The Evolution of Larval Competition Strategies in *Callosobruchus maculatus* and *C. analis*

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You know I'm born to lose,
and gamblin's for fools,
but thats the way I like it baby, I don't wanna live forever.

(Lemmy from Motörhead, demonstrating his understanding of the subtleties of evolutionary game theory)

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The Evolution of Larval Competition Strategies in *Callosobruchus maculatus* and *C. analis* - Nicholas Colegrave

Summary

Callosobruchus maculatus and *C. analis* present an interesting problem to the evolutionary ecologist. The larvae of both species complete their development within the seeds of various legumes such as black-eyed beans. However, the two species compete over the resources within the bean in very different ways. *C. maculatus* larvae compete in a scramble process; the larvae avoid each other within the bean and several adults can emerge from a single bean. In contrast the larva of *C. analis* compete actively within the bean, seeking each other out and fighting until only one larva is left alive. As a consequence, only a single *C. analis* adult will emerge from each bean, no matter how many larvae were initially present. In this thesis I try to determine the types of selective forces that can cause two species to evolve such different competition strategies when competing over similar resources.

In Chapter 3 it is suggested that differences in the cost of exploitation competition suffered by the two species could explain why they originally evolved different larval competition strategies, but that these differences are not enough to maintain the strategies under current conditions. It is suggested that historical constraints may have limited *C. analis* to using an ancestral contest competition strategy that is maladaptive on the large hosts which this species currently uses.

In chapter 4 the effect of host size on the cost of exploitation competition is investigated further. As expected, the cost of exploitation competition increases as bean size decreases.

In chapter 5 the cost of fighting is measured for *C. analis* larvae. Although the fitness of a larva that fights over a bean and wins is affected by having fought, the magnitude of the effect is small, and probably of little evolutionary consequence.

In chapter 6 a game theory model is presented that investigates the effect of asymmetries in fighting and passive competitive ability on the evolution of competition strategies. The results suggest that such asymmetries will increase the possibility that aggressive competition strategies will evolve and could also explain the conditional strategies used by some strains of *C. maculatus.*

In chapter 7 a genetic model is presented that investigates the effects of population structure on the evolution of competition strategies. The results of the model suggest that the patchy population structure, typical of stored product pests such as *Callosobruchus* beetles, can favour the evolution of scramble competition strategies.

Finally the factors that may affect the competition strategy that a species evolves are discussed in more general terms.

Contents

Chapter 1. General introduction

1.1. An introduction to competition

Since the publication of Darwin's "On the Origin of species" (Darwin 1859), competition by organisms for scarce resources has been recognised as the major force driving the evolution of the complex adaptations seen throughout the animal kingdom. Darwin recognised that the resources required by organisms are generally in limited supply, and this leads to individuals having to compete to obtain them. If individuals differ in their ability to compete, some individuals will obtain more of the resource than others and ultimately the successful competitors will leave more offspring in the next generation than the unsuccessful competitors. Assuming that the traits that made the successful individuals good competitors are heritable, this will ultimately lead to a population in which all individuals have the traits making them better competitors. Thus, competition results in the evolution of traits that enable organisms to become better at competing for the resources that they require.

Competition has been defined as, "an interaction between individuals brought about by a shared requirement for a resource in limited supply, and leading to a reduction in the survivorship, growth and/or reproduction of the individuals concerned" (Begon et al. 1986). It can occur between individuals of different species (interspecific competition), but is probably more intense between individuals of the same species (intraspecific competition), simply because their requirements for resources are likely to be similar.

1.2. Asymmetric and symmetric competition

While competition is, by definition, costly to all individuals this does not mean that all individuals will suffer from the effects of competition to the same degree. Even within a single species there will be differences in the competitive abilities of individuals; this means that some individuals do better than others. Competition in which individuals are not equal is termed asymmetric competition and is characterised by some individuals suffering very little from competition, whilst others suffer a great deal. (Begon 1984, Begon et al. 1986). When competition is extremely asymmetric, the successful competitors may actually obtain as much of the resource as they would have without competition, while unsuccessful competitors may get nothing at all. However, this does not mean that the successful competitor has not paid a cost of having competed; the individual will have invested time and energy in competing, and so may have a lower fitness than if it had not had to compete. Whilst many experimental and theoretical studies have assumed that competition is symmetrical, with all competitors being equal, the reality is probably that most competition is asymmetrical (Begon 1984, see also Lawton and Hassell 1981 for interspecific competition).

1.3. Open and closed systems

Competition for resources can be viewed as occurring in either an open or a closed system. An open system is characterised by the fact that individuals can stay and compete over the resource, or leave and go in search of other resources. For example, an important resource for female *Agelenopsis* spiders is the site of a web (Riechert 1978). If two spiders meet in a web, each has the option of staying and fighting over the resource, or leaving in search of another web site. In contrast, in a closed system individuals are not able to leave the resource and avoid competition. The larvae of many parasitoid wasps are limited for the whole of their development to the host larva selected by their parent (Godfray 1987a, b). Similarly many leaf miners complete their development within a single leaf (Faeth 1990) and young birds will often have to compete with siblings within their nest for food from their parent. In fact, closed systems are probably most commonly experienced by juvenile organisms, as their limited mobility prevents them from avoiding competition by moving to another area to feed.

Whilst much competition probably occurs in open systems, closed systems provide many advantages for the study of competition. In particular, the effect of competition on the fitness of individuals can be assessed without many of the confounding effects that would arise if individuals were able to leave the resource.

1.4. Processes of competition

In general, when faced with competition for a resource an organism can choose to compete in one of two ways. It can attempt to monopolise the resource by actively excluding other competitors such that successful competitors gain sole access to the resource, whilst unsuccessful competitors are excluded or even killed. Alternatively an individual can compete by attempting to gain as much of the resource as possible without actively interfering with other competitors. In the first case competitors affect each other's fitnesses by actively interfering with each other, in the second, competitors affect each other indirectly by depleting the available resource.

