OVIPOSITION BEHAVIOR OF *ORELLIA RUFICAUDA* ON CANADA THISTLE

by

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Oviposition behaviour of Orellia ruficauda on Canada thistle

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ABSTRACT

This research addresses the problem faced by insects allocating eggs to hosts of variable quality, when that quality also changes as the day proceeds. Under such conditions, how useful is partial information on the relative value of an encountered host? *Orellia ruficauda* (Fab.) is a tephritid fly of European origin whose larvae parasitize the seed heads of Canada thistle (*Cirsium arvense*) (L.) Scop. (Asteraceae), feeding solely upon fertile seeds. Flies preferentially attack, and their larvae do best in seed heads that are about to open, a transient stage that lasts about one day. Flies can identify and tend to avoid seed heads that have been parasitized by conspecifics. The capacity of seed heads to support larvae is highly variable. However, local presence or absence of a pollen source has a strong effect on seed set and therefore on carrying capacity. Adults may be able to discriminate pollination probability. When the effect of fly density is controlled using Taylor's power law, egg distributions are significantly more aggregated in high quality localities, where male plants are locally present, than in low quality localities. Seed head size also influenced host quality, but flies were not apparently sensitive to this factor, as density of eggs in the field was not significantly greater in the largest seed head size class. A larva's final mass has a significant effect upon its lifetime reproductive success. Large larvae produce more eggs as adults than do small larvae.

I used field and laboratory-derived parameters to generate functions predicting the utility of a given clutch size laid into an encountered seed head. Here, the shape of a function (and therefore the optimal clutch size) depends upon the information available to the ovipositing fly at the time of the encounter. I used Monte Carlo simulation to 1) determine if increased use of information translates to increased reproductive success, and 2) generate egg distribution patterns to compare with field distributions.

In general, increased use of information confers an advantage (i.e., highest lifetime reproductive success) when relative density of ovipositing flies is high. However, less information-rich strategies proved superior under some circumstances. Furthermore, relative success was frequency-dependent, even at high densities. This suggests that some strategies can coexist and enjoy equal fitness in the field. Finally, it proved difficult to identify one strategy as most likely to occur in nature, as all strategies generate egg distribution patterns consistent with field patterns.

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CHAPTER 1

INTRODUCTION

An ideal parasitic insect should be able to locate every available host, evaluate perfectly each host's capacity to support larvae and allocate that number of eggs to each host which will maximize its lifetime reproductive success. In reality, parasitic insects foraging for hosts are constrained by a number of ecological factors that reduce the accuracy of their assessment of the true value of a given host. The first and most obvious of these is that the insect may be uncertain as to the exact number and quality of offspring that a just-encountered host can support. Secondly, the rate with which an insect encounters hosts, and the time required to exploit those hosts can never be deterministic. Therefore, an insect must "decide" how many eggs to commit to a host of uncertain value when it may (or may not) encounter a better (or inferior) host at some unknown time in the future. If the insect makes the "wrong" decision, one which leads to less than maximal fitness, it wastes time and eggs on an inferior host when better hosts are available. The converse mistake will cause the insect to spend too much time searching for superior hosts. Clearly, an insect's reproductive allocation can only be based on its best estimate of host quality and general availability, while it operates within perceptual and temporal constraints. This begs the question of how good must a parasite be at making such estimates, or how much information is necessary?

Lack (1947) first proposed a solution to the problem of how many eggs to commit to a discrete clutch. He applied this solution specifically to nesting birds, but it applies equally well to the problems faced by insects laying eggs in hosts (Charnov and Skinner 1984, Parker and Courtney 1984, Skinner 1985, Godfray 1987). He showed that the clutch size which provides maximal fitness to a parent will be the one that maximizes the product of offspring number and the probability of those offspring surviving. This "Lack Optimum" is the simplest solution to the problem and ignores such factors as parental survivorship, quality of surviving offspring and time costs. The latter two factors are most important when this idea is applied to insect systems, where multiple clutches are the rule, rather than the exception.

Charnov and Skinner (1984, 1985) Skinner (1985) and Parker and Courtney (1984) applied the marginal value theorem (Charnov 1976, Parker and Stuart 1976) to Lack's (1947) solution with respect to oviposition of parasitic insects. In their models, insects were supplied with an effectively infinite number of eggs. They solved for optimal clutch size under time limitation and variable host quality, and found that they could closely mimic the observed variation in clutch sizes in the field (Charnov and Skinner 1984). This theory was further refined by Mangel (1987) and Mangel and Clark (1988), who used a stochastic dynamic optimization approach to predict how egg limitation acts to modify clutch size decisions generated by the above model.

Other refinements include the presence of previously-exploited hosts, which retain some residual value (Parker and Courtney 1984, Skinner 1985, Mangel and Roitberg 1989) and the different effects of strong and weak larval competition on the parental allocation decision (Smith and Lessells 1984, Waage and Godfray 1984, Ives 1989, Godfray 1987).

Most of these studies assume that the value of the host item is more or less readily assessable by the parent insect when it makes its oviposition decision. Unnattacked hosts have a fixed value and already-attacked hosts (which I will call marked hosts, since they are often made recognizable by virtue of a marking pheromone (Prokopy 1975, 1977)) have a residual value associated with them which is also assumed to be more or less fixed (but see Mangel and Clark 1988). In this thesis I will describe a model host-parasite system wherein the quality of unattacked hosts is not readily assessable, and the residual quality of marked hosts is even harder to estimate because of variation in the initial clutch size and its covariation with the density of conspecifics in the parasite's locality.

My model insect is a tephritid fly, *Orellia ruficauda* Fab., a parasite (*sensu* Price 1980) of the seed heads of Canada thistle (*Cirsium arvense* (L.) Scop.). I will show that the capacity of thistle seed heads to support larvae varies with availability of male plants in the general vicinity (and therefore presumably with pollination intensity), seed head size, and with a combination of other, random factors that operate on individual host plants. Pollen availability and seed head size may or may not be readily assessable by the parent insect. Flies may also be able to incorporate information on their own local density into oviposition decisions. The general question that I wish to address in this thesis is the relative value of these sources of information in a highly stochastic system. How is limited information best used? When unexplained variance in host quality is high, increasingly subtle uses of what information is available must provide increasingly diffuse benefits. To properly address this question, it will be neccessary to stray from pure empiricism, and I will finish by comparing the relative costs and benefits of purely hypothetical strategies.

Ideally, scientific research progresses through five phases: 1) general observation of a system, 2) an intuitive recognition of an apparent pattern which gives rise to a general hypothesis of an underlying process, 3) a more directed gathering of data to establish baseline parameters, 4) use of those parameters to develop a more rigorous theoretical model which can generate testable hypotheses, and 5) testing of hypotheses, ideally by predicting the reaction of the system of interest to a controlled manipulation or series of controlled manipulations, in such a way that alternate hypotheses can be rejected.

This thesis progresses through the first four phases in a more or less workmanlike fashion, but actual testing of hypotheses generated by theory is left to inference rather than experiment. Having made this flaw explicit, I will now argue that, within recognizable limitations, this approach still has utility, if only for its heuristic value. I will develop this idea in the five remaining chapters. Chapter two reviews relevant information about the fly and its host plant. The third chapter reports on field data largely gathered during the first 2 summers of research. Chapter four describes field and laboratory experiments designed to place meaningful figures on life-history parameters, with a view towards building a theoretical model of clutch-size decisions. The fifth chapter then describes the formulation of, and the predictions generated by a series of models that predict fitness consequences expected from clutches of a given size, when flies can incorporate increasingly complex levels of information. These models are then used to compare the viability of hypothetical oviposition strategies using Monte Carlo simulation. The results of these simulations are presented in the final chapter. Chapter six also discusses potential sources of error which may affect the validity of any conclusions generated by this synthetic approach.

CHAPTER 2

GENERAL BIOLOGY OF THE HOST AND ITS PARASITE

2.1 The Host

Canada thistle (*Cirsium arvense* (L.) Scop.) is a weedy plant thought to have originated in the Mediterranean, spread into the river valleys of Central Europe after the last glaciation, and finally radiated outward with the development of agriculture (Seitz and Komma 1984). It is the sole dioecious member of its genus (Lloyd and Myall 1976), although there are a number of closely-related gynodioecious species (Correns 1916, Lloyd and Myall 1976). It became a serious weed in North America shortly after the first Europeans settled (Detmers 1927, Hayden 1934, Peschken 1984). Canada thistle's long-standing persistence in the face of constant human opposition is probably due to its ability to disperse to, and aggressively colonize fugitive habitats, such as cultivated fields. Plants can disperse seeds over remarkably long distances (Bakker 1960, Sheldon and Burrows 1973), and reproduce vegetatively once established in a locality (Detmers 1927, Hayden 1934, Bakker 1960, Hodgson 1968, Amor and Harris 1975).

Separation between the two sexes in thistle is not perfect in that "males" can produce low numbers of viable achenes (Correns 1916, Lloyd and Myall 1976, Lalonde and Roitberg in prep.). Females do not produce any pollen at all, however

(Hayden 1934), and must receive pollen to produce seeds (Derscheid and Schultz 1960, Lalonde and Roitberg 1989,in prep.). How far pollen can effectively disperse from male plants under field conditions is not known, although some evidence suggests that fertilization rate is significantly reduced when separation distance reaches about 100 metres (Hayden 1934, Bakker 1960, Amor and Harris 1974). The effect of male proximity on seed production on a local scale (i.e., when males are locally interspersed with females, but clumped in distribution) is not yet known.

Seed abortion after fertilization is often highly correlated with resource limitation in many plant species (Stephenson 1981, Lee and Bazzazz 1986, Harper and Wallace 1987). However, although a large (and variable) proportion of achenes will abort after fertilization, the proportion of achenes that abort prior to full provisioning varies from individual to individual and is not affected by either the rate of pollen transfer (Lalonde and Roitberg in prep), or by available resources (Lalonde and Roitberg 1989). Seed abortion may be an expression of a high degree of genetic load in Canada thistle populations (Wiens et al. 1987).

The inflorescence of *C. arvense* is technically a capitulum, or flower head, which is an aggregation of component flowers, each of which arises from an ovary containing a single ovule, or potential seed. The seed heads on a thistle shoot develop in a determinate fashion, resulting in what appears to be a cymose inflorescence (Hayden 1934). Technically, this higher-level arrangement of inflorescences (i.e., seed heads) should be be termed a *conflorescence*. However, I feel that this is a clumsy and unfamiliar term. Thus, in the interests of accessibility, I will term the arrangement of seed heads (or flower heads) on a shoot an inflorescence for the remainder of this thesis. On a cyme, the first seed head to develop is normally the primary seed head (i.e., the apical head). Its development is followed by the heads that are terminal on the lateral shoots (secondary heads), beginning with the heads that are nearest to the top of the plant. The heads on each lateral shoot develop after the secondary head in a pattern which recapitulates the development of the entire inflorescence. Because of this process of seed head development, at any given time tertiary and quaternary heads can be blooming on the upper portions of the shoot while secondary heads bloom further down. Thus, especially after the earliest-developing heads near the top of the shoot have finished blooming, the distribution of blooming flower heads along a shoot appears to be random to the casual observer, such that heads of a particular stage of development are not confined to one region of the shoot.

The number and size of healthy seeds produced when plants experience high levels of pollination under laboratory conditions is largest in primary seed heads and declines in secondary and tertiary heads (Lalonde and Roitberg 1989). This pattern may not emerge under field conditions, because seed size is also strongly influenced by maternal effects (Hodgson 1964, Lalonde and Roitberg 1989). Furthermore, variation in the suitability of growing conditions over the season may further serve to mask this effect.

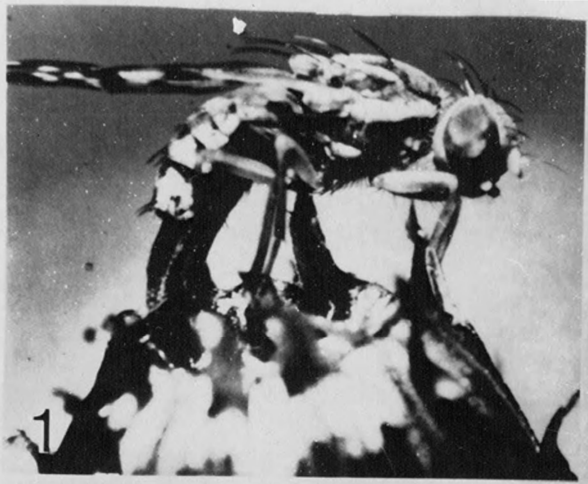
2.2 The Parasite

Like its thistle host, *Orellia ruficauda* Fab. is of European origin, and has been collected in North America since 1885 (McFadden and Foote 1960). In Europe, it is one of a complex of species that utilize thistle heads as a resource for raising offspring (Zwölfer 1965, 1983, Angermann 1986, Straw 1989a). There, *O. ruficauda* is thought to be a fugitive species because of its poor ability to compete with other thistle head feeders (Angermann 1986). Until recently, such superior competitors were absent from the North American system (Maw 1976, Peschken 1984, Forsyth and Watson 1985). However, the accidental introduction of a seed and receptacle-feeding weevil, *Larinus planus*, to North America in the early 1970's (Wheeler and Whitehead 1985) and its subsequent spread to British Columbia in the mid 1980's has reduced the fly to a fugitive species, at least in the lower mainland area of British Columbia (Lalonde unpublished). The results presented below may therefore be more of historical interest *vis à vis* the natural history of the *O. ruficuda* - thistle system in North America.

Female *Orellia ruficauda* flies oviposit into the seed heads of female Canada thistle plants (Figure 2.1). After oviposition they will generally circumscribe the upper rim and sides of the head with the tip of their extended ovipositor (Figure 2.2). The fluid deposited by this process is believed to be a marking pheromone (Angermann 1986), but fly response to this putative mark has not yet been demonstrated. However, many fruit-infesting tephritids (Prokopy 1977), and at least some other seed-parasitic tephritid species (Straw 1989b, Pittara and Katsoyannos 1990), are known to avoid ovipositing into hosts that have been similarly marked.

Eggs are placed individually between the florets, about 0.5 cm above the developing ovary. Larvae move to a still-soft ovary and feed internally during the entire 1st instar (Figure 2.3). This feeding elicits hypertrophic growth of the ovary which becomes gall-like in appearance (Figure 2.4). This feeding behavior and the host's subsequent growth response is reminiscent of the response elicited by closely-related gall-forming *Urophora* flies (Redfern 1968, Shorthouse 1977). However, *Urophora* flies feed solely within their galls whereas *O. ruficauda* maggots eventually leave their "galled" ovary and feed on ripe achenes during the 2nd and 3rd instar. Achene feeding characteristically proceeds by excavation of the soft embryo through a single circular hole abraded through the pericarp (Figure 2.5). The number of achenes consumed by a single maggot varies with achene size; typically 4-12 are

Figures 2.1 - 2.6. Natural history of *Orellia ruficauda*. 2.1, Oviposition by female flies into unopened seed heads. 2.2, Dragging of ovipositor around the rim of the head typically follows oviposition. 2.3, 1st instar larva boring into an immature ovary. 2.4, Hypertrophy of ovary infested by a 1st instar larva. 2.5, Characteristic feeding damage on mature achenes produced by 2nd and 3rd instar larvae. 2.6, Remnant of initially-infested ovary.



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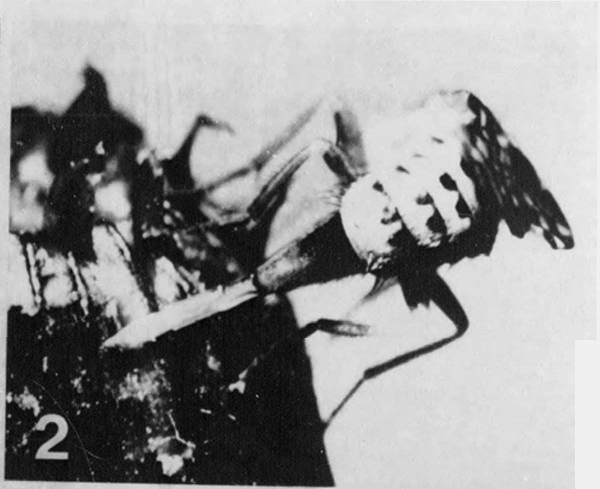

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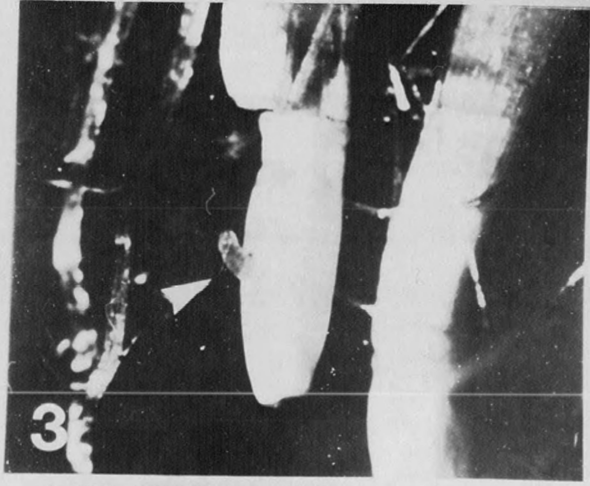

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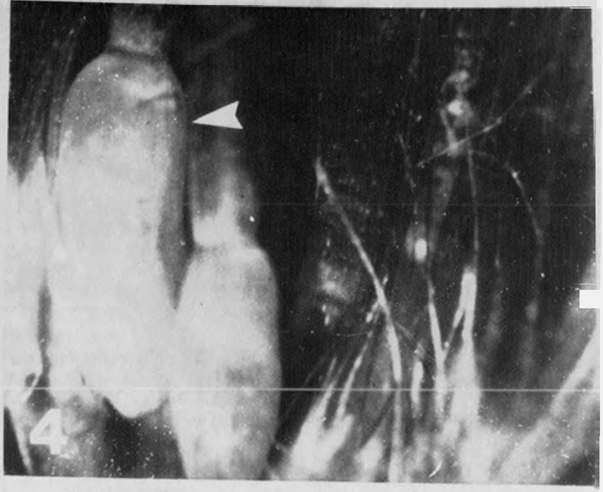

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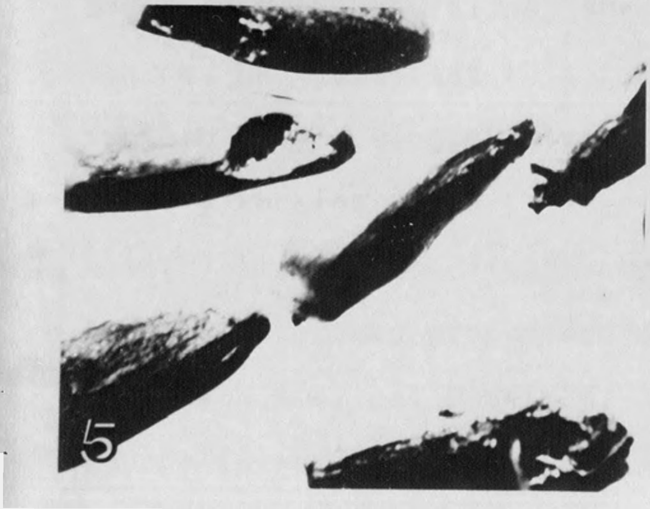

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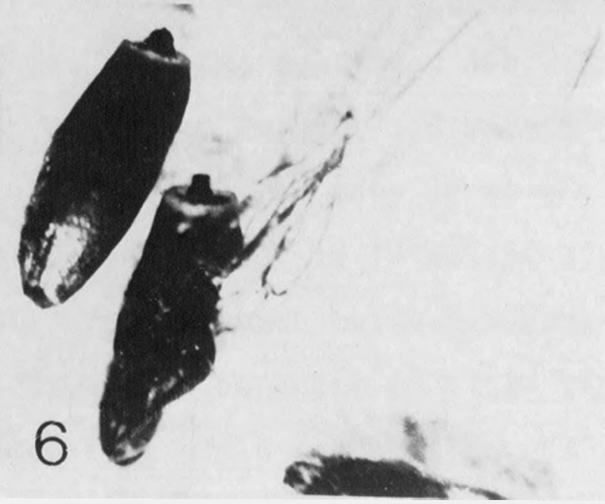

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consumed. Third instar larvae form cocoons of pappus hairs when fully-grown. The maggots overwinter inside these structures, and pupate and emerge in the spring. I was able to determine the number of larvae initially feeding within a seed head, because each larva leaves a shrivelled, but recognizable remnant of the initial hypertrophied ovary (Figure 2.6).

Feeding behavior of *Orellia* maggots suggests that seed production may limit fly numbers at the population level. Forsyth and Watson (1985) report a correlation between seed set and larval density. However, the actual quantitative relationship between seed production and potential larval density within individual seed heads has not been worked out. Reports conflict on a qualitative scale about the strength of this relationship. Kandybina (1970) asserts that a head will support only a single larva. Angermann (1986) reports that flies in Europe generally will commit only a single egg per head, even under crowded conditions, when oviposition sites are presumably scarce. He feels that this implies that one seed head can support only a single larva. In contrast, Forsyth and Watson (1985), working in North America, revovered as many as seven healthy larvae from field-sampled seed heads. It is not likely that thistle seed production differs that much between Europe and North America. Possibly, oviposition behavior of flies in Europe is shaped more by the potential of interspecific competition than is the behavior of North American flies. Thus, the reluctance of European flies to commit many eggs to a seed head may be an expression of risk-spreading behavior (Root and Karieva 1984).

Male plants set far fewer seeds than do female plants (Lloyd and Myall 1976) and are thus poorer substrates for fly oviposition. Angermann (1986) suggests that flies in Europe can discriminate male and female flower heads. He recovered no maggots from male heads in localities that supported high larval densities in female heads. However, because he did not dissect for eggs, these results could also reflect larval survivorship, rather than host selection by the parent. Forsyth and Watson (1985) suggest that low densities of flies in certain areas may be the result of such gender mistakes on the part of female flies. I have observed such "mistakes", but rarely, and only in cases where female flies were gravid for several days without encountering a female head. I will present evidence in Chapter 2 that indicates that female flies recognize and avoid oviposition into male seed heads. Moreover, male presence is likely to enhance pollination success, and by extension, the quality of individual seed heads. The presence of male plants in a locality is thus far from being a detriment to the flies, so long as female plants are also present.

Larvae are subject to mortality risks while inside the host seed head. Two species of eulophid endoparasite *Crataepus marbis* and *Tetrastichus venustus* parasitize and kill 3rd instar larvae. Third instar larvae are also prone to disease mortality from an unknown species of pathogen. Infected larvae become translucent and die prior to pupating. Whether or not either of the parasitoid species or the disease express a numerical response to host larval aggregations at the level of the seed head is not known.

Thus, I report on a system where flies must exploit ephemeral, patchy resources (seed heads). As such it is similar to a large number of systems already described in the literature. There is a vast literature describing search behaviour of adults (Varley 1941, Parker and Stuart 1976, Roitberg et al. 1982, 1984, Mangel and Roitberg 1989, Straw 1989b), fitness of larvae (Weis et al. 1983, Godfray 1986, Averill and Prokopy 1987, Simberloff and Stiling 1987, Romstöck-Völkl 1990), and emergent egg distribution patterns in such systems (Varley 1941, Myers and Harris 1980, Atkinson and Shorrocks 1984, Angermann 1986, Straw 1989b, Romstöck-Völkl and Wissel 1989, Averill and Prokopy 1989, Roitberg et al. 1990). I will be incorporating aspects of all of these approaches in this thesis. However, the true value of this particular system is that larval resources are quantifiable, as is larval reproductive success in relation to resource availability. This means that I will be able to develop quantitative theoretical predictions regarding ovipositional choices by adult flies. Thus, I hope to achieve an amalgamation of empirical and theoretical approaches using this model system.

CHAPTER 3

FIELD STUDIES

3.1 Introduction

Although there is some natural history information available on the biology of *Orellia ruficauda*, the specific ecological factors affecting larval success (and therefore adult fitness) that may be accessable to ovipositing females as predictors of offspring fitness are not well quantified. The purpose of this chapter is to identify which potential factors are most important to *O. ruficauda*'s fitness. Several were alluded to in the previous chapter, but I will now be explicit.

The first and most obvious question to ask is: what are the direct constraints on the number of offspring that can be produced from a given seed head? The answer to this requires an understanding of how crowding can affect larval growth, survival and development through 1) Competition for limited food, 2) Cannibalism, 3) Interference effects, 4) Disease, and 5) Parasitism. In the field studies described in this chapter I use larval survivorship and mature weight in the cocoon as my measure of larval success. I will provide support for this assumption in Chapter four.

Competition for food may occur because a larva is committed to feeding within the particular seed head selected for it by its parent. Logically, there must be some upper limit to the number of larvae that can share one seed head. How is the success of *O. ruficauda* larvae affected by seed production?

In many plant systems, seed production varies predictably with position of the seed-bearing structure on the plant (Harper et al. 1970, Hendrix 1979, 1984, Lalonde and Roitberg 1989) and with pollinator availability (Bierzychudek 1981, Hainsworth et al. 1985). In other species seed production is not pollinator-limited, but instead is limited by resource availability (Stephenson 1981, Zimmerman and Pyke 1988). Therefore, while it may seem logical to assume that in a dioecious species like *C. arvense*, distance separating male and female plants may be a reliable indicator of pollen availability, resource-limitation may mask any effects of distance to a pollen-source. Thus, seed set of *Aralia nudicaulis* was not correlated at all with distance between males and females (Barrett and Thomson 1982). What factors are accurate predictors of seed production in Canada thistle?

Plant parasites in general have been shown to preferentially attack hosts that have (or have a high probability of having) the highest concentration of larval resources (Whitham 1978, 1980, Myers 1985). Seed predators in particular select host fruits that are likely to yield more seeds (Hare and Futuyma 1978, Hare 1980, Herrera 1984), and even fruits that received a maximum of pollinator visits when in flower (Zimmerman 1980, Hainsworth et al. 1984). Is *O. ruficauda* sensitive to any proximate cues which correlate with seed head quality?

Many parasitic species (Fisher 1971, Quiring and McNeil 1984, Hubbard et al. 1987, Bai and Mackauer 1990), and some fruit-infesting tephritid species (Averill and Prokopy 1987) are known to kill, and sometimes cannibalize, conspecifics when more than one larva occupies a host. *Orellia ruficauda* is known to be gregarious within thistle heads in North America (Forsyth and Watson 1985). However, this does not preclude at least some agonistic behaviour. If cannibalism, lethal fighting, or highly asymmetrical competition for food occurs, one would expect differences between the mean density of eggs in heads on a given sampling day and the density of mature 3rd instar larvae at the end of the season.

Larval success within a given head may be limited by larval density in ways other than by cannibalism and food exploitation. For example, excessive crowding may limit mature larval weight (and therefore fitness) through interference effects if larvae waste energy in competing for locally-scarce food. Also, larvae in more crowded heads may be more susceptible to the attack of disease or parasites. What then, are the effects of larval crowding on mature weight and on the rate of disease and parasitism?

Are there ways in which female flies can avoid or ameliorate the potentially detrimental effects of crowding on their offspring? I will demonstrate in Chapter four that female flies deposit a marking pheromone after oviposition. Considering the simplest scenario, flies may employ contact with this mark as a cue to avoid ovipositing into a previously-attacked seed head. If flies respond to marks in this fashion one would expect eggs (or larvae, if survivorship is high) to be overdispersed amoung seed heads. This is the egg distribution pattern which tends to emerge in systems where insects are known to employ marking pheromones (Zimmerman 1979, Bauer 1986, Averill and Prokopy 1989, Messina 1989). However, aggregated egg distribution patterns are also reported from such systems (Averill and Prokopy 1989, Straw 1989b). Egg distribution patterns may change with density, however, as an individual's propensity to accept or reject a host type may be a function of its availability (Straw 1989b). Since I will be looking at different densities of eggs in my field samples, the problem of how to index aggregation emerges. Indices of aggregation are, in general employed in situations where mean density is held constant, or otherwise assumed to be not important. Problems of independence arise when the aggregation at sites with different mean densities are compared (Myers 1978). Taylor's log-transformed mean vs log variance regression technique (Taylor 1961,1984), is one commonly employed method, specifically developed to measure the effect of changing density on aggregation. It is often assumed to have an underlying behavioural basis (Gillis et al. 1986). I recognize that many different processes contribute to an emergent distribution pattern (Rhomberg 1984, Soberón and Loevinsohn 1987, Hurlbert

1990). Thus, while I will use this method as an indicator of how (or if) flies respond to their own density when attacking seed heads, I will also try to eliminate possible effects of spatial patterns of hosts on parasite distribution.

3.2 Materials and Methods

I surveyed a number of sites at 3 different localities in the lower mainland of British Columbia in 1984. I identified a clone as an aggregation of thistle shoots expressing similar floral and vegetative traits. A minimum of 4 such female clones were identified and sampled throughout the season at each locality. Male thistle clones were sampled at some locations as well. Twenty five shoots within each of the sample clones were tagged at the beginning of the season and followed throughout that season. At each sample date, any heads that had just initiated blooming were marked by attaching 1 x 0.3 cm plastic tags to their peduncles with fine wire and their position on the inflorescence was then recorded. Tagged heads were collected 5 to 20 days later and taken back to the laboratory for dissection. Most heads were harvested before seed release. Any post-release heads were excluded from subsequent analyses, because both seeds and larvae may have left the head prior to harvesting.

In the 1985 field season I selected 2 sites at the Reifel bird refuge on Westham Island in Delta, British Columbia. The first site was an open field located between a corral and the margin of a stand of red alder (*Alnus rubra*). The second site was located along one of the dikes and was partially shaded by a sparse plantation of Douglas fir (*Pseudotsuga menziesii*). For the remainder of this thesis, I will refer to these 2 sites as the Corral site and the Dike site, respectively. At each site, 100 female thistle shoots were randomly selected for study at the beginning of the season before any blooming occurred. I subsequently recorded the spatial location of each of these shoots at the end of the field season. At the time that the plants were chosen, I also established 50 1 m^2 quadrats at each site. Quadrat location was randomized by generating cartesian coordinates using the random number generator function on a hand-held calculator. I visited the refuge sites weekly until the first blooms were noted, whereupon I sampled each site weekly until no blooming flower heads could be found.

