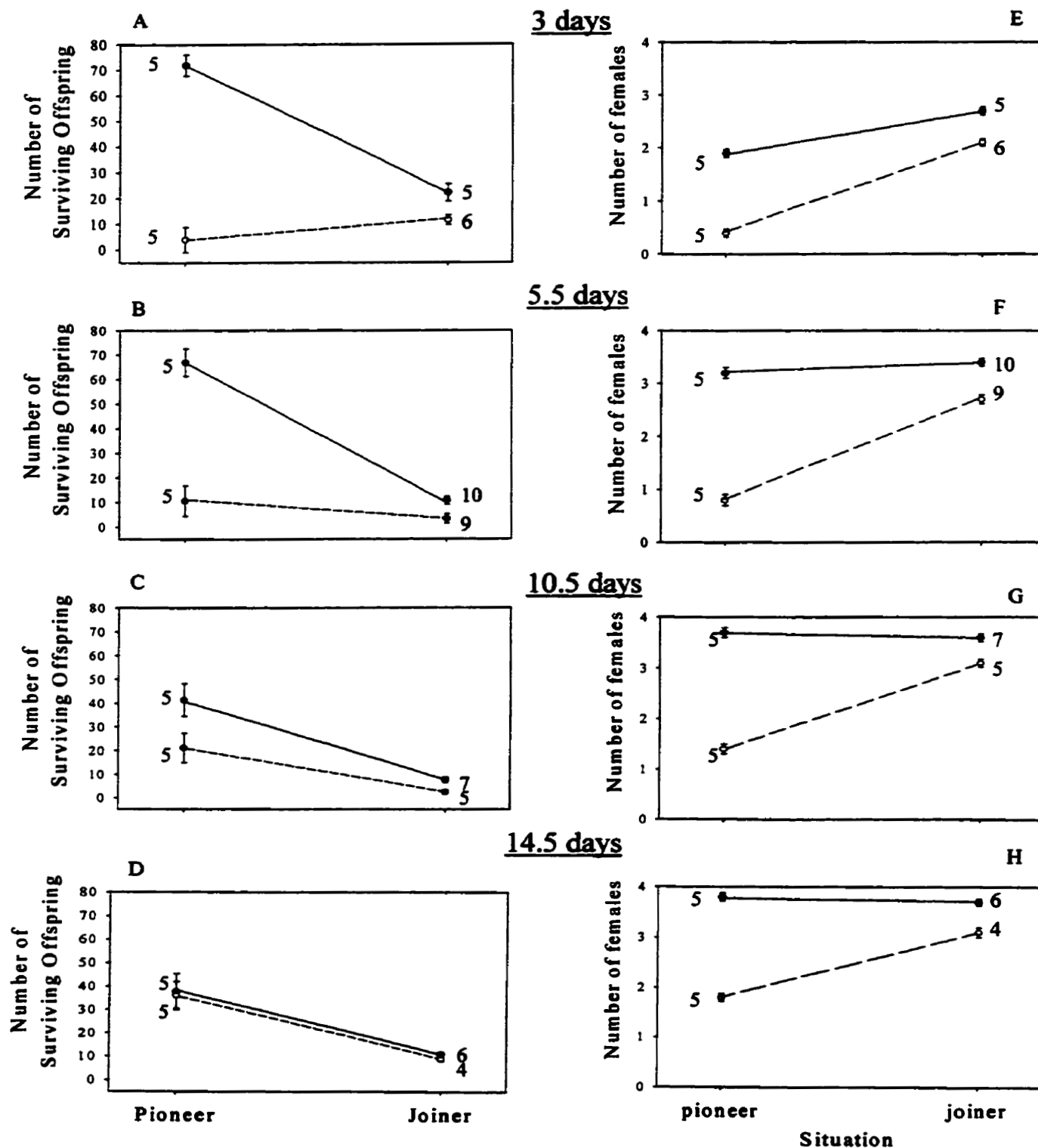
Fig. 3.4. Fitness and mate attraction results from the simulation model. Simulations were performed for 4 different flight times (3, 5.5, 10.5 and 14.5 days). Flight times controlled for the time available to attract mates (or other male beetles for pioneer beetles). Displayed are the mean number of offspring and mean number of mates, collected from 10 replicates for each male in the simulation (numbers represent # of males in each simulation; included are standard error bars). Large males are represented by solid circles and solid lines, small males are represented by hollow circles and dashed lines (lines are added for ease of visual comparison).

Chapter 4

General conclusions

The findings of my two studies suggest that joining an aggregation results in a net cost to pine engravers, both in terms of the effects of increasing aggregation size (Chapter 2) as well as relative to being a pioneer (Chapter 3). I tested three hypotheses as to how aggregations may benefit mating and breeding success of pine engravers and therefore why aggregations form. The hypotheses were: that aggregations increase the probability of males acquiring mates; that individuals differed in signalling ability, and low quality signallers were parasitizing the signal of high quality males; and that the cost of settling alone was higher than settling within an aggregation (in terms of number of surviving offspring). All three of these hypotheses were rejected as reasons for aggregation formation in pine engravers. I demonstrated that mating success declined with increasing aggregation density, and that it declined for large and small males equally (Chapter 2), although large males had higher mating success than small males (Chapters 2 and 3). If small males are exploiting the signal of large males, small male mating success is predicted to increase with increasing aggregation density. A decline in mating success for small males with increasing aggregation size rejects the hypothesis that small males were joining aggregations to exploit the signal of large males (Chapter 2). I used a simulation model to calculate fitness returns (number of offspring that survive to pupation) for pioneers and joiners of an aggregation (for both large and small males). The lower mating success for males that pioneered a site relative to that of males joining aggregations was more than offset by the benefits of reduced offspring competition when settling alone (Chapter 3).

Why then do aggregations form in this species? There are two categories of alternative explanations. The first is the common supposition that there is some other benefit of being with conspecifics (Prokopy and Roitberg, 2001). The idea that there is some mutual resource enhancement, such as seen in aggressive bark beetles, is clearly not applicable to bark beetles breeding in dead trees. Several studies, including this one, have demonstrated that for non-aggressive bark beetles the presence of conspecifics reduces resource availability resulting in a large reduction in the number of offspring produced per male or per female (Beaver, 1974; DeJong and Grijpma, 1986; Robins and Reid, 1997; Chapter 3). Another commonly proposed benefit is reduced predation. This is unlikely for bark beetles that are confined under the bark where the suggested mechanisms that include faster predator detection, predator confusion, and the dilution of risk (Pulliam and Caraco, 1984; Alcock, 1993) would not apply.

A less commonly considered type of explanation for aggregation formation relates to the uncertainty of finding a breeding site. This uncertainty may be the result of several different mechanisms. Most simply, if suitable breeding habitat is limited then there may be no habitat that is available for all individuals to settle alone or as a potential pioneer. However, in pine engravers, I observed that aggregations reached high densities while there was habitat available that was less densely inhabited (Chapter 2). In 1999 there were several suitable sites that remained uncolonized while other sites reached aggregation densities of upwards of 6 males per 100 cm^2. Therefore, individuals were not forced to join aggregations due to an actual lack of resources.

Another source of uncertainty relates to the remaining time in the flight season. Four flight times were used in the simulation model, and only with the shortest flight time

(3 days) was pioneering more costly than joining an aggregation (and then only for small males) (Chapter 3). Pine engravers overwinter in the duff of the forest floor, and emerge to search for habitat and mates. The cue used for emergence is most likely temperature of the duff (Botterweg, 1982). Overwintering sites are distributed across the forest and it is not unreasonable to assume that these sites will heat differently. In this scenario beetles will emerge at different times (Safranyik et al., 1996) without knowledge of whether other members of the population have already emerged. This situation also does not allow beetles to know the remaining flight duration. For small beetles, the risk of a short remaining flight time may favour a risk averse strategy due to a low chance of mate attraction and a decreased in fitness as a pioneer compared to joining an aggregation. Large males in this scenario should still opt to pioneer because of their high fitness returns as pioneers when flight time is short. However, large males were observed joining aggregations (Chapter 2).

Finally, uncertainty in finding host trees may be related to search costs. An increase in search costs for a suitable habitat can reduce choosiness of habitat quality by searching individuals (Pomiankowski, 1987), or individuals may be forced to rely on additional cues of conspecifics to find suitable habitat (Stamps, 2001). Suitable habitat for bark beetles is unpredictable in both location and abundance within a forest (Atkins, 1966), and the cost of locating this habitat has been demonstrated to explain much of the mortality in bark beetle life tables (Raffa and Berryman, 1987). Previous work on flight and dispersal of engraver beetles has indicated that flight ability is size specific, as is successfully finding appropriate habitat (Anderbrant and Schlyter, 1989; Robertson and Roitberg, 1998). As beetles fly in search of habitat they reduce their fat content (Atkins,

1969; Thompson and Bennett, 1971). A reduction in fat has also been demonstrated to reduce a male's ability to produce pheromones (Gries et al., 1990), thereby reducing a male's signalling ability. This results in a trade-off for searching males in which males can expend more energy to find a pioneering site and thereby reduce their attractiveness or ability to acquire mates, or they can accept a habitat that can be found quickly and have a strong attractive ability. This cost may result in males choosing a habitat that is easily found, over a site that may be more beneficial in terms of fitness gains but more difficult to locate (Stamps, 2001). It may also be more important to find site quickly and attract females quickly, especially if female availability is unpredictable, because time spent searching may result in no females being available once a site is located. One way to reduce all of these search costs is to use the presence of conspecifics at a site as an indicator of habitat quality (Boulinier and Danchin, 1997; Stamps, 2001). Using the presence of conspecifics to select habitat will lead to individuals becoming aggregated at previously discovered resources.