Nicholson (1954) termed these two competition strategies contest and scramble competition respectively. However, whilst Nicholson's definitions of contest and scramble competition related to the actual process by which individuals compete, recently several authors have redefined these terms in relation to the outcome of competition at the population level. With a contest outcome the number of survivors of competition may initially increase as the number of competitors increases but then remains constant as the number of competitors increases further, whilst, with a scramble outcome, the number of survivors after competition may initially increase with increased number of competitors, but then begins to decrease again until at very high population densities no individual gains enough of the resource to survive (figure 1.1). This redefinition of the terms has caused confusion in the literature, not least because a contest outcome may arise from either a contest or a scramble process. In this thesis the terms are used exclusively to describe the process of competition rather than its outcome.

Other authors have used the term interference competition, to describe situations where individuals compete by actively interfering with other competitors and exploitation competition when individuals compete by exploiting the resource without interference (Miller 1967). These terms were originally defined in relation to interspecific competition and roughly equate to the contest process/ scramble process dichotomy of Nicholson (1954).

Both types of competitive process are found throughout the animal kingdom. In many species of animal, males fight over groups of females and winning males gain sole access to the females, whilst in other species, males compete for females simply by attempting to attract as many females as possible, without directly interfering with other males. Even similar species can compete in very different ways. In some birds, nestlings compete for food from the parents in a scramble process (e.g. Palmer 1941), with individuals attempting to beg louder than each other, whilst in other species, particularly raptors, chicks may attempt to kill one another and siblicide within a nest is not uncommon (e.g. Meyburg 1974, Mock 1984). Godfray (1987b) has described a dichotomy of competition behaviours in the larvae of parasitoid wasps. In gregarious species, the larvae do not interfere with each other and compete in a scramble process with several adults emerging from a single host, whilst in solitary species, larvae fight to the death and, as a consequence, only a single adult emerges from each host. The type of competition strategy that a species adopts will have important consequences for the population dynamics of that species, therefore it is important for evolutionary ecologists to understand the types of selective forces and ecological factors that affect the type of competition strategy that a species evolves.

1.5. Larval competition in *Callosobruchus* beetles

Beetles of the genus *Callosobruchus* are stored product pests of various legumes cultivated by man (Southgate 1978, 1979). Females lay their eggs on the surface of beans, and once the eggs hatch the larvae burrow through the testa into the bean where they feed until pupation. Several eggs can be laid on a single bean and, as beans are closed systems with a larva restricted to a single bean for the whole of its pre adult development, larval competition can be intense. The consequences of this larval competition are particularly important in these beetles as they do not feed as adults and so the resources obtained as a larva must sustain the adult for the whole of its life. *Callosobruchus* beetles make an ideal model system for investigating the evolution of competition strategies as different species within the genus compete in different ways as larvae (Smith & Lessells 1985). The larvae of *C. maculatus* compete in the way typical of most other *Callosobruchus* species, with larvae avoiding each other within a bean and competing in a scramble process, exploiting the resource without directly interfering with each other. In contrast, the larvae of *C. analis* compete using a contest process; larvae seek each other out within the bean and fight to the death (Umeya et al 1975). As a result, whilst more than 15 adult *C. maculatus* can emerge from a single black-eyed bean, generally only a single *C. analis* adult ever emerges from a single host. In this thesis I aim to determine some of the selective forces that may have been responsible for the evolution of such different larval competition strategies in two such similar species of beetle.

1.6. The approach

When investigating the evolution of a trait or behaviour, the evolutionary ecologist is faced with an obvious problem; the forces that produced the evolutionary outcome observed today were operating in the past, and so cannot be observed directly. As a consequence the researcher must use more indirect approaches to make inferences about what may have occurred in the past. One approach that has been particularly fruitful is the use of theoretical modelling in conjunction with experiments designed to test the assumptions and predictions of the models. This mixture of theoretical modelling and experimental investigation was the approach used in this study.

1.6.1. Theoretical models

The use of theoretical models allows the evolutionary ecologist to construct possible scenarios for the way in which evolution may have operated in the past. When considering why a species has evolved to compete in a certain way the researcher often begins by considering other ways in which the organism could behave, the organism's strategy set (Parker 1984, Grafen 1991). Factors thought to be important in the evolution of the character are then incorporated into the model as parameters, and assumptions are made about the effect of each factor on the fitness of individuals using different strategies. The strategy expected to evolve under different conditions can then be determined by altering the values of the parameters in the model, and seeing the effect on the fitness of the different strategies.

If the fitness of an individual depends only on the way in which it behaves, and is independent of the way other individuals behave, optimality models can be used to determine the best way to behave under different conditions (Maynard Smith 1978, Parker and Maynard Smith 1990). However, when considering the evolution of a competition strategy, the fitness of an individual will depend not only on the way in which it behaves but also on the strategy used by its competitors. In this situation optimality models no longer apply and instead an evolutionary game theory approach must be used (Maynard Smith 1982).

Evolutionary game theory (Maynard Smith 1982, Riechert & Hammerstein 1983, Parker 1984) was developed from economic game theory (Von Neuman & Morgenstern 1953) specifically to investigate competitive behaviour in animals. Instead of looking for the optimal strategy for a certain set of conditions, game theory looks for the evolutionarily stable strategy (ESS: Maynard Smith 1982). This is defined as a strategy such that, if all members of a population adopt it, no mutant strategy can invade under the influence of natural selection (Maynard Smith 1982). An individual using the ESS is effectively maximising its expected fitness given the way in which other individuals are behaving, rather than its expected fitness per se. Game theory models are typically classified into two types; models in which the fitness of a strategy depends on a series of pairwise interactions (pairwise models), and models in which the fitness depends on some average property of the whole population (playing the field models). The types of competitive interaction studied in this thesis fit into the former category because larval competition will occur between two or a few individuals within a single bean.

Game theory models are an example of phenotypic models (Grafen 1991), where the evolution of the strategy or phenotype is modelled without considering the genetic system underlying the character. More accurately, game theory models assume that the phenotype is inherited asexually via a haploid genotype. Phenotypic models are particularly common in studies of the evolution of behaviour, simply because the genetic system behind the character is often unknown and is likely to be complicated. Whilst no evolutionary biologist believes that behaviour is really inherited in this way, the fact that models with explicit genetic systems often give identical results to their simpler phenotypic equivalents (Maynard Smith 1981, 1982, Thomas 1985a, b, c, d) suggests that it is often safe to ignore the genetics of the character. However, there are some instances in which a model assuming asexual reprodution will not suffice; for example in chapter 7 of this thesis the effect of population structure on the evolution of competition strategies, including the effect of the point in the population cycle at which a female mates, is investigated theoretically. To investigate such an effect it is obviously impossible to assume that inheritance is asexual. In this situation, the approach of assuming that the behaviour is controlled by the simplest possible diploid genetic system, with behaviours controlled by different alleles can offer a tractable alternative. In this case, an allele that, once fixed in the population cannot be replaced by a rare mutant allele, will be evolutionarily stable, and the strategy that this allele represents can be viewed as an ESS.