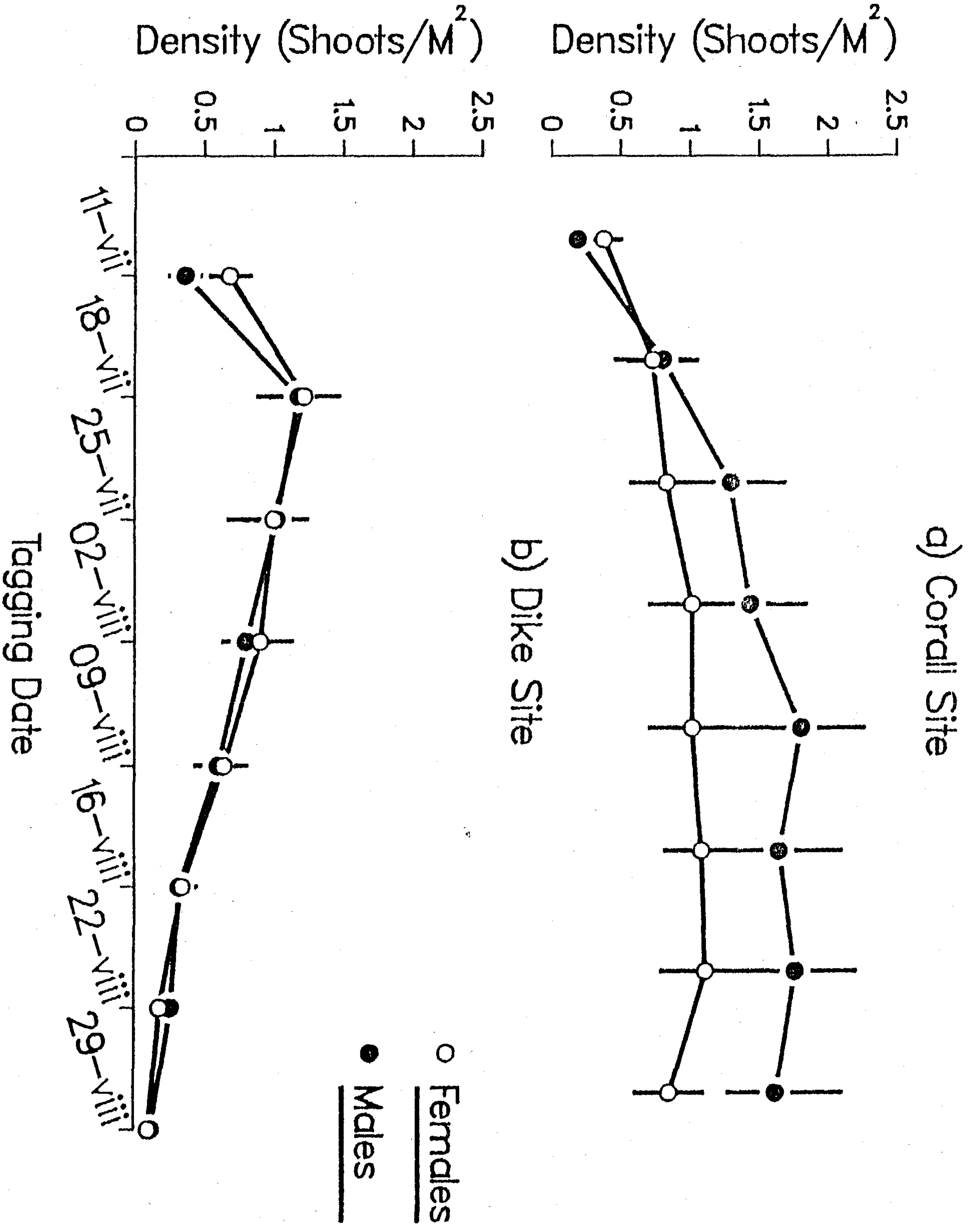
Once thistles began blooming the quadrats were censused for number of vegetative shoots and number of female and male shoots in bloom on each sampling day. Study plants were examined and any flower heads that had just initiated blooming were tagged. In this manner, I obtainde a series of cohort samples of heads that I presumed were no longer available to flies and would experience the same pollination regime. I based my assumption upon my observation that flies only oviposited into heads 1 day prior to blooming. The validity of this assumption is demonstrated in Chapter four. The position of each of these heads on the plant was then recorded. I sampled heads either early (on the day of tagging), or late (after the head had opened to release seeds) from a cohort sample to compare larval densities. A discrepancy in larval density would indicate a possible effect of larval competition on mortality. At the time of tagging, the distance from each study plant to the nearest male plant in bloom was measured. All heads left on study plants were reexamined the following week and fastened shut with plastic twist-ties to prevent the release of mature seeds. It was neccessary to wait 1 week for the pappus on a tagged head to grow out completely. Also, this waiting period probably minimized disturbance to 1st instar larvae and pollinators. Seed heads that were sampled immediately were taken back to the laboratory and dissected. The number of florets and the number of fly eggs in each head were then recorded. Besides providing a basis for comparison, late-sampled heads could provide much more information on non-lethal crowding effects and on pollination success as well as the availability of larval resources. Consequently, any larvae in a late-sampled seed head were dissected out, counted, and weighed to the nearest 0.1 mg. In addition to this, the number of pappus plumes (= florets), the number of plump seeds, the number of seeds consumed by fly larvae, and the number of aborted seeds were counted. The healthy seeds were then weighed collectively to the nearest 0.1 mg.

I also made a number of bulk collections of female flower heads, mainly to obtain flies for behavioural experiments, from near the Reifel refuge sites and on the SFU campus. These proved useful for determining parasitoid and disease effects, since my twist-tie technique effectively excluded both of these mortality factors from the samples collected on the bird refuge. All such bulk collections were made towards the end of the summer (late August and early September) during 1984, 1985, and 1986. At the time of sampling I made no attempt to collect seed heads randomly, but instead attempted to collect only heads that contained at least one larva. I dissected subsamples of these heads, recorded the number of larvae, then stored each larva individually inside a gelatin capsule until either pupation, parasitoid emergence or death from disease occurred.

3.3 Results

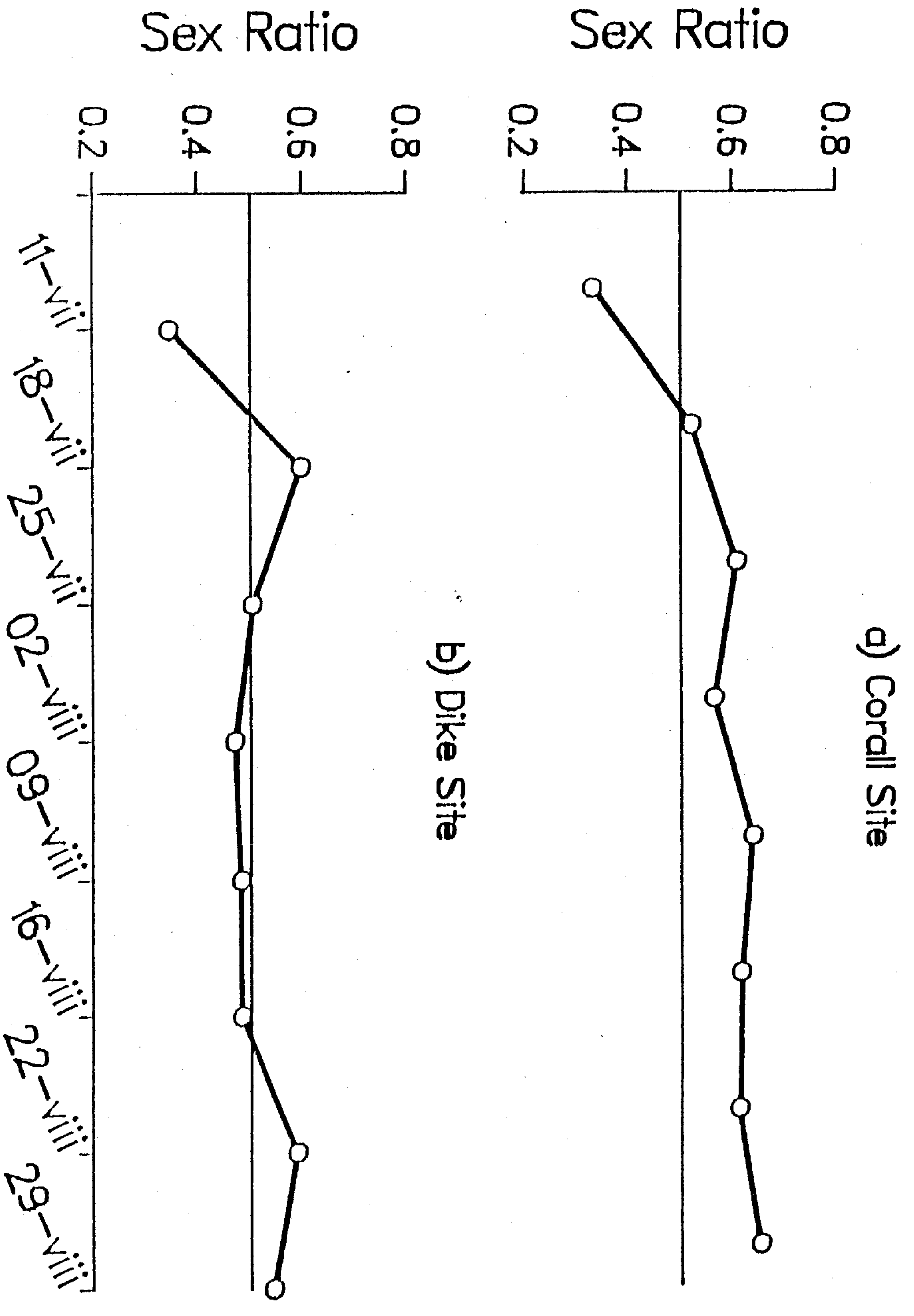
I estimated the density of flowering male and female shoots on the 2 Reifel refuge sites from the quadrat data (Figure 3.1). The operational sex ratio (blooming male shoots/total blooming shoots) neither changed materially with season on either site nor deviated far from 50:50 (Figure 3.2). I combined the data summarized in Figure 3.1 with data obtained at the same sampling dates from the individual plants, to estimate seed production/m^2 on each sampling day and the impact and duration of the fly's effect on thistle seed production. This is summarized in Figure

Figure 3.1. Density of blooming male and female shoots over the season. The bars denote 1 standard error.



a) Corall Site
b) Dike Site
Density (Shoots/M^2)
Density (Shoots/M^2)
0
0.5
1
1.5
2
2.5
11–vii
18–vii
25–vii
02–viii
09–viii
16–viii
22–viii
29–viii
Tagging Date
○ Females
● Males

Figure 3.2. Operational Sex ratio (blooming shoots) over the season.



a) Corall Site

b) Dike Site

3.3. Note that at no time did the flies have more than a minimal effect on seed production at either site, even though fly densities were comparable to those in other sites used in the course of this study and thus cannot be considered to be exceptionally low.

I tested the hypothesis that larval cannibalism occurs by comparing the number of larvae present at the end of the season with the number of eggs initially laid into a seed head. If larval density were reduced in late samples compared with early samples, one could not say that this was due to cannibalism. However, if larval density stayed the same, one could say with fair confidence that cannibalism did not take place. I found a significant difference between mean density in early- and late-sampled heads on only two sampling dates, one at each site (Mann-Whitney "U" test, $p < 0.05$, Table 3.1). Both of these indicated an increase in larval density. At one site this difference was highly significant ($p < 0.001$), probably due to careless treatment on my part of the early sample (The sample froze, turning into a black, smelly mass upon thawing, making dissection difficult. This did not happen to any of the other samples.). Thus, while I often grouped data from early and late samples for all the other sample dates, I was careful to use only the late sample data from this site in any subsequent analyses. At the other sample date the difference was significant, but at a relatively low level ($p = 0.043$) and considering that there were 10 cohort samples, the result was

Figure 3.3. a,c - Seed production (achenes/M^2) and b,c - seed consumption by *Orellia ruficauda*, estimated from quadrat and whole plant data. The bars represent 1 standard error. a,b, Corral site; c,d, Dike site.

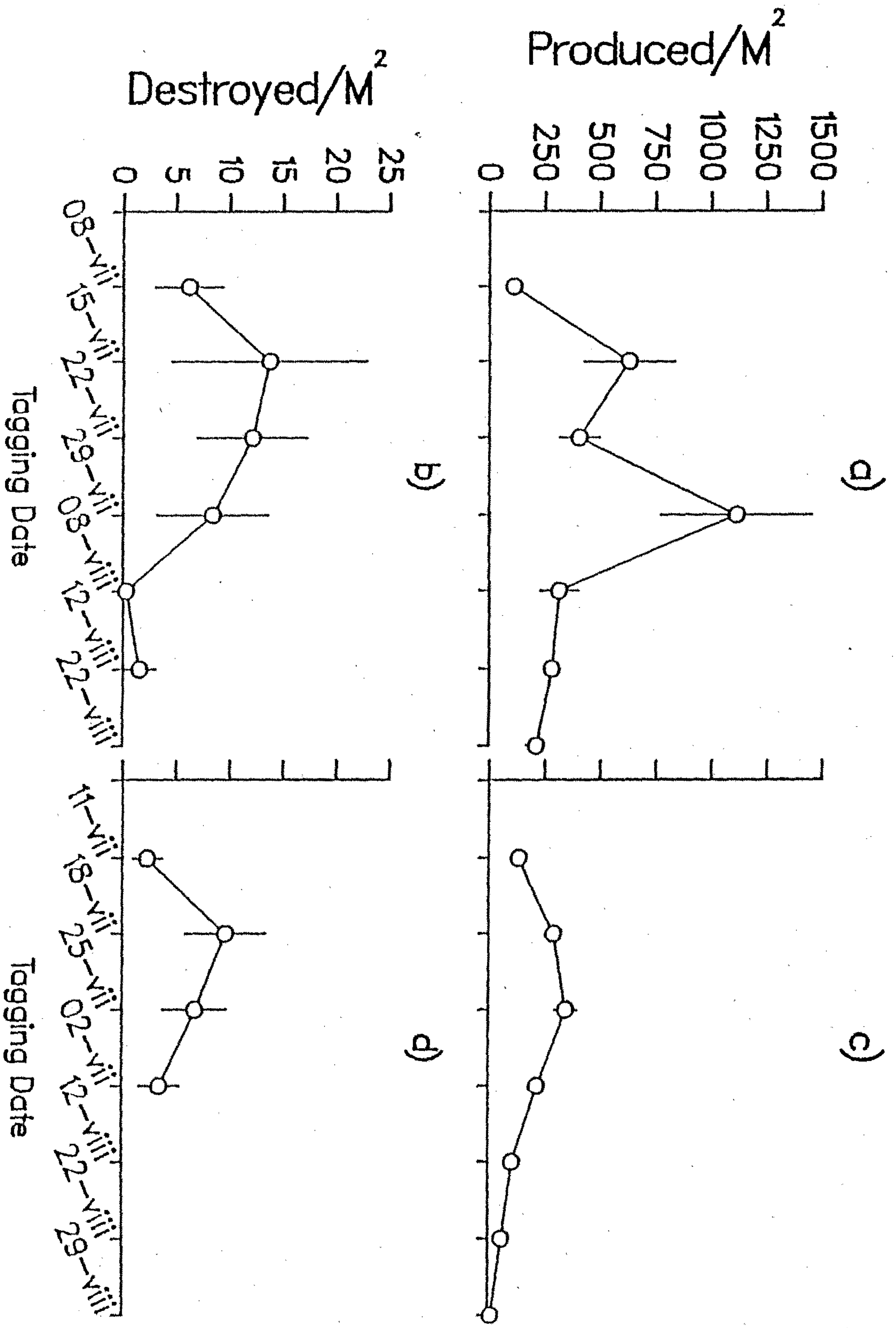

Produced/M^2
0
250
500
750
1000
1250
1500
a)
c)
Destroyed/M^2
0
5
10
15
20
25
b)
d)
08-vii
15-vii
22-vii
29-vii
08-viii
12-viii
22-viii
11-vii
18-vii
25-vii
02-vii
12-viii
22-viii
29-viii
Tagging Date
Tagging Date

Table 3.1. Density of *O. ruficauda* eggs in heads sampled at the time of flowering vs. larval density in heads sampled after seed release. Values in brackets are standard errors. Mean densities were compared using Mann-Whitney "U" tests for each tag date.

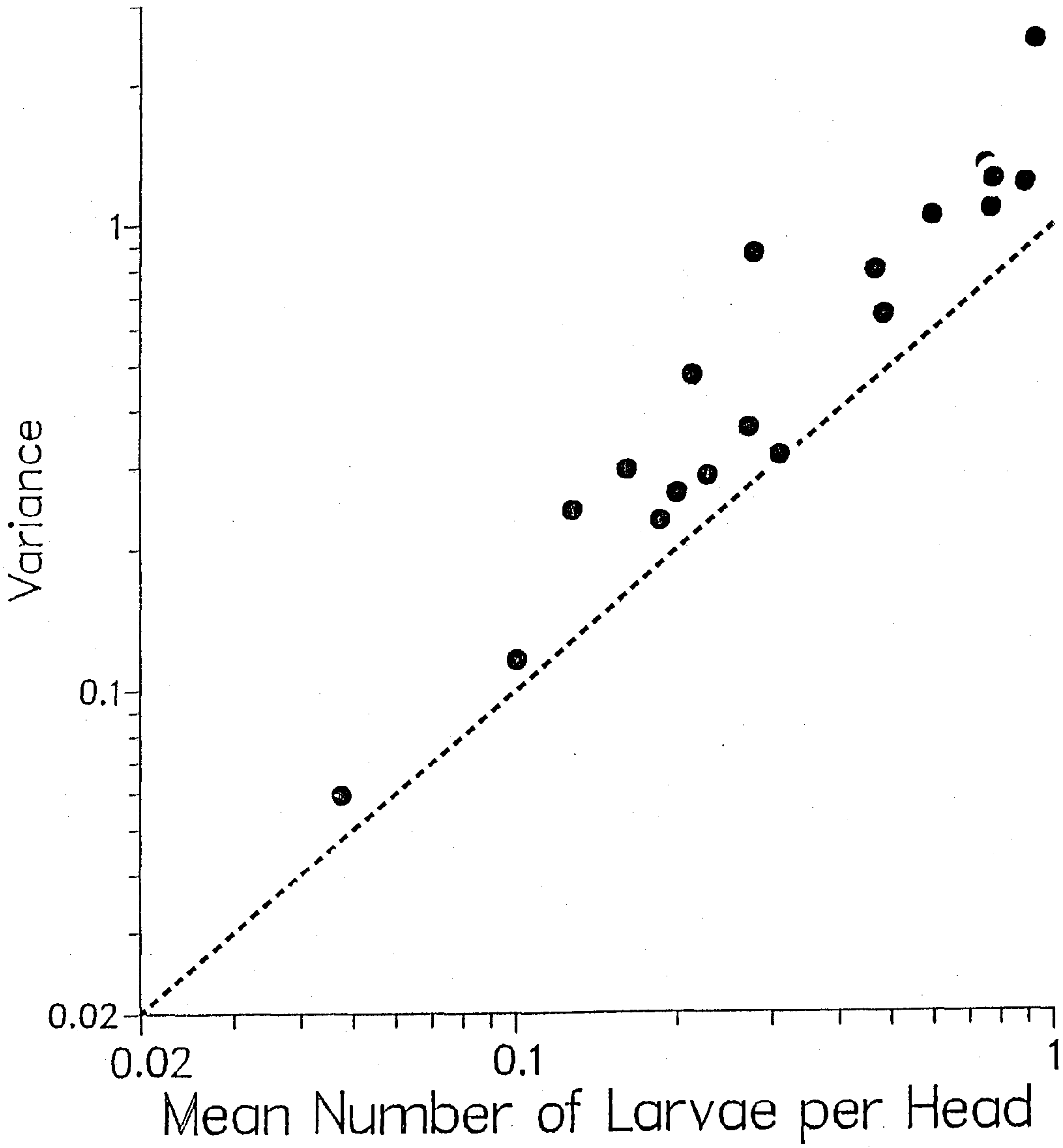
Site	Tag date	n	Early	n	Late	P
Corral	08-vii-85	18	0.833(1.15)	48	0.750(1.12)	0.795
"	15-vii-85	73	0.164(0.58)	98	0.592(1.02)	0.001
"	22=vii-85	65	0.462(0.81)	99	0.495(0.85)	0.919
"	29-vii-85	77	0.208(0.55)	99	0.192(0.49)	0.935
"	08-viii-85	32	0.031(0.18)	58	0.017(0.13)	0.668
"	12-viii-85	29	0.138(0.44)	44	0.068(0.26)	0.570
Dike	11-vii-85	24	0.083(0.28)	63	0.190(0.59)	0.653
"	18-vii-85	49	0.122(0.39)	84	0.357(0.69)	0.043
"	25-vii-85	48	0.229(0.52)	80	0.225(0.55)	0.773
"	02-viii-85	24	0.125(0.61)	39	0.128(0.41)	0.424

therefore probably due to chance. Overall, there was no consistent direction to the difference between mean infestation rate in early and late sampled heads. Thus, I concluded that egg survivorship is quite high and there is no measurable cannibalism, at least not at the densities found in the field.

I calculated mean and variance of larval density per head at each site sampled by the individual head tagging method. This included sites tagged in 1984 as well as the 1985 sites on Westham Island. I regressed log variance against log mean egg density (Figure 3.4). The slope of this power law plot is not significantly different from 1 ($p = 0.075$), but the intercept is significantly greater than 0 ($p < 0.001$). Any log mean vs log variance regression line that falls above the mean = variance line (i.e., when the intercept is > 0) indicates aggregation. Thus eggs of *Orellia ruficauda* are significantly aggregated in their distribution.

I tested the hypothesis that observed aggregation is simply a spurious result of a mere spatial patterning of infestation within the site (which could lead to apparent aggregation). The data from the field study of 1985 were used for this test, because the exact location of each plant was known for both the dike and corral sites. Only the data from the 4 highest infestation dates at each of the 2 sites were analyzed, since egg density on the remaining days was quite low, and distributions were not significantly different from a Poisson (G test, $p > 0.05$). A series of plant neighborhoods of increasing

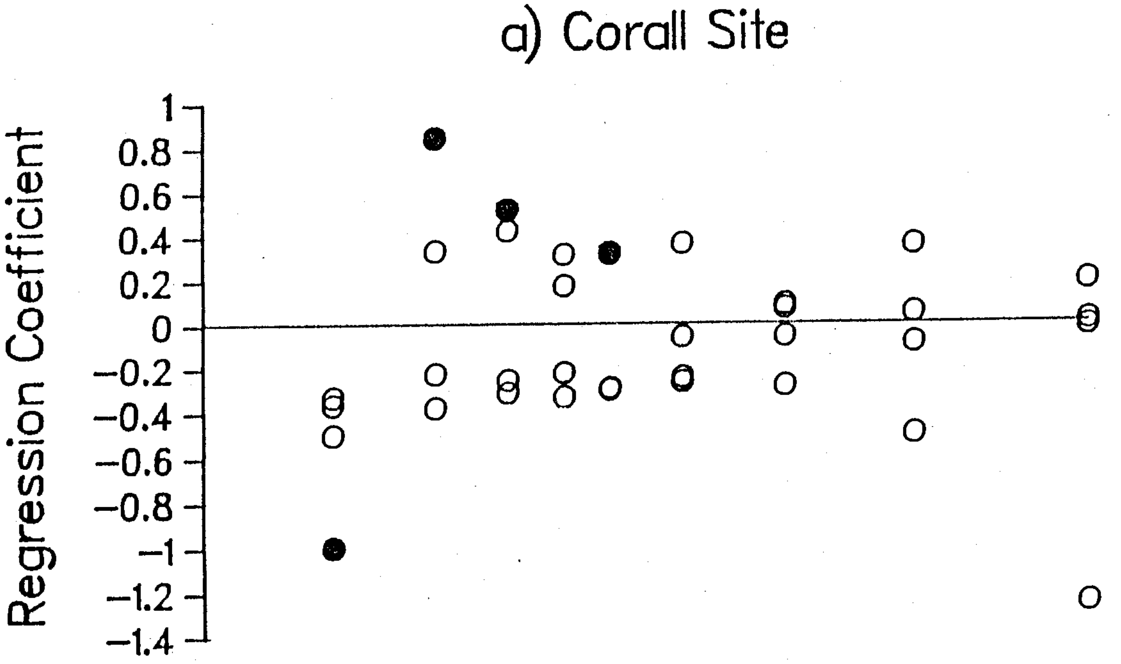
Figure 3.4. Power law plot of log density of larvae per head vs log variance. The slope of the fitted regression line is not significantly different from a slope of 1 (change in mean = change in variance), but the intercept is significantly greater than 0. The dashed line indicates mean = variance.


1
0.1
0.02
0.02
0.1
1
Variance
Mean Number of Larvae per Head

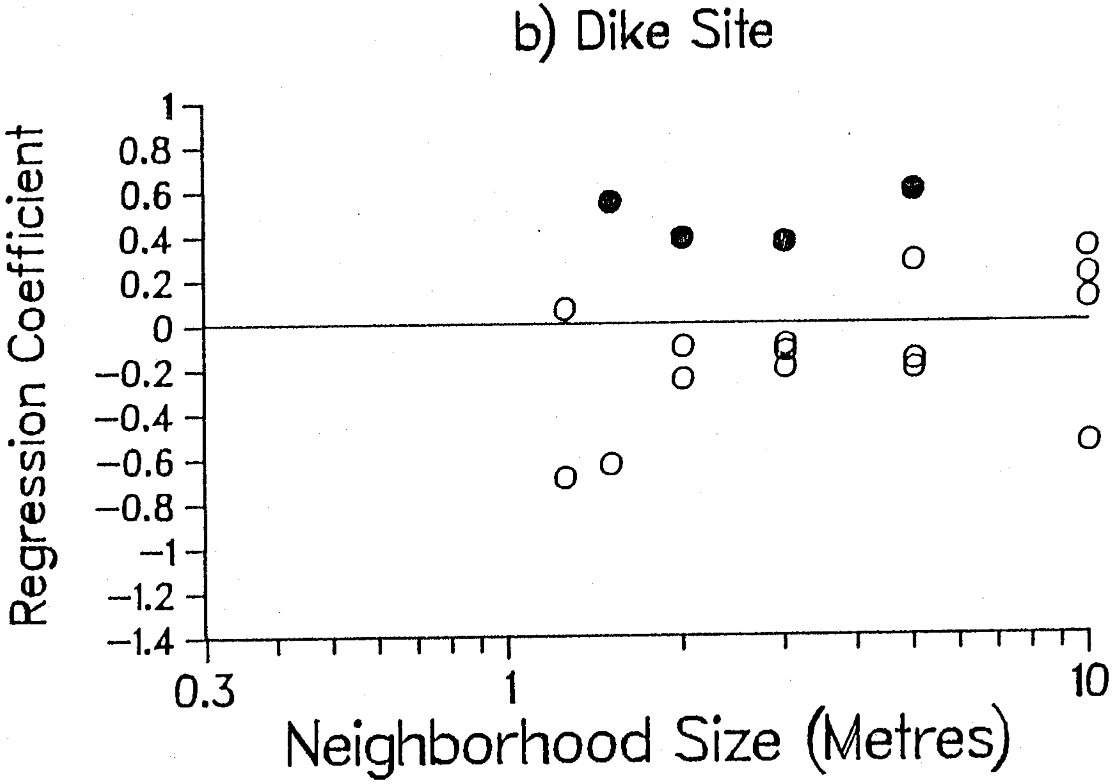
diameter was established around each plant. The identity of all plants within each of these plant neighborhoods was recorded. Then for each neighborhood size, infestation rate on individual plants was correlated with the mean infestation rate in their neighborhoods. A significant positive correlation between infestation rate on individual plants and infestation rate within a neighborhood would indicate an underlying spatial cause for the observed aggregation of eggs. Correlations were only significant at 2 of the sample dates, and there was no consistent pattern to the sign of the regression coefficients (Figure 3.5). Neither the value of the regression coefficient nor the significance level was related to infestation rate on the site at any sampling date. Thus, I conclude that aggregation of eggs was not a result of a spatial effect.

Distance to nearest male plant measures were log-transformed to normalize these data. The log-transformed distance to the nearest male plant was significantly negatively correlated with the proportion of fertilized ovules at both sites on the earliest sampling dates, and was significant overall for both sites (Table 3.2). However, the magnitude of even the most significant correlations are not great (at most, 16% of the variation in seed set was explained by distance to nearest male and overall, only 3% of the variation was explained). The effect on seed abortion rate was less clear-cut. Seed abortion rate was significantly correlated with distance to nearest male on both sites, especially on the dike site.

Figure 3.5. Plots of regression coefficients (slopes) between infestation rate on individual plants and average infestation rate within their neighborhoods, calculated for increasing neighborhood size. Solid points are statistically significant correlations ($p < 0.05$). a) Corral site, b) Dike site.



a) Corall Site



b) Dike Site

Table 3.2. Coefficients of determination, signs, and attained significance levels of regressions of Log transformed distance to nearest male against the Arcsine-Square Root transformed proportion of achenes which were fertilized. Calculations were made separately for each tagging day at each site.

Site	Tag Date	n	Sign	r^2	P
Corral	08-vii-85	48	-	0.15	0.007
"	15-vii-85	93	-	0.08	0.006
"	22-vii-85	99	-	0.11	0.006
"	29-vii-85	92	-	0.00	0.787
"	08-vii-85	57	-	0.00	0.741
"	12-viii-85	39	-	0.05	0.159
"	22-viii-85	21	+	0.00	0.928
Total Corral		449	-	0.03	0.000
Dike	11-vii-85	63	-	0.16	0.001
"	18-vii-85	82	-	0.00	0.842
"	25-vii-85	74	-	0.14	0.008
"	02-viii-85	37	-	0.07	0.102
"	09-viii-85	15	-	0.13	0.186
Total Dike		272	-	0.05	0.000

However, this correlation was negative at the dike site and positive on the corral site (Table 3.3).