In this study I have rejected the hypothesis that aggregations in pine engravers can be explained by enhanced mate attraction, suggesting instead that all males should be pioneers or solitary if they have the ability to locate an appropriate site. Few studies of species with breeding aggregations have taken into account the fitness realized by solitary individuals, and therefore my work contributes significantly to that end. However it leaves unanswered the question of why aggregations form. I have suggested that the best hypothesis relates to the probability of finding available habitat in the presence and absence of conspecifics. I have elucidated the post-settlement consequences of aggregation formation in terms of both competition (Beaver, 1974; DeJong and Grijpma,

1986; Robins and Reid, 1997; Chapter 3) and mate attraction (Chapters 2,3). By

knowing the post-settlement consequences of habitat choice, we can better evaluate pre-

settlement processes, such as habitat search, which is the direction future research should

explore with regards to aggregation formation in non-aggressive bark beetles.

References

Alcock, J. (1982). Natural selection and communication among bark beetles. *Florida Entomologist*, **65**, 17-32.

Alcock, J. & Gwynne, D.T. (1991) Evolution of insect mating systems: the impact of individual selectionist thinking. In: *Reproductive behaviour of insects: Individuals and populations* (Ed. by Bailey, W.J. & Ridsdill-Smith, J.), pp. 10-41. London: Chapman & Hall.

Alcock, J. (1993). *Animal behavior: An evolutionary approach*. Sunderland: Sinauer Associates, Inc.

Alcock, J. (1997). Competition from large males and the alternative mating tactics of small males of Dawson's burrowing bees (*Amegilla dawsoni*) (Apidae, Apinae, Anthophorini). *Journal of Insect Behavior*, **10**, 99-113.

Alexander, R. D. (1975). Natural selection and specialized chorusing behavior in acoustical insects. In: *Insects, science and society* (Ed. by Pimental, D.), pp. 35-77. New York: Academic Press.

Anderbrant, O., Schlyter, F. & Birgersson, G. (1985). Intraspecific competition affecting parents and offspring in the bark beetle *Ips typographus*. *Oikos*, **45**, 89-98.

Anderbrant, O. (1988). Survival of parent and brood adult bark beetles, *Ips typographus*, in relation to size lipid content and re-emergence or emergence day. *Physiological Entomology* **13**: 121-129.

Anderbrant, O. & Schlyter, F. (1989). Causes and effects of individual quality in bark beetles. *Holarctic Ecology*, **12**, 488-493.

Andersson, M. (1994). *Sexual Selection*. New Jersey: Princeton University Press.

Aspi, J. & Hoffman, A. A. (1998). Female encounter rates and fighting costs of males are associated with lek size in *Drosophila mycetophaga*. *Behavioral Ecology and Sociobiology*, **42**, 163-169.

Atkins, M. D. (1966) Behavioural variation among scolytids in relation to their habitat. *Canadian Entomologist*, **98**, 285-288.

Atkins, M.D. (1969). Lipid loss with flight in the Douglas-fir beetle. *Canadian Entomologist*, **101**, 164-165.

Bailey, W.J. & Ridsdill-Smith, J. (eds) (1991). *Reproductive behaviour of insects: Individuals and populations*. London: Chapman & Hall.

Beaver, R. A. (1974). Intraspecific competition among bark beetle larvae (Coleoptera: Scolytidae). *Journal of Animal Ecology*, **43**, 455-467.

Berryman, A. A. & Pienaar, L. V. (1973). Simulation of intraspecific competition and survival of *Scolytus ventralis* broods (Coleoptera: Scolytidae). *Environmental Entomology*, **2**, 447-459.

Berryman, A. A. (1976). Theoretical explanation of mountain pine beetle dynamics in lodgepole pine forest. *Environmental Entomology*, **5**, 1225-1234.

Berryman, A. A., Dennis, B., Raffa, K.F. & Stenseth, N.C. (1985). Evolution of optimal group attack, with particular reference to bark beetles (Coleoptera: Scolytidae). *Ecology*, **66**, 898-903.

Birgersson, G., Schlyter, F., Bergstrom, G. & Lofqvist, J. (1988). Individual variation in aggregation pheromone content of the bark beetle, *Ips typographus*. *Journal of Chemical Ecology*, **14**, 1737-1761.

Bonduriansky, R. & Brook, R. J. (1999). Why do male antler flies (*Protopiophila litigata*) fight? The role of male combat in the structure of mating aggregations on moose antlers. *Ethology, Ecology and Evolution*, 11, 287-301.

Borden, J. H. (1974). Aggregation pheromones in the Scolytidae. In: *Pheromones* (Ed. by Birch, M. C.), pp. 135-160. Amsterdam: North-Holland.

Bossert, W. H. & Wilson, E. O. (1963). The analysis of olfactory communication among animals. *Journal of Theoretical Biology*, 5, 443-469.

Botterweg, P. F. (1982). Dispersal and flight behaviour of the spruce bark beetle *Ips typographus* in relation to sex, size and fat content. *Zeitschrift fuer Angewandte Entomologie*, 94, 466-489.

Boulinier, T. & Danchin, E. (1997). The use of conspecific reproductive success for breeding patch selection in terrestrial migratory species. *Evolutionary Ecology*, 11, 505-517.

Bradbury, J. W. (1981). The evolution of leks. In: *Natural selection and social behavior: Recent research and new theory* (Ed. by Alexander, R. D. & Tinkle, D. W.), pp. 138-169. New York: Chiron Press.

Buck, J. & Buck, E. (1978). Toward a functional interpretation of synchronous flashing by fireflies. *American Naturalist*, 112, 471-492.

Cade, B. S. & Richards, J. D. (1996). Permutation tests for least absolute deviation regression. *Biometrics* 52: 886-902.

Cade, W. (1980). Alternative male reproductive behaviour. *Florida Entomologist* 63: 30-45.

Clark, C. W. & Mangel, M. (1984). Foraging and flocking strategies: information in an uncertain environment. *American Naturalist*, **123**, 626-641.

Cole, W. E. (1973). Crowding effects among single-age larvae of the mountain pine beetle *Dendroctonus ponderosae* (Coleoptera: Scolytidae). *Environmental Entomology*, **2**, 285-293.

Danchin, E. & Wagner, R. H. (1997). The evolution of coloniality: the emergence of new perspectives. *Trends in Ecology and Evolution*, **12**, 342-347.

Dawkins, R. (1980). Good strategy or evolutionary stable strategy? In: *Sociobiology: Beyond nature/nurture?* (Ed by Barlow, G.W. and Silverberg, S.), pp.331-367. Boulder: Westview.

De Jong, M. C. M. & Saarenmaa, H. (1985). A mechanistic simulation model for the movement and competition of bark beetle larvae (Coleoptera, Scolytidae). *Ecological Modelling*, **27**, 109-138.

De Jong, M. C. M. & Grijpma, P. (1986). Competition between larvae of *Ips typographus*. *Entomologia Experimentalis Applicata*, **41**: 121-133.

Deutsch, J. C. (1994). Uganda kob mating success does not increase on larger leks. *Behavioral Ecology and Sociobiology*, **34**, 451-459.

Dominey, W. J. (1984). Alternative mating tactics and evolutionary stable strategies. *American Zoologist*, **24**, 385-396.

Doolan, J. M. (1981). Male spacing and the influence of female courtship behavior in the bladder cicada, *Cystosoma saundersii* Westwood. *Behavioral Ecology and Sociobiology*, **9**, 269-276.

Ehrlich, P. R. & Wheye, D. (1986). "Non-adaptive" hilltopping behaviour in male checkerspot butterflies (*Euphrydryas editha*). *American Naturalist*, **127**, 477-483.

Fairchild, L. (1984). Male reproductive tactics in an explosive breeding toad population. *American Zoologist* **24**: 407-418.

Filip, G. M. & Schowalter, T. D. (1993). Synopsis. In: *Beetle-pathogen interactions in conifer forests*, pp. 231-238: Academic Press.

Forester, D. C. and Lykens, D. V. (1986). Significance of satellite males in a population of spring peepers (*Hyla crucifer*). *Copeia* **3**: 719-724.

Fretwell, S. D. & Lucas, H. L. J. (1970). On territorial behaviour and other factors influencing habitat distribution in birds. I. Theoretical development. *Acta Biotheoretica*, **19**, 16-36.

Gibson, R. M. & Jefferson, D. R. (1990). Lek formation by female choice: a simulation study. *Behavioral Ecology*, **1**, 36-42.

Greenfield, M. D. & Shelly, T. E. 1985. Alternative mating strategies in a desert grasshopper: evidence of density-dependence. *Animal Behaviour*, **33**, 1192-1210.

Gries, G., Bowers, W. W., Gries, R., Noble, M. & Borden, J. H. (1990). Pheromone production by the pine engraver *Ips pini* following flight and starvation. *Journal of Insect Physiology*, **36**, 819-824.

Haack, R. A., Wilkinson, R. C., Foltz, J. L. & Corneil, J. A. (1987). Spatial attack pattern, reproduction, and brood development of *Ips calligraphus* (Coleoptera: Scolytidae) in relation to slash pine phloem thickness: A field study. *Environmental Entomology*, **16**, 428-436.

Harari, A. R., Ben-Yakir, D. & Rosen, D. (2000). Male pioneering as a mating

strategy: the case of the beetle *Maladera matrida*. *Ecological Entomology*, **25**, 387-

394.