1.6.2. Experimental investigations.

Once a model has been constructed which seems consistent with contemporary observations, it is not enough to accept that the model is a true representation of the way in which evolution actually occurred. Instead, the model must be used to make predictions that can be tested. There are three main approaches used in evolutionary ecology to test models; i) selection experiments, ii) comparative studies and iii) experimental tests. Selection experiments generally attempt to alter the factors thought to be important in the evolution of the character under investigation, in the hope of producing a change in the character in line with the predictions of the model. Although selection experiments can provide a large amount of information about the validity of the model, they are generally extremely time consuming (to select for a change in behaviour can take many generations) and are particular likely to be unsuccessful for qualititive traits as they rely on the presence of genetic variation which, although assumed to have been present at the time when the character evolved, may not be present in the contemporary population. Comparative studies use variation in characters between species, and look for relationships between characters and the factors thought to be important to their evolution (Felsenstein 1985, 1988, Grafen 1989, Harvey & Pagel 1991). Such studies have been extremely successful in testing many ideas in evolution, but they do require a large amount of information about character values for many species that is often not available. Experimental tests use experimental manipulations to either test the assumptions of the model, or to measure the effect of altering factors on the fitness of individuals. In this study experimental techniques were used to test the assumptions and predictions of a model of the evolution of larval competition strategies.

1.7. Previous models of competition

There have been many attempts to produce theoretical models to explain how various aspects of the way in which organisms compete may have evolved. Many of these models have concentrated on the way in which organisms should behave, given that they are either competing in a contest process (e.g. Maynard Smith & Price 1973, Maynard Smith & Parker 1976, Hammerstein 1981, Enquist & Leimar 1990) or a scramble process (Fretwell & Lucas 1970) over the resource. However, several models have explored the types of factors that could determine which strategy, contest or scramble, a species will evolve. Godfray (1987b) produced a simple genetic model to explain why the larvae of some parasitoid insects will fight to the death within a host (solitary species), whilst others will coexist, and compete passively (gregarious species). Godfray (1987b) found that the stability of the two strategies depended critically on the optimum clutch size of the parent, which will in turn depend on the quality of the host. At large clutch sizes the gregarious strategy was stable against invasion by the solitary strategy, whilst at small clutch sizes the solitary strategy could invade. However, the model also exibited hysteresis; the gregarious strategy was often unable to invade a population of solitary strategists, even at high optimum clutch sizes. The problem of whether a chick in a nest should share food with its siblings, or attempt to monopolise the food by interfering with or killing other chicks has also been investigated theoretically (O'Connor 1978, Dickens & Clark 1987, Godfray & Harper 1991). While differing in details, these models all showed that siblicide is likely to evolve when the fitness of chicks that share the resources in the nest is low relative to the fitness of a chick that has the nest to itself. In this system too, the model of Godfray and Harper (1991), predicted hysteresis with it being far harder for a non siblicidal gene to invade a siblicidal population, under conditions in which the non siblicidal strategy would be stable, than vice versa. More generally, models have been used to investigate under what conditions organisms are expected to exclude other individuals from resource patches and behave territorially (Davies & Houston 1984). These models predict that individuals should contest the resource, and behave territorially if the reduction in fitness caused by sharing the territory is high relative to the costs of defending the territory: this is the the concept of economic defendability (Brown 1964, Davies & Houston 1984).

Whilst these models were produced to investigate different systems, their general conclusions are similar. The way in which organisms should compete will depend on the reduction in fitness suffered by individuals that share the resource, compared to individuals with sole access to the resource.

1.8. The Smith and Lessells model of Larval competition in internally feeding granivores

Smith and Lessells (1985) produced a simple game theory model to try to investigate the types of selective forces that may be important in determining the type of competition strategy that a species evolves. The model was developed with *Callosobruchus* beetles in mind and provides the basis for much of the work described in this thesis. Smith and Lessells began by defining two larval competition strategies: *Attack* strategists attempt to find and kill other larvae within a bean, whilst *Avoid* larvae attempt to avoid one another within a bean, and compete in a scramble process. They then constructed a simple game theory model to determine what factors would affect which of the two strategies would be an evolutionarily stable strategy (ESS; Maynard Smith 1982). The simplest version of their model assumed that competition occurred between pairs of larvae, with each bean containing exactly two larvae before competition, and it is this version of the model that is described here. However, versions of the model with more than two larvae per bean produced qualitatively similar results.

The fitness of larvae using the two different competition strategies were defined relative to the fitness of an *Avoid* larva that develops alone within a bean (defined as having a fitness of 1). If two *Avoid* larvae share a bean, there is no interference between the larvae and each suffers a reduction in fitness, E, due to exploiting the same resource. If two *Attack* larvae share a bean they fight, and one kills the other and each larva is assumed to have the same probability of winning the fight. The surviving larva does not suffer any cost of having fought, and thus has a fitness of 1. If a bean contains one *Attack* and one *Avoid* larva, the larvae are assumed to always meet, and fight to the death. The probability that an *Attack* larva wins an encounter, with an *Avoid* larva was defined as W, and *Attack* larvae were always assumed to be at least as likely to survive the encounter as *Avoid* larvae ($0.5 \leq W \leq 1$). The payoffs to the two strategies in competition with each other are shown in Table 1.1.