The infestation rate of flower heads on both sites was significantly positively correlated with the distance to nearest male plant on one of the sample days ($p = 0.011$), but the same site yielded a significant negative correlation on the previous sample date ($p = 0.042$, Table 3.4). These were the only 2 significant correlations between infestation and distance to nearest male plant.

I compared the density of eggs dissected from female seed heads in 1984 with egg density in male heads at the same sample locality and date, for four different localities. No eggs were found in any of the male heads, even though female heads often supported substantial numbers of eggs (Table 3.5).

The weight of seed consumed by larvae was estimated as the product of number of seeds consumed and the average seed weight (determined from unconsumed seeds in each head). Total weight of mature larvae per head was regressed against total weight of consumed seed. This relationship was highly significant and explained 91% of the variation in larval weight (Figure 3.6). The regression model (Larval Mass = Seed Mass Consumed x 0.554 - 0.00024), was used to calculate the maximum potential carrying capacity of each seed head in the population. I took the mode of the distribution of larval weights (5.7 mg, Figure 3.7), and then calculated the weight of thistle seed necessary for one

Table 3.3. Coefficients of determination, signs, and attained significance levels of regressions of log-transformed distance to nearest male against the Arcsine-Square Root transformed proportion of fertilized achenes which subsequently aborted.

Site	Tag Date	n	Sign	r^2	p
Corral	08-vii-85	48	+	0.18	0.002
"	15-vii-85	93	+	0.08	0.007
"	22-vii-85	99	+	0.09	0.003
"	29-vii-85	92	+	0.00	0.525
"	08-viii-85	57	-	0.00	0.981
"	12-viii-85	39	+	0.01	0.637
"	22-viii-85	21	-	0.24	0.023
Total Corral		449	+	0.02	0.001
Dike	11-vii-85	63	-	0.13	0.003
"	18-vii-85	82	-	0.31	0.000
"	25-vii-85	74	-	0.04	0.099
"	02-viii-85	37	-	0.24	0.002
"	09-viii-85	15	-	0.35	0.021
Total Dike		272	-	0.16	0.000

Table 3.4. Coefficients of determination, signs, and attained significance levels of the regression of the log-transformed distance to the nearest male plant against the infestation rate (# of eggs or larvae) in each seed head.

Site	Tagging Date	n	Sign	r^2	p
Corral	08-vii-85	66	-	0.000	0.897
"	15-vii-85	193	+	0.017	0.207
"	22-vii-85	179	-	0.042	0.042
"	29-vii-85	197	+	0.070	0.011
"	08-viii-85	95	+	0.031	0.192
"	12-viii-85	48	+	0.000	0.962
Total Corral		778	+	0.004	0.256
Dike	11-vii-85	87	-	0.003	0.645
"	18-vii-85	134	+	0.004	0.571
"	25-vii-85	131	-	0.004	0.610
"	02-viii-85	74	+	0.015	0.466
Total Dike		426	+	0.000	0.989

Table 3.5. Number of eggs per head in male and female seed heads sampled from the same locality. Values in brackets are standard errors.

Site	Eggs/Male Head	n	Eggs/Female Head	n
1	0	34	0.60 (0.143)	50
2	0	51	1.07 (0.312)	45
3	0	35	1.28 (0.145)	68
4	0	60	0.09 (0.054)	75

Figure 3.6. Scatter plot of estimated weight of consumed achenes in a seed head against the total larval weight in that head. Data from both sites are combined.

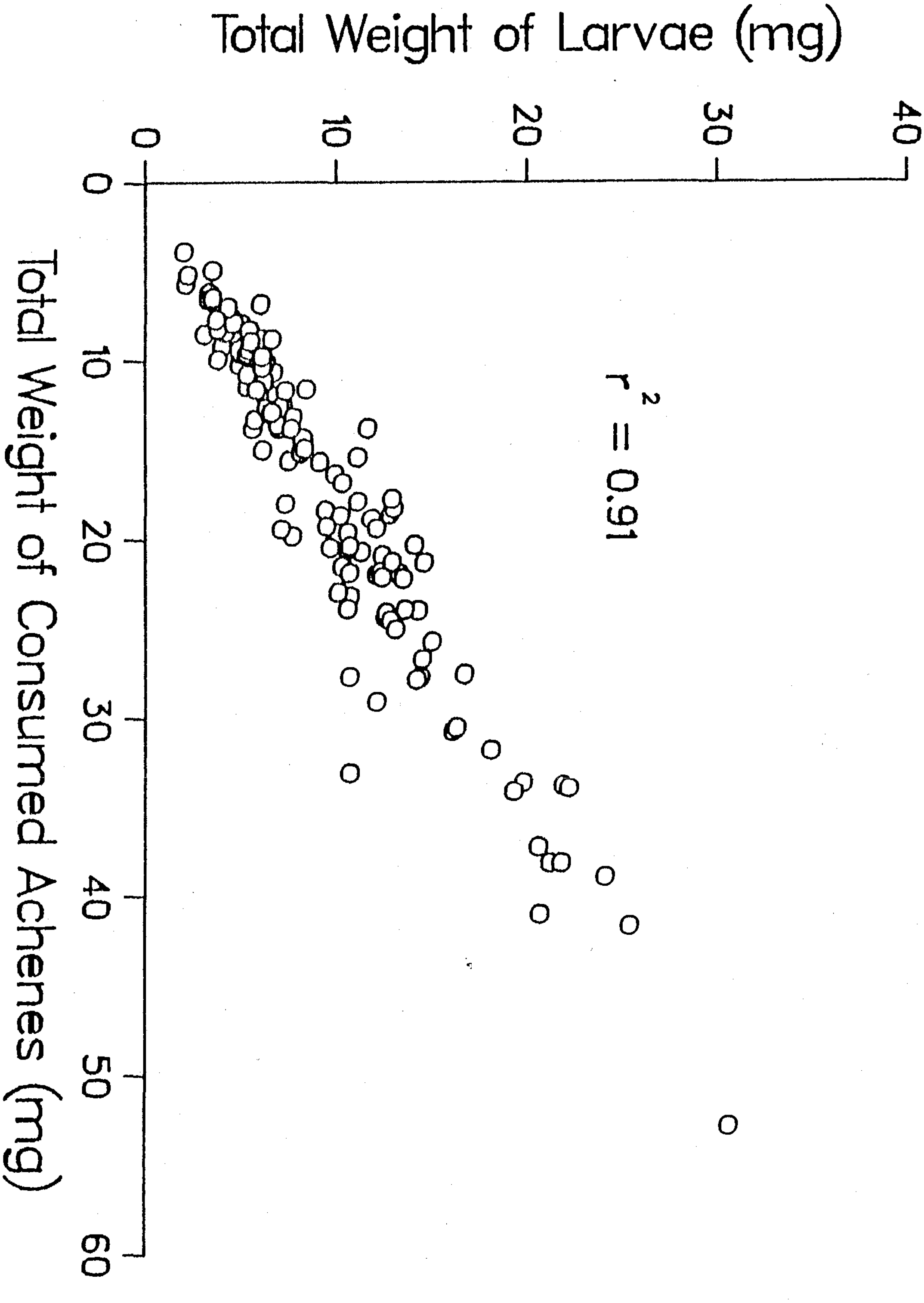

Total Weight of Larvae (mg)
0
10
20
30
40
Total Weight of Consumed Achenes (mg)
0
10
20
30
40
50
60
r² = 0.91

Figure 3.7. Frequency distribution of mature larval weight for late-sampled seed heads from both Corral and Dike sites. Modal larval weight at maturity was 5.7 mg.

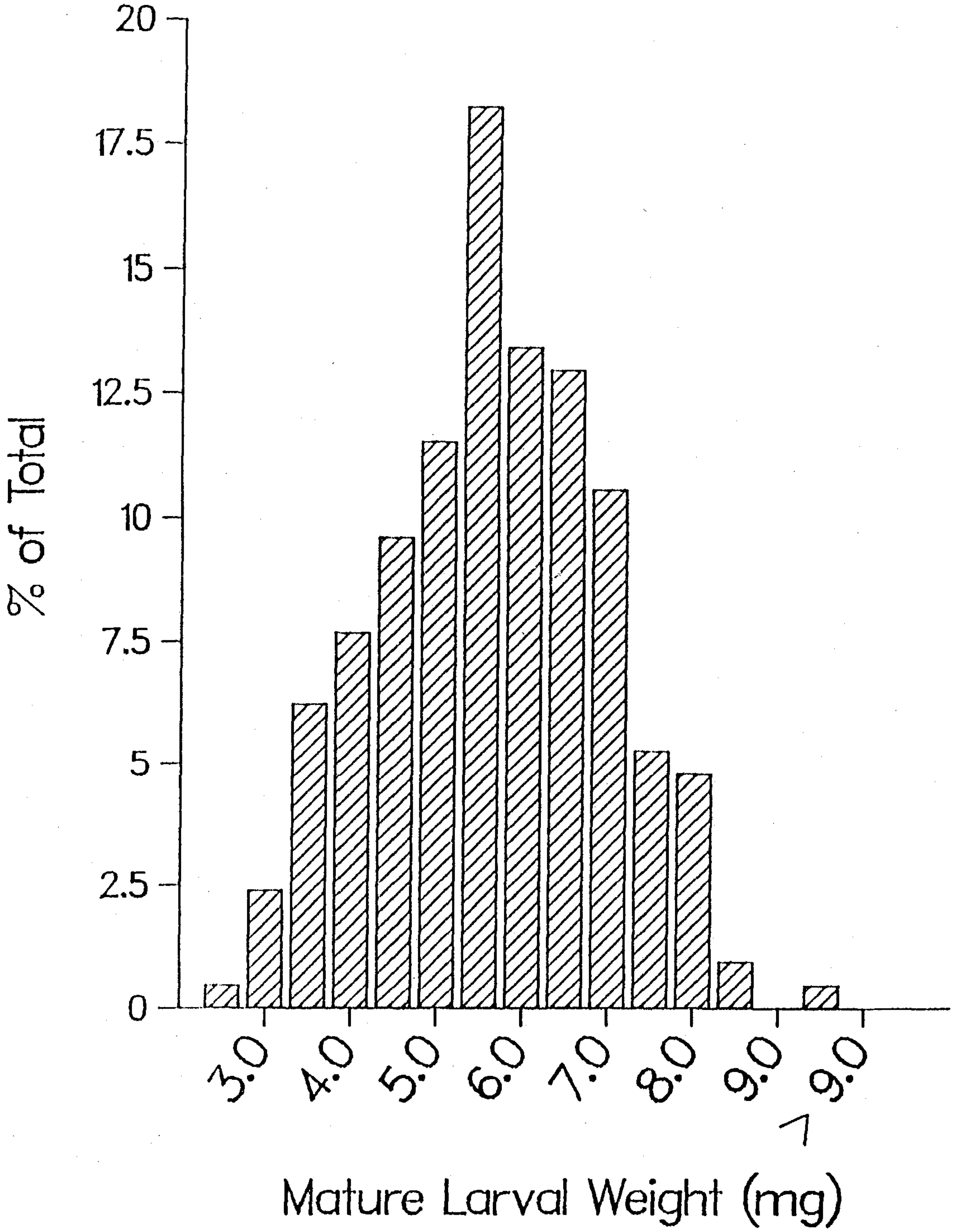

% of Total
20
17.5
15
12.5
10
7.5
5
2.5
0
3.0
4.0
5.0
6.0
7.0
8.0
9.0
> 9.0
Mature Larval Weight (mg)

Figure 3.8. Distribution of seed heads by their theoretical carrying capacity (defined as the maximum # of larvae that can be supported to reach modal weight). a) Corral site, b) Dike site.

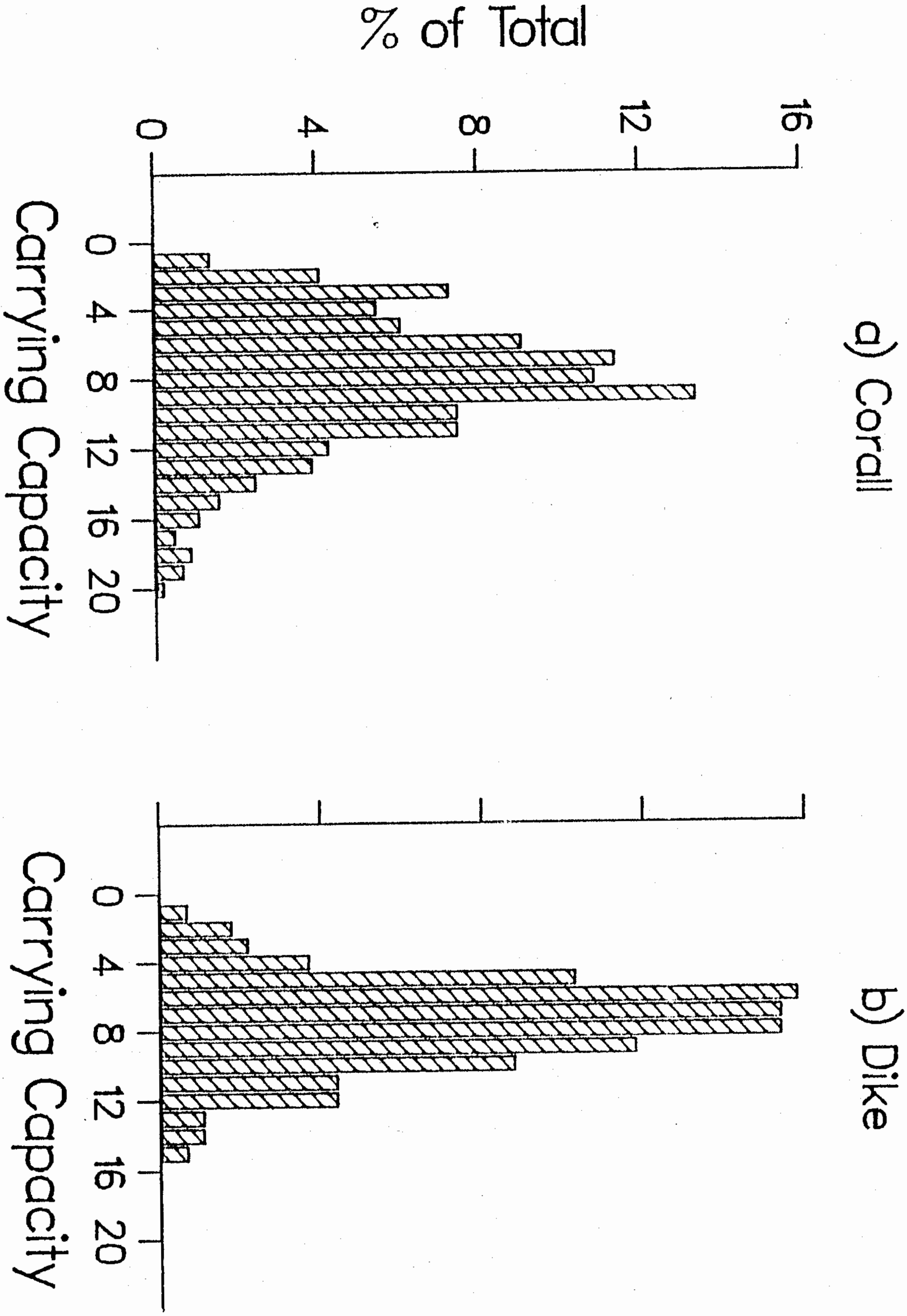

% of Total
0
4
8
12
16
a) Corall
0
4
8
12
16
20
Carrying Capacity
b) Dike
0
4
8
12
16
20
Carrying Capacity

Figure 3.9. Mean carrying capacity in primary, secondary, and tertiary seed heads for the first four tagging dates at each site. Points sharing the same letter are not significantly different ($p < 0.05$, Scheffé). a) Corral Site, b) Dike site.

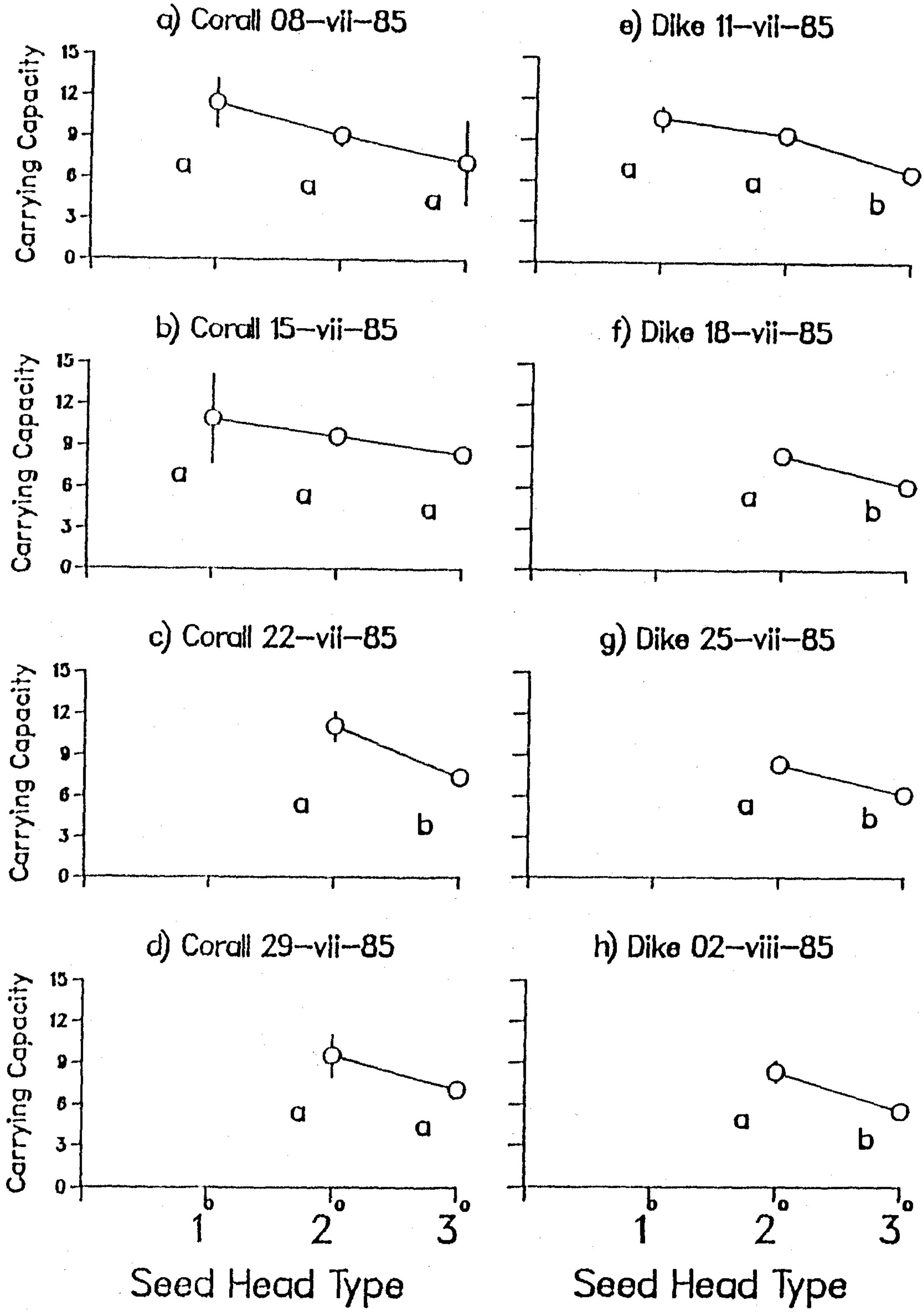
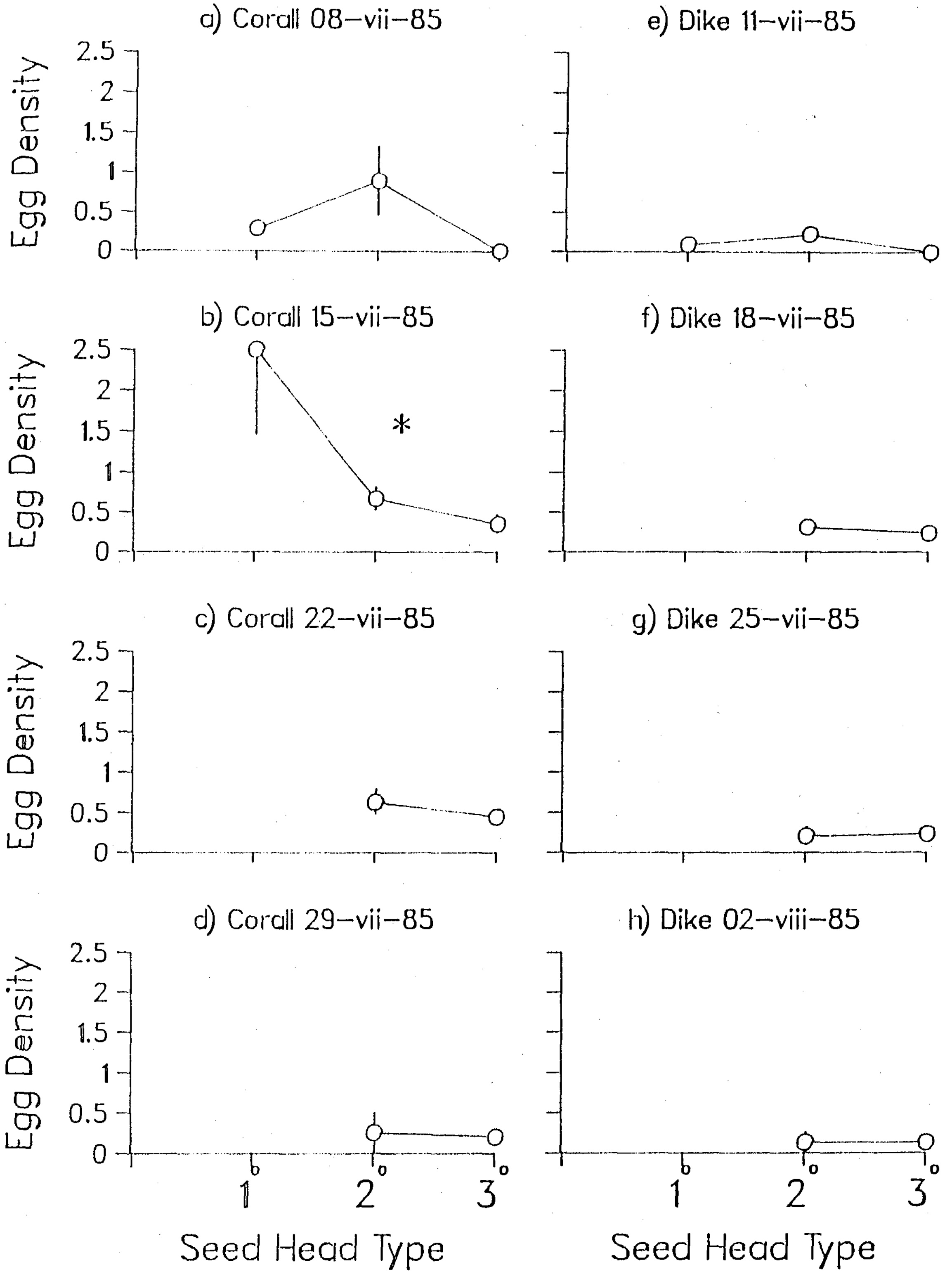

a) Corall 08–vii–85
e) Dike 11–vii–85
b) Corall 15–vii–85
f) Dike 18–vii–85
c) Corall 22–vii–85
g) Dike 25–vii–85
d) Corall 29–vii–85
h) Dike 02–viii–85
Carrying Capacity
0
3
6
9
12
15
a
b
1
2
3
Seed Head Type

Figure 3.10. Infestation in primary, secondary, and tertiary seed heads for the first four tagging dates at each site. An asterisk indicates a significant difference in infestation between seed head classes. ($p < 0.05$, Kruskal-Wallis). a) Corral site, b) Dike site.


a) Corall 08–vii–85
e) Dike 11–vii–85
b) Corall 15–vii–85
f) Dike 18–vii–85
*
c) Corall 22–vii–85
g) Dike 25–vii–85
d) Corall 29–vii–85
h) Dike 02–viii–85
Egg Density
2.5
2
1.5
1
0.5
0
b
o
o
1
2
3
Seed Head Type

larva to achieve modal weight. This factor was used to transform total weight of mature seed in each head to total number of modal-sized larvae able to mature in each seed head, i.e., the carrying capacity of the head. The distribution of seed heads by their theoretical carrying capacity is given in Figure 3.8.

Carrying capacity and infestation rate were calculated for all primary, secondary and tertiary heads for the first four sampling days at each site (Figures 3.9 and 3.10). The carrying capacity does show a tendency to decline from primary to tertiary seed heads, but this tendency is significant on only a few of the sample dates. Infestation frequency goes in the expected direction (i.e., is highest in primary seed heads) significantly on only one of these sample dates, and frequently goes in the opposite direction (although not in a significant way) on the other sample dates.

I used floret number, and mean achene weight as independent variables in a multiple regression model to predict their combined effects on carrying capacity, infestation, and larval mass. Both independent variables were highly significant when the model was used to predict carrying capacity and larval success (Table 3.6). However, there is no evident effect of these two factors on host selection, as indexed by infestation intensity. Egg number per head correlates positively with floret number, but probably only because both factors are significantly correlated with tagging date (Table 3.7).

Table 3.6. The combined effects of seed mass and floret number on the carrying capacity of individual seed heads and on larval success (measured as 3rd instar mass) within infested seed heads.
(* $p < 0.05$, *** $p < 0.0001$)

	n	r (florets)	r (seed mass)	multiple r^2
Carrying Capacity	708	0.6413 ***	0.2890 ***	0.4945 ***
Larval Success	133	0.1568 *	0.1850 *	0.0587 *

Table 3.7. Correlation matrix of interactions between seed size, floret number, tagging date and egg density. Significant correlations are followed by an asterisk.
($p < 0.05$, Spearman's Rho)

	Seed Size	Floret #	Tagging Date	Egg #
Seed Size	---	0.0234	-0.1226 *	0.0319
Floret #		---	-0.5606 *	0.1568 *
Tagging Date			---	-0.2088 *

Table 3.8. Larval density per head (crowding level) and mature larval mass (mg.). Means are not significantly different in any cell (Scheffé, $p < 0.05$).

	Crowding			Level				
Site	1	(n)	2	(n)	3	(n)	4+	(n)
Corral	5.222	(45)	5.903	(36)	6.038	(13)	6.072	(2)
Dike	5.178	(23)	5.116	(19)	6.900	(1)	---	

Table 3.9. Larval density per head and the proportion of larvae which experience mortality due to parasitism from *Crataepus marbis* and *Tetrasticus venustis*. The hypothesis that larvae at all levels of crowding at a given site experience identical rates of parasitism was tested by calculating 1-way ANOVAs on the arcsine-square root transformed proportions for each site.

	Crowding Level								
Site	1	(n)	2	(n)	3	(n)	4+	(n)	P
1	0.123	(65)	0.130	(138)	0.105	(54)	0.197	(23)	0.571
2	0.282	(78)	0.189	(114)	0.126	(58)	0.150	(54)	0.047
3	0.331	(139)	0.277	(74)	0.306	(24)	0.375	(8)	0.824
4	0.513	(39)	0.457	(23)	0.190	(7)	0.150	(3)	0.314
5	0.282	(39)	0.340	(53)	0.130	(16)	0.370	(9)	0.267
6	0.364	(77)	0.333	(30)	0.392	(17)	0.563	(4)	0.756
7	0.278	(18)	0.136	(22)	0.259	(9)	0.000	(4)	0.454

Table 3.10. Larval density per head and the proportion of larvae which experience mortality due to disease. The hypothesis that mortality due to disease is independent of crowding was tested by calculating 1-way ANOVAs on the arcsine-square root transformed proportion of larvae which died from disease for all crowding levels for each site.

	Crowding Level								
Site	1	(n)	2	(n)	3	(n)	4+	(n)	P
1	0.169	(65)	0.083	(138)	0.086	(54)	0.075	(23)	0.166
2	0.218	(78)	0.140	(114)	0.098	(58)	0.095	(54)	0.087
3	0.065	(139)	0.088	(74)	0.056	(24)	0.000	(8)	0.724
4	0.103	(39)	0.109	(23)	0.143	(7)	0.333	(3)	0.633
5	0.256	(39)	0.226	(53)	0.354	(16)	0.156	(9)	0.605
6	0.221	(77)	0.150	(30)	0.118	(17)	0.000	(4)	0.499
7	0.056	(18)	0.205	(22)	0.074	(9)	0.438	(4)	0.023

I compared the weights of healthy larvae sampled from heads containing one to four or more larvae, using data obtained from the Reifel refuge sites. I could not detect any effect of crowding on larval success in any of these field samples (Scheffé, $p < 0.05$, Table 3.8). No larvae in any of the Westham Island samples were parasitized or diseased. I therefore used larvae from bulk samples to make similar analyses to detect density effects on larval mortality due to either of the two endoparasitoids (Table 3.9), or by disease (Table 3.10). No consistent effect of larval crowding on any of these mortality factors was found.

3.4 Discussion

Fly impact on predispersal seed mortality over the season was never great at either site on the Reifel Island refuge. At no point during the season did flies consume even a fraction of the total number of seeds available, at either the population level, or the level of the individual seed head. Although seed predators can have strong effects on seed production (Hawthorne and Hayne 1978, Hare 1980, Zimmerman 1980, Hainsworth et al. 1984), and even in rare cases on actual recruitment of new individuals into the population (Louda 1982), this is clearly not the case here. Under-utilization of host material in plant-parasitic species like *Orellia ruficauda* has been found in many other systems (Monro 1967, Bauer 1986, Solbreck and Sillén-Tullberg 1986, Simberloff and Stiling 1987).