Heath, R. & Alfaro, R. I. (1990). Growth response in a Douglas-fir/lodgepole pine stand

after thinning of lodgepole pine by the mountain pine beetle: A case study. *Journal of*

Entomological Society of British Columbia, **87**, 16-21.

Hernandez, M. L., Houston, A. I. & McNamara, J. M. (1999). Male rank and optimal lek

size. *Behavioral Ecology*, **10**, 73-79.

Hibino, Y. (1986). Female choice for male gregariousness in a stink bug, *Megacoptera*

punctissimum (Montandon) (Heteroptera, Plataspidae). *Journal of Ethology*, **4**, 91-95.

Hirschberger, P. (1998). Spatial distribution, resource utilisation and intraspecific

competition in the *Aphodius ater*. *Oecologia*, **116**, 136-142.

Hoglund, J. & Robertson, J. G. M. (1990). Female preferences, male decision rules and

the evolution of leks in the great snipe *Gallinago media*. *Animal Behaviour*, **40**, 15-22.

Hoglund, J., Montgomerie, R. & Widemo, F. (1993). Costs and consequences of variation

in the size of ruff leks. *Behavioural Ecology and Sociobiology*, **32**, 31-39.

Janetos, A. C. (1980). Strategies of female mate choice: A theoretical analysis.

Behavioural Ecology and Sociobiology, **7**, 107-112.

Kimsey, L. S. (1980). The behaviour of male orchid bees (Apidae, Hymenoptera, Insecta)

and the question of leks. *Animal Behaviour* **28**: 996-1004.

Krupa, J. J. (1989). Alternative mating tactics in the Great Plains toad. *Animal Behaviour*

37: 1035-1043.

Lanctot, R. B., Scribner, R. T., Kempanaers, B. & Weatherhead, P. J. (1997). Lekking

without a paradox in the buff-breasted sandpiper. *American Naturalist*, **149**, 1051-

1070.

Landolt, P. J., Reed, H. C. & Heath, R. R. (1992). Attraction of female papaya fruit fly

(Diptera: Tephritidae) to male pheromone and host fruit. *Environmental Entomology*,

21, 1154-1159.

Lanier, G. N. & Cameron, A. (1969). Secondary sexual characteristics in the North

American species of the genus *Ips* (Coleoptera: Scolytidae). *Canadian Entomologist*,

101, 862-870.

Lank, D. B. & Smith, C. M. (1992). Females prefer larger leks: field experiments with

ruffs (*Philomachus pugnax*). *Behavioural Ecology and Sociobiology*, **30**, 323-329.

Lucas, J. R., Howard, R. D. & Palmer, J. G. (1996). Callers and satellites: chorus

behaviour in anurans as a stochastic dynamic game. *Animal Behaviour*, **51**, 501-518.

Manly, B.F. (1991). *Randomization and Monte Carlo methods in biology*. London:

Chapman and Hall.

Maynard Smith, J. (1974). The theory of games and the evolution of animal conflicts.

Journal of Theoretical Biology, **47**, 209-221.

Maynard Smith, J. (1982). *Evolution and the theory of games*. Cambridge: Cambridge

University Press.

McNamara, J. M. & Houston, A. I. (1996). State-dependent life histories. *Nature*, **380**,

215-221.

Muller, K. L., Stamps, J. A., Krishnan, V. V. & Willits, N. H. (1997). The effects of conspecific attraction and habitat quality on habitat selection in territorial birds (*Troglodytes aedon*). *American Naturalist*, **150**, 650-661.

Parker, G.A. (1984). Living in groups: Is there an optimal group size? In: *Behavioural ecology an evolutionary approach* (Ed. by Krebs, J. R. & Davies, N. B.), pp. 122-147. Oxford: Blackwell Scientific Publications.

Parker, G.A. & Sutherland, W.J. (1986). Ideal free distributions when individuals differ in competitive ability: phenotype-limited ideal free models. *Animal Behaviour*, **34**, 1222-1242.

Parrish, J. K. & Edelstein-Keshet, L. (1999). Complexity, pattern, and evolutionary trade-offs in animal aggregation. *Science*, **284**, 99-101.

Pomiankowski, A. (1987). The cost of choice in sexual selection. *Journal of Theoretical Biology*, **128**, 195-218.

Popp, M. P., Wilkinson, R. C., Jokela, E. J., Harding, R. B. & Phillips, T. W. (1989). Effects of slash pine phloem nutrition on the reproductive performance of *Ips calligraphus* (Coleoptera: Scolytidae). *Environmental Entomology*, **18**, 795-799.

Prokopy, R. J. & Roitberg, B. D. (2001). Joining and avoidance behavior in nonsocial insects. *Annual Review of Entomology*, **46**, 631-665.

Pulliam, H. R. & Caraco, T. (1984). Living in groups: Is there an optimal group size? In: *Behavioural ecology an evolutionary approach* (Ed. by Krebs, J. R. & Davies, N. B.), pp. 122-147. Oxford: Blackwell Scientific Publications.

Raffa, K., F. & Berryman, A. A. (1987). Interacting selective pressures in conifer-bark beetle systems: a basis for reciprocal adaptations? *American Naturalist*, **129**, 234-262.

Raffa, K. F., Phillips, T. W. & Salom, S. M. (1993). Strategies and mechanisms of host colonization of bark beetles. In: *Beetle-pathogen interactions in conifer forests*, pp. 103-128. London: Academic Press.

Raffa, K. F. & Dahlsten, D. L. (1995). Differential response among natural enemies and prey to bark beetle pheromones. *Oecologica*, 102, 17-23.

Reid, M. L. (1991). Female choice and male parental care in a bark beetle. Ph.D. Thesis, pp. 114: Simon Fraser University (Burnaby).

Reid, M. L. & Roitberg, B. D. (1994). Benefits of prolonged male residence with mates and brood in pine engravers (Coleoptera: Scolytidae). *Oikos* 70: 140-148.

Reid, M. L. & Roitberg, B. D. (1995). Effects of body size on investment in individual broods by male pine engravers (Coleoptera: Scolytidae). *Canadian Journal of Zoology*, 73, 1396-1401.

Reid, M. L. & Stamps, J. A. (1997). Female mate choice tactics in a resource-based mating system: Field tests of alternative models. *American Naturalist*, 150, 98-121.

Reid, M. L. & Robb, T. (1999). Death of vigorous trees benefits bark beetles. *Oecologia*, 120, 555-562.

Robertson, I. C. (1998). Flight muscle changes in male pine engraver beetles during reproduction: the effects of body size, mating status and breeding failure. *Physiological Entomology*, 23, 75-80.

Robertson, I. C. & Roitberg, B. D. (1998). Duration of parental care in pine engraver beetles: why do larger males care less? *Behavioural Ecology and Sociobiology*, 43, 379-386.

Robins, G. L. & Reid, M. L. (1997). Effects of density on the reproductive success of

pine engravers: is aggregation in dead trees beneficial? *Ecological Entomology*, **22**,

329-334.

Roseland, C. R., Bates, M. B. & Oseto, C. Y. (1990). Role of a male-produced

pheromone of the red sunflower seed weevil (Coleoptera: Curculionidae) in host

finding. *Environmental Entomology*, **19**, 1675-1680.

Rudinsky, J. A. (1962). Ecology of Scolytidae. *Annual Review of Entomology*, **7**, 327-

348.

Saarenmaa, H. (1983). Modeling the spatial pattern and intraspecific competition in

Tomicus piniperda (Coleoptera: Scolytidae). *Communicationes Instituti Forestalis*

Fenniae, **118**, 1-40.

Safranyik, L. (1976). Size- and sex-related emergence, and survival in cold storage, of

mountain pine beetles. *Canadian Entomologist*, **108**, 209-212.

Safranyik, L., Shore, T. L. & Linton, D. A. (1996). Ipsdienol and lanierone increase *Ips*

pini Say (Coleoptera: Scolytidae) attack and brood density in lodgepole pine infested

by mountain pine beetle. *Canadian Entomologist*, **128**, 199-207.

SAS (1996) JMP version 3.1. SAS Institute, Cary, NC

Shelly, T. E. (1989). Waiting for mates: Variation in female encounter rates within and

between leks of *Drosophila conformis*. *Behaviour*, **111**, 34-48.

Stamps, J. A. (1987). Conspecifics as cues to territory quality: a preference of juvenile

lizards (*Anolis aeneus*) for previously used territories. *American Naturalist*, **129**, 629-

642.

Stamps, J. (2001). Habitat selection by dispersers: integrating proximate and ultimate

approaches. *Dispersal: individual, population and community*. J. Clobert, E. Danchin,

A. Dhondt and J. Nichols, Oxford University Press.

Stillman, R. A., Clutton-Brock, T.H., & Sutherland, W.J. (1993). Black holes, mate

retention, and the evolution of ungulate leks. *Behavioural Ecology*, **4**, 1-6.

Svensson, B. G. & Petersson, E. (1992). Why insects swarm: testing the models for lek

mating systems on swarming *Empis borealis* females. *Behavioural Ecology and*

Sociobiology, **31**, 253-261.

Swaby, J. A. & Rudinsky, J. A. (1976). Acoustic and olfactory behaviour of *Ips pini*

(Say) (Coleoptera: Scolytidae) during host invasion and colonisation. *Zeitschrift fuer*

Angewandte Entomologie, **81**, 421-432.

Tallamy, D. W. & R. F. Wood. (1986). Convergence patterns in subsocial insects. *Annual*

*Review of Entomol*ogy **31**: 369-390.