Smith and Lessells then used these pay-offs to calculate the average fitness of *Avoid* strategists (S_{Avoid}) and *Attack* strategists (S_{Attack}) in a population containing a proportion p *Avoid* strategists and (1-p) *Attack* strategists. The average fitnesses were determined as:

$$S_{Avoid} = p.(1-E) + (1-p)(1-W) \qquad \text{i}$$

$$S_{Attack} = p.W + (1-p)/2 \qquad \text{ii}$$

Thus, the average fitness of each strategy depends, not only on E and W but also on the frequency of the two strategies in the population. If there is no *Attack* larval superiority, ($W = 0.5$) the ESS depends simply on the value of E (figure 1.2a and b.). If E is less than 0.5 (figure 1.2a.), *Avoid* strategists are fitter than *Attack* strategists at all frequencies, so, no matter what the initial frequencies, the population will evolve to consist entirely of *Avoid* individuals; *Avoid* is the only ESS. Similarly, if $W = 0.5$ but $E > 0.5$ *Attack* is the sole ESS (figure 1.2b.). If there is some degree of *Attack* larval superiority, *Attack* is always a possible ESS (figure 1.2c. and d.), but if the cost of exploitation competition is also low ($E < 1-W$), *Avoid* is also a possible ESS (figure 1.2c.). Under conditions in which *Attack* and *Avoid* are both possible ESS's the one that the population evolves to will depend on the initial frequencies of the two strategies; if *Attack* is initially at high frequency then the achieved ESS is *Attack*,

Table 1.1. Pay-off matrix for the Smith and Lessells model of larval competition. The matrix shows the expected pay-off to a larva adopting a particular strategy against both sorts of opponent. E is the cost of exploitation competition and W is the probability that an *Attack* larva kills an *Avoid* larva.

Larva's strategy	Opponent's strategy	
	Avoid	*Attack*
Avoid	1-E	1-W
Attack	W	1/2

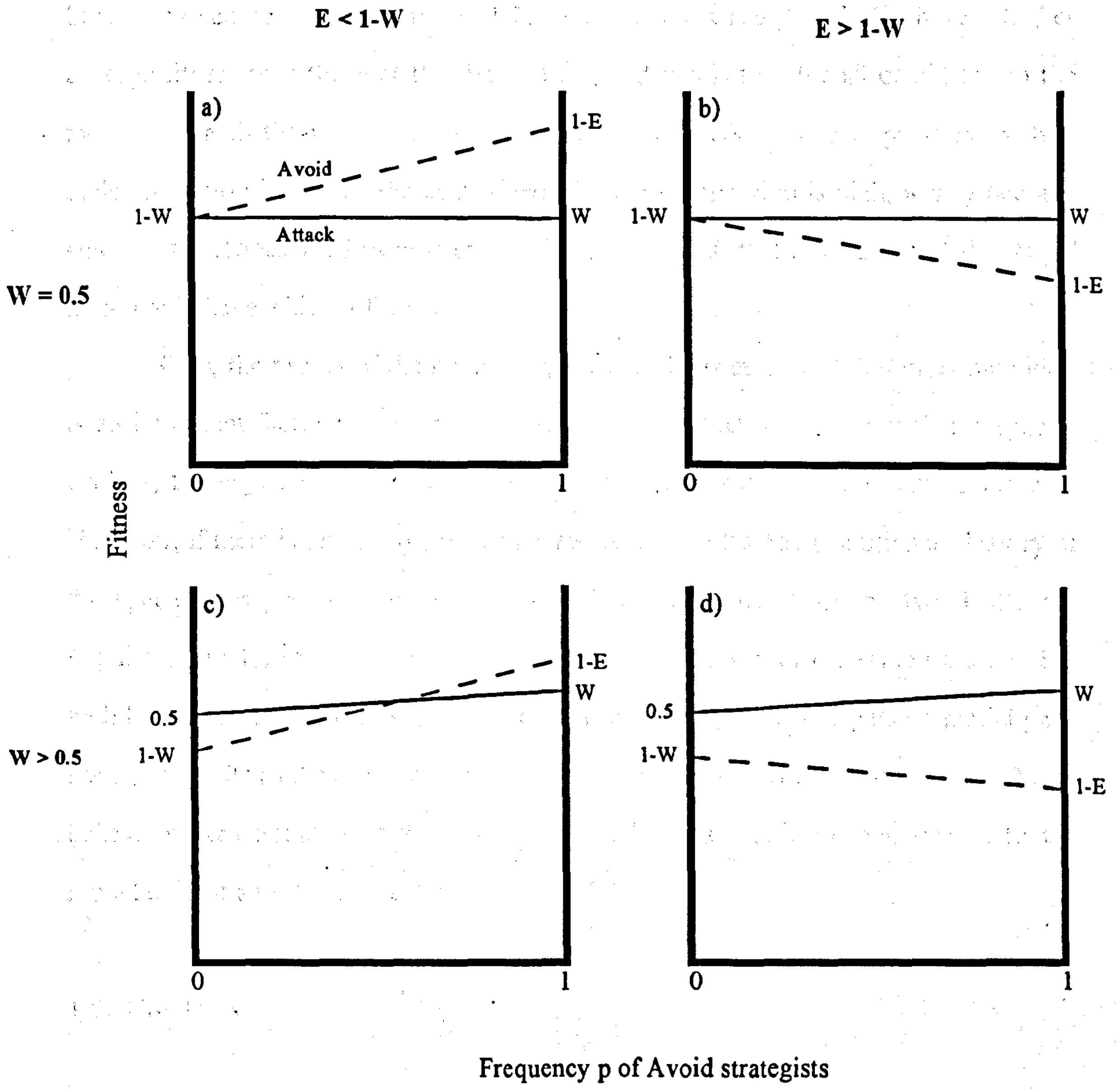

Figure 1.2. The fitness versus frequency curves for the Smith and Lessells model (after Smith & Lessells 1985 Fig. 26.6). Fitness of *Avoid* (broken lines) and *Attack* (solid lines) are plotted against p the frequency of *Avoid* strategists. The strategy with the higher average fitness will increase in frequency. If W > 0.5 *Attack* is an ESS (b and d), whilst if E < 1-W *Avoid* is an ESS (a and c). If both conditions are true *Attack* and *Avoid* are alternative ESS's (c), although in this situation individuals at the *Attack* ESS will always have a lower fitness than individuals at the *Avoid* ESS.

otherwise it is *Avoid.* Also, under some conditions *Attack* and *Avoid* are alternative ESS's this does not mean that individuals at the alternative ESS's will have the same fitness. As can be seen from figure 1.2c., individuals at the *Avoid* ESS have a higher average fitness than those at the *Attack* ESS, and this is true for all conditions in the model in which the two strategies are both possible ESS's. If a population evolves under conditions in which the cost of exploitation competition is high, it may become stuck at the *Attack* ESS even if conditions change such that individuals at the *Avoid* ESS would have a higher fitness.