Why are larval densities so low if a head can support eight larvae (as the average head on the Reifel sites can). Others have shown significant crowding effects on larval success (Weis et al. 1983, Godfray 1986). Parasitism pressure has also been invoked as an explanation for dispersion of larvae (Cornell 1982, Thompson 1987, but see Romstöck-Völkl and Wissel 1989), as has the probability of cannibalism (Smith and Lessells 1984, Waage and Godfray 1984). However, *O. ruficauda* larvae do not experience any measurable detrimental effects from crowding, at least not in any of the field samples. Larvae were neither smaller in crowded heads, nor were they more prone to mortality from disease or parasitoids, at least not within the densities found in the field. Cannibalism does not seem to occur in this species, although it is documented for some fruit-infesting tephritids (Averill and Prokopy 1987). Whether or not cannibalism, or crowding in general, can affect larval success at densities higher than I have found in the field has yet to be determined.

The distribution of larval carrying capacities estimated from my field data (see Figure 3.7) may provide an explanation. Adult flies may be allocating eggs to seed heads based on the probability distribution of host quality. In other words flies may be sensitive to the variation in the carrying capacity of individual hosts as well as to the mean. The possibility of food limitation of larval success will provide the basis of my theoretical development in Chapter 5.

What can be gleaned from the field data so far? First we can conclude with some assurance that even though larval success was not affected by food limitation in the field, the potential for food limitation exists. A very high proportion ($r^2 = 0.91$) of the variation in larval production is explained by achene consumption, and achene production is limited and varies between heads. Other factors that may limit larval density in a given seed head are not apparent, at least not at the density levels measured. I recognise that this is not yet conclusive, because the larval densities encountered in the field are far lower than the theoretical limit imposed by achene availability.

A second conclusion that can be drawn is that adult flies allocate their eggs in such a way that egg distribution amoung heads tends to be slightly aggregated. This pattern is probably not a manifestation of simple avoidance of attacked seed heads on the part of the parents. Avoidance behavior would be expected to produce a decrease in the aggregation of larvae with increased density. If anything, the trend is towards increased aggregation as density increases, although this trend is not significant. Of interest, Straw (1989b) demonstrated that the seed predatory tephritid *Tephritis bardanae* deposited and responded to a marking pheromone, but also tended to aggregate its eggs in the field. It is possible that aggregation could result from flies incorporating the information provided by a marking pheromone. Flies avoiding oviposition into marked heads may respond by allocating larger clutches to unmarked heads as such heads become relatively rare.

Pollination was significantly affected by proximity to blooming male plants (Table 3.2), and also significantly affected the seed abortion rate on some sample days on the dike site (Table 3.3). However, I feel it unlikely that either factor is biologically important to ovipositing flies. When male plants are present locally, the reduction in mean pollination success with increased distance from the nearest male (about 10% over 20m), is quite minor compared with the background variation. Seed abortion rate was often strongly affected by the distance to the nearest functional male, but the direction of this variation was not predictable. I show elsewhere that seed abortion rate is not affected by pollination intensity *per se* (Lalonde and Roitberg 1989). It is possible that the significant effects of distance on seed abortion is a paternal effect arising from the genetic load in the 2 local thistle populations (Wiens 1984, Wiens et al. 1987). If this were true, one might well expect to often find significant relationships, but be unable to predict the direction. Given limited gamete selection on the part of females, close proximity to particular males may thus produce either higher or lower rates of seed abortion than average, because distant pollen will tend to be excluded. This will be especially prevalent in situations where there is a high degree of genetic variability within the population, but local genetic composition has low diversity. Canada thistle's clonal growth pattern may generate such diversity on a local scale.

Potential for a high degree of variability in expressed characters within this species is well-documented (Hodgson 1964). In any case, the field evidence suggests that seed abortion rate is a random factor that increases the variability of seed head quality.

Given the slight effect of distance to nearest male on average seed set, and the high degree of unexplained variation, it is not surprising that flies apparently did not respond to the proximity of male shoots in a locality (Table 3.4). Female flies are, however, able to discriminate male seed heads from female seed heads. Eggs were conspicuously absent from samples of male heads taken from sites of high infestation in female heads. A complete absence of male plants in a locality may severely limit seed set and indicate extremely poor conditions to a fly foraging for oviposition sites. Thus, a fly that encounters no males at all while foraging may expect a lower profitability from host heads. Both of these premises will be explored in Chapter 5.

Finally, seed production (both number and weight) is potentially reduced across primary, secondary, and tertiary seed heads (Lalonde and Roitberg 1989), and this pattern was expressed to a weak, but consistent degree in the field. Different thistle clones express strong differences in both seed size and floret number, so it is not too surprising that this pattern did not emerge strongly. Infestation pattern did not tend to follow this weak trend; possibly female flies do not have a good perception of the relative position of a flower head on a shoot. Considering that thistle shoots tended to grow very close together, this is not surprising. Seed head size, as indexed by the multiple regression using floret number and seed weight may give a better proximate cue to ovipositing flies about seed head quality, since both carrying capacity and larval success are significantly related to these factors. Here I assume that floret number and seed weight vary directly with seed head size, and are thus assessable by the ovipositing fly. Nevertheless, when the confounding effect of tagging date is considered, there was no effect of either floret number or seed size on the allocation pattern of female flies in the field. Flies were not obviously preferentially attacking larger seed heads. I will develop these ideas further in Chapter five.

In the next chapter, I will use laboratory, and controlled field experiments to measure some life-history and behavioural parameters associated with this system. I will use these parameters, along with field data described in this chapter to develop a theoretical measure of the fitness consequences of parental clutch-size decisions.

CHAPTER 4

LAB AND FIELD MEASUREMENTS OF FLY BEHAVIOUR AND LIFE-HISTORY PARAMETERS

4.1 Introduction

The object of this thesis is to develop a theoretical prediction of how flies should go about allocating eggs to hosts during a day. Field data obtained so far will aid in development of such a theory, but it will first be neccessary to quantify a number of life-history and behavioural parameters in order to make this theory as realistic as possible by reducing the number of unknown factors.

First, although there is strong inferential and phylogenetic support for the notion that these flies employ a marking pheromone, so far I have presented no proof of this. This is critical, since the presence of a pheromone mark can give information on the quality of the marked host, and the frequency of encounters with marks can indicate the general quality of the locality.

I cannot assume that a mature larva's size is directly proportional to its reproductive success when I calculate parental returns from different clutch sizes. This is clearly not the case; there must be some minimum size, below which flies are simply not able to produce eggs. Furthermore, there may well be some kind of interaction between size and adult longevity which would certainly affect the fitness of offspring reared under conditions where food is scarce.

A major assumption made in previous insect clutch-size models is that handling time is dependent upon the number of eggs laid by and insect during an oviposition event (Charnov and Skinner 1985, Parker and Courtney 1984, Skinner 1985). If handling has a fixed time cost independent of clutch size, then my model will generate a very different prediction of how many eggs a fly should allocate to a host.

The factors outlined above are basic to the structure of any theoretical model of this system. However, it is also neccessary to obtain some numerical values for other parameters in order to employ a sensitivity analysis that encompasses reality. For example, the number of eggs available for oviposition will affect a female fly's allocation decision. If flies are strongly egg-limited, the type of theoretical approach to clutch size used by Charnov and Skinner (1984) and Skinner (1985) will not be applicable to this system (Mangel and Clark 1988). On the other hand, if time costs (either search, or handling) are so large that they limit the number of hosts that can be processed within a day (i.e., if eggs are typically left over), then egg limitation will not be particularly important.

I have so far assumed that the vulnerability of heads to fly attack ends shortly after blooming has started and begins about a day prior to this. I have based this assumption upon my field observations where I found flies to be remarkably selective. In the field, wild flies only selected flower heads which were unopened or in the process of opening. However, the duration of a host's vulnerability to fly attack dictates how rapidly the environment as perceived by the flies will change at a given conspecific density. For example, if heads remain vulnerable to attack for several weeks, as is the case for many fly - fruit systems (Averill and Prokopy 1989), or even several days, as is the case for many seed head parasites (Straw 1989c), then the relative frequency of attacked heads will change very little over the day. In contrast, if heads reach their vulnerable stage overnight and remain vulnerable for only a single day, then a fly should encounter almost no marked hosts at the beginning of a given day, and (if fly density is high) will be able to find almost no unattacked hosts towards the end of that day. In this chapter I will test my assumption that heads are vulnerable for a single day by 1) determining the duration of different blooming stages in the field, 2) measuring the responses of flies to different seed head developmental stages, and 3) determining the fate of eggs laid into non-preferred host stages.

Finally, host heads experienced a relatively high rate of pollen transfer in the localities studied in Chapter 3. What is the expected value of a randomly-encountered seed head when male plants (local pollen) are not locally present? Isolated female stands occur fairly frequently (Amor and Harris 1975, Hayden

1934), and flies forage in such patches. What is the expected value of a randomly-encountered seed head in a locality where males are not locally present? Is it to a fly's advantage to be sensitive to such variation? Are fly responses to male thistle availability measurable at the population level? Here, I will measure the effect of local presence of male plants on pollination success and the distribution of carrying capacities, and the distribution of eggs. I will use information on carrying capacities in localities where male plants are locally absent to develop and evaluate my clutch-size models, in Chapters 5 and 6.

Thus, this chapter considers a number of loosely-related factors whose common theme is their potential effects on the reproductive success of female flies. My aim is to incorporate these data, along with the field data obtained in the previous chapter, into a theoretical prediction of optimal clutch size.

4.2 Materials and Methods

Wild, lab-maintained flies were used in all of my experiments. To obtain these flies, larval-infested thistle heads were collected in bulk at the end of the season and stored in the refrigerator at 3°C until the following spring. I reared flies by placing seed heads into 25 cm^2 plexiglass cages, and kept the heads moist by spraying daily with distilled water until emergence finished. Emerging flies were removed daily and placed into cages supplied with yeast hydrolysate-sugar feeding strips (Prokopy and Boller 1971), and wicks kept moist with distilled water. Flies were placed individually into cages which contained at least five heads in host condition for 24 hours prior to any trial involving a choice between two oviposition substrates. I assumed that this allowed flies to reduce their egg load and thereby increased their threshold for rejecting substandard hosts (cf. Roitberg and Prokopy 1983). Flies required two weeks to reach maximum egg production and were able to maintain this rate for at least one week, typically longer. Thus, to standardize as much as possible, only recently-mated (on the previous day) flies of two to three weeks of age were used.

4.2.1 Recognition of Prior Parasitism

Here, I tested the ability of flies to discriminate heads which had been previously infested. I took avoidance of oviposition to indicate recognition of prior parasitism. Female flies were presented with a sequence of either 1) a previously-attacked seed head followed by an unattacked seed head, or 2) an unattacked seed head followed by an attacked head. An attacked head was one which another female fly had previously probed and then circumscribed with the tip of her extended ovipositor. Any trials in which the test fly did not oviposit into either seed head were discarded from the data set. A G test of independence (Sokal and Rohlf 1981) was used to test the hypothesis that flies responding to the first presentation sequence acted significantly differently from flies responding to the second sequence. I predicted that flies should tend to avoid oviposition into previously-attacked flower heads. Heads used in this experiment were collected from the field, from a site where flies were infrequent. To further minimize the risk of "wild" marks affecting the outcome, such heads were collected 24 hours prior to attaining the stage which I had previously observed to be most vulnerable to fly attack. All heads were then washed in distilled water, and used one day later.

4.2.2 Seed Head Phenology

Here, I measured preference and suitability of heads at different developmental stages. I arbitrarily divided seed head development into the following categories;

1) **U** - unopened: The involucral bracts still completely enclose the florets.
2) **O** - opening: Bracts are in the process of opening; some, but not all florets are fully open; some stigmas may show above the lip of the corolla.
3) **B** - blooming: All florets are expanded and most of the stigmas are now visible.
4) **W** - withering: Florets and stigmas now show some signs of necrosis.
5) **M** - maturing: Florets all withered and the pappus hairs now extend above the rim of the involucre.

The duration of the opening, blooming and withering stages was measured in the field by tagging 40 unopened seed heads and following their progress until they were clearly in the maturation stage.

I tested the acceptability of heads at different developmental stages in a manner similar to the marking pheromone assay. In these trials, flies were pre-, and post-tested with an unattacked seed head which was one day away from opening, the stage already observed to be preferred in the field. Any fly failing to oviposit in either the pre-, or post-test head was discarded. At least 20 heads in each of the developmental categories listed above were presented to individual flies. Each test head was tagged and kept in water after presentation and its stage of development was recorded 24 hours after presentation. Since some developmental stages were lengthier than others, each test head was classified by its transition state, i.e., its stage at the point of testing and its stage 24 hours later. Thus, for example, a head that was blooming on the test day and withering on the next was classed as "B - W".

To test the suitability of heads at different developmental stages, I induced mated female flies to oviposit into seed heads of all stages on intact plants. Attacked plants were maintained in a growth chamber at 24°C on a 16:8 light:dark regime. Attacked heads were hand-pollinated using freshly-collected pollen on an artist's paint brush. To ensure that no seeds would be lost prior to collection, heads were bound with plastic twist-ties. Seeds were harvested when ripe (i.e., when the involucral bracts opened), about 20 days after blooming. Living and dead larvae (and eggs) were dissected out and any living larvae were weighed to the nearest 0.1 mg on an analytical balance.

4.2.3 Handling Time and Clutch Size

I recorded the time required by a fly to probe a seed head in any choice test involving presentation of heads to flies. I included all of the time that a fly spent attempting to insert its ovipositor into the head with actual probing time. After the trial, presented heads were dissected to determine the number of eggs left by the fly.

4.2.4 Larval Size Effects on Adult Fecundity and Longevity

Mature 3rd instar larvae were dissected from infested seed heads, weighed individually, and placed inside a tagged gelatine capsule to pupate and emerge. On the morning of its emergence, a female fly was chilled briefly to inhibit movement and was marked on the pronotum with a dab of acrylic paint. Five colours were used: white, blue, red, yellow, and green. Marked female flies were then stored, five to a cage, with an equal number of males, a feeding strip, and a moistened water wick. Cages were scanned every hour or so and any pairs in copula were gently removed, and placed in an individual cage. Such cages were supplied with all of the usual amenities, and in addition five unattacked thistle seed heads in host condition were placed inside the cage and replaced daily. Seed heads were removed after 24 hours and dissected, and any eggs present were recorded. This protocol was continued until the female fly died. If the male predeceased the female, he was replaced on the same day.

4.2.5 Male Thistles, Pollination, and Carrying Capacity

Four sites were selected on the SFU campus where I could easily manipulate presence of male thistles. On 2 sites, male plants were present locally, but females were otherwise isolated such that the next nearest source of pollen was at least 50m away. The other 2 sites were isolated from the nearest source of pollen by at least 50m. The first treatment consisted of exposing a tagged cohort of seed heads to existing conditions. When all heads in a tagged cohort had entered the maturing stage of development and were no longer receptive to pollen, the site was then manipulated to either reduce, or augment pollen availability. Existing males were simply removed in the naturally high pollen availability sites and placed into buckets of water and set among the plants in the low pollen availability sites. Thus, each site was subjected to both a high, and a low pollen availability treatment. As before (Chapter 3), heads were bound with plastic twist-ties to prevent early seed release. When heads matured completely and the bracts had opened, they were harvested and plump achenes, aborted achenes and florets were counted. All plump achenes in a head were then weighed collectively to the nearest 0.1 mg on an analytical balance.

To determine the distribution pattern of larvae in what I assumed to be low quality sites, I scanned for laying female flies in sites where male thistles were not locally present. I tagged a minimum cohort of 50 heads at such sites, bound heads with twist-ties after one week, and sampled and dissected heads when seed maturation was indicated. Seven sites were found where I could determine the mean and the variance in per-head infestation.

4.3 Results

4.3.1 Prior Parasitism

Flies which were presented with the Attacked - Unattacked sequence of seed heads behaved significantly differently than did flies presented with the reverse sequence (Table 5.1). The reason for this difference is the clear propensity for flies to avoid probing seed heads that had already been attacked.

4.3.2 Seed Head Phenology

Flies showed a clear preference for flowerheads that either had just begun to open, or were one day away from opening (Figure 4.1b). The most preferred stage of seed head development is also the most transient: it lasts about one day (Figure 4.1a), and the bulk of flowerhead development through this transition appears to occur overnight (my observation). Maggots reared from such heads presumably enjoy an advantage since such larvae weighed significantly more than did larvae reared from forced oviposition into less-preferred seed heads (Figure 4.1c). There was no confounding effect of larval crowding on the relationship between mature larval weight and seed head stage at the densities achieved in this experiment (two-way ANOVA, $p > 0.05$). No head had more than five eggs. The above result does, however, overestimate the success of larvae reared from oviposition into the oldest heads, since only the weights of larvae that survived to 3rd instar are presented. In fact survivorship was affected as well. Probed heads up to the

Table 4.1. Response of female *Orellia ruficauda* flies to sequential presentation of previously-attacked and unattacked flower heads. The hypothesis that flies respond to reciprocal sequences in a similar manner is rejected ($G = 23.58$, $p < 0.001$)

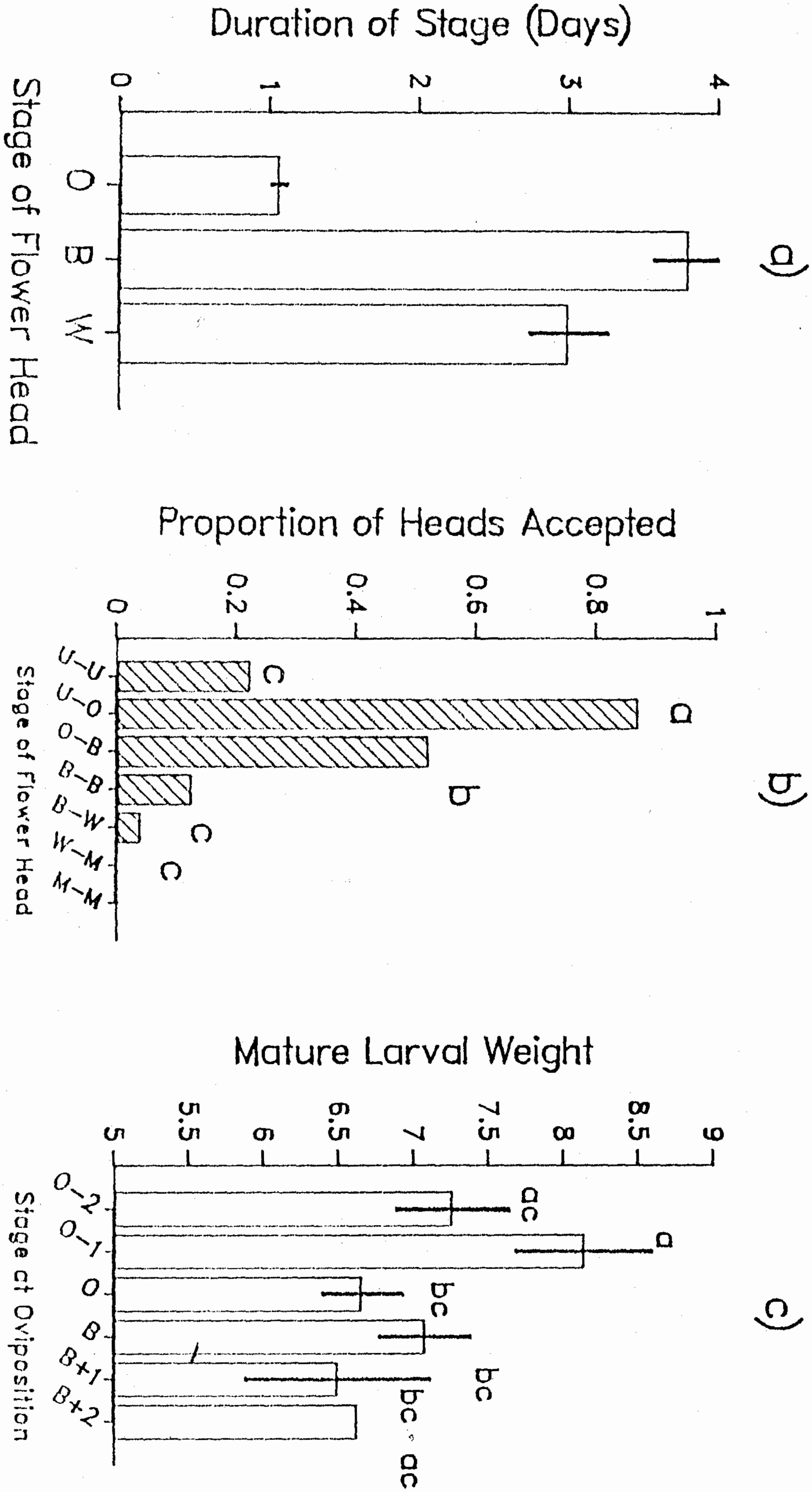
		Oviposition Response		
Presentation Sequence	N	1st Only	2nd Only	Both Heads
Attacked - Unattacked	24	3	16	5
Unattacked - Attacked	21	14	1	6

Figure 4.1 a) Duration of opening, blooming, and withering stages of seed head development. Bars represent 1 standard error.

b) Proportion of adult flies that oviposited into seed heads of different developmental stages. Y-axis gives the proportion of heads within a category that were found acceptable by female flies. X axis divisions give the transition state of the presented seed head (i.e., its condition on the day of presentation and its condition 24 hours later. Bars sharing the same letter are not significantly different (Unplanned Comparison test of Homogeneity, $p > 0.05$).

c) Mature larval weight resulting from oviposition into heads at different developmental stages. X -axis division labels modified by a minus sign and a numeral denote oviposition into a seed head **n** days before the onset of that stage. Division labels modified by a plus sign denote oviposition **n** days after the onset of that developmental stage. Bars denote 1 standard error. Bars sharing the same letter are not significantly different (Scheffé test, $p > 0.05$).

U - unopened, O - opening, B - blooming, W - withering, M - maturing.


Duration of Stage (Days)
0
1
2
3
4
O
B
W
Stage of Flower Head
a)
Proportion of Heads Accepted
0
0.2
0.4
0.6
0.8
1
U-U
U-O
O-B
B-B
B-W
W-M
M-M
Stage of Flower Head
c
a
b
c
c
b)
Mature Larval Weight
5
5.5
6
6.5
7
7.5
8
8.5
9
O-2
O-1
O
B
B+1
B+2
Stage at Oviposition
ac
a
bc
bc
bc
ac
c)

blooming stage produced living larvae at higher frequencies (about 55%) than did older heads which were similarly probed and marked (B+2 and greater, about 10%). This difference was significant (Unplanned Comparison Test of Homogeneity, $G = 15.34$, $p < 0.01$, Sokal and Rohlf 1981). Within the same categories, heads which were probed and dragged and subsequently dissected (from the preference trials) produced equal (and high) proportions of eggs (88% from the unopened to the full bloom stage vs 90% from later stages; Unplanned Comparison Test of Homogeneity, $G = 0.0102$, $p >> 0.05$; Sokal and Rohlf 1981).

4.3.3 Handling Time and Clutch Size

There is no relationship between the time that a fly spends probing a seed head and the number of eggs that it eventually allocates to that head (Kruskal-Wallis, $p = 0.1636$, Figure 4.2a) This relationship is not significant either when probing time is combined with time spent marking the head after oviposition, (Kruskal-Wallis, $p = 0.5564$) or if total time spent examining, probing, and marking a head are combined (Kruskall-Wallis, $p= 0.7112$). Furthermore, duration of per-egg probing time varied tremendously from fly to fly (Figure 4.2b).

4.3.4 Life History and Larval Size

When females are presented with a male immediately after emergence, and are fed *ad libidum*, they begin producing eggs after about one week, and typically produce eggs throughout their remaining life (Figure 4.3). Total fecundity of adult

Figure 4.2. a) Time spent probing (exclusive of marking); indexed by clutch size. There is no apparent relationship between time probing and number of eggs laid (Kruskal-Wallis p = 0.1636). Bars represent one standard error
b) Frequency distribution of handling times (defined as time spent probing a seed head, divided by the number of eggs laid).

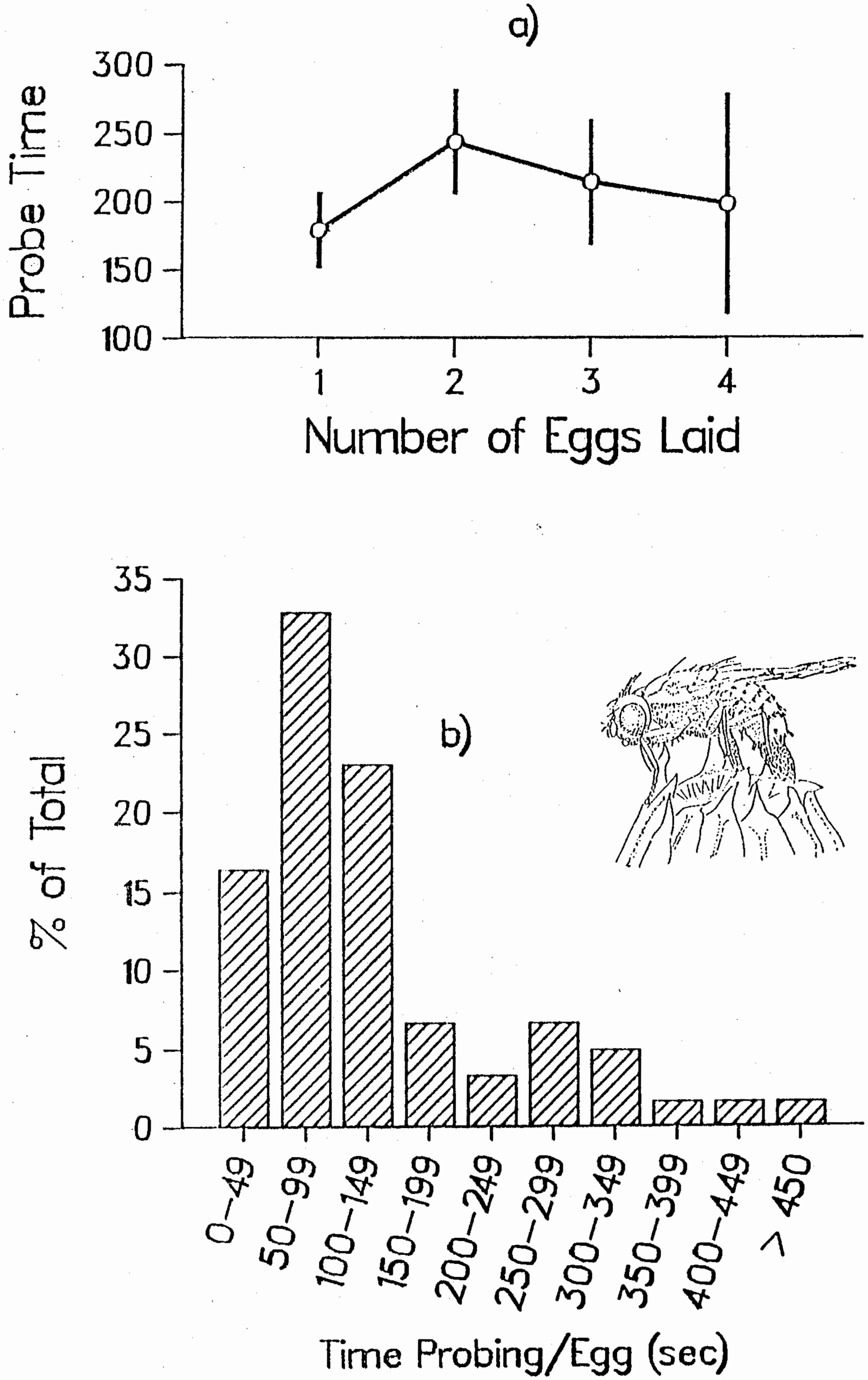
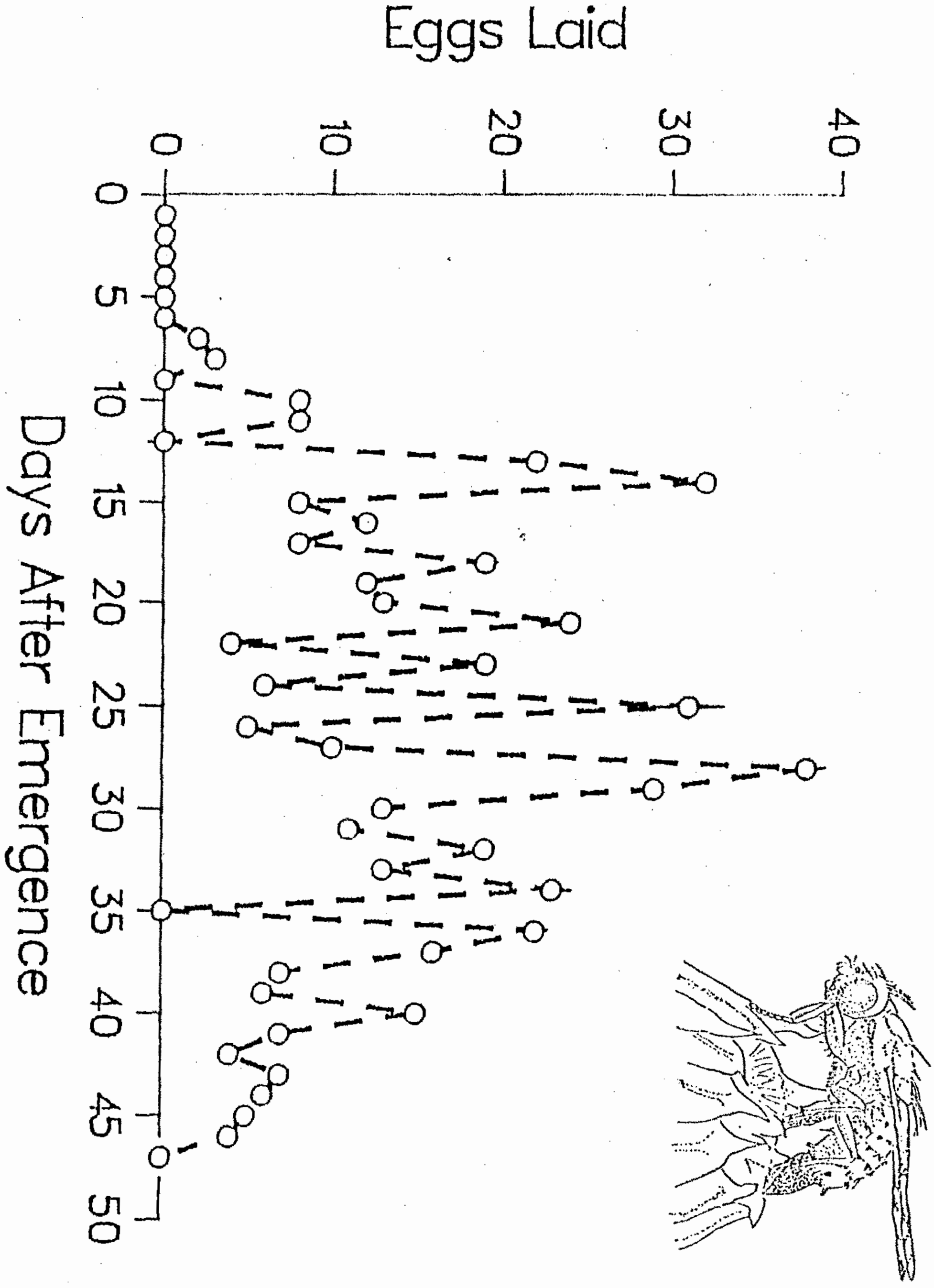

a)
Probe Time
300
250
200
150
100
1
2
3
4
Number of Eggs Laid
b)
% of Total
35
30
25
20
15
10
5
0
0–49
50–99
100–149
150–199
200–249
250–299
300–349
350–399
400–449
> 450
Time Probing/Egg (sec)

Figure 4.3. Daily egg production of a typical *Orellia ruficauda* female.