Thompson, S.N. & Bennett, R.B. (1971). Oxidation of fat during flight of male Douglas-

fir beetles, *Dendroctonus pseudotsugae*. *Journal of Insect Physiology*., **17**, 1555-1563.

Thornhill, R. & Alcock, J. (1983). *The evolution of insect mating systems*. Cambridge:

Harvard University Press.

United States Geological Survey (2000). *Blossom statistical software*. Fort Collins:

Midcontinent Ecological Science Center.

http://www.mesc.usgs.gov/blossom/blossom.html

Westcott, D. A. (1994). Leks of leks: a role for hotspots in lek evolution? *Proceedings of*

the Royal Society of London B, **258**, 281-286.

Widemo, F. & Owens, I. P. F. (1995). Lek size, male mating skew and the evolution of

lekking. *Nature*, **373**, 148-151.

Wiklund, C. & Fagerstrom, T. (1977). Why do males emerge before females? A

hypothesis to explain the incidence of protandry in butterflies. *Oecologia*, **31**, 153-

158.

Wilensky, U. (1997). StarLogoT. Evanston, IL: Center for Connected Learning and

Computer Based Modeling, Northwestern University.

http://ccl.northwestern.edu/cm/starlogoT

Wood, D. (1982). The role of pheromones, kairomones, and allomones in the host

selection and colonization behaviour of bark beetles. *Annual Review of Entomology*,

27, 411-446.

Zhang, Q. H., Byers, J. A. & Schlyter, F. (1992). Optimal attack density in the larch bark

beetle, *Ips cembrae* (Coleoptera: Scolytidae). *Journal of Applied Ecology* **29**, 672-678.

Appendix 1

Competition Model

While mate attraction is relatively easy to monitor for pine engravers, larval competition and survival are far more difficult. To collect the males that initiated a nuptial chamber (for size measurements) and the females associated with those males, gallery systems needed to be excavated before larval development was complete. Therefore, to collect information on males and females, it is impossible to also collect information on their larvae's survival, resulting in the need to model larval survival. If larval development is allowed to continue to pupation, it is difficult to determine which larvae belong to which female (and which male) because larval paths cross repeatedly, again necessitating a model for larval survival. The models typically used for bark beetle systems are dynamic simulation models because the death of one larva increases resources available for other larvae (De Jong and Saarenmaa, 1985; however see Berryman and Pienaar, 1973). Previous bark beetle competition models (Saarenmaa, 1983; De Jong and Saarenmaa, 1985) ignore any time lag in settlement of male beetles or the influence of mate attraction ability, both in terms of number of mates attracted and timing of those attractions based on individual male quality.

I constructed a dynamic simulation model that examined mate attraction and competition influences on fitness for males of high and low quality that settle within aggregations or that settle as pioneers. This model used natural settlement patterns observed at aggregation sites during the 1999 field season. Males were assigned probabilities of attracting mates based on empirical data for both male size and whether the male is a pioneer or a joiner of an aggregation. Simulations that had a male begin as a

pioneer were able to attract other males and start an aggregation (based on field observed patterns from my 1999 field season).

Like other bark beetle competition models (De Jong and Saarenmaa, 1985), my model assumed that for larvae the phloem layer of the tree is a two dimensional surface and that all larval movement is for the acquisition of food. Larval death occurs when larvae are unable to find food within a set number of moves due to entering an area already consumed by other larvae or by female adults. The model simulated 50 days from the beginning of colonization of a site, which was sufficient time for all larvae to pupate. The sources of the parameter values for variables used in the model are described in Appendix 2.

This model was constructed using the object based programming language called StarLogoT2001 (Wilensky, 1997). The model calculated the number of eggs that were fathered and the number of offspring that survived until pupation for each male. The following is the code for the competition program and several screen shots from the running program (Fig. A1.1) as well as the programs interface (Fig. A1.2).

Program Code

```
;; Simulation of pine engraver bark beetles (competition model)
;;Requires an input text that is imported.  Use actual settlement patterns with reversed X and Y coordinates.
;;Also need to
;;import a procedures page.
;
;===================================================================
;
; global variables
;===================================================================
;

globals [group-size simtime iterator
          male-count pio-large-mate-prob pio-small-mate-prob
          agg-large-no-mate-prob agg-large-one-mate-prob
          agg-large-two-mate-prob agg-large-three-mate-prob
          agg-small-no-mate-prob agg-small-one-mate-prob
          agg-small-two-mate-prob agg-small-three-mate-prob
          time-interval arrivalClock numberofmales]



;===================================================================
;
; patch variables
;===================================================================
;


patches-own [bite stepon]



;===================================================================
;
; turtle variables
;===================================================================
;



turtles-own [number orientation stop? age origin no-food-step food-step
large-larva small-larva maleID femaleID larvaeID close_encounters isDead arrivalTime]

breeds [male-large male-small females larvae]

;===================================================================
;
; general setup
;===================================================================
;

to setup

          setup-bark
          ifelse (pioneerRun = 1)
                          [ setarrivalClock  0]
                          [ setarrivalClock  1 ]
          create-male-beetles
          initialize-prob
          setsimtime 0
          settime-interval 1
          set-random-seed-observer seed
          setnumberofmales 0
end
```

```
;===============================================
; setup the bark patches
;===============================================

to setup-bark
  setbite 0

  scale-pc brown bite 0 10

end

;===============================================
; create male beetles and disperse them on the bark
;===============================================

to create-male-beetles

  if (breed = male-large) [setc orange]
  if (breed = male-small) [setc white]

        setnumber 0
        setorientation 0
        setstop? 0
        setage 0
        setlarge-larva 0
        setsmall-larva 0
        setisDead 0
end

;===============================================
; setting up female attraction
;===============================================

to initialize-prob

;;;probability of a pioneer male attracting females

        setpio-large-mate-prob 37
        setpio-small-mate-prob 5

;;;probability of a male attracting a mate in an aggregation


        setagg-large-no-mate-prob 92
        setagg-large-one-mate-prob 75
        setagg-large-two-mate-prob 30
        setagg-large-three-mate-prob 5
        setagg-small-no-mate-prob 75
        setagg-small-one-mate-prob 55
        setagg-small-two-mate-prob 10
        setagg-small-three-mate-prob 1
end
```

```
;;========================================
;; male, female, and larvae
;;========================================

to update

        if (simtime > 100) [ stop ] ;; end the run after 50 days
        if ( (breed = male-small or breed = male-large) )
        [

        if ( (arrivalTime <= arrivalClock and pioneerRun = 0) or
        (pioneerRun = 1 and ((numberofmales) >= (aggmales)) and (arrivalTime <= arrivalClock)))
                [
                if (simtime <= flight)

        if (breed = male-large)
                                [large-attract]

        if (breed = male-small)
                                [small-attract]
                ]
                ]

        if (pioneerRun = 1 and ((numberofmales) < (aggmales)) and
        arrivalTime <= arrivalClock)

        [
                if (simtime <= flight)
                [
                pio-attract

                male-attract
                ]
        ]

]


if (breed = females) [ setage (age + 1) repeat 5 [walk]]


update-display


if (breed = larvae)
                [
                setage (age + 1)
                if(age >= 9)
                                [repeat 2 [larvae-movement]]

                ]
        if (simtime = 100)
                [ displaystats ]
        setsimtime simtime + 1
```

```
        if (arrivalClock > 0 )
                [ setarrivalClock arrivalClock + 1 ]


        if ((numberofmales >= aggmales) and arrivalClock = 0)
            [
                setarrivalClock arrivalClock + 1
    ]
        type random 100
        print "||
end

to displaystats
        setiterator 0
setiterator iterator + 1]
co
        print "|Breed Small-Larva Large-Larva isDead MaleID |
            repeat count-turtles
                    [
                                    type breed-of iterator
                                    type "|        |
                                    type small-larva-of iterator
                                    type "|        |
                                    type large-larva-of iterator
                                    type "|        |
                                    type isDead-of iterator
                                    type "|        |
                                    type maleID-of iterator
                                    print "||
                                    setiterator iterator + 1
                    ]

end
```

;;═══
;;Male attraction section
;;═══

```
to male-attract

        if (breed = male-large) and (number <= 3)
        [
                if ((random 100) <= pio-large-mate-prob)
                                [
                        tsetnumberofmales numberofmales + 1
                                ]
        ]

if (breed = male-small) and (number <= 3)
        [if ((random 100) <= pio-small-mate-prob)
                                [
                        tsetnumberofmales numberofmales + 1

                                ]
```

```
        ]

end

;;==================================================================
;;Female attraction section
;;==================================================================

to pio-attract

if (breed = male-large) and (number <= 3)
        [if ((random 100) <= pio-large-mate-prob)
                [setnumber (number + 1)
                        orientAndHatch 2
                ]
        ]

if (breed = male-small) and (number <= 3)
        [if ((random 100) <= pio-small-mate-prob)
                [setnumber (number + 1)
                        orientAndHatch 2
                ]
        ]

end

;;;;Attraction for large male


to large-attract

        if (number = 3)
                [ifelse ((random 100) <= agg-large-three-mate-prob)
                        [setnumber (number + 1)
                                orientAndHatch 2
                        ]

                                [setc gray]
                ]


        if (number = 2)
                [ifelse ((random 100) <= agg-large-two-mate-prob)
                        [setnumber (number + 1)
                                orientAndHatch 2
                        ]

                                [setc gray]
                ]


        if (number = 1)
                [ifelse ((random 100) <= agg-large-one-mate-prob)
                        [setnumber (number + 1)
                                        orientAndHatch 2
```

```
                            ]

                                    [setc gray]
                            ]


        if (number = 0)
                [ifelse ((random 100) <= agg-large-no-mate-prob)
                        [setnumber (number + 1)
                                            orientAndHatch 2
                        ]

                                [setc gray]
                        ]


end



;;;;small male attraction

to small-attract


        if (number = 3)
                [ifelse ((random 100) <= agg-small-three-mate-prob)
                        [setnumber (number + 1)

                                            orientAndHatch 1
                        ]
                                [setc gray]
                        ]


        if (number = 2)
                [ifelse ((random 100) <= agg-small-two-mate-prob)
                        [setnumber (number + 1)

                                            orientAndHatch 1
                        ]
                                [setc gray]
                        ]


        if (number = 1)
                [ifelse ((random 100) <= agg-small-one-mate-prob)
                        [setnumber (number + 1)

                                                orientAndHatch 1
                        ]
                                [setc gray]
                        ]
```

```
        if (number = 0)
                [ifelse ((random 100) <= agg-small-no-mate-prob)
                        [setnumber (number + 1)


                                        orientAndHatch 1
                ]
                        [setc gray]
                ]

end
```