Thus, the results of the model suggest that the cost of exploitation competition is an important factor in determining the type of competition strategy that a species evolves, the higher this cost the more likely a species will evolve a contest strategy. However, if there is any degree of *Attack* larval superiority, the evolutionary history of the species can play an important role in determining which of the two ESS's the population evolves to. Smith (1990) also produced a model of the same situation, but with behaviour controlled by a simple diploid genetic system. The genetic model gave the same results as the original game theory model, whether the allele producing Avoid behaviour was dominant or recessive. Thus adding a simple genetic system to the model did not alter the model's outcome.

1.9. The Aims

The general aim of this study was to investigate some of the factors that affect whether a species evolves a contest or scramble competition strategy using *Callosobruchus* beetles as a model system. The problem was investigated using both experimental and theoretical techniques.

The aim of the experimental work was to evalute the success of the Smith and Lessells model in explaining the evolution of larval competition strategies in *Callosobruchus* beetles by testing experimentally some of its predictions and assumptions. The cost of exploitation competition was measured for both *C.*

maculatus and *C. analis*, to see whether inherent differences in this cost could explain the different larval competition strategies of the two species (Chapter 3). The cost of exploitation competition suffered by *C. maculatus* larvae was also measured on hosts of different species and sizes, to examine the effect of host size on the evolution of larval competition strategies (Chapter 4). Finally the assumption that fighting over a bean is not costly to the victor was investigated by measuring this cost in *C. analis* larvae (Chapter 5).

The Smith and Lessells model is a simple game theory model and the main aim of the theoretical work was to extend this model to provide a better understanding of the evolution of larval competition strategies. In particular, models were produced to investigate the effects of asymmetries in fighting and passive competitive ability (Chapter 6) and of a subdivided population structure (Chapter 7) on the evolution of competition strategies.

Chapter 2. Materials and methods

2.1. General biology of *Callosobruchus maculatus* and *C. analis*

Bruchid beetles of the genus *Callosobruchus* are stored product pests found throughout the tropics and subtropics (Southgate 1978, 1979). The genus probably had its origins in Asia and Africa, but has since become pan-global with the unintentional aid of man (Southgate 1978). *C. maculatus* is now known to occur in Asia, Africa, Europe, Australasia and the Americas, whilst *C. analis* is most common in Asia, but is also occasionally found in Africa (Southgate 1978).

The adult females of both species lay their eggs on the surface of various legumes cultivated by man. The hosts of *C. maculatus* include black-eyed bean (*Vigna unguiculata*), mung bean (*V radiata*), adzuki bean (*V. angularis*) soya bean (*Glycine max*) and brown lentil (*Lens esculenta*), whilst *C. analis* is generally found only on black-eyed beans and mung beans. However, both species are able to use other hosts when presented with them (Janzen 1977, Umeya et al 1975).

About three days after eggs are laid, the developing larvae of both species are clearly visible within the egg, due to the presence of the conspicuous dark cephalic shield (Van de Meer 1979), and two to three days after this the larva begins to chew through the testa and enter the cotyledon tissue within the bean (Howe & Currie 1964). As the larvae burrow into the bean, they eject seed matter into the chorion of the egg, causing it to change from translucent white to opaque (either white or brown depending on the colour of the cotyledon tissue). Once within the bean the larvae of the two species show different feeding behaviour, with larvae of *C. maculatus* feeding at the surface of the bean, just below the testa, and *C. analis* larvae burrowing to the centre of the bean to feed. The larvae of both species pass through three or four further instars within the bean and then pupate (Howe & Currie 1964, Begum et al. 1982, Wightman 1978). The adult beetles then emerge from the bean through a small emergence hole cut into the testa. The developmental times of both species are affected by temperature and humidity (El-Sawaf 1956, Giga & Smith 1983), but at 30°C, 70% rh, *C. maculatus* pass from egg to emergence in about 22 days, whilst *C. analis* take about 28 days (pers. obs.). After emerging, the adults can mate at once and will live for about 6 days for *C. maculatus* and 15 days for *C. analis* (Giga & Smith 1983, and pers. obs.). The adults of both species do not normally feed after emergence.

2.2. Stock cultures

The *C. maculatus* strain used in this study derives from a stock cultured at Imperial college at Silwood park since 1977 and is the same Campinas strain as that used by Bellows (1982a, b), and Giga and Smith (1981, 1987). The strain was originally collected from Brazil in 1974 (Wilson 1989, Ovenden 1991), and has been cultured at Sheffield University since July 1984. The exact geographical origin of the *C. analis* culture is unknown, but it too came from Imperial college in July 1984 (C.M. Lessells pers. com.). Cultures of both *C. maculatus* and *C. analis* were maintained, and experiments conducted, in a constant environment room at 30°C, 70%rh, using black-eyed beans as a host until September 1994, after which point failure of the humidifying equipment meant the conditions were changed to 30°C, 35% ± 5 rh. The change in conditions occured between experiments, and the only experiment carried out under the new conditions was the experiment on three different sized black-eyed beans, described in chapter 4.

The same general culturing regime was used for both species. Every week about 200 adult beetles were removed from a stock culture set up four (in the case of *C. maculatus*) or five (in the case of *C. analis*) weeks earlier. In general these adults would have emerged less than four days previously. The adults were then placed in a new culture box with approximately 1000 black-eyed beans, and allowed to oviposit for one week. All beetles (most of which had died by this point) were then removed from the beans. The beans were then left for a further three (*C. maculatus*) or four (*C.

analis) weeks at which point the next generation of adult beetles would have emerged and the process could be repeated.

This procedure means that each culture was made up of four (*C. maculatus*) or five (*C. analis*) subcultures, each set up a week apart. Whilst this ensures a constant supply of newly emerged beetles every week it does have the problem that, because subcultures are genetically isolated, there may be some degree of genetic divergence between them. To reduce the effect of this on experimental results beetles used within an experiment were all obtained from the same subculture whenever possible.

2.3. General methods

2.3.1. Sexing adults

The adults of *C. maculatus* are sexually dimorphic in their elytral markings (Southgate et al. 1959, Halstead 1963) and so can be easily and reliably sexed. However, male and female *C. analis* do not differ in appearance (Southgate et al. 1959), and for this species beetles had to be dissected at the end of an experiment to determine their sex, with males identified by the presence of the chitinised aedegus.