Eggs Laid
0
10
20
30
40
0
5
10
15
20
25
30
35
40
45
50
Days After Emergence

flies varied significantly with prepupal mass (Figure 4.4). The regression equation explained only about 32% of the variation, however. Although there was no interaction between prepupal mass and adult longevity (Figure 5.5), mortality variation contributed a large component of the variation in total fecundity. A multiple regression model including prepupal size and longevity explained 77% of the variation in total fecundity ($p < 0.00001$). To reduce this effect, I calculated the average rate of egg production for each fly, exclusive of the pre-reproductive period. Regression of egg production rate against prepupal weight improves the explanatory power of the model ($r^2 = 0.54$, Figure 5.6).

4.3.5 Pollen Donors, Pollination Rate, and Carrying Capacity

When male plants were interspersed with female plants in a locality, both the fertilization rate (Figure 4.7), and the quality of individual heads (in terms of their ability to support larvae; Figure 4.8) increased. This treatment effect was highly significant for both characters ($p < 0.0001$, Mann-Whitney U) at all 4 sites.

Distribution of larvae was significantly less aggregated in low quality sites than in high quality sites (males present) (Figure 4.9). The log-transformed mean-variance regressions were not significantly different in slope ($p = 0.0984$; ANCOVA), but were significantly different in intercept ($p < 0.001$).

Figure 4.4. Total fecundity of individually-caged flies presented with 5 flower heads in host condition every day until the fly died, regressed against their prepupal weight.

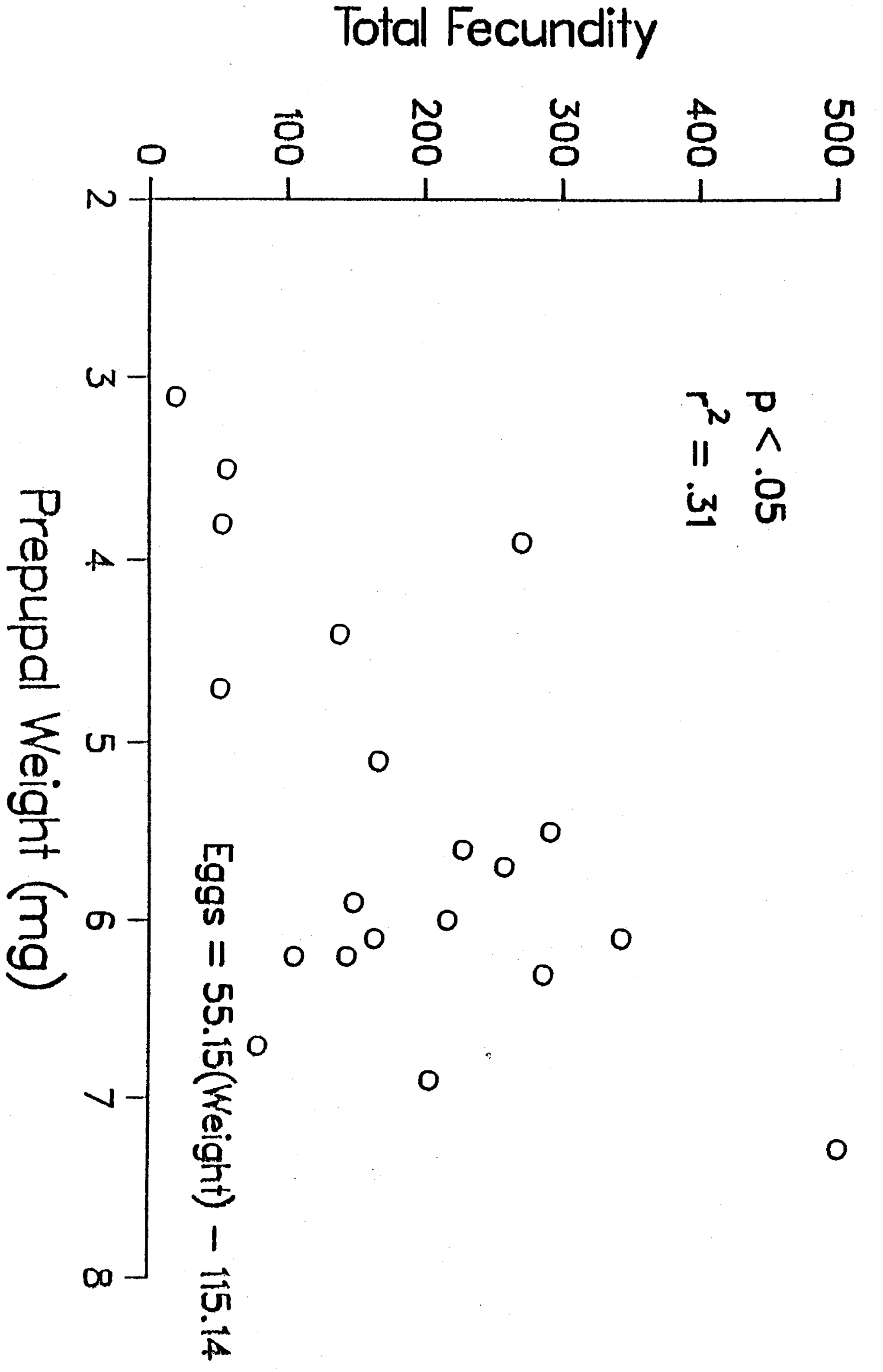

Total Fecundity
500
400
300
200
100
0
2
3
4
5
6
7
8
Prepupal Weight (mg)
P < .05
r² = .31
Eggs = 55.15(Weight) − 115.14

Figure 4.5. Scatter plot of adult longevity vs prepupal mass.

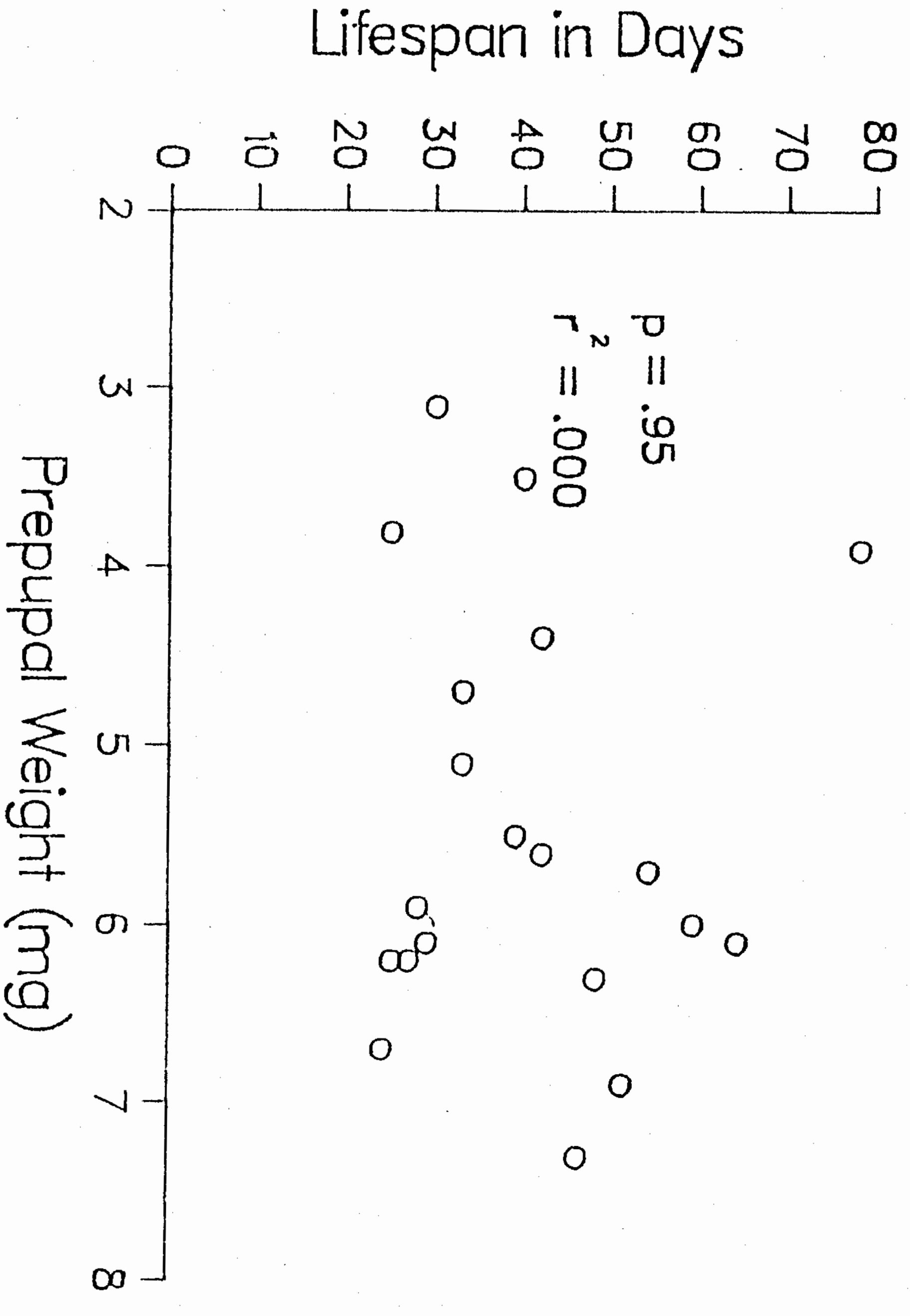

Lifespan in Days
0
10
20
30
40
50
60
70
80
Prepupal Weight (mg)
2
3
4
5
6
7
8
P = .95
r^2 = .000

Figure 4.6. Scatter plot of average rate of egg production against prepupal mass.

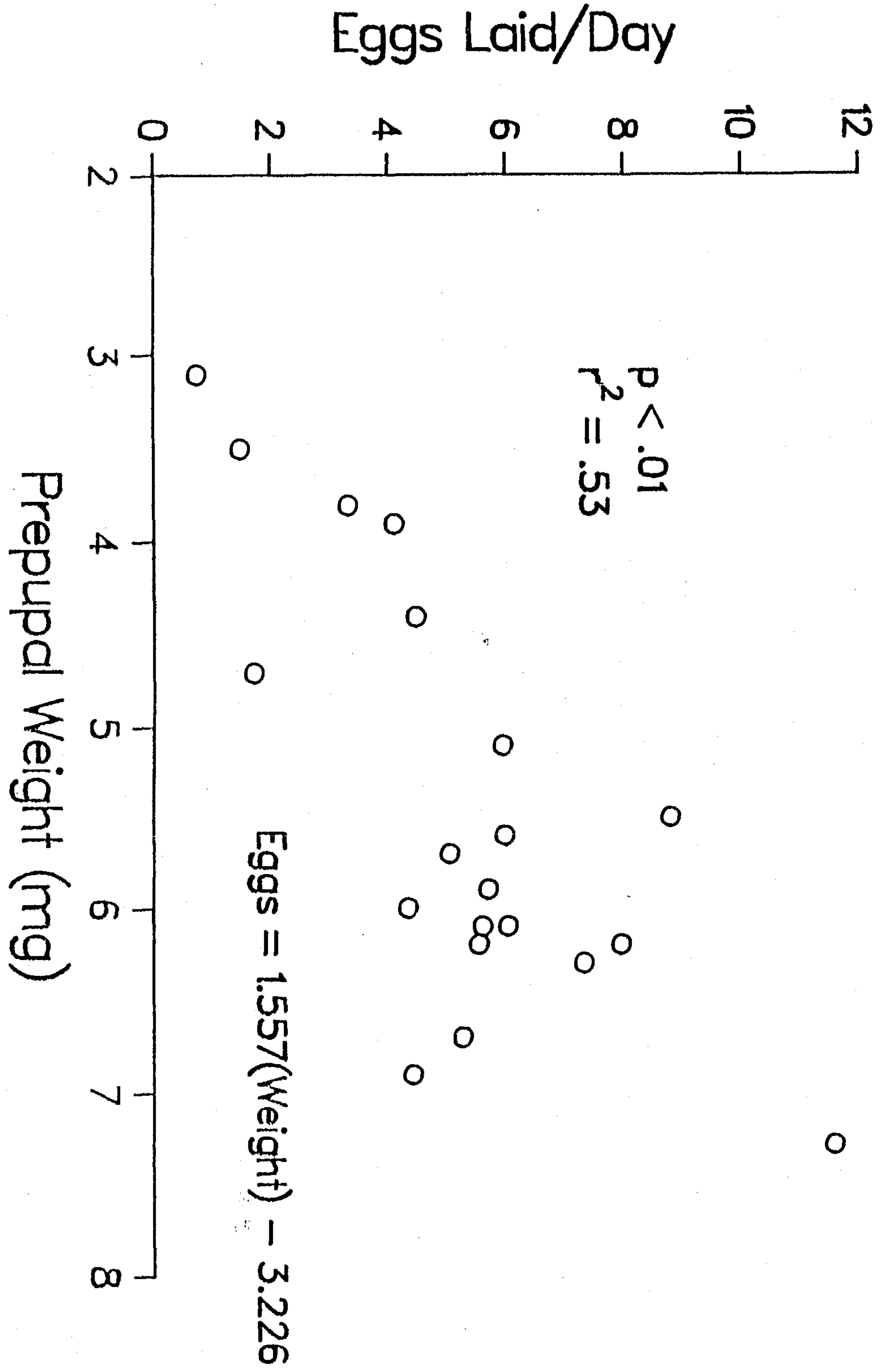

Eggs Laid/Day
0
2
4
6
8
10
12
Prepupal Weight (mg)
2
3
4
5
6
7
8
$P < .01$
$r^2 = .53$
Eggs = 1.557(Weight) − 3.226

Figure 4.7. Effect of manipulation of pollen transfer on *C. arvense* seed head fertility at 4 different field sites.

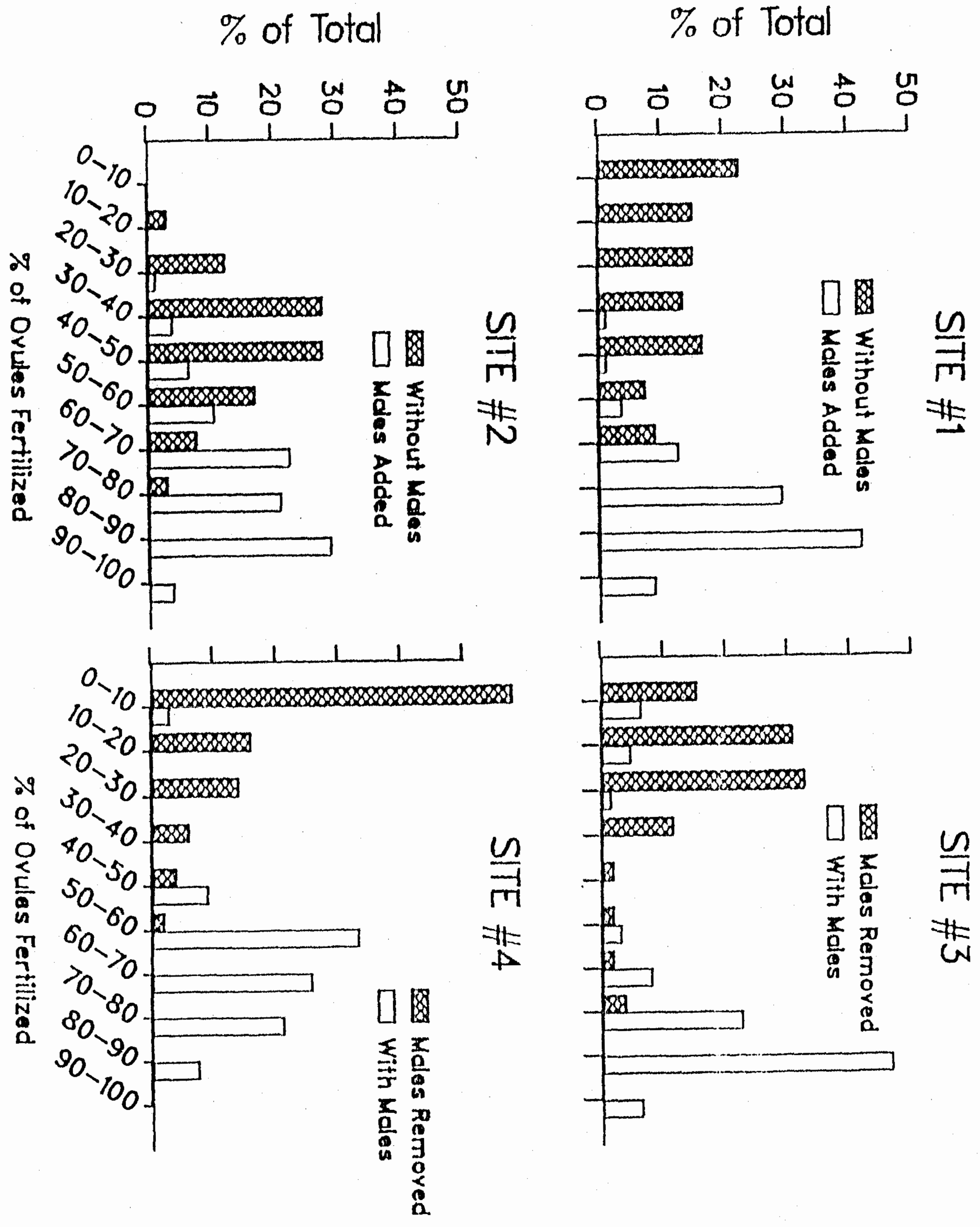

SITE #1
▨ Without Males
☐ Males Added
SITE #3
▨ Males Removed
☐ With Males
% of Total
0
10
20
30
40
50
SITE #2
▨ Without Males
☐ Males Added
SITE #4
▨ Males Removed
☐ With Males
% of Total
0
10
20
30
40
50
0-10
10-20
20-30
30-40
40-50
50-60
60-70
70-80
80-90
90-100
% of Ovules Fertilized
% of Ovules Fertilized

Figure 4.8. Effect of manipulation of pollen transfer on capacity of seed heads to support larvae at 4 different field sites.

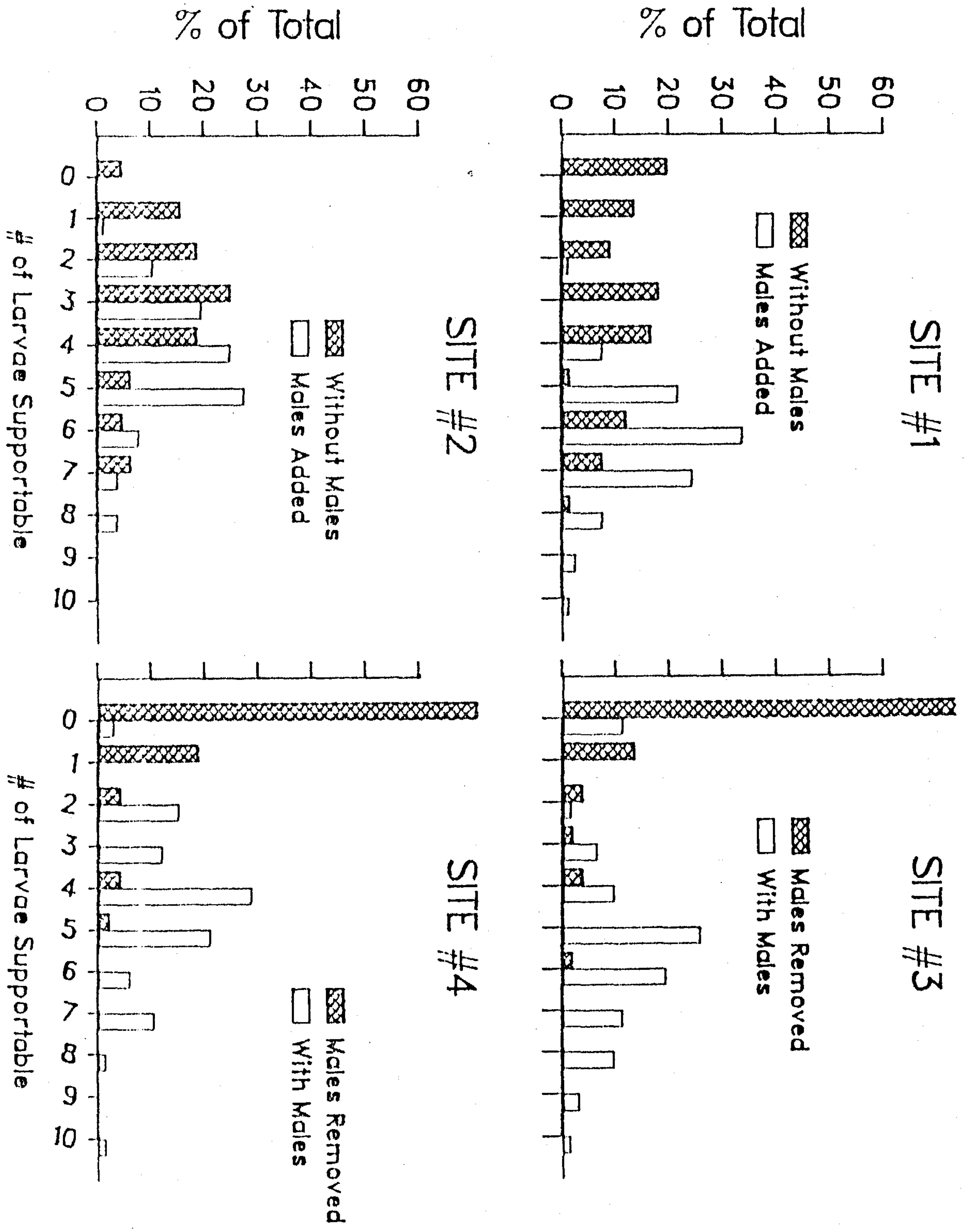
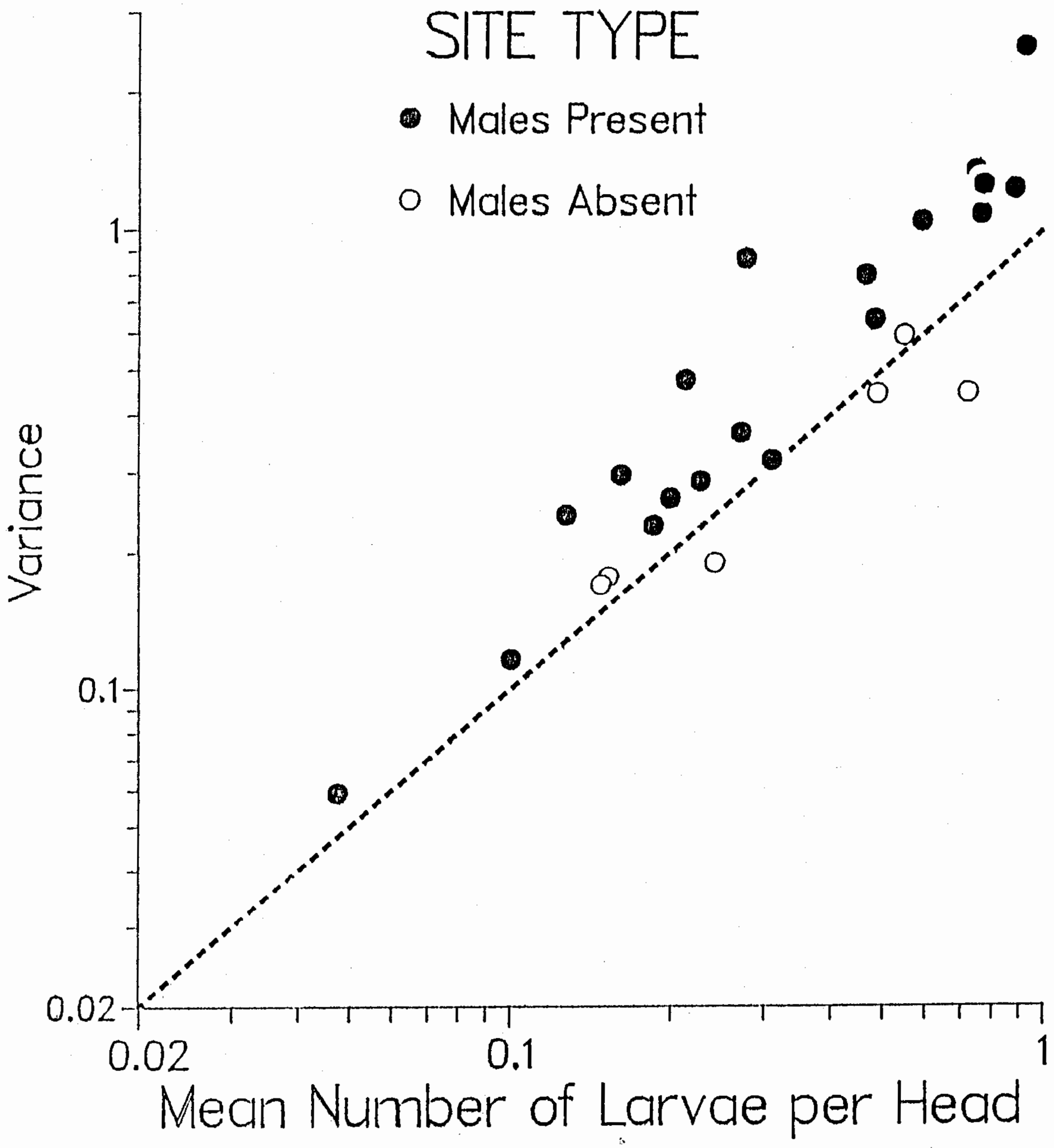

SITE #1
Without Males
Males Added
SITE #2
Without Males
Males Added
SITE #3
Males Removed
With Males
SITE #4
Males Removed
With Males
% of Total
% of Total
0
10
20
30
40
50
60
# of Larvae Supportable
# of Larvae Supportable
0
1
2
3
4
5
6
7
8
9
10

Figure 4.9. Log mean vs. Log variance scatter plot for infestation rate in high quality (closed circles) and low quality (open circles) localities. Regressions are significantly different in intercept ($p < 0.001$), but not in slope ($p = 0.0984$; ANCOVA). The dashed line indicates complete randomness (mean = variance).


SITE TYPE
● Males Present
○ Males Absent
Variance
1
0.1
0.02
0.02
0.1
1
Mean Number of Larvae per Head

4.4 Discussion

The complete protocol for establishing the existence of a marking pheromone should include a trial wherein flies are also presented with marked heads which have had the putative pheromone removed (Prokopy 1975, Prokopy et al. 1982). Here I show that flies can recognize heads that have been attacked. Since my flies do not pierce any tissues with their ovipositor, and do lay down a trail of liquid after oviposition, the odds are great that they do employ a marking pheromone. For purposes of this thesis, it is not neccessary to demonstrate that the liquid trail is the cause of this recognition, since I am only interested in whether or not flies can recognize heads that have been attacked. How flies go about using this information is another question, however. In addition to simple host avoidance, other tephritid species respond to contact with pheromone-marked hosts by reducing the amount of time spent in a locality (Roitberg et al. 1982) and increasing their propensity to fly long distances (Roitberg et al. 1984). Within a locality, flies will adjust their propensity to superparasitize hosts, depending upon their frequency of encounter with marked hosts (Roitberg and Prokopy 1983, Mangel and Roitberg 1989). I will cover some scenarios relevant to the *O. ruficauda -C. arvense* system in the next two chapters.

Heads are most acceptable to ovipositing flies when they are a single day from opening. This is period of acceptability is very short and I feel fairly safe in my assumption that flies can experience rapid changes in their rates of encounter with marked hosts as the day proceeds. The rate of this change will be most dependent upon the number of flies that are present in the locality, and suggests a very complex problem for the flies with respect to allocation of effort over the day (which will not be dealt with extensively in this thesis). If flies lay more at the beginning of the foraging day, they capitalize on the relatively high availability of clean heads, but run the risk of superparasitism. Flies that wait until the day is almost over minimize the risk of superparasitism, but may not find many hosts. Clearly, an individual fly's allocation strategy depends upon how other flies in the locality allocate their eggs over the day. Furthermore, the propensity of other flies to exploit marked heads will also determine an individual's best strategy. Analysis of this "dynamic game" is quite complex. The interested reader is referred to chapter 9 of Mangel and Clark (1988) for a solution to a highly simplified version of this very complex problem.