;===
; hatch female beetles
;===

```
to orientAndHatch :orig
setfemaleID maleID
        if (number = 1)
        [ifelse (chance 60) [setorientation 60] [setorientation 270]]

        if (number = 2)
        [ifelse (orientation = 60)
        [ifelse (chance 70)
        [setorientation 300] [setorientation 180]]
        [ifelse (chance 60)
        [setorientation 30]  [setorientation 150]]
        ]

        if (number = 3)
        [if (orientation = 300) [setorientation 181]
        if (orientation = 180)
        [setorientation 300]
        if (orientation = 30)
        [setorientation 151]
        if (orientation = 150)
        [setorientation 30]
                ]

        if (number = 4)
        [if (orientation = 181)
        [ifelse (chance 60)
        [setorientation 120] [setorientation 240]]
        if (orientation = 300)
        [ifelse (chance 60)
        [setorientation 0] [setorientation 240]]
        if (orientation = 151)
        [ifelse (chance 60)
        [setorientation 210] [setorientation 90]]
        if (orientation = 30)
        [ifelse (chance 60)
        [setorientation 330] [setorientation 90]]
                ]

        hatch [setbreed females
```

```
        if (number = 1) [setheading orientation setc red]

        if (number = 2) [setheading orientation setc yellow]

        if (number = 3) [setheading orientation setc blue]

        if (number = 4) [setheading orientation setc green]

        if (number > 4) [setc white]
    ]
        setorigin :orig
end
```

;═══
; make female beetles consume phloem
;═══

```
to bitebark


tsetbite-at  0  0 (bite + 1)

if ((heading >= 337 or heading <= 22) or (heading >= 157 and
heading <= 202))
[tsetbite-at 1 0 (bite + 1)  tsetbite-at -1 0 (bite + 1)]


if  (heading > 22 and heading <= 67)
[tsetbite-at -1 1 (bite + 1)  tsetbite-at 1 -1
(bite + 1) tsetbite-at -1 0 (bite + 1) tsetbite-at 0 -1 (bite + 1)]


if (heading > 202 and heading <= 247)
[tsetbite-at -1 1 (bite + 1)  tsetbite-at 1 -1 (bite + 1) tsetbite-at 0 1 (bite + 1) tsetbite-at 1 0 (bite + 1)]


if ((heading > 67 and heading <= 112) or (heading > 247 and heading <= 292))
[tsetbite-at 0 1 (bite + 1)  tsetbite-at 0 -1 (bite + 1)]

if  (heading > 292 and heading < 337)
[tsetbite-at -1 -1 (bite + 1)  tsetbite-at 1 1 (bite + 1) tsetbite-at 1 0 (bite + 1) tsetbite-at 0 -1 (bite + 1)]


if (heading > 112 and heading < 157)
[tsetbite-at -1 -1 (bite + 1)  tsetbite-at 1 1 (bite + 1) tsetbite-at 0 1 (bite + 1) tsetbite-at -1 0 (bite + 1)]

end
```

;;═══
;;Female walk and egglaying
;;═══

```
to walk
```

```
ifelse (pen_down?) [pu] [pd]

  if (stop? < 1))
  [
                        bitebark

  if (layeggs? = 1)
  [if (age > 2)
                        [if (chance eggprob)
     [hatch
       [setbreed larvae
                   setlarvaeID femaleID
        ifelse (origin = 1) [setc brown] [setc white]
        ifelse (chance 50) [setheading (heading + 90)] [setheading
                   (heading - 90)]
        tsetbite 0
        setnumber 0
        setage 0
        pd fd 1
        ]
    ]
                   ]
  ]

        if (heading > 270) [setheading heading - 2]
        if ((heading <= 270) and (heading > 180)) [setheading heading+ 2]
        if ((heading <= 180) and (heading > 90)) [setheading heading - 2]
        if (heading <= 90) [setheading heading + 2]

        evaluate

        ]
end
```

```
;=================================================================
; Female Beetle Move
;=================================================================

to move :avoid
  ifelse (:avoid = 0)
  [
  if(breed = females)
[
    if ((random 100) < wiggleprob) [wiggle]

                go

  ]
  ]
  [

        if (age > 10)
        [
                ifelse  (simtime mod 2 = 0)
```

```
                [
                        setheading atan ycor xcor
                        setclose_encounters close_encounters + 1
                        ]
                        [

                        setheading atan ycor xcor
                        setclose_encounters close_encounters + 1
                        ]
                        if (close_encounters > max_encounters)
                        [ setstop? 1 ]
                ]

                        go

        ]
end


;===================================================================
;make female beetle move
;===================================================================

to go
  fd stepsize
  tsetstepon 1
end


;;==================================================================
;;larval movement
;;==================================================================

to larvae-movement

  if (stop? < 1))
                        [
                        fd 1
                        tsetbite-at 0 0 (bite + 1)

                        ifelse((bite-at 0 0) > 1)
                        [ setno-food-step (no-food-step + 1)]
                        [
                        setfood-step (food-step + 1)
                        if(no-food-step > 0) [setno-food-step (no-food-step - 1)]
                        ]

                        if ((no-food-step >= starvation) and (food-step < minfood))
                        [setisDead 1
                        setstop? 1]
                        if ((no-food-step >= starvation) and (food-step > minfood))
                        [setsmall-larva 1 setstop? 1]

                        if(food-step >= maxfood)
                                [setlarge-larva 1 setstop? 1]

                        if((bite-at 0 0) > 1) [wiggle]
                        ]
```

```
end
```

```
;
; utility function: random number
;
```

```
to chance :n
  output ((random 100) <= :n)
end
```

```
;
;make beetles wiggle
;
```

```
to wiggle
  ifelse ((random 100) < 50) [lt random wiggleangle] [rt random
wiggleangle]
end
```

```
;
;update the display
;
```

```
to update-display
  scale-pc brown bite 0 10
end
```

```
;
;start movie
;
```

```
to start-movie
  open-movie "bark
end
```

```
to end-movie
        close-movie
end
```

```
;
;;Evaluation function.  female determines if the next step is a good
one.
;
```

```
to evaluate

            if (heading > 292 and heading < 337)
            [
                    ifelse (not(bite-at -3 3 = 0))

                    [
                    move 1
                    ]
```

```
                [ move 0 ]
        ]

if (heading >= 337 or heading <= 22)
[
                ifelse (not((bite-at  -1 4 = 0) and (bite-at 0 4 = 0) and
                (bite-at 1 4 = 0)))

                [
                move 1
                ]
                [ move 0 ]
        ]

if (heading > 22 and heading <= 67)
[
                ifelse (not(bite-at 3 3 = 0))

                [
                move 1
                ]
                [ move 0 ]
        ]

if (heading > 67 and heading <= 112)
[
                ifelse (not((bite-at  4 -1 = 0) and (bite-at 4 0 = 0) and
                (bite-at 4 1 = 0)))

                [
                move 1
                ]
                [ move 0 ]

        ]

if (heading > 112 and heading < 157)
[       ifelse (not(bite-at 3 -3 = 0))

                [
                move 1
                ]
                [ move 0 ]
        ]

if (heading >= 157 and heading <= 202)
[
                ifelse (not((bite-at  -1 -4 = 0) and (bite-at 0 -4 = 0) and
                (bite-at 1 -4 = 0)))

                [
                move 1
                ]
                [ move 0 ]
        ]
```
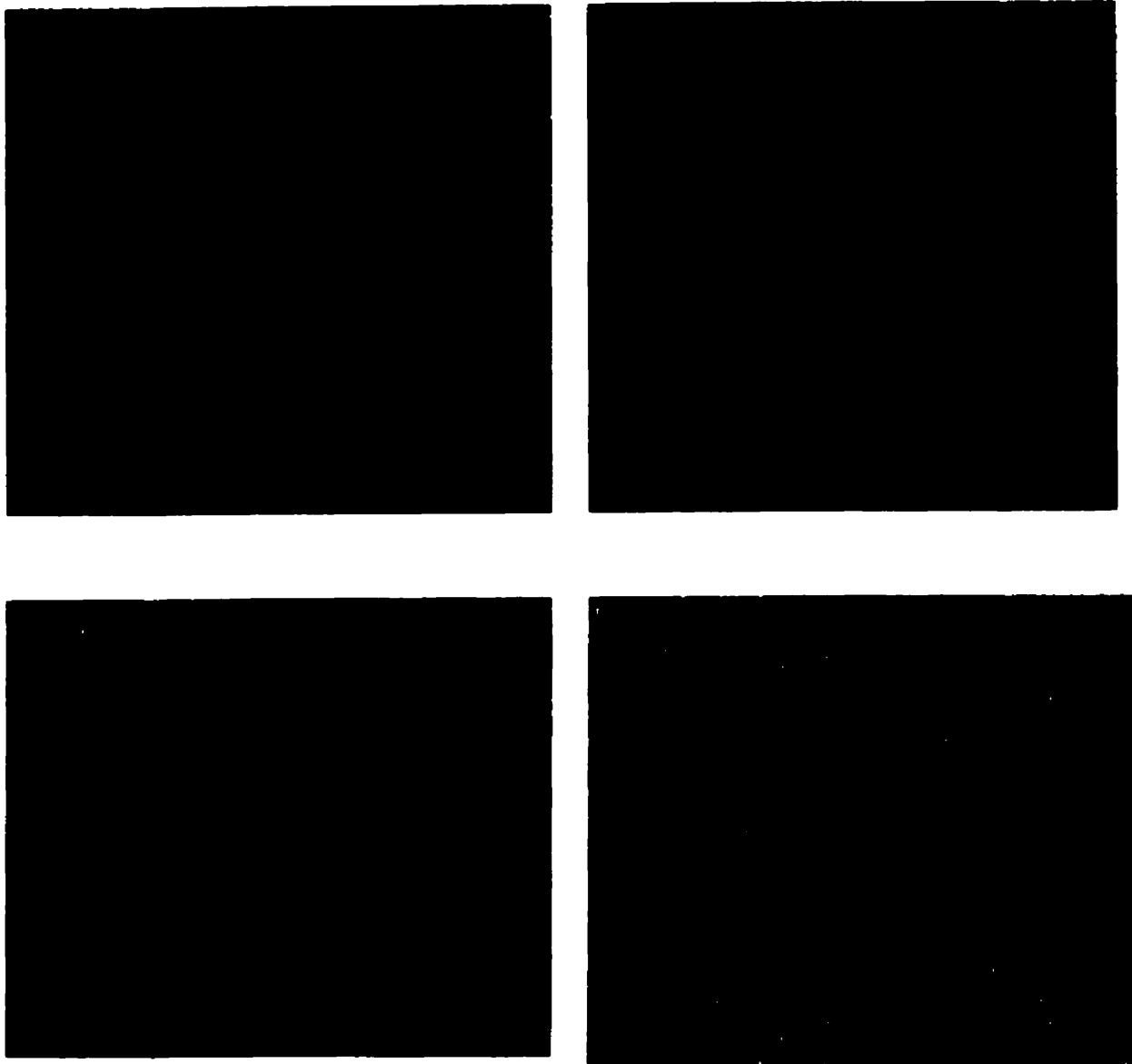
```
if (heading > 202 and heading <= 247)
[
        ifelse (not(bite-at -3 -3 = 0))

                [
 move 1
                ]
                [ move 0 ]

]

if (heading > 247 and heading <= 292)
[
        ifelse (not((bite-at  -4 -1 = 0) and (bite-at -4 0 = 0) and
        (bite-at -4 1 = 0)))

                [
 move 1
                ]
                [ move 0 ]

]

end
```