2.3.2. Estimating fitness

Two main measures of fitness were used in this study; survival of larvae to emergence and female emergence size, measured as left elytron length. Both have been shown to be affected by competition in previous studies (Mitchell 1975, Credland et al 1986, Giga & Smith 1991, Messina 1991). Female emergence size is known to be a good indicator of lifetime fecundity in many insects, including *C. maculatus* (Credland et al 1986, Colegrave 1993). To determine the relationship between female lifetime fecundity and emergence size in the two species used in this study, virgin females (less than 12h since emergence) of both species were mated to virgin males (less than 12h since emergence) and each given 100 black-eyed beans on which to oviposit. After the females died, their left elytron was removed and measured using a Kontron Videoplan image analysis system (Kontron 8057 Eching, Munchen, Germany) attached to a Reichert Jung Polyvar compound microscope (Reichert AG, Wien, Austria). The number of eggs laid by each female was then counted. In both species there was a positive relationship between female lifetime fecundity and female emergence size (figures 2.1. & 2.2.). Moreover the intercepts of the two regression lines do not differ significantly from zero, suggesting that female lifetime fecundity is directly proportional to emergence size.

In later experiments the development time of larvae was also measured. However, as the effect of changes in development time depend on the rate of growth of the population, it is difficult to translate effects on development into effects on fitness.

2.3.3. Computing and statistics

All simulations described in this thesis were written in ANSI C++, and run on the University of Sheffield's Silicon Graphics computer. Random numbers were generated where required using the ran2 procedure (Press et al. 1992). All statistical analyses were carried out using SPSS (SPSS Inc, 1989). Statistical methods were obtained from Sokal and Rohlf (1981), Snedecor and Cochran (1967), Siegal and Castellan (1988) and Walpole and Myers (1972).

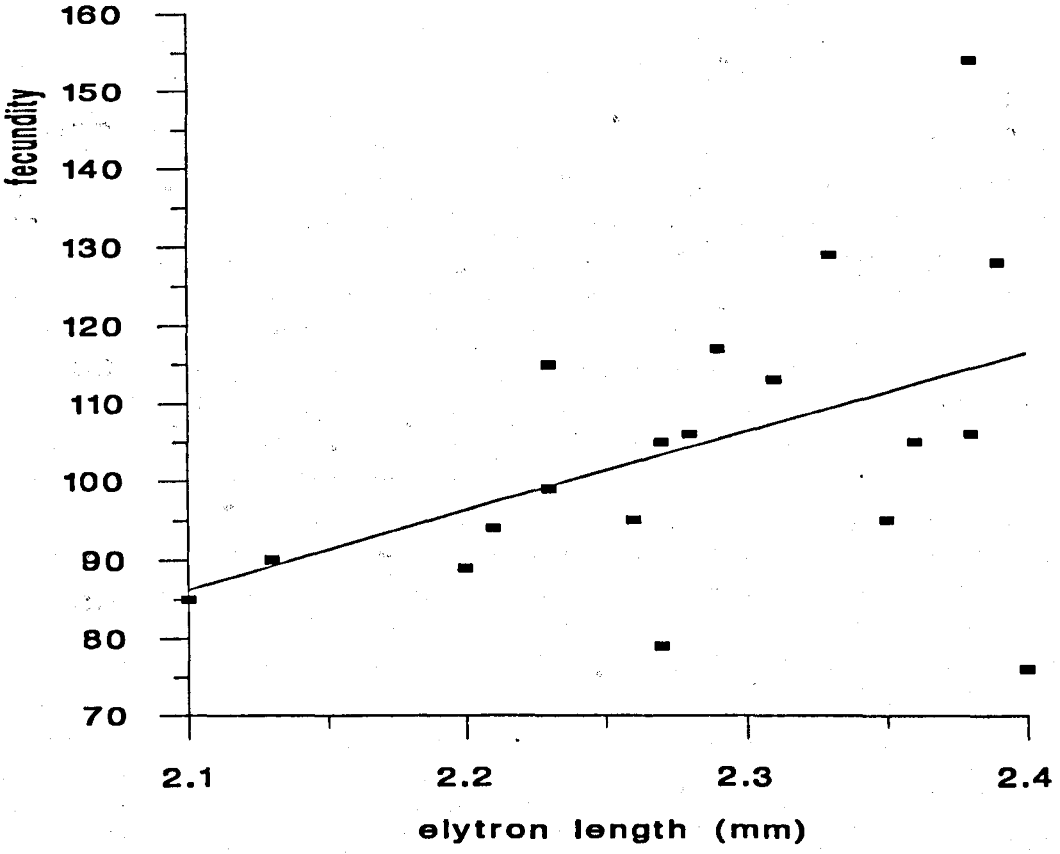

Figure 2.1. The relationship between female lifetime fecundity and left elytron length for *C. maculatus*. Fecundity = -127+101.0(elytron length): $F_{1,19} = 4.95$, $P = 0.038$. The intercept of the line with the y axis does not differ significantly from zero (t = 1.22, df = 19, $P = 0.24$) and so lifetime female fecundity is directly proportional to female elytron length.