Neither total time spent by a fly on a head, nor probing time was correlated with clutch size. However, my acceptance of the null hypothesis that handling time does not increase with clutch size is not particularly confident because of the ambiguous significance level ($p = 0.1636$), and the lack of power associated with nonparametric tests. A true correlation between clutch size and handling time may still exist. Such a relationship would be masked if variation between individuals in their per-egg probing time was strong, as is indeed the case. A possible source of the observed variation in handling time may be different levels of egg availability. A fly with few eggs available may not process a host head as fast as it possibly can. Another possibility is that the fixed handling time costs associated with inserting the ovipositor between the bracts and florets of the flower head may vary strongly between heads because of variation in degree of compaction, or from differences in the ability of individual flies to insert the ovipositor into the flower head. In any case, such a large fixed handling time cost is probably much greater in magnitude than any variable time cost associated with clutch size. Because of this, I assume in the models to be developed in the next 2 chapters that handling time is essentially independent of clutch size for *O. ruficauda*.

The life history experiment showed that prepupal body size strongly affects adult fecundity. This is consistent with the findings for another tephritid, *Rhagoletis pomonella* (Averill and Prokopy 1987). However, Averill and Prokopy (1987) also found a significant negative relationship between body size and survivorship. I found no such relationship in *O. ruficauda*, at least under laboratory conditions. I will build the fecundity-size relationship into the theory to be developed in the next chapter. This experiment also showed that some individuals display strong between-day variation in egg laying

(Figure 4.3). Because day-to-day conditions were kept as constant as possible, I infer from this that egg laying reflects egg availability. Thus, in wild populations, individual oviposition decisions could well be shaped by egg limitation on one day and by time limitation on another day. Potential effects of variation in egg availability on clutch size will be explored in the final chapter.

The presence of male thistles in a locality has a strong effect upon the expected quality of a randomly-encountered host head. Since flies apparently alter their oviposition behaviour in low-quality host patches (cf. Figure 4.9), I infer that flies may be sensitive to this factor.

The purpose of the final two chapters is to construct and test a model predicting optimal oviposition behaviour in this system. In the final chapter, I will propose potential fly oviposition strategies wherein flies employ different levels of information availability and express different abilities to process that information. These strategies will be evaluated within the observed range of variation for such potentially-important factors as host pollination level, fly handling time, egg limitation, and conspecific density. The purpose is twofold: first, to evaluate the relative success of such potential strategies and second, to see if an egg distribution pattern consistent with field distributions will be generated by one or more of the strategies.

CHAPTER 5

THEORETICAL IMPLICATIONS OF FIELD- AND LABORATORY-OBTAINED DATA

5.1 Introduction

The purpose of this chapter is to use the data and conclusions of my field survey (Chapter 3), and my laboratory and field manipulations (Chapter 4), to develop a theoretical model of the oviposition behaviour (i.e., decisions on clutch size) of *Orellia ruficauda*. This model will be used to generate a framework which I will use in Chapter 6 to address the question of the importance of information to the reproductive success of *Orellia ruficauda* flies.

Field data show a remarkable lack of any density effects on larval success in the field. At no point were larvae limited by decreased food, or increased cannibalism, disease, or parasitism at higher densities. This suggests (and the estimation of larval carrying capacities supports this) that females distribute their eggs at densities far below the theoretical upper limit on the capacity of individual host flower heads to support their offspring. Notwithstanding the above, oviposition behavior must, at some level, be shaped by the carrying capacity of individual host heads, because larval food in such heads is limited. I suggest that the propensity of *O. ruficauda* to commit few eggs to individual seed heads is selected for by the possibility of food limitation. I will begin by assuming that flies are not able to assess anything about the quality of individual host heads and develop the theory from there in a bottom-up approach.

5.2 The Model

The simplest possible model assumes a relatively low level of available information. From the field data on the distribution of carrying capacity (Figure 3.8), and from the results of my manipulation of pollen availability in the field (Figure 4.8), I know that a randomly-encountered seed head will have a maximum capacity of about eight larvae in a high-quality locality, and about two to three larvae in a low-quality locality. However, a randomly-encountered seed head in either case can have resources sufficient to provision anywhere from 0 to 15 larvae. Per-offspring fitness returns from a clutch of **c** eggs, laid into a head which has **R** resources (i.e., f(c,R)) will be maximal as long as **R** represents a resource level that is greater than or equal to the amount neccessary to support **c** larvae. Larval densities in excess of food availability will presumably make all individuals undersized, since contest competition does not apparently occur in this species. Per-offspring fitness levels will thus decline when **R** is less than **c**. I can include the linear relationship between larval size and lifetime adult fecundity (Figures 4.4 and 4.6) to describe how larval success declines when resources within a head are limiting. I can then solve numerically for expected parental fitness returns from a clutch, **c**, laid into a randomly-encountered seed head by summing, for all possible resource states, the product of clutch size, **c**, probability of **R** resources being present, **p**(**R**), and the fitness expected from a clutch of **c** eggs sharing **R** resources, **f**(**c**,**R**) (Yoshimura and Shields 1987, Lalonde 1991). Thus,

$$1)\ \tilde{\omega}_c = \sum_{R=0}^{15} c \cdot p(R) \cdot f(c,R)$$

Incorporating some of the information gained in chapter three and four makes further refinements possible.

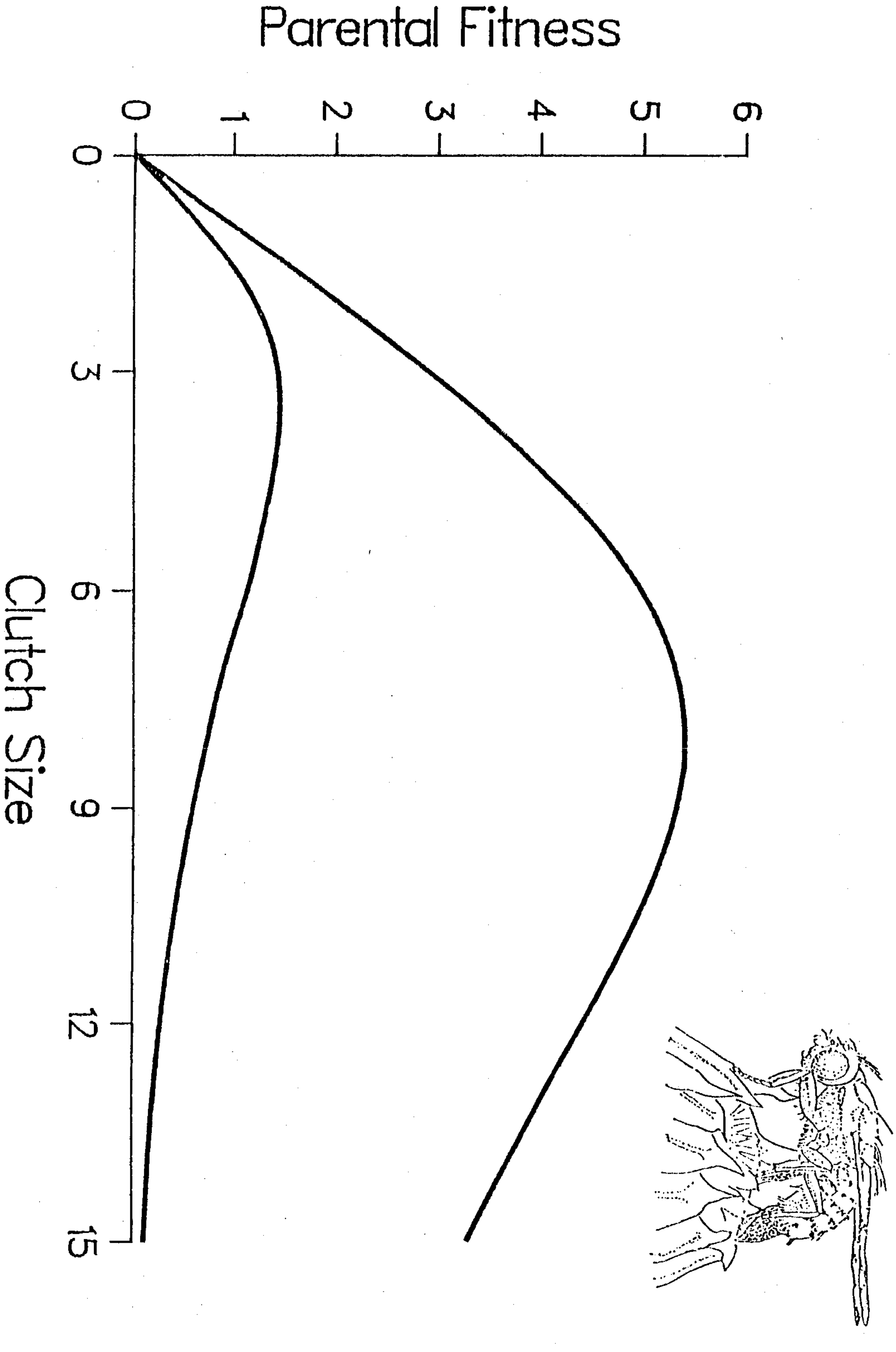
Even when adequate resources are available in a seed head, as in the field trials described in Chapter 3, there is still a certain degree of variance expressed in larval mass at maturity (see Figure 3.7). Thus, final larval size is not completely determined by food availability. Since I consider **f**(**c**,**R**) (i.e., offspring reproductive success) and offspring mass to be essentially equivalent, variation in larval size should translate directly into variation in offspring reproductive rate. Thus, if we let **f**(**c**,**R**) = M and allow the value of **M** to be distributed according to some probability density function, where the probability that **M** = **m** is σ_m. The mean value of **M** will be set by the resource level in the head, relative to the size of clutch and will take on the value of my assumed optimal larval size whenever **R** > **c**. The associated variance is assumed to vary in direct proportion to the mean. With this further level of variation built into the parental fitness model, equation 1) becomes

$$2)\ \tilde{\omega}_c = \sum_{R=0}^{15} c \cdot p(R) \cdot [\int_{m=0}^{\infty} m \cdot \sigma_m \, dm]$$

Figure 5.1 illustrates the fitness return expected from laying a given clutch of eggs in a randomly-encountered seed head where the value of the head is not known to the fly. The upper curve represents this relationship for a fly searching for hosts in a high-quality locality (i.e., a locality with male thistles locally present), and the lower curve represents this relationship in a low-quality locality. Here, I assume that the distribution of resource availability and larval mass to be normal. Means and variances were estimated from the distribution of carrying capacities on the dike site (Figure 3.8b) for resource availability in a high quality locality and from the four plots where males were not locally present (Figure 4.8) for resource availability in a low quality locality. Mean and variance of mature larval mass when resources are not limiting was estimated from field data (Figure 3.7).

Note that each curve has a static optimum (a point where a given clutch will produce maximal fitness) which is approximately 8 eggs per host in the high quality locality and 3 eggs per host in the low quality locality. These static optima place a theoretical upper limit on clutch size, since a fly laying superoptimal clutches will depress her own fitness. However, since both curves increase monotonically to these

Figure 5.1. Clutch size and parental fitness in high and low quality localities. The top curve represents the calculated fitness function for eggs laid in a high quality locality (male thistles present), and the bottom curve represents the fitness function for a low quality locality (male thistles locally absent).


Parental Fitness
0
1
2
3
4
5
6
Clutch Size
0
3
6
9
12
15

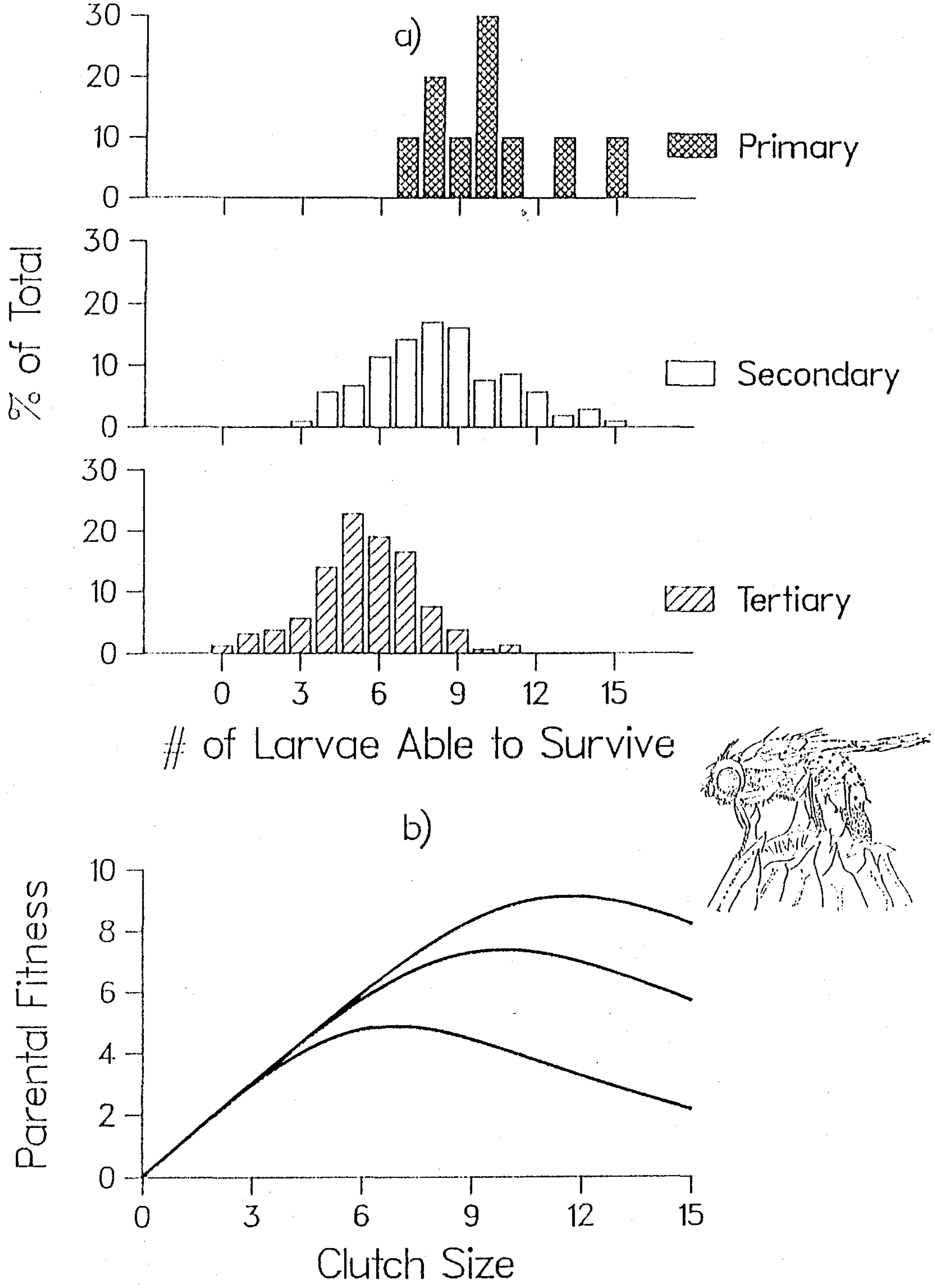
optima (i.e., per-egg fitness returns decrease), it is not likely that an egg-limited fly such as *Orellia ruficauda* will lay at the limiting clutch size, unless she cannot find very many host heads during the day.

This theoretical approach to describing clutch-size decisions can help to explain egg allocation patterns in the field. For example, recall from Chapter 3 that seed head size, as indexed by position on the inflorescence, floret number and achene mass, had a significant effect upon the carrying capacity of a given seed head. This factor did not, however, accurately predict larval infestation patterns in the sampled field population (Chapter 3). Why should this be so? As already shown, head size can be conveniently partitioned by separating heads into their primary, secondary, and tertiary size classes. The distribution of calculated carrying capacities in seed heads (sampled from the Dike site), separated by their size classes is illustrated in Figure 5.2 a. I used the mean carrying capacity and its variance, estimated for each head size-class from field data, to calculate parental fitness curves for the 3 seed head types using equation (2). The fitness functions are displayed in Figure 5.2 b. Clearly, fitness returns at low allocation levels are essentially identical for the 3 seed head types. Only at higher allocation levels is there any benefit to be derived from being selective. For example, a fly should discriminate tertiary heads from primary and secondary once average allocation levels exceed a clutch size of four eggs. Again, egg-limited flies

Figure 5.2, a,b. Distribution of seed head carrying capacity in primary, secondary, and tertiary seed heads and their corresponding fitness curves.

a) Carrying capacity broken down by seed head class

b) Expected parental fitness from clutches of eggs laid into the 3 seed head types. Top curve, primary heads; middle curve, secondary heads; bottom curve, tertiary heads.


a)
30
20
10
0
Primary
30
20
10
0
% of Total
Secondary
30
20
10
0
Tertiary
0
3
6
9
12
15
# of Larvae Able to Survive
b)
10
8
6
4
2
0
Parental Fitness
0
3
6
9
12
15
Clutch Size

probably seldom, if ever achieve per-head allocation levels of five eggs in nature. Discrimination on the basis of head size is therefore not likely to be demonstrable under field conditions. Furthermore, selection for such discrimination is likely to be quite weak.

I do not include an estimate of the fitness curves for the three head size-classes in low quality localities, because estimated carrying capacities do not differ much, if at all, between heads when pollination levels are very low ($p > 0.05$, ANOVA) for 3 of 4 sites where pollination was manipulated (Figure 4.7). Furthermore, while I do not reject the idea that significant differences in carrying capacity between primary, secondary, and tertiary heads may exist at low pollination levels, such differences will be even less likely to affect allocation decisions by an adult fly.

So far, this description of my system is too simplistic. In addition to hosts that are unattacked, flies will also tend to encounter hosts which have already been visited and attacked. Given the putative host-marking behaviour described in the first chapter, the well-documented propensity for other tephritids to mark hosts (Roitberg and Prokopy 1987), and the evidence presented in the preceding chapter (Table 4.1), it seems reasonable to suppose that individual oviposition decisions are mediated by a response on the part of female flies to their rate of encounter with pheromone-marked seed heads. Rejecting the idea that flies discriminate host size, flies now encounter two different types of hosts with two different utilities: 1) unattacked hosts which have the utility function described in Figure 5.1, and 2) marked hosts which have an as-yet undefined utility function. There are two alternatives within this scenario, both of which occur in other systems. The first is that flies express a simple threshold response to the presence or absence of a mark on a seed head, rather than any quantitative response to the amount of pheromone (Averill and Prokopy 1987). The second is that flies can directly assess the degree of prior parasitization by the density of marking pheromone on the seed head (Prokopy et al., 1982).

I will first consider scenario one. Lack of information on the degree of prior parasitization imposes additional variance, since the number of eggs in an infested head is unpredictable. Thus equation (2) now has additional uncertainty because attacked heads already have **x** eggs present. The value of **x** is generated from the probability density function ρ_x. Thus, the fitness of a clutch **c** of eggs laid into a marked head ($\tilde{\omega}_{\mathbf{c}_+}$), will be the product of the integral of the probabilities for all possible values of **x** with the expected fitness returns for a clutch of **c+x** eggs. Here, we let **f(c+x,R)** be represented by the distribution **M′**. Thus

$$3)\ \tilde{\omega}_{c_+} = \sum_{R=0}^{15} \int_{x=1}^{\infty} \rho_x \cdot c \cdot p(R) \cdot \left[\int_{m'=0}^{\infty} m' \cdot \sigma_{m'}\, dm'\right] dx$$

Egg number in an attacked head can be partially predicted by the frequency of attacked heads in a locality. A regression of mean number of eggs in attacked heads against the arcsine square root transformed proportion of heads that were attacked, yields a significant ($p < 0.05$, $r^2 = 0.26$), positive slope (Figure 5.3). This suggests that flies may be able to use their encounter rate with attacked heads to improve their ability to assess the utility of a marked seed head. I built this regression model into the utility equation and generated a numerical solution to equation (3) for fitness returns expected from a given clutch laid into a marked head when marked heads have been encountered at a given frequency or "attack rate". The fitness surfaces for high-, and low-quality localities are illustrated in figures 5.4a, and 5.4b respectively. Note that there is actually very little effect of intensity of attack on the shape of the utility function. This is because the regression model is a relatively poor predictor of infestation rate ($r^2 = 0.26$). Consequently the effect of frequency of encounter with attacked heads on the optimal clutch size is not large.

When flies can assess the number of eggs already inside a seed head more or less directly (eg. from the concentration of marking pheromone), the situation simplifies tremendously. Here, the value of a clutch of **c** eggs laid into a marked head is the product of the per-egg returns from a head with **c** + **x** eggs, times **c**, where **x** is the number of eggs already present. Again,

Figure 5.3. Proportion of seed heads attacked, and number of larvae inside attacked seed heads. Data were obtained from field studies described in Chapter 3. (Larvae per head = Proportion infested x 1.2028 + 1.26)

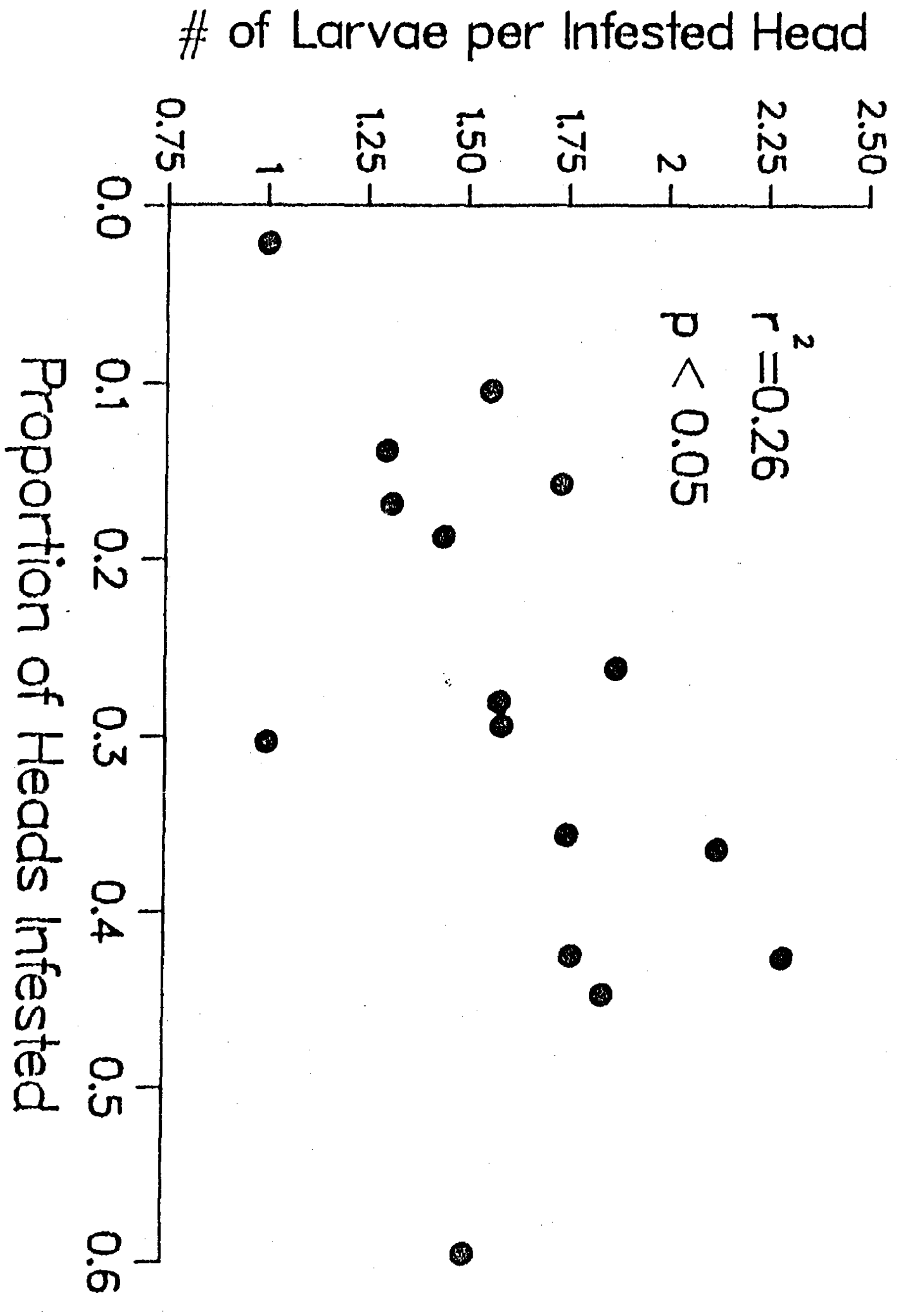
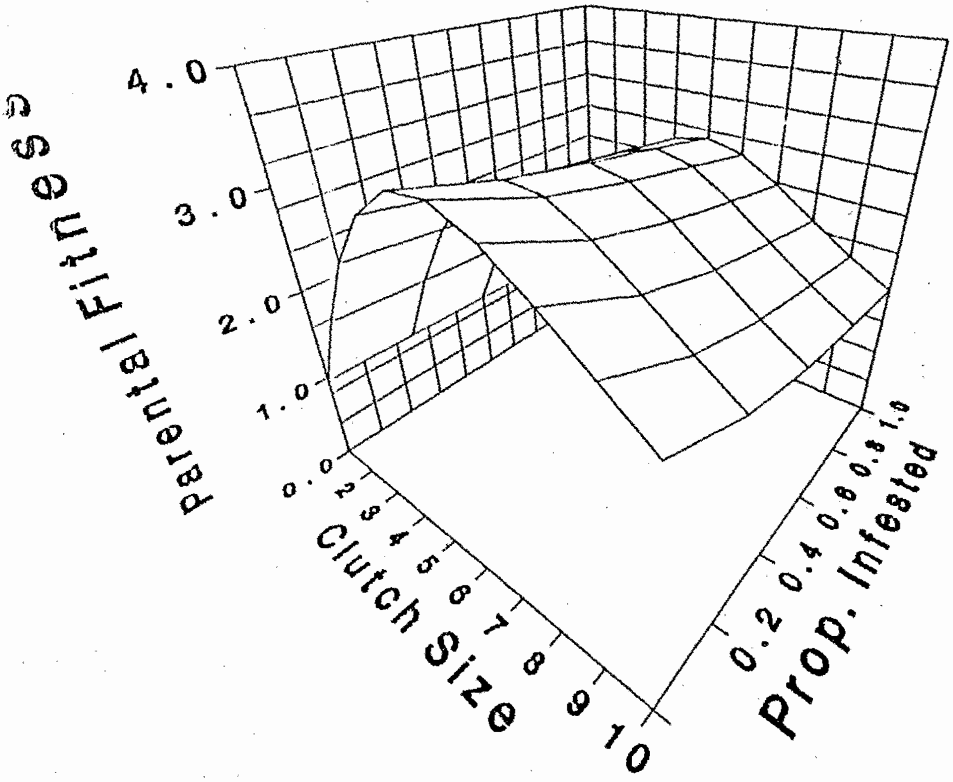

# of Larvae per Infested Head
0.75
1
1.25
1.50
1.75
2
2.25
2.50
$r^2 = 0.26$
$p < 0.05$
0.0
0.1
0.2
0.3
0.4
0.5
0.6
Proportion of Heads Infested

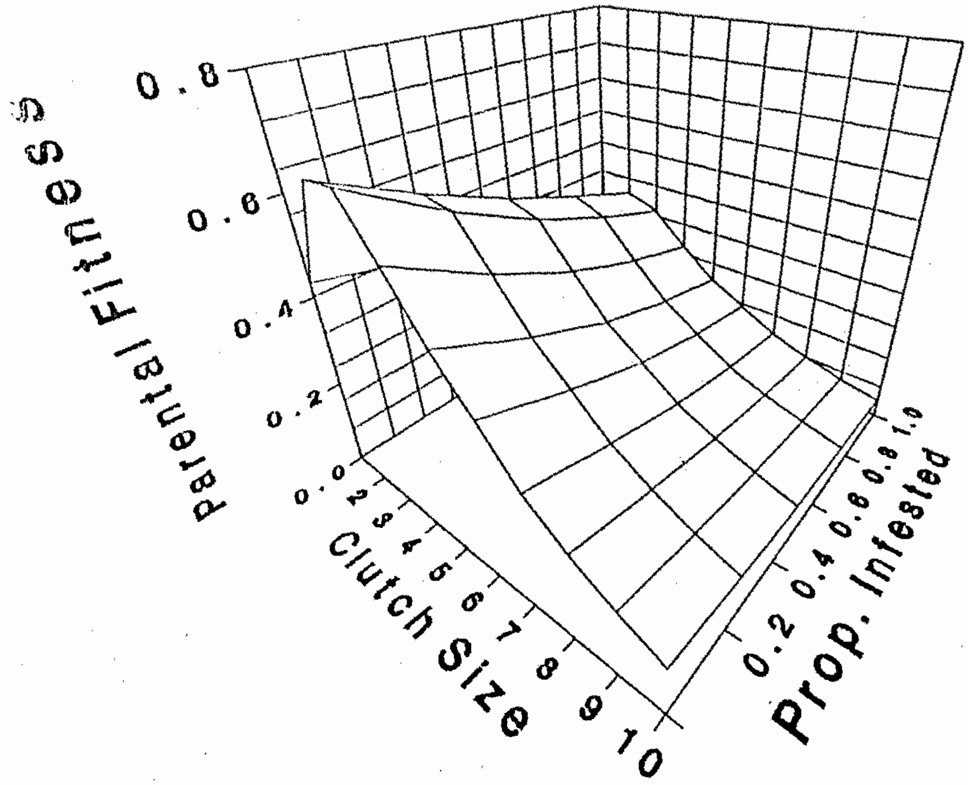
Figure 5.4. Expected fitness returns from clutches laid into previously infested heads. Flies have no direct way of assessing the number of eggs already present, but can estimate infestation levels from frequency of encounter with infested heads (attack rate).

a) Expected fitness returns in a high-quality locality.

b) Expected fitness returns in a low-quality locality.