Fig A1.1. Screen shots of the competition model. Single dots represent the arrival locations of male beetles (large and small males are different colours, not discernible here). Females are attracted to the males location and begin their galleries (thick lines), males can attract a maximum of 4 females each. Each female lays eggs as she moves, on either the right or left of her gallery. Eggs hatch, and the larvae move consuming phloem (thin lines), until they acquire enough resources to pupate. These screen shots represent an aggregation run for 4 different durations: 3 days, 4 days, 6.5 days and 10 days (earliest top left, latest bottom right).
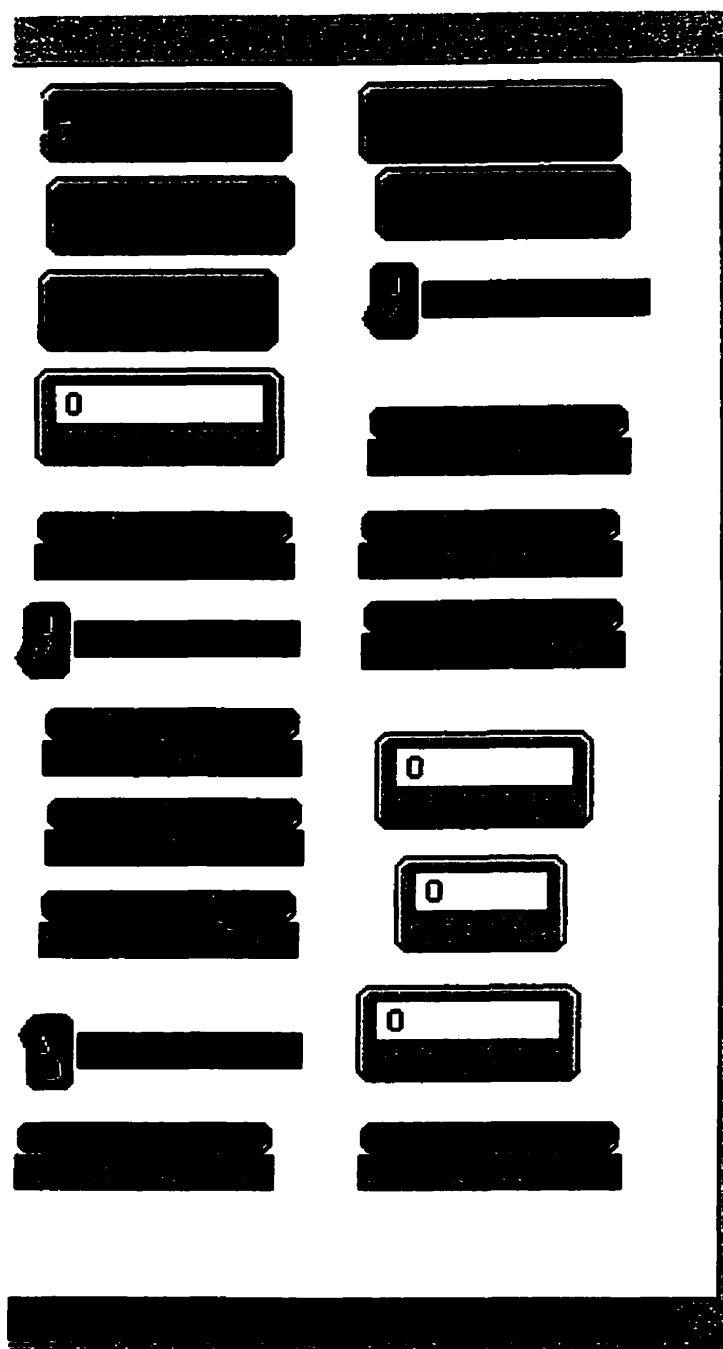
Fig A1.2. StarLogoT interface for competition model. Sliders and switches can be adjusted to change the model's parameters. The interface shown here is set for an aggregation run that will have females available until simulation time 28 (14.5 days).

Appendix 2

Competition Model Parameters

2a) Female Attraction Within an Aggregation

I determined the mating probabilities for large and small males within an aggregation by examining the number of females attracted for males that had settled naturally on recently fallen lodgepole pine (*Pinus contorta* var *latifolia*). Twice a day, the locations of new male settlers were identified by the presence of frass and pinned with a coloured pin representing the date of settlement. Three sites had their settlement tracked. The number of females for each male was tallied and I measured each male's pronotum width to the nearest 0.02 mm using a dissecting scope and an ocular micrometer, and determined their fresh weight (to the nearest 0.1 mg using an AND ER-120A Electronic Balance). I divided males into two size classes. Large males had a pronotum width greater than 1.51 mm and weighed more than 5.2 mg, while small males had a pronotum width less than 1.46 mm and weighed less than 4.8 mg (Fig 2.1). I then determined the proportion of males of each size class, that had attracted at least one, two, three or four females for males that were residents for 0.5 days to 22 days (Fig. A2.1). I fit sigmoidal curves to the data to create a cumulative probability curve. From each of the cumulative probability curves, I took the largest half day probability increase for all the time steps (for each number of females) and used that value as the attraction probability for attracting a given female (i.e. first, second, third) on any given day.

The calculated probability of having a given number of females on any given day was then used to create a cumulative probability curve of having a given number of

females over twenty days. I compared the original cumulative probability curve for each female to the cumulative probability curve created using the largest half day probability for each given female, and the resulting curves were comparable. The attraction of the fourth female was dealt with differently due to inability to fit a sigmoidal curve to the data (see Figs. A2.1 and A2.2). I assigned a probability value less than the value for the third female, and a value that when run through the model produced results similar to results observed during site excavations. The model used the probability of attracting one female on any given day if the male currently has no mates. Once the male attracted his first female the model uses the probability of having at least two mates on any given date. If the male has two or three mates the probability for having three or four mates is used (respectively).