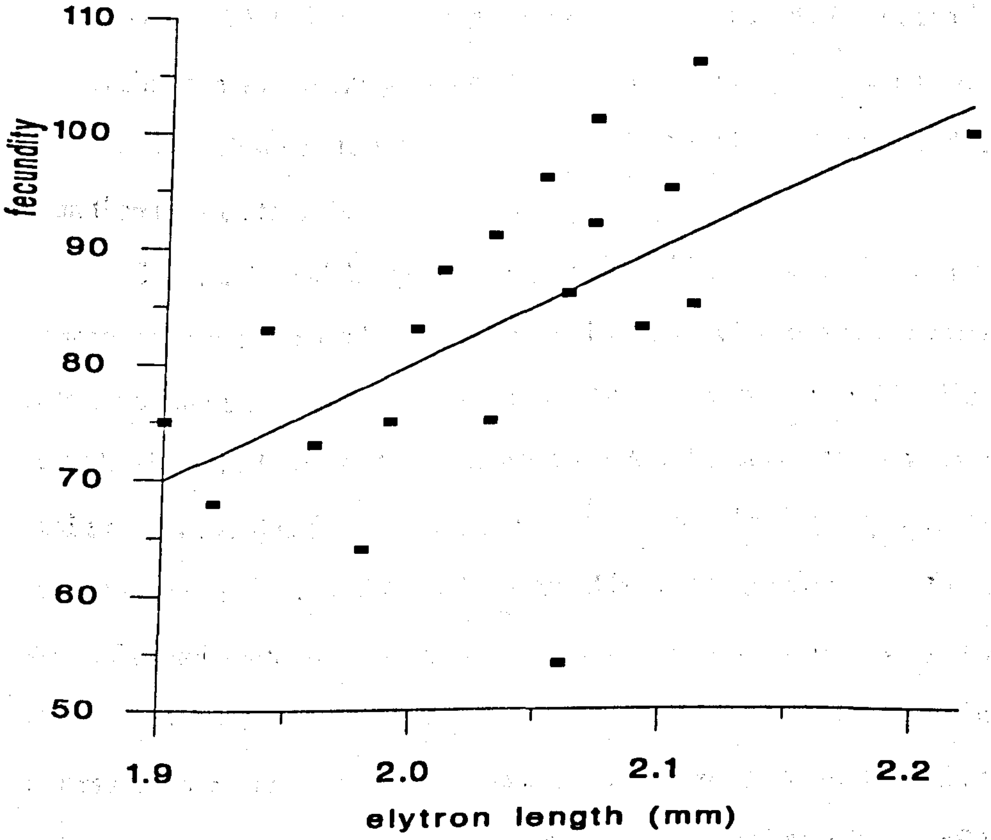

Figure 2.2. The relationship between female lifetime fecundity and left elytron length for *C. analis*. Fecundity = -118+101.4(elytron length): $F_{1,18} = 9.15$, $P = 0.007$. The intercept of the line with the y axis does not differ significantly from zero ($t = 1.77$, $df = 18$, $P = 0.094$) and so lifetime fecundity is directly proportional to female elytron length.

Chapter 3. Experimental measurement of the cost of exploitation competition in *Callosobruchus maculatus* and *C. analis*

(Based on Colegrave 1995)

3.1 Introduction

One of the major aims of theoretical modelling in evolutionary ecology is to try to determine which factors in an organism's environment could have been important in producing the evolutionary outcomes that we see today. Once a model has been produced which seems to explain the way in which evolution has proceeded the model can then be used to make experimentally testable predictions.

The Smith and Lessells (1985) model of larval competition in granivorous insects attempted to explain why several larvae of *Callosobruchus maculatus* will coexist within a single bean, using the *Avoid* competition strategy (Smith and Lessells 1985), whilst the larvae of *C. analis* use the *Attack* larval competition strategy (Smith and Lessells 1985) and fight to the death within a bean leaving only a single surviving adult to emerge. Smith and Lessells modelled larval competition using 2 variables; the cost of exploitation competition (E) and *Attack* larval superiority (W). The cost of exploitation competition represents the reduction in fitness of an *Avoid* larva which shares a bean with another *Avoid* larva compared to what its fitness would have been had it developed without exploitation competition (defined as a fitness of 1). *Attack* larval superiority is simply the probability that an *Attack* larva beats an *Avoid* larva in a fight, and allows for the fact that by specialising in fighting behaviour, *Attack* larvae may be better fighters than *Avoid* larvae. The results of the model are summarised in figure 3.1.

In general, as the cost of exploitation competition increases, the *Attack* larval competition strategy becomes more likely to be the evolutionarily stable strategy (ESS, Maynard Smith 1982). A higher cost of exploitation competition in *C. analis* than in *C.*

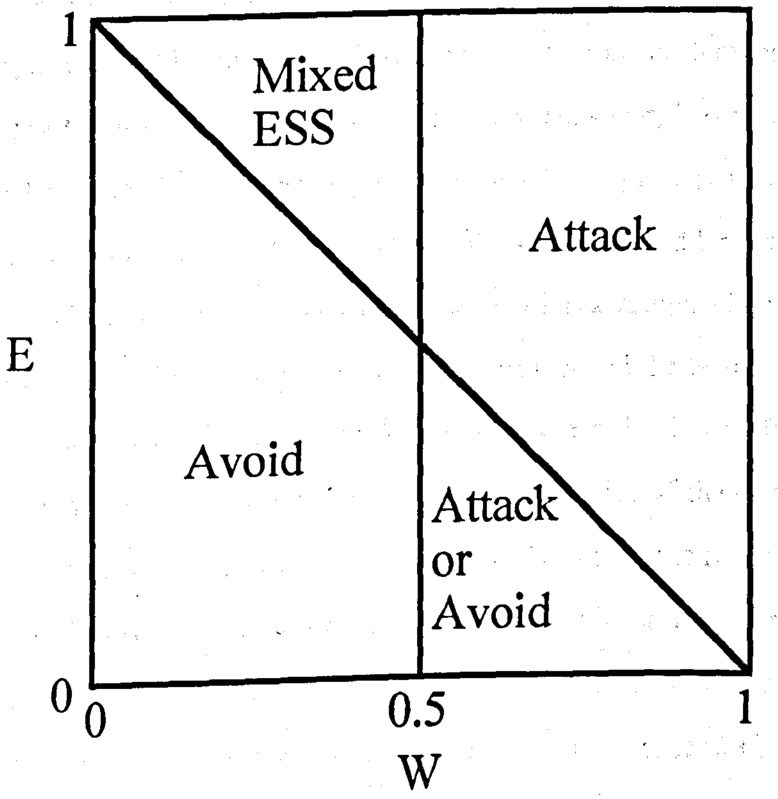

Figure 3.1. The Smith and Lessells model. E is the cost of exploitation competition and W the level of *Attack* larval superiority. Zones represent the ESS under different conditions. Although the original Smith and Lessells model did not include values of W < 0.5, these are included in this figure for completeness.

maculatus could thus explain their different larval competition strategies. Previous authors have successfully measured the cost of exploitation competition in *C. maculatus* (Credland, et al. 1986, Giga & Smith 1991, Messina 1991) by measuring the relative fitness of larvae raised with and without exploitation competition. However, this cannot be done for *C. analis* as the larvae kill each other leaving a single larva to develop without exploitation competition. However, it is possible to get two *C. analis* larvae to share a bean sequentially, by allowing one larva to develop alone within a bean and then, once it has emerged, allowing a second larva to develop in the same bean. The reduction in fitness of the second larva compared to the first can be used as a measure of the cost if the two larvae had shared the bean simultaneously. If the same is done with *C. maculatus* larvae, then the reduction of fitness of second larvae through a bean can be compared for the two species. If the cost of exploitation competition in *C. analis* is higher than in *C. maculatus* then the reduction in fitness of the second *C. analis* larva will be expected to be higher than for the second *C. maculatus* larva. Finally, the sequential development method can be calibrated for *Avoid* competition by comparing the relative fitness of the second *C. maculatus* larva with the fitness of *C. maculatus* larvae raised in simultaneous competition (i.e. sharing the bean with one other larva).