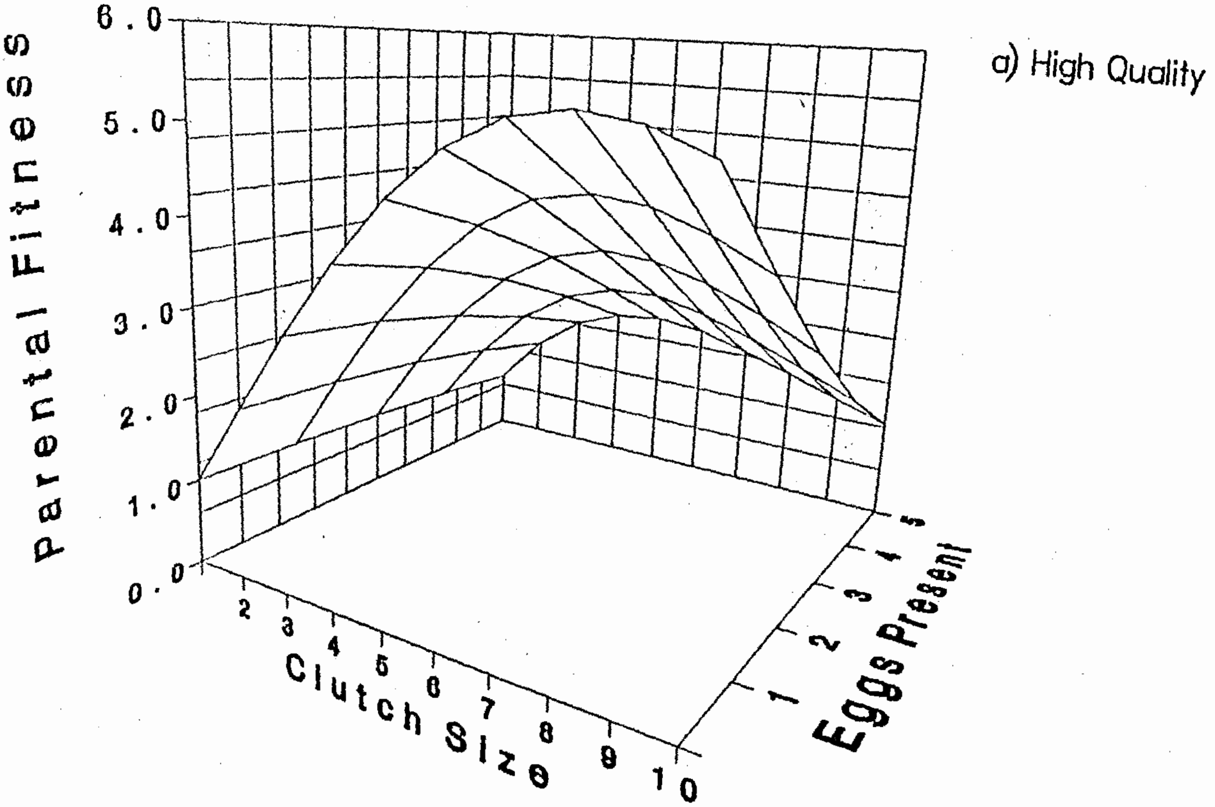


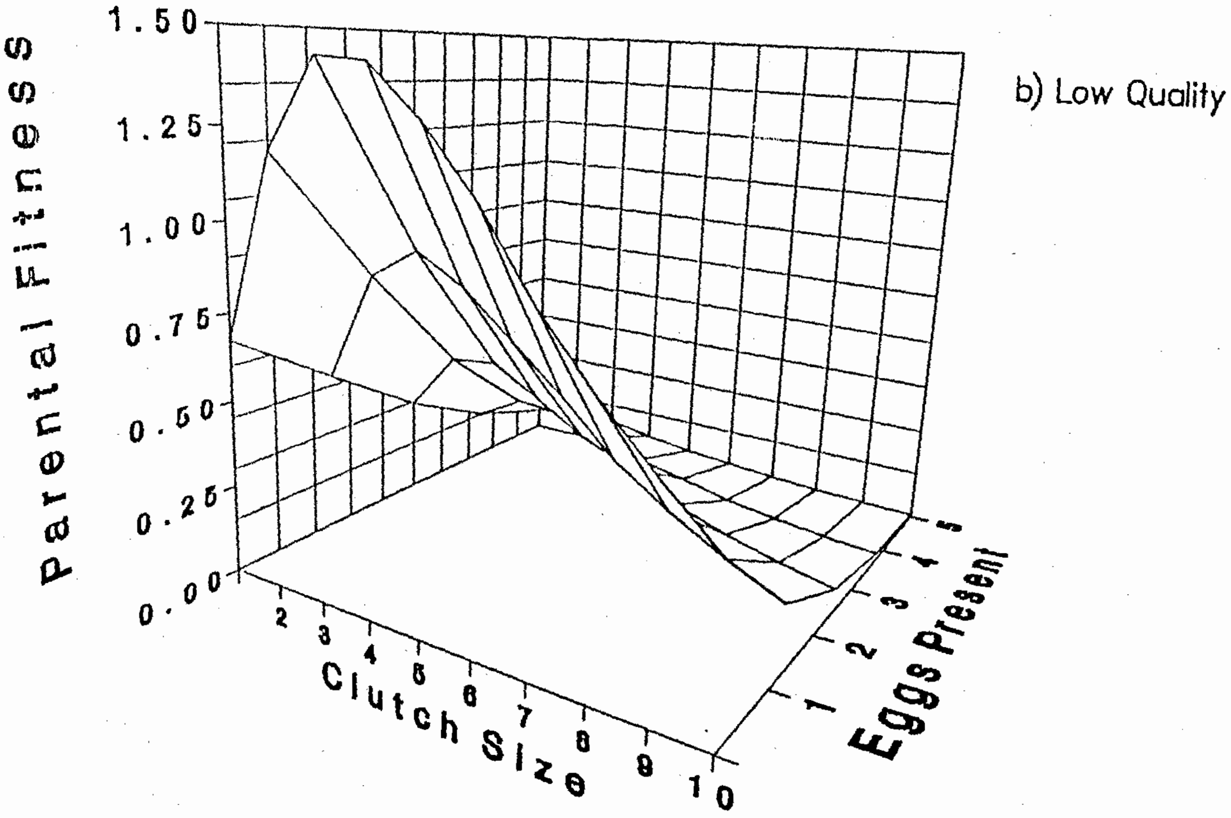
a) High Quality



b) Low Quality

Figure 5.5. Fitness returns expected from a clutch laid into a previously-infested seed head when the level of prior parasitization can be assessed directly, presumably by the concentration of pheromone present.
a) Expected returns in a high-quality locality.
b) Expected returns in a low-quality locality.


a) High Quality
Parental Fitness
6.0
5.0
4.0
3.0
2.0
1.0
0.0
Clutch Size
2
3
4
5
6
7
8
9
10
Eggs Present
1
2
3
4
5


b) Low Quality
Parental Fitness
1.50
1.25
1.00
0.75
0.50
0.25
0.00
Clutch Size
2
3
4
5
6
7
8
9
10
Eggs Present
1
2
3
4
5

let **f(c+x,R)** be represented by the distribution, **M′**

$$4)\ \tilde{\omega}_{c_+} = \sum_{R=0}^{15} c\cdot p(R)\cdot\left[\int_{m'=0}^{\infty} m'\cdot\sigma_{m'}\,dm'\right]$$

The fitness surfaces illustrated in Figure 5.5a,b clearly show that there is a strong effect of increasing levels of pre-parasitization on the expected fitness of the current clutch. Note also that this surface is considerably steeper at the lower levels of pre-infestation than are the surfaces illustrated in Figure 5.4. The reduction in variance from knowing how many eggs are already present confers a strong advantage to the female fly. Finally, the perceivable changes in the fitness of a given clutch size at different parasitism levels are far more dramatic when female flies have access to this level of information (cf. Figure 5.4a,b).

5.3 Discussion

What does this simplified treatment of clutch size decisions tell us? First, If we assume that the laying of each egg imposes a handling time cost, and that there is a non-zero between-flowerhead travel-time cost, we have the patch residence time problem formalized by Charnov (1976) and Parker and Stuart (1976). In this case, we simply apply it to a clutch size problem. Thus, as with the classic foraging problem, an individual's allocation decision will depend upon the amount of time that the fly has spent travelling between hosts (Charnov and Skinner 1984, Parker and Courtney 1984, Skinner 1985). I have shown, however, that there is no reason to suppose that per-head handling time and clutch size are tightly correlated in this system (Figure 4.2a). Time effects are thus assumed from now on to be simply the interaction effect of a fixed handling time, egg availability, and host availability on allocation decisions. Since flies in the field commonly lay both single-egg and multiple-egg clutches, such time costs may vary in importance, depending on individual circumstances.

I can also infer here something about the cost of superparasitism in high-quality localities. Fitness returns expected from a given clutch laid into a previously-parasitized, high-quality head are quite high when compared with the returns expected from an identical clutch laid into an uninfested head (see figure 5.5a). In light of this, why should flies selectively avoid previously-parasitized seed heads? Even species that typically mark hosts often do not use, or apparently respond to marking pheromone on very high quality hosts (Zimmerman 1980, Prokopy et al. 1982). The utility of being able to recognize conspecific marks in this system when host quality is high will be tested in the final chapter.

While many of the parameters affecting larval fitness have been estimated and incorporated into the clutch-size allocation model, less is known about how female flies integrate available information into an oviposition strategy. At this point I have developed a series of static models that can be used to calculate the perceived utility of a single encountered seed head. Information use can place this perceived utility into a relative context. For example, in Figure 5.4 b, maximal fitness returns are obtained from a clutch size of 2 eggs under all circumstances. However, a 2 egg clutch will only be optimal if the fly only encounters a single marked head. This will usually not be the case. Absolute fitness returns expected from laying an egg into a marked head in a low-quality locality are extremely low, especially at high infestation rates. Flies should only lay a clutch which yields per-egg fitness returns that are at least equal to what they can expect from an average encounter. Thus, a fly that encounters marked heads at a high frequency, but can also expect to encounter a sufficient number of unmarked heads to accomodate all of her eggs will avoid parasitizing marked heads entirely. A more formal treatment of this will be presented in the next chapter where I will develop the simulation model.

It is possible to postulate a number of different oviposition strategies from the material presented so far. The purpose of the next chapter is to attempt to identify the most likely of these. However, there are still a number of aspects of the *Orellia ruficauda* - Canada thistle system that I do not know about.

In terms of information, I do not know whether flies can discriminate;

1) Frequency of attacked seed heads in a locality relative to unattacked seed heads

2) Number of eggs present in already-attacked seed heads

A portion of the Monte Carlo simulations described in the next chapter will be devoted to finding out if it is important for the flies to know this.

Furthermore, physical constraints can affect oviposition strategy. Flies vary tremendously from individual to individual (Figure 4.4, 4.6) and from day to day (Figure 4.3) in the number of eggs that they produce. Since conditions were kept as constant as possible during the life-history study, I assume that eggs allocated/day is an adequate index of eggs available/day. Clearly, a fly that has 30 eggs available for oviposition will be more likely to be time-constrained than will be a fly that has only one or two eggs ready for laying. Can the range of variation in egg availability observed under laboratory conditions affect the success of a fly's oviposition strategy?

The purpose of the next chapter is thus to integrate the discrete fitness functions that I have derived for flies that have encountered unattacked and attacked seed heads into an allocation strategy that will act to maximize daily fitness returns. By changing the informational and physical constraints operating on the system I hope to see if increased information availability translates into increased fitness returns. Finally, patterns of infestation emerging at the population level are generated by the behavior of individuals. A correspondence between an infestation pattern generated by model flies adopting a given strategy and the infestation pattern observed in the field may indicate a similar correspondence in underlying behaviour.

CHAPTER 6

SIMULATION AND SYNTHESIS

6.1 Introduction

Initially, I asked what value information (and the ability to process that information) has when a parasite is foraging for hosts in a variable environment. I have subsequently defined many of the physical and life-history parameters of this model host-parasite system and used those parameters to generate utility functions for flies using seed heads - as utility would be perceived by flies that can access different levels of information. Here, I assume that a fly will act within its perceptual and informational constraints to maximize its reproductive success. Given this, I can now compare the viability (do they maximize fitness?) and the appropriateness (do they mimic flies in the field?) of flies adopting a number of possible oviposition strategies; strategies which incorporate a range of perceptual and information-integrative abilities.

Since it is difficult, if not impossible, to prevail upon real flies to adopt particular strategies, the only way to compare the success of purely hypothetical strategies is to resort to Monte Carlo simulation. Ideally, as much realism should be built into the model as is possible. In all of the four strategies compared in this chapter, I assume that flies optimize their reproductive allocation. What I vary is the quality of the information available to them.

In this chapter I use two approaches to evaluate the validity of my hypothetical strategies. First, I compare relative fitness over a range of ecological conditions and physiological states. The assumption here is that, given an adaptationist point of view, I expect the strategy that confers highest fitness in the simulation will be the strategy most likely to be selected in nature. Secondly, I compare the egg distribution patterns generated by the behaviour of "flies" using these hypothetical strategies, with egg distribution patterns observed in the field in high and low quality localities. I assume that the strategy that produces the pattern most similar to that observed in the field will be the strategy most similar to that employed by actual flies in nature.

The process of adjusting allocation of offspring to hosts in response to perceived host availability is straightforward. As pointed out by Charnov and Skinner (1984) and Parker and Courtney (1984), such an allocation decision is no different from a foraging problem. A large body of literature deals with this (Stephens and Krebs 1986), and here I have flies adopting a relatively simple procedure. What I address in this chapter is the problem faced by a fly that encounters hosts that are unexploited and hosts previously attacked by a conspecific. Potentially, both the frequency of encounter with attacked heads and the attacked heads themselves can provide information to the fly. On one level, an increasing rate of encounter with marked heads may decrease the perceived density of unattacked seed heads. Furthermore, encounters with attacked heads may also tell the fly something about the residual utility of such heads as hosts. How should a fly allocate eggs to heads as the relative proportion of attacked heads changes over the day?

If a fly can recognize that a head has been attacked, but cannot estimate the number of eggs that are already present, its best option may be to forgo any residual utility that a head may have, and simply avoid ovipositing in it entirely. This will be a viable strategy as long as the fly encounters sufficient unattacked seed heads during its foraging day. A fly may adopt a more sophisticated approach however, and make some evaluation of the profitability of an attacked head relative to that of an unattacked head. Flies do superparasitize in this, and other systems (Roitberg and Prokopy 1983, Mangel and Roitberg 1989), particularly when host encounters are rare. As outlined in Chapter 5, flies could calculate profitability of marked heads either by estimating density of conspecific eggs from frequency of encounter with attacked heads, or by directly assessing prior infestation level in some way, such as using the concentration of marking pheromone. Thus, we have three ways of dealing with previously-attacked heads:

1) Avoid laying entirely ("Avoid")
2) Estimate profitability from relative frequency and use as required ("Estimate")
3) Estimate profitability directly from the number of eggs

that are already present, and use as required ("Measure"). In these Monte Carlo simulations, I will also add a null strategy for purposes of comparison, i.e.,

4) Treat all encountered heads as uninfested ("Ignore")

I will be comparing computer-generated egg distribution patterns, and fitness returns for flies following these four strategies in all of the model runs described below.

6.2 The Simulation Model

6.2.1 The basic model

The basic simulation routine begins with the creation of an array of host seed heads. Each head is randomly assigned an "age" (time when it is susceptible). I run the model over five foraging "days", thus this number takes on a value between 1 and 5. This fixes the mean frquency of susceptible heads in the population at 20% for any foraging day. To minimize the number of permutations, I did not vary this parameter. However, I did complete a few runs with host heads at lower frequencies and found that the model results were insensitive to this factor. Finally, the head is assigned a carrying capacity, drawn from a normally-distributed random number generator, with mean and variance derived from field data.

6.2.2 The oviposition decision

The simulation model is run by releasing a "fly" which is equipped with a given strategy and a given set of behavioural and physiological constraints into the "environment". The decision process followed by the fly is illustrated in Figure 7.1. The actual clutch size decision is determined by the particular global strategy that the fly follows. However, all strategies have some common features.

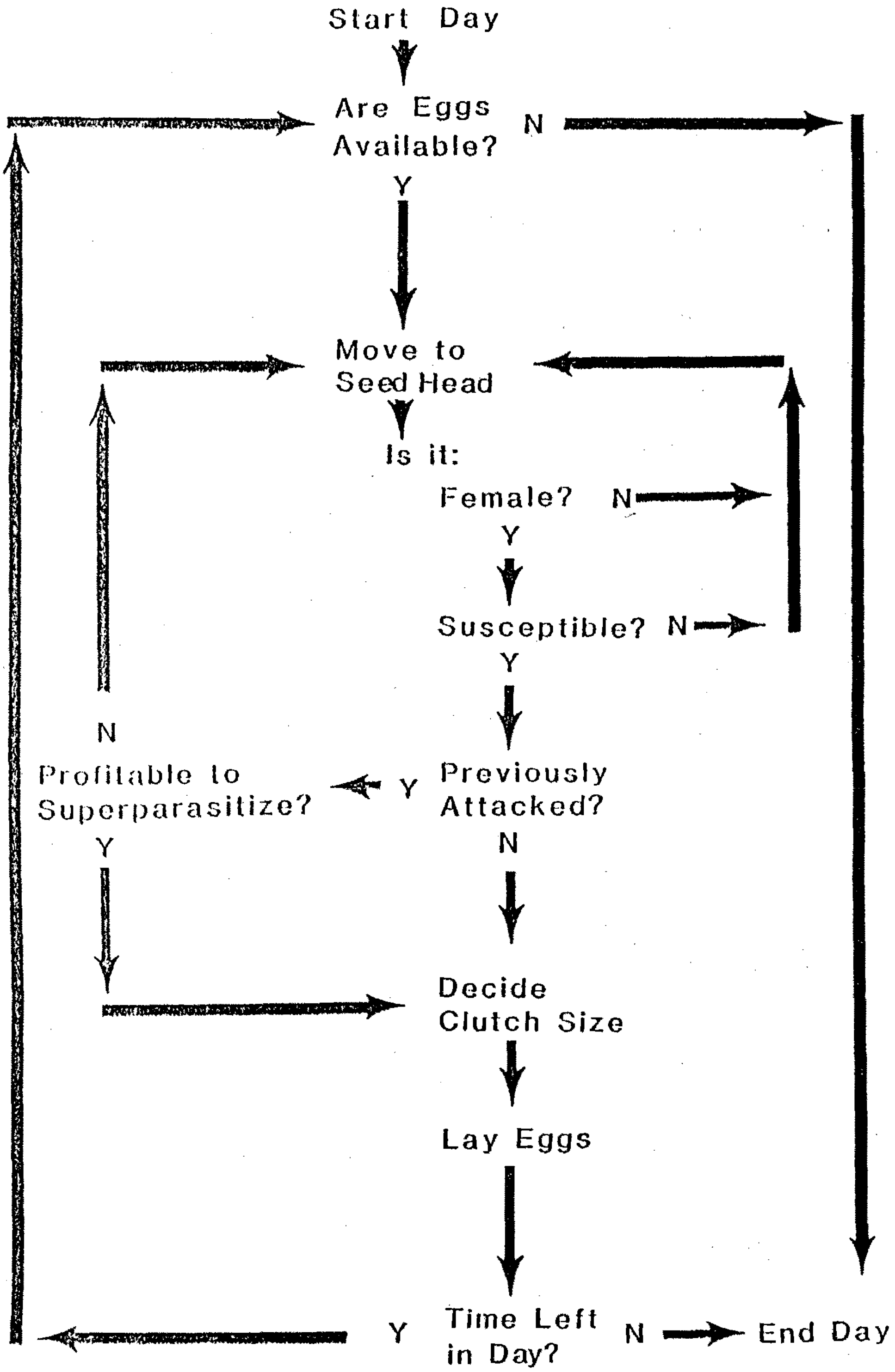
I assume that flies are selected to maximize lifetime fitness, within their physiological and informational constraints. I further assume that flies achieve this by maximizing the reproductive value (Fisher 1930) of a given allocation decision. In other words, a fly with limited eggs available should consider, not only returns expected from the present clutch of eggs, but also the effect of present allocation on future egg availability (and resulting lost opportunities). Thus, each time a clutch size decision is made, a fly should maximize the sum of the fitness returns expected from the current oviposition event and returns expected from future ovipositions that will occur that day. Optimal clutch size will thus be

$$5)\ C^{*} = c,\mathrm{MAX}[\tilde{\omega}^{o}_{c} + \tilde{\omega}_{(e-c)/n}\cdot n]$$

where

$n <= (e-c)$

Figure 6.1. Decision algorithm for a fly foraging for hosts in a thistle patch.


Start Day
Are Eggs Available?
N
Y
Move to Seed Head
Is it:
Female?
N
Y
Susceptible?
N
Y
N
Profitable to Superparasitize?
Y
Previously Attacked?
N
Y
Decide Clutch Size
Lay Eggs
Y
Time Left in Day?
N
End Day

Here, $\tilde{\omega}^{o}_{\mathbf{c}}$ is the expected fitness returns from a clutch size of **c** eggs laid into the currently-encountered seed head. The numerical value of $\tilde{\omega}^{o}_{\mathbf{c}}$ is determined by the equation appropriate to the strategy being run through the simulation (one of the equations outlined in Chapter 5). The reproductive success expected from all future ovipositions is $\tilde{\omega}_{(\mathbf{e}-\mathbf{c})/\mathbf{n}} \cdot \mathbf{n}$ where **e** is the number of eggs currently in the abdomen, and **n** is the number of times a fly can expect to encounter a host head in the time remaining to it. **n**, is estimated by dividing the average of the search interval and the handling time costs associated with each previous oviposition, i, into the time remaining in the day. Thus;

6) $n = (T - t)/i$

where t is the current time in the searching day, and T is the time at the end of the day.

If the fly has not yet attacked a host in a given foraging day, it estimates future reproductive success as the returns expected from laying a single-egg clutch into a clean head, multiplied by the number of eggs that will remain in its abdomen. After the first oviposition event, future reproductive success is estimated as the average per-egg fitness returns realized during the day, multiplied by the number of eggs that remain in the abdomen. This is a fair approximation as long as time remaining in the foraging day is not less than that required to find enough heads to maintain the current allocation level.

If the expected number of future encounters with hosts is not sufficient for the fly to be able to allocate its eggs at the present level, it will have to be less choosy in future encounters, or else it will not derive the maximum benefit from its eggs. In this case, a model fly estimates future reproductive success as the product of the number of probable remaining encounters with a host and the returns expected from dividing remaining eggs evenly over the remaining encounters (To simplify matters, I do not build the possibility of egg resorption into the model.). In this scenario, flies that can discriminate previously-attacked heads calculate the proportion of future encountered heads that will be attacked already, and the degree of prior parasitism. Flies then discount the expected fitness returns from future clutches by the proportion expected to be allocated to previously-attacked heads. Fitness returns to be expected from laying into a randomly encountered, previously-attacked head are estimated from prior estimates of parasitism levels in such heads. The simplifying assumption is that there will be no differential allocation between marked and unmarked heads in the future, except in the case of the "avoid all attacked heads" strategy. Finally, egg maturation only occurs overnight. Thus, there is no production of new eggs during the foraging day. A more advanced model is presented by Charnov and Skinner (1988), which incorporates a maturation factor that increments **e** as the day proceeds.

6.2.3 Sensitivity Analysis

Flies forage in situations where conspecific density and egg availability vary a great deal. A robust oviposition strategy should ideally be one which succeeds over the natural range of variation in these density factors. Thus, I included a range of egg availabilities and conspecific densities in the sensitivity analysis. Finally, handling time was a highly variable factor (Figure 5.2), showing a tenfold range of variation. Here, I varied handling time in the simulation in order to determine whether such variation affects the relative success of the four allocation strategies to any significant degree.

6.2.4 Validation

I evaluated fitness returns of different strategies first, by comparing the relative success of populations adopting a single strategy, and second, by examining the relative success of pairs of strategies competing within a single population. I ran the different model versions for "sites" that had male plants present locally, and for "sites" where male plants were not present. I deemed a successful strategy to be one that did best in both high and low quality situations, because flies will likely encounter both in nature.

In addition to comparing fitness of different strategies, I also compared egg dispersion patterns at the population level. I already have some indirect evidence that flies recognise (Table 3.5) and respond in some way to the local presence of male thistle plants in a locality (Figure 4.9). The regressions fitted through the log mean - log variance scatter for sites with and without male plants gave me a template to help validate my model results. Thus, in addition to maximizing a fly's fitness, a realistic oviposition strategy should also produce significantly different egg distribution patterns in high and low quality localities. This difference should correspond with that observed in nature.

6.2.5 Execution and Analysis

I first compared fitness of populations of pure strategies. I ran the simulation model for a minimum of 20 times for each unique combination of handling times of 0.001, 0.01, and 0.1 of the foraging day, egg loads in the abdomen of 4, 8, 16, and 32 eggs, and host availabilities of 12.5, 25, 50, and 100 seed heads per day/fly. I compared the reproductive success of flies at a given host density using a 3-way analysis of variance (main factors were Strategy, Handling time and Egg load).

For pairs of strategies in competition within a single population, I fixed handling time at 0.01 of the total foraging day and set egg availability at 16 eggs/day. Host availability was set at 12.5, 25, 50, and 100 hosts per fly per day. Relative frequency of each strategy was kept at 50%. The reproductive success of each strategy was evaluated using 2-way Analysis of Variance for each pairwise interaction, with strategy and host availability as main effects. Again, the model was run for each combination for a minimum of 20 iterations.

The relative frequency of a strategy in a population may determine its success when in competition with other strategies. Thus, frequency-dependent effects on pairwise interactions were also evaluated, but only for the interaction between the "estimate" and the "avoid" strategies and the "measure" and the "avoid" strategies. In this run, host availability was kept constant at 12.5 hosts per fly per day. Each fly had 16 eggs available to it each day, and handling time was set at 0.01 of the total foraging day. Each strategy varied in frequency from 6.25% of the population to 93.75% of the population. Again, a minimum of 20 runs of each combination were carried out, and the relative success of each strategy at a given frequency was evaluated with a paired t test.

I compared the log mean vs log variance scatters generated by the simulations in high and low quality localities for each unique combination of egg availability, handling time and strategy, using an analysis of covariance. I also compared the generated egg distributions to those observed in the field.

6.3 Simulation Results

6.3.1 Sensitivity

The relative success of, and distribution pattern generated by different strategies is extremely insensitive to variation in handling time. The only noticable effect of handling time occurred when egg availability was relatively high. In this circumstance, long handling times made for large clutches, even when seed head availability was also high.

The relative success of the 4 different strategies when pure was, however, sensitive to host availability and egg number. Representative data are shown in Figure 6.2. When local patch quality and host availability were high, all strategies did equally well (Figure 6.2a). When competition for limited hosts was high, the "avoid" strategy did poorest when patch quality was high (Figure 6.2a), but was second only to the "measure" strategy (the one with the highest quality information) when local patch quality was low (Figure 6.2b). The naive strategy, "ignore" did surprisingly well, and actually surpassed the "avoid" strategy when competition for limited hosts was high in high quality localities.

Host availability again strongly affected the success of different strategies when in competition, but not always in the way indicated by the fitness returns generated in "pure" populations (Figure 6.3). The relatively sophisticated strategies, "estimate" and "measure", did quite well when

Figure 6.2 a,b. Reproductive success of 4 oviposition strategies with high (25/day) and low (12.5/day) host availabilities. a) High quality hosts. b) Low quality hosts.