2b) Female gallery direction

I examined 23 nuptial chambers that were created on a 2 m section of tree that had fallen during the winter of 1998 / 1999. New nuptial chambers were noted and marked twice a day as above. The log was excavated after 22 days and males and females were collected. The galleries created by females were measured. The longest galleries from each nuptial chamber were considered to be the first arriving females, the second longest gallery was the second female to join that nuptial chamber, etc. The direction that each arriving female chose to create its gallery was determined by assigning it a number on a circle with twelve sections (hours on a clock face). These twelve sections divided the perimeter of the male's nuptial chamber. Twelve o'clock represented an area that faced the upper surface of the log (recall that the tree is lying down). The assignment of

number 11 was given to females that started their galleries from the upper left corner of the nuptial chamber, number 12 was assigned for females that started their galleries straight upwards from the nuptial chamber, and the number 1 represented females that started their galleries in the upper right corner of the nuptial chamber. Three o'clock pointed the crown of the tree, 6 o'clock pointed toward the underside of the tree, and 9 o'clock pointed towards the roots of the tree (Fig. A2.3).

The direction that second, third and fourth arriving males females began their galleries was recorded as was the distance (in number of 'hours') that the arriving female began her gallery compared to the current residents. The first arriving female would not have a distance value because there were no other females to be compared with, whereas the fourth arriving female would have three distances measured because it could be compared to each of the three earlier arriving females. Distances were measured by counting the number of 'hours' between the new arrival and the previous females, in either a clockwise or counter-clockwise direction (whichever was shorter).

Using a stem and leaf plot I was able to determine that there were two 3 'hour' areas that contained most gallery starts for the first arriving female. After grouping the number of females that started galleries toward these three adjacent 'hours', 47% of gallery starts occurred towards 1,2, and 3,o'clock, and 30% of gallery starts toward 7,8, and 9 o'clock. Thus, first arriving females tended to begin their galleries in one of two directions that are opposite one another, towards the crown of the tree or towards the roots of the tree. Second females to arrive had their direction of gallery initiation calculated in the same way as the first arriving female. The second female had a 45% chance of occupying the 11 o'clock area (10, 11, and 12 o'clock), and a 23% chance of

occupying the 5 o'clock area (4, 5, and 6 o'clock). The third and fourth arriving

females did not tend to start their galleries in a specific direction, but did place their

galleries in relation to where the first and second females started their galleries.

The females that arrived second started their galleries 4 'hours' (mean $\pm$ SE= 4.0 $\pm$

0.18, n = 22) from the first female, as did the third female (3.9 $\pm$ 0.23, n = 17). The third

females also started their galleries 4 'hours' (4.1 $\pm$ 0.26, n = 17) from the second female to

arrive. The fourth female to arrive chose to settle far from first and second females (3.4 $\pm$

0.46, n = 8; 4.5 $\pm$ 0.46, n = 8 respectively) and closer to the third female (2.5 $\pm$ 0.57, n =

8).

I used these data in the model to give arriving females a starting place. First

arriving females had a 60% chance of starting at 2 o'clock and a 40% chance of starting at

9 o'clock. This translated to coordinates x = -1, y = +3 (for 2 o'clock) and x = 0, y = -3

(for 9 o'clock). The direction the first female started in the model was recorded. For the

second female I made the starting position dependent on the direction the first female

started. If the first female started at 2 o'clock, 70 % of the second females started at 10

o'clock, and 30 % started at 6 o'clock. If the first female settled at 9 o'clock there was a

60% chance that the second female would start at 1 o'clock, or a 40% chance that she

would start at 5 o'clock. The second female's location was recorded in order to determine

a starting place for the third female. The third female settled either at 6 o'clock if the

second arriving female started at 10 o'clock; or at 5 o'clock if the second female started at

1 o'clock; or at 10 o'clock if the second female started at 6 o'clock; or at 1 o'clock if the

second female started at 5 o'clock. The fourth female settled with a 60% chance at 4

o'clock or a 40 % chance at 8 o'clock if the third female started at 6 o'clock. If the third

female started at 10 o'clock the fourth female had a 60% chance of settling at 12

o'clock and a 40 % chance of settling at 8 o'clock. If the third female started at 5 o'clock

the fourth female had a 60% chance of settling at 7 o'clock and a 40 % chance of settling

at 3 o'clock. If the third female started at 1 o'clock the fourth female had a 60% chance of

settling at 11 o'clock and a 40 % chance of settling at 3 o'clock.

2c) Female Movement and Egg Laying

Female movement was designed to have a predisposition to move along the grain

of the wood. The distance a female could move in a single time step (1/2 day) was

determined by examining the distance females had travelled in a known amount of time

on experimental logs. For this experiment I released approximately 20 males on a 1 m

section of log in the laboratory. Males were released over a period of 1 week, and the

placement of their nuptial chamber was recorded. Starting the day after the first males

were released and continuing for approximately 10 days, I released females on the log

and recorded which nuptial chamber they entered and the time that they entered it.

Between 2 and 3 weeks after the experiment was initiated, all the males' nuptial chambers

were excavated, males and females were collected, and gallery characteristics such as

gallery length and egg density were measured. This experiment was replicated 3 times.

From these replicates, I was able to determine gallery lengths and exact residence time

for 16 females. These data allowed me to calculate a daily rate of gallery extension

(mean = 9.03 mm / day, SE = 0.91 mm). In the model I used a gallery extension rate of

5mm / half day (each step had to be a minimum of 1 mm, so I rounded up to 5 mm from

4.52 mm). This rate was comparable to rates collected from other experiments and

observations (see below and unreported data). Females continued moving until they encountered a total of four other galleries (female or larval galleries) at which time they stopped moving and egg laying and were considered to have left the log.

Egg laying was set as a probability of laying an egg at each 1 mm female step. Using the gallery systems from the above mentioned experiments I measured the number of eggs laid per 1mm of the egg bearing section of a gallery. Egg density was 0.26 eggs / mm (SE = 0.042, n = 13), therefore I set the probability of laying an egg at each step at 25%. Whether the egg was placed on the right of left side of the gallery was determined randomly. Egg laying did not begin until the female had already spent a full day of gallery construction. This was equivalent to 10 mm of gallery construction, which is similar to the value determined by Reid and Robb (1999) of a 11.3 mm ($\pm$ 1 mm) of pre-egg bearing gallery.

2d) Larval Movement and Food Consumption

I analyzed data collected by M.L. Reid to determine the time required for an egg to hatch, larval movement, and minimum and maximum food requirements for larvae. M.L. Reid stripped a 25 cm by 20 cm section of phloem and bark layer off a lodgepole pine tree and mounted it on a slightly curved piece of Plexiglas. The section was fastened to the Plexiglas with the phloem side down in order to be able to observe beetle behaviour under the bark. The bark section was fastened to the Plexiglas using clamps and window putty to prevent desiccation. Males were implanted on the bark and allowed to create a nuptial chamber. Once the male had created a nuptial chamber, females were introduced to the male. These bark samples were maintained at room temperature (ca.

21°C). Females that entered the nuptial chamber had their gallery progress measured using a different coloured pen for each day's progress. Also recorded was egg placement and larval movement (also marked daily with uniquely coloured pen). From these data I calculated the time required for an egg to hatch (mean 4.6 days, SE = 0.065, n = 67). I measured the average distance that a female moved per day (mean 13.2 mm / day, SE = 2.15, n = 5) as well as the average distance the larvae moved each day (mean 4.53 mm / day, SE = 0.13, n = 220 daily moves for 67 larvae). The date at which the larvae pupated was also recorded on the Plexiglas sheet. I calculated the total distance travelled by the larvae before pupation, and therefore obtained an estimate of how much consumed phloem was required for the larvae to pupate. The range of distance travelled was 40 mm to 65 mm (n = 67), and I used these values as minimum distance required to successfully pupate and as the maximum distance a larvae will travel before pupating.

Larvae were observed to initially moved perpendicular to the female's gallery. For the model larvae started perpendicular to their mother's gallery and continued in this direction until they encountered an area of already consumed phloem, at which point they randomly changed their heading by 50° in either direction (left or right was randomly determined). Each larval step on a phloem rich area was tallied, until the maximum food value (65 phloem rich steps) was reached, at which time the larva stopped and was considered a pupa. If the larva encountered a phloem poor area, the number of steps in the phloem poor area were tallied, until the starvation value (10 steps in phloem poor area) was reached. If the starvation value was reached after the minimum food value had been reached (40 steps in a phloem rich area), the larva was considered a pupa. However, if the minimum food value was not reached by the time the starvation value

reached, the larva was considered dead. If the larva had a positive value for the number of steps in a phloem poor area and then encountered a phloem rich area, the value in the phloem poor area was reduced by 1 for each step in the phloem rich area until it reached zero. The steps in a phloem rich area were not tallied until the number of steps in a phloem poor area reached zero.
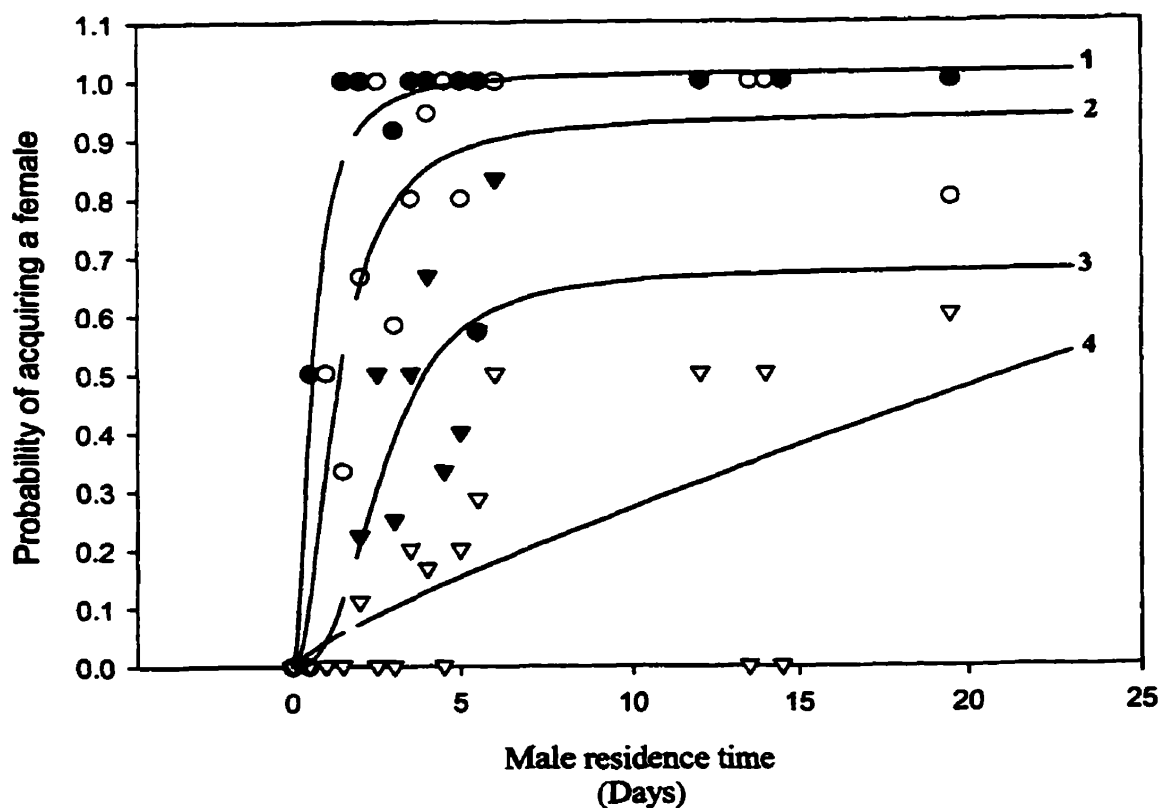
Fig A2.1. The speed at which large males attracted females within an aggregation was calculated by determining the proportion of males that had attracted at least one, at least two and at least three and four females for each given residence time. The largest increase in the probability from one time step to the next was used as the probability of attracting that particular female (i.e. 1st, 2nd, 3rd or 4th female). Solid circles represent the percentage of males that had attracted at least one female for a given residence time. Open circles represent 2 females, solid triangles 3 females and open triangles 4 females. The numbers beside each curve indicates what female that curve represents.
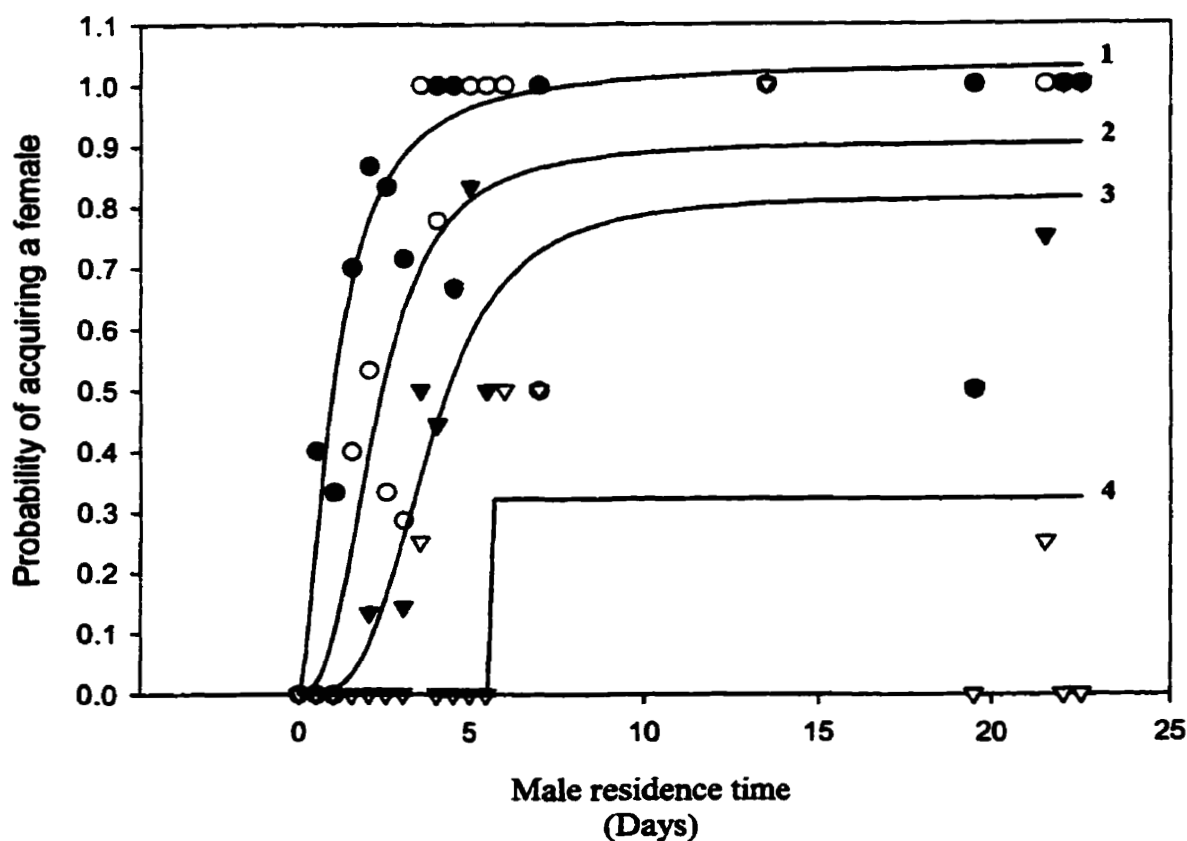
Fig A2.2. The speed at which small males attracted females within an aggregation was calculated by determining the proportion of males that had attracted at least one, at least two and at least three and four females for each given residence time. The largest increase in the probability from one time step to the next was used as the probability of attracting that particular female (i.e. 1st, 2nd, or 3rd but not the 4th female (see text)). Solid circles represent the percentage of males that had attracted at least one female for a given residence time. Open circles represent 2 females, solid triangles 3 females and open triangles 4 females. The numbers beside each curve indicates what female that curve represents.
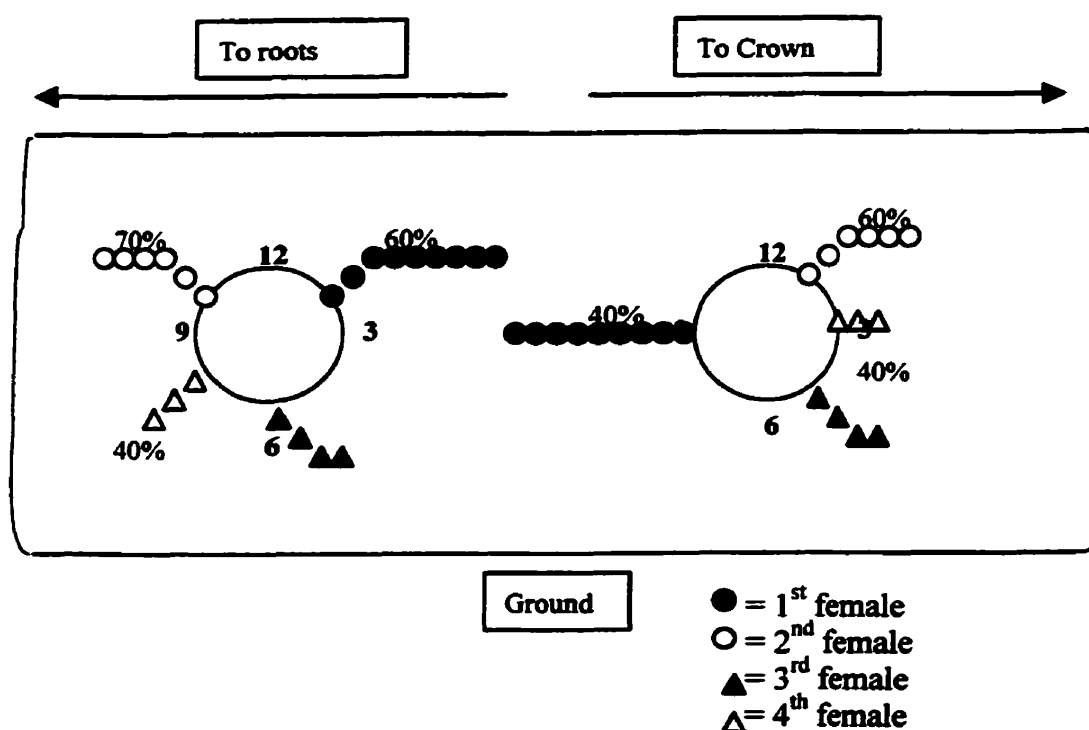
Fig A2.3. Female gallery direction determination for the simulation model. The longest gallery was determined to be the first female to arrive, the second longest gallery the second female, and so on. Gallery starting positions were mapped out on a clock face (bolded numbers) and the probability of a female starting her gallery in a particular direction was determined (see Appendix 2b). The percentages included on these two examples represent the probability used in the model for each female's starting position, given the starting place of the last female to arrive (see Appendix 2b). The third female does not have an associated percentage because its starting position is directly determined by where the 1st a 2nd female settle (e.g. if the 1st female starts at 2 o'clock and the 2nd female starts at 8 o'clock, the only place a female can settle is at 6 o'clock).