This chapter describes a series of experiments designed to answer the question: can differences in the cost of exploitation competition in *C. analis* and *C. maculatus* explain their different larval competition strategies? Sequential competition experiments were carried out on both species of beetle to provide comparable measures of the cost of exploitation competition, and simultaneous competition experiments were carried out on *C. maculatus* to calibrate the sequential experiments. All experiments were carried out on a large host, black-eyed bean (*Vigna unguiculata*: mass ± se; 234mg ± 1.19, n = 50) and also on a small host, mung beans (*V. radiata*: 62.5mg± 0.63, n = 50), to provide two sizes of hosts with differing expected levels of exploitation competition.

3.2. Methods

3.2.1. Sequential development

100 adult *C. analis* (within 12h of emergence) were allowed to oviposit on 200 host beans for 24h. The beetles were then removed and the beans examined. Any beans that did not carry eggs were returned to the beetles for a further 6h of oviposition. This was repeated until all beans carried at least one egg. All eggs were laid within a period of 36h. The beans then had their egg load reduced to one by removal of excess eggs with a scalpel and were placed in individual cells of a partitioned petri dish in conditions suitable for larval development (30°C, 70%rh). This procedure removes any systematic difference in bean quality caused by females laying fewer eggs on poorer quality hosts. After seven days the beans were re-examined and any carrying unhatched eggs were removed from the experiment. After a further 21 days the beans were monitored daily and any emergent adults removed. The length of the left elytron of each adult was measured. Once adults had ceased emerging, all beans from which beetles had emerged were collected for the next stage of the experiment. Any beans from which no beetle had emerged were kept for a further seven days to ensure no further emergence, and then discarded. 100 *C. analis* adults (less than 12h old) were then allowed to oviposit on the remaining beans for 24h, after which the beetles were removed and the beans examined. Any beans not carrying eggs were returned to the beetles for a further 6h of oviposition, and this was repeated until all beans carried at least one egg. As *C. analis* adults showed reduced oviposition on used mung beans, not all beans carried eggs within 36h. Beans that did carry eggs after 36h were therefore used as a subgroup. The remaining beans were given to a new set of adults (less than 12h old) for a further bout of oviposition until they also all carried at least one egg. Thus two subgroups were set up, the beans within each subgroup carrying eggs laid within 36h of each other. All beans in both subgroups were then modified to

have an egg load of one and the larvae were allowed to develop exactly as in the previous part of the experiment. Once again all emergent adults were measured.

The *C. maculatus* sequential experiment was carried out using exactly the same method, but due to the shorter development time of *C. maculatus* larvae the beans were monitored for emergence daily 21 (rather than 28) days after the eggs were laid. As *C. maculatus* adults showed less aversion to laying on used beans, all second eggs were laid within 36h and it was not necessary to set up subgroups.

3.2.2. Simultaneous development

100 adult *C. maculatus* (less than 12h old) were allowed to oviposit on 200 host beans for 24h. The beetles were removed and the beans examined. Any beans that did not carry eggs were returned to the beetles for a further 6h of oviposition. This was repeated until all beans carried at least two eggs. All eggs were laid within 36h. Each bean then had its egg load reduced to two by removal of excess eggs with a scalpel. The beans were then placed in individual cells of a partitioned petri dish and placed in conditions suitable for larval development. After seven days the beans were re-examined and any carrying unhatched eggs were discarded. After a further 14 days the beans were monitored daily and any emergent adults removed on the day of their emergence. All adults were measured.

3.2.3. Analysis

Both the survival of larvae and the size of emergent adults were used as measures of fitness in the statistical analysis. Size was used as a measure of fitness as lifetime fecundity is strongly correlated with size in both species (Credland et al. 1991, Colegrave 1993 and chapter 2 for *C. maculatus* and *C. analis*). As males and females of *C. analis* are impossible to distinguish reliably without dissection, and there is no sex difference in size, with or without competition (two-way anova: sex $F_{1,40} = 0.79$, $P = 0.38$), size data for the two sexes were pooled for *C. analis* in the statistical analysis.

However, as *C. maculatus* shows sexual dimorphism with males smaller than females, and the effect of size on a male's fitness is unknown, only the data on *C. maculatus* female size were used.

3.3. Results

3.3.1. Large host: black-eyed bean

In both *C. analis* and *C. maculatus* the second larvae to pass through the beans showed a reduction in the size of emergent adults compared to first larvae (Table 3.1a: two-way anova: larval sequence $F_{1,372} = 23.0$, $P < 0.0001$) suggesting that they are suffering a reduction in fitness due to reduced resources. However second *C. analis* larvae did not show a greater reduction in size than second *C. maculatus* larvae (Table 3.1a: two-way anova: species by larval sequence interaction $F_{1,372} = 0.18$, $P = 0.68$). There was no difference between the species in the survival to emergence when comparing first larvae to second larvae, as shown by the non-significant 3-way interaction in a 3-way loglinear model (table 3.2a: G = 1.17, df = 1, $P = 0.28$: Sokal & Rohlf 1981). Thus it appears that in black-eyed beans the cost of exploitation competition is similar in *C. analis* and *C. maculatus*. Furthermore, second *C. maculatus* larvae did not differ in either survival to emergence ($chi^2 = 2.83$, df = 1, $P > 0.05$) , or emergent female size (t = 0.96, df = 161, $P = 0.34$) when compared to *C. maculatus* larvae raised in simultaneous competition with another larva (Tables 3.1b & 3.2b), suggesting that the estimate of the cost of exploitation competition obtained by the sequential development method is a good estimate of the true cost of