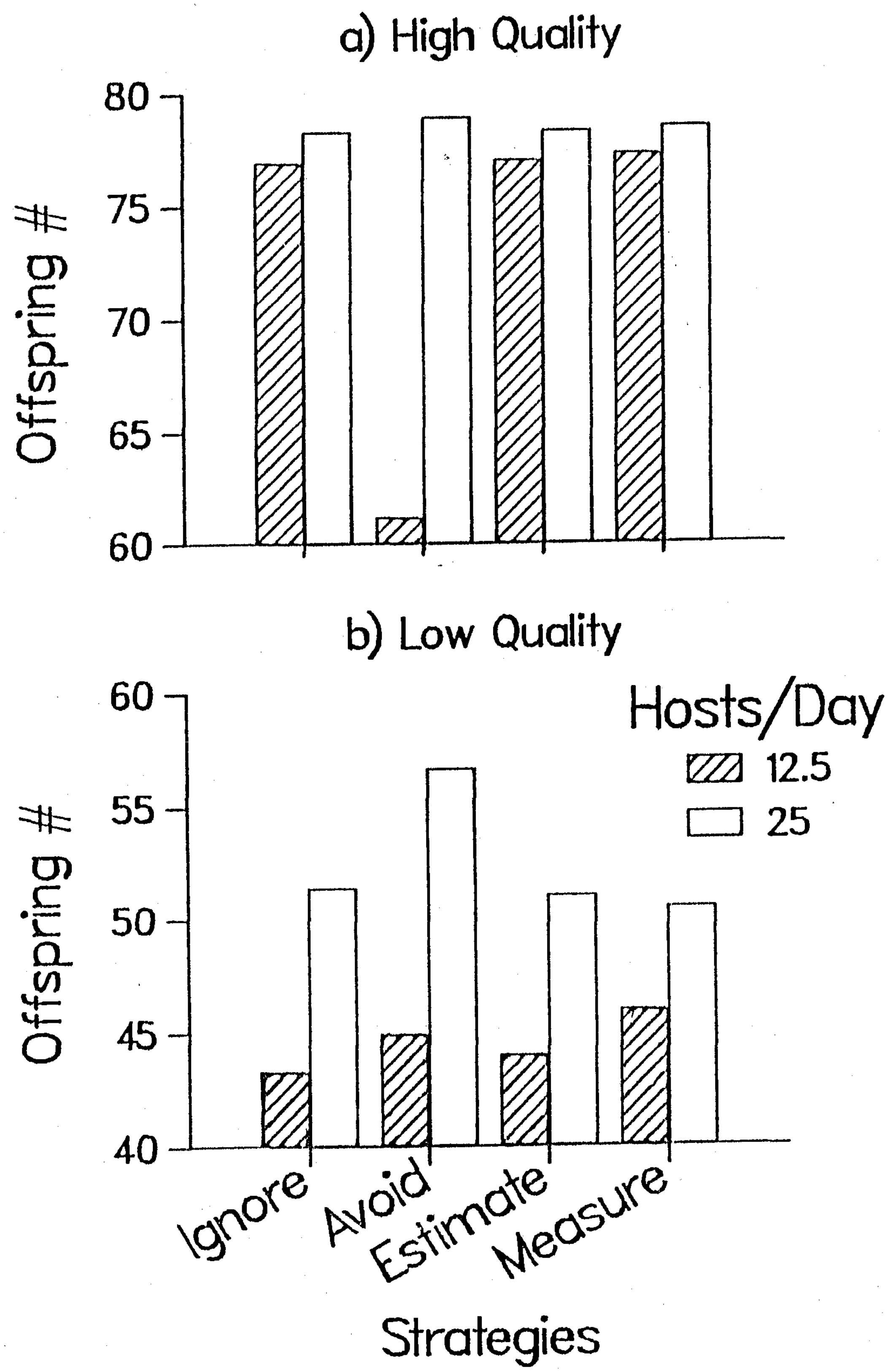
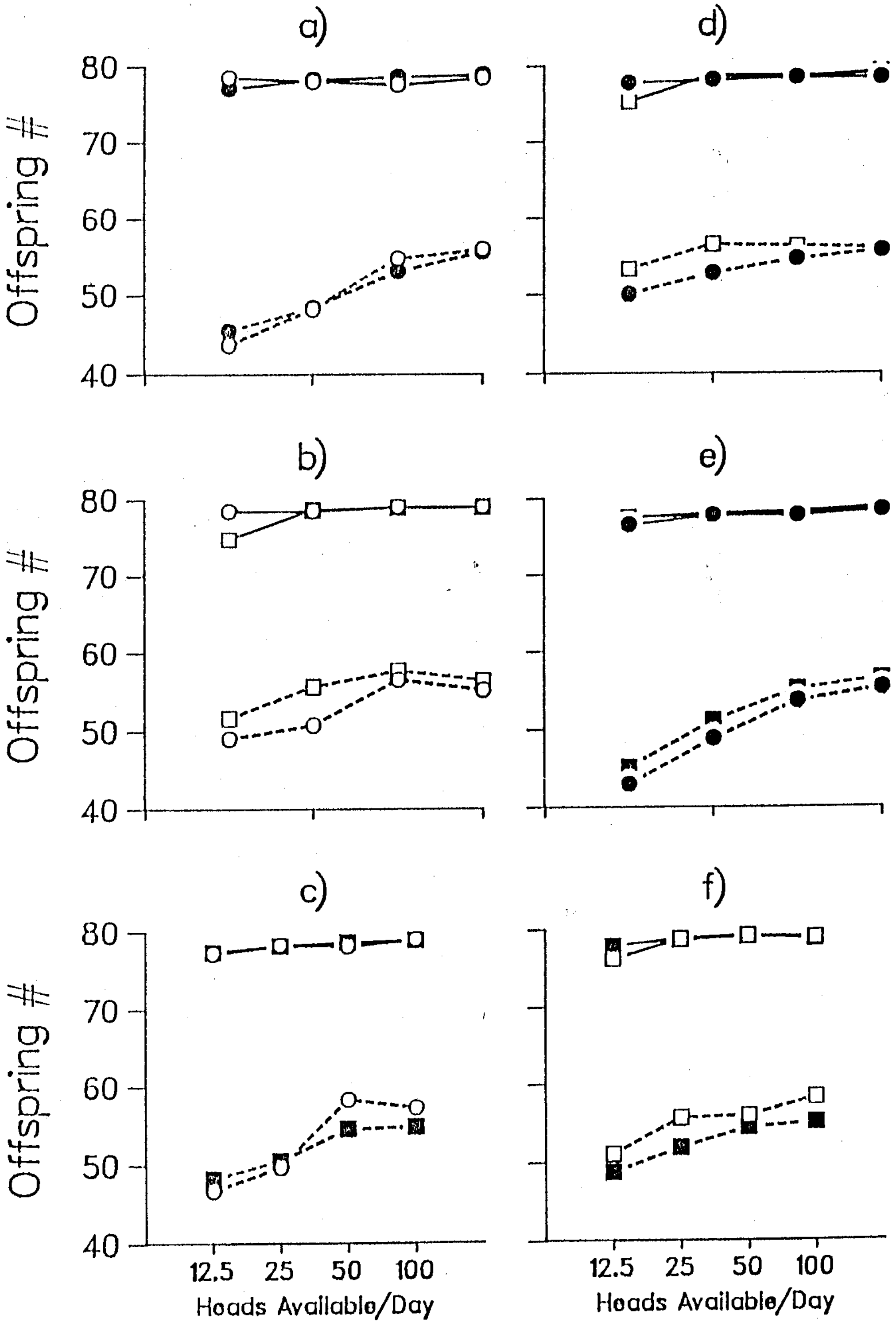

a) High Quality
Offspring #
80
75
70
65
60
b) Low Quality
Offspring #
60
55
50
45
40
Hosts/Day
12.5
25
Ignore
Avoid
Estimate
Measure
Strategies

Figure 6.3 a-f. Reproductive success of pairs of strategies in competition. Equal proportions interact in all cases. Strategies are: 1) Ignore (open circles), 2) Estimate (closed circles), 3) Avoid (open squares), and 4) Measure (closed squares). All flies have 16 eggs per day available and experience a per-clutch handling time cost of 0.01 of the foraging day. Solid lines denote interactions in localities with high quality hosts and dashed lines denote interactions in localities with low quality hosts. a) Ignore vs Estimate, b) Ignore vs Avoid, c) Ignore vs Measure, d) Estimate vs Avoid, e) Estimate vs Measure, f) Measure vs Avoid.


a)
d)
b)
e)
c)
f)
Offspring #
80
70
60
50
40
12.5
25
50
100
Heads Available/Day

competing with "avoiders" in high quality localities, especially when host availability was low (Figure 6.3 d,f). However, both of these 2 information-rich strategies did poorly when competing with "avoiders" in low quality localities at all levels of host availability (Figure 6.3 d,f). Again, the most naive strategy, "ignore", did quite well under conditions of high host availability. In fact, this strategy actually did slightly better than "estimators" and "measurers" when these competed within a low quality locality and host availability was high (Figure 6.3 a,c). Advantages to discrimination were conferred here only when host availability was low.

The outcome of these interactions was sensitive to the relative frequency of each interacting strategy in the population. When "avoiders" competed with "estimators" and "measurers", no strategy fared best at all frequencies. All strategies tested did poorly when they occurred at a high frequency in the population. "Avoiders" started to lose out to "estimators" and "measurers" in high quality localities once their frequency increased past 25% of the population. This switch in advantage occurred at a much higher frequency in low quality localities (i.e., > 50%) for both interactions (Figure 6.4 a-d).

Figure 6.4 a-d. Reproductive success of strategies in the Avoid vs vs Estimate interaction and the Avoid vs Measure interaction over a range of relative frequencies. Host availability is set at 12.5 hosts per fly per day. Flies have 16 eggs available per day and experience a handling time cost of 0.01 of the foraging day. Open squares- Avoid; Closed squares- Measure; Closed circles- Estimate. a) Avoid vs Measure - High quality hosts, b) Avoid vs Measure - Low quality hosts, c) Avoid vs Estimate - High quality hosts, d) Avoid vs Estimate - Low quality hosts.

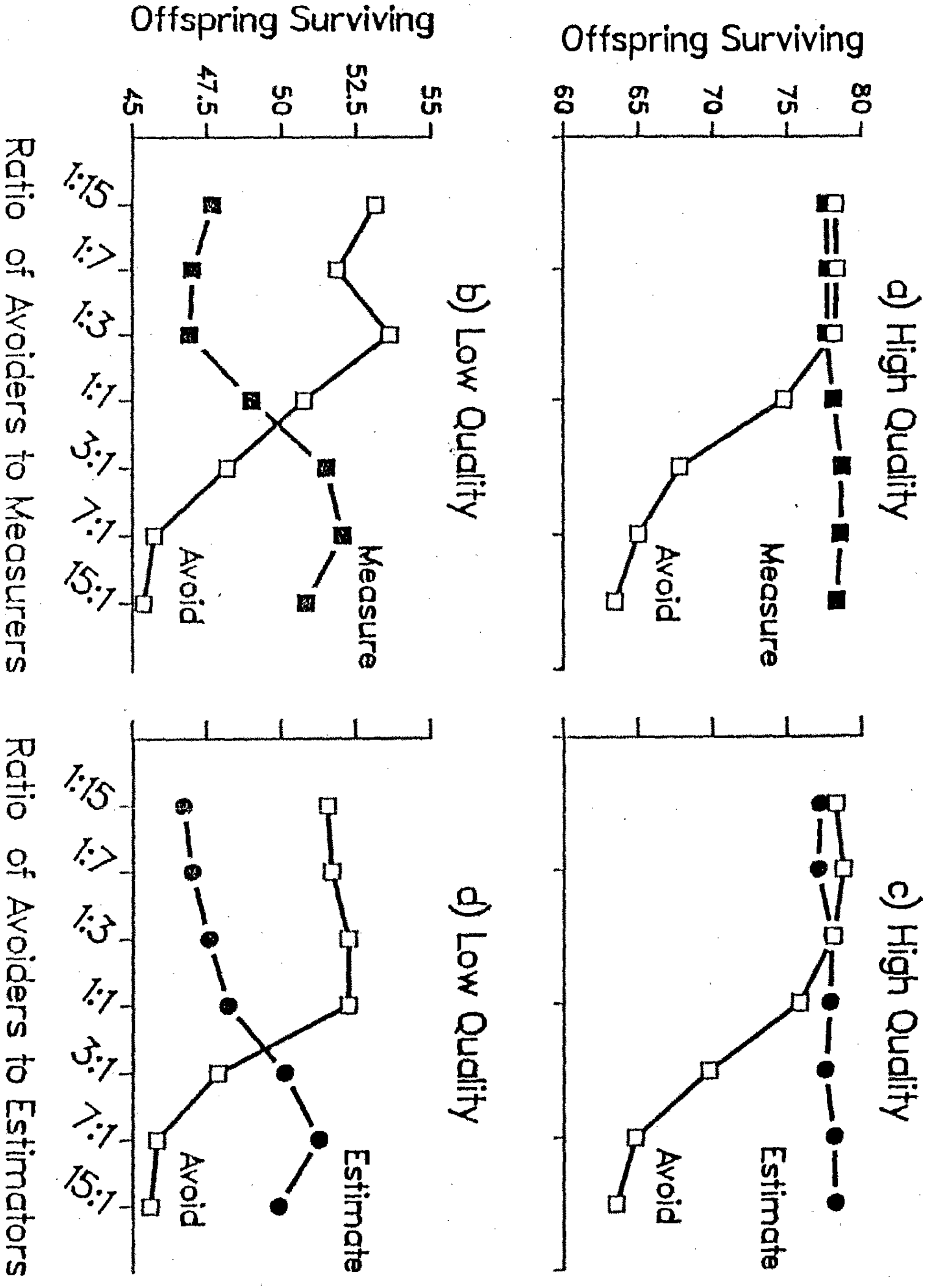
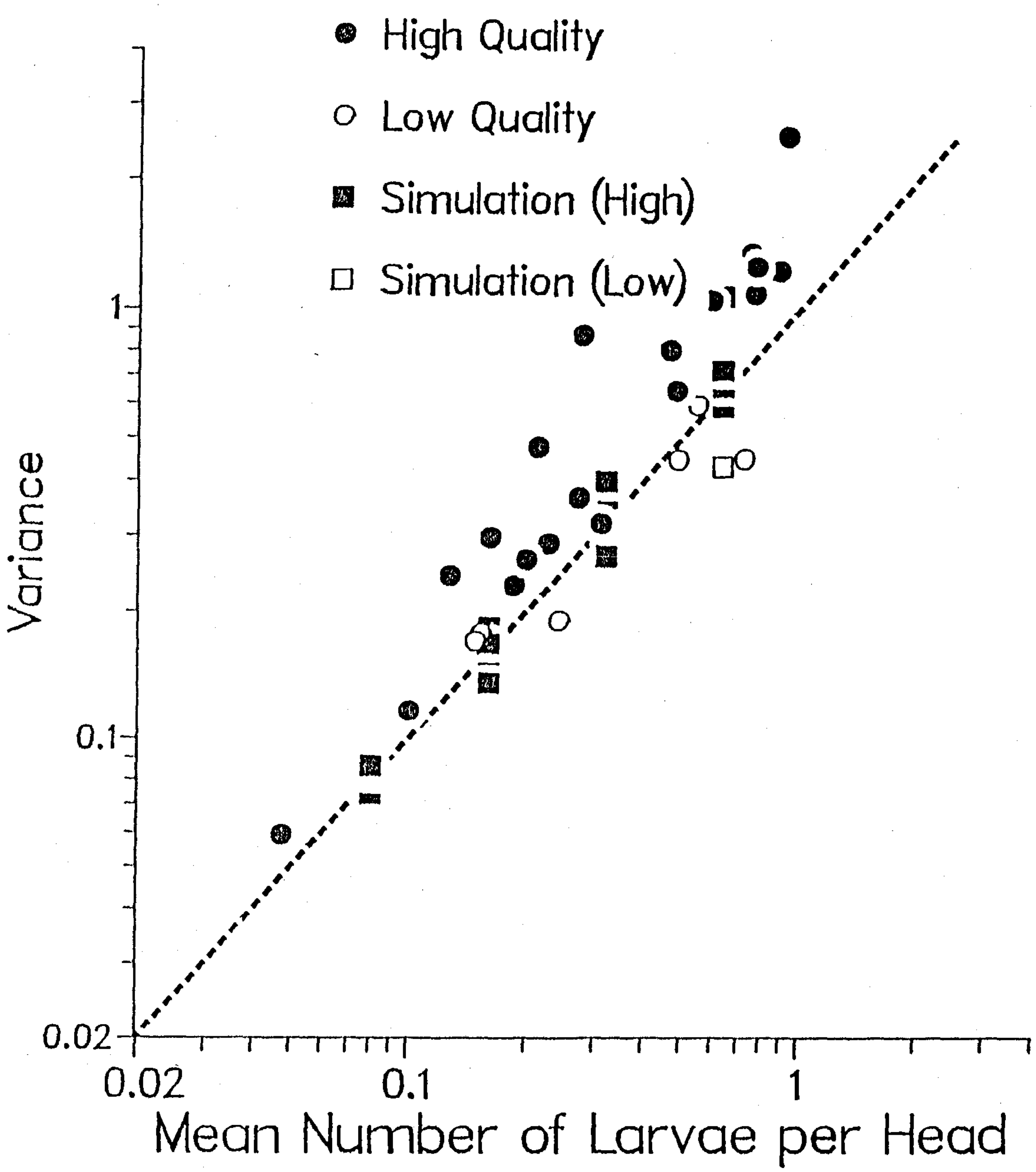
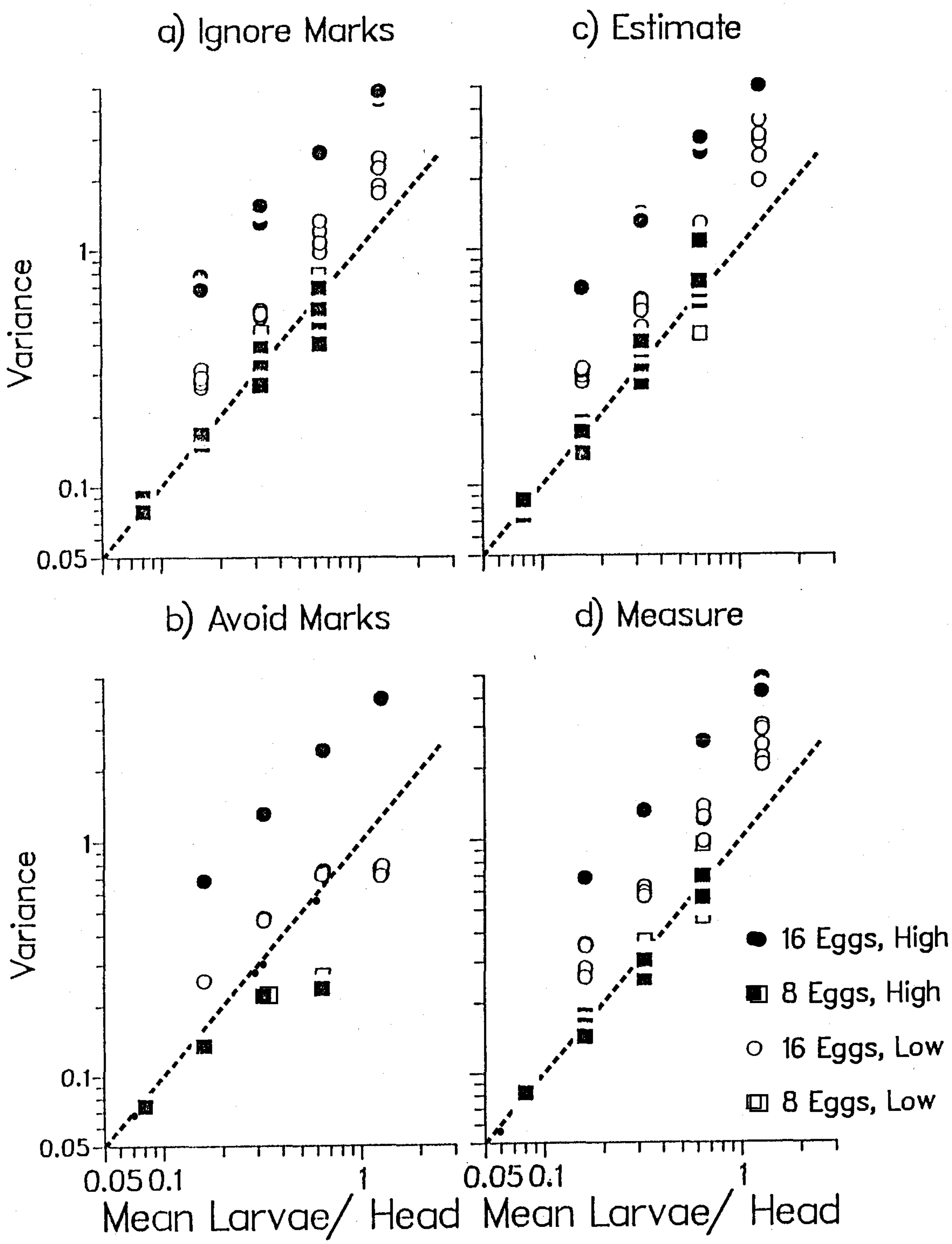

a) High Quality
b) Low Quality
c) High Quality
d) Low Quality
Offspring Surviving
Offspring Surviving
60
65
70
75
80
45
47.5
50
52.5
55
Measure
Avoid
Estimate
Avoid
Measure
Avoid
Estimate
Avoid
1:15
1:7
1:3
1:1
3:1
7:1
15:1
Ratio of Avoiders to Measurers
Ratio of Avoiders to Estimators

Figure 6.5 a-d. Log mean vs Log variance scatter plots for the 4 strategies. In all cases, per-host handling time was kept at 0.01 of the foraging day. Filled circles: flies with 16 eggs available per day foraging in a high quality locality. Open circles: 16 eggs, low quality locality. Filled squares: 8 eggs, high quality locality, Open squares: 8 eggs low quality locality. a) Ignore, b) Avoid, c) Estimate, d) Measure.



● High Quality
○ Low Quality
▨ Simulation (High)
☐ Simulation (Low)
Variance
1
0.1
0.02
0.02
0.1
1
Mean Number of Larvae per Head

Figure 6.6. Scatter plot of Log mean vs Log variance data from the field (circles) and a representative scatter of log mean vs log variance data generated by the simulation model (squares). Model parameters used were: "Estimate" strategy, 8 eggs per fly *per day, handling time 0.01 of the total foraging day.* Filled symbols denote high quality hosts, open symbols denote low quality hosts.


a) Ignore Marks
c) Estimate
b) Avoid Marks
d) Measure
Variance
Variance
1
0.1
0.05
1
0.1
0.05
0.05
0.1
1
0.05
0.1
1
Mean Larvae/ Head
Mean Larvae/ Head
● 16 Eggs, High
■ 8 Eggs, High
○ 16 Eggs, Low
□ 8 Eggs, Low

6.3.2 Egg Distribution Pattern

Egg distribution patterns generated by flies laying in high and low quality localities were relatively insensitive to the strategy adopted by those flies. Egg distributions generated in high quality localities became significantly more aggregated than corresponding distributions generated in low quality localities, as egg availability increased. Figure 6.5 (a-d) shows scatters for all four strategies, for egg availabilities of 8 eggs per day per fly and 16 eggs per day per fly. In all cases, an egg availability of 8 eggs per fly per day resulted in an egg distribution pattern which closely resembled that found in the field (Figure 6.6). However, at this level of egg availability, the pattern generated in a high quality locality was not significantly more aggregated than that generated in a low quality locality (ANCOVA, $p > 0.05$).

6.4 Discussion

Depending upon the parameters used, no strategy fits the criterion of enjoying highest fitness over the complete range of parameters, nor does any strategy uniquely produce an egg distribution pattern which matches that encountered in the field. In fact, over a wide range of conditions, all strategies enjoy essentially equal fitnesses. In a similar way, all strategies can produce patterns which correspond closely to those encountered in the field. The use of simulation to compare potential strategies has, however generated some interesting, counterintuitive results.

My model results indicate a paradox: strategies that use information in a sophisticated way do not always do as well as those which use information in a simpler way. Specifically, flies that do not attempt to evaluate the utility of previously-attacked seed heads and simply avoid using them do better, in many instances, than flies that are able to make extremely accurate assessments of the utility of such heads. Secondly, flies that are not sensitive to the presence of marking pheromone and do not themselves lay marks ("ignorers") do as well as, and when hosts are common do better than, strategies that lay and recognise marks. What causes these results and is this relevant to the natural situation?

It is relatively easy to understand how "avoiders" can outcompete "estimators" and "measurers" when we compare the fitness of individuals in populations that adopt pure strategies. While flies that superparasitize may be maximizing their current and future fitness, they are also reducing the fitness of the individual(s) that contributed to the clutch of eggs already present in the head. Thus, consider the case of a fly at high densities which is encountering nothing but attacked seed heads, and has a number of eggs in its abdomen. There will always be some residual fitness returns to be expected from laying eggs in a previously-attacked seed head, The fly will thus always superparasitize if it can do no better. However, by doing so the fly reduces the fitness of eggs already in the head. Thus, a pure population of superparasitizers ("estimators" and "measurers") will often do much worse than a pure population of "avoiders". Consequently, we have here a case where a strategy can act to depress its population-level recruitment rate, while its component individuals successfully maximize their reproductive success.

A more familiar expression of a strategy which limits population recruitment occurs in the sex allocation patterns expressed by nearly all organisms. It is clearly advantageous for all individuals to raise mainly daughters, since this will maximize the absolute number of their grandchildren. This will only be viable, however, if all individuals in the population adopt this strategy. Most organisms, however are selected to produce equal proportions of sons and daughters, because of the fitness loss which would be suffered by any individual that deviated in its allocation pattern from this equilibrium (Fisher 1930, Charnov 1982).

The outcome of the interaction between "avoiders" and either "measurers" and "estimators" is frequency-dependent. "Avoiders" outcompete "measurers" and "estimators" only at relatively low frequencies in the population. In such circumstances, a certain proportion of heads parasitized by the "avoid" strategy will be superparasitized by its competitor, but this cost is shared by both interacting strategies in a more-or-less even fashion. If this were not the case, one would expect "avoiders" to do poorest when rare. What causes the decreased viability of "avoiders" at high frequencies is the opportunity cost imposed upon this strategy from avoiding previously-parasitized hosts. When "avoiders" are rare, the availability of unattacked seed heads is relatively high, because the competing strategies will superparasitize and will thus tend to exploit fewer hosts. Conversely, a nearly pure population of "avoiders" will exploit available clean heads far more rapidly and will do relatively poorly.

A less intuitive result occurs at low host densities where "ignorers" do as well as (or better than, when host quality is low) either "measurers" or "estimators". The informational constraints imposed on all strategies may be the cause. Stephens and Krebs (1986) and Stephens (1989) discuss situations where increased information (in their case, sampling frequency) in variable and changing environments will not necessarily translate to increased fitness. In this case, the additional information that a mark provides may not be valuable enough to offset costs resulting from any inaccuracies. I refer here to the time lag implicit in the information used by the fly. In this case, flies laying eggs assume a relatively high availability of hosts at the beginning of the day, and revise this estimate as the day proceeds. Thus, if clean heads are perceived to be relatively common at the start of the day, initial clutch sizes will tend to be relatively small, and laid solely into clean heads. As unparasitized hosts are encountered less frequently, flies will eventually perceive higher profitability from laying larger clutches and, in the case of "estimators" and "measurers", from superparasitizing. Such flies will thus incur a cost due to the increased probability of competition. The only strategy that will tend not to change its clutch size over the day will be the strategy where flies ignore the existence of marks completely (i.e., "ignore"). Because of this, a fly adopting the "ignore" strategy will not tend to aggregate its eggs at the end of the day. In most circumstances, this alone will not confer any advantage, but when hosts are common and of low quality, the "ignore" strategy actually outcompetes "estimators" and "measurers", because there is a high cost of aggregation, and such a large number of hosts that the rate of random superparasitization will be relatively low. The margin of advantage in this circumstance is slight, however. "Avoiders" are never outcompeted by "ignorers", so a large clutch size at the end of the day is not a sufficient factor to tip the scale towards the random strategy: a tendency to superparasitize is also necessary. Nevertheless, we do have here a situation where there is an actual disadvantage to obtaining extra (incomplete) information when the environment is constantly changing.

For this time lag in information acquisition to operate, my flies of neccessity must not employ a long-term memory. In deterministic environments, where conditions prevailing on a given day are highly correlated with what was experienced on the previous day, a fly will only suffer an information lag cost on its first day of searching for hosts and should thus employ some form of long-term memory. The utility of such long-term memory will decline and eventually become detrimental as host availability and conspecific density is less and less consistent from day to day. I have not addressed this issue in this thesis, but I suspect that this will be a fertile area for future research.

Apart from illustrating potential costs of imperfect information, what else can be gleaned from this exercise? As I have already pointed out, all strategies tended to do at least as well as the others, depending upon conditions. Extreme conditions selected for particular strategies (i.e., generated clear "winners"), but no strategy turned out to be a consistent winner. I have already shown that flies do not ignore previously-parasitized seed heads, but how else real flies use this information is problemical. Finally, one could postulate a number of other possible oviposition strategies. For example, flies could adopt a conditional strategy wherein they show a propensity to recognize marked hosts under low-quality conditions, and become "ignorers" in high-quality localities.

The results generated by the pairwise interactions of the different strategies suggest that some strategies can coexist under some circumstances. Certainly "avoiders" could coexist with either "estimators" or "measurers" under a range of conditions. Even flies which do not make or even recognize marks could persist under low-density conditions. A similar result was generated from models developed by Roitberg and Mangel (1988) wherein they found that, in theory at least, a low frequency of non-marking *Rhagoletis* could persist within a population of marking individuals. Thus, the possibility that there is no "pure" oviposition strategy present in *Orellia* populations must be considered.

Theoretical considerations of parasite clutch-size have consistently focussed on systems where estimation of host quality by the parasite is perfect (Charnov and Skinner 1984, Parker and Courtney 1984, Skinner 1985, Mangel 1987,1989, Mangel and Roitberg 1989). Fewer studies have addressed the situation where host quality (in terms of number of larvae able to fully mature in an encountered host) is only loosely correlated with host-associated traits that are perceivable at the time of oviposition. Host quality can be masked at such times if oviposition occurs early in the host's development and final host quality exhibits strong, unpredictable variation. Inasmuch as many insect-host plant systems display this characteristic (Dethier 1959a,b, Rausher 1980), my study should have some general applicability. Further theoretical development needs to be done, however. One feature common to many such systems, which is absent from the *O. ruficauda* - *C. arvense* sysem, is the option of offspring being able to fine-tune the parent's clutch-size decision by emigration from the host (Dethier 1959b, Wellington 1977). While larval mobility undoubtably reduces variance in larval success, it generates its own suite of problems, vis à vis clutch size. One such is the possible interaction between clutch size, the degrees of relatedness between offspring in a clutch and parent-offspring conflict (Roitberg and Mangel, in prep.).

The last major take-home message from the present work is that the use of reductionism has strong limitations. In this case I found it difficult to extend theory developed to elucidate individual dynamics (host selection strategies), to help explain a population-level phenomenon (spatial distribution of eggs). Roitberg et al. (1990) make this point in their examination of a field test of oviposition theory attempted by Borowicz and Juliano (1986), wherein the latter failed to detect density-dependence in a population of dogwood maggot flies, which were probably behaving in a density-dependent fashion on an individual basis (Roitberg et al. 1982). Borowicz and Juliano's (1986) field set up controlled for host density, but the density of the parasite population was not known. Roitberg et al. (1990) were able to show that varying this factor could generate vastly different patterns of infestation in the field. By the same token, when interpreting field data in light of possible underlying individual behaviour, it is necessary to consider a range of reasonable alternative behaviours. When more than one alternative behaviour generates patterns which correspond to an observed pattern, it is difficult to come to very specific conclusions. In the present study none of the four strategies generated vastly different egg distribution patterns. All strategies could generate patterns that roughly corresponded with those observed in the field. Clearly, more tightly-controlled experimental work needs to be done before any unequivocal conclusions can be reached about how *Orellia* flies go about foraging for hosts.

In conclusion, I should step back a bit from the pessimistic tone of the last paragraph. I set out to ask something about the value of information in a specific, variable system. In order to do this, it was necessary to develop a theory and to look for some consistent relationships within the context of that theory. Thus, I observed a field distribution of eggs and inferred some possible causative behaviours. I then measured a number of life-history and ecological parameters and used these data to generate hypothetical strategies, which I compared using simulation methods. Instead of finding one robust strategy which did best under all circumstances, I obtained results that indicated first, that different strategies did best depending upon what conditions prevailed, and second, that certain strategies could coexist. Inasmuch as both results are generated by the high degree of uncertainty associated with this system, they suggest something about what we can expect to find in nature. For natural selection to operate consistently, there has to be a similarly consistent relationship between variation in a trait and its effectiveness. Highly variable systems lack this consistency and thus may not select for one particular mode of dealing with the world. Thus, we frequently find differences between individuals in nature in their ability to perceive and process information. This study suggests that such differences may not represent variation around a selected optimum, but rather that the diversity itself may be the end product of selection.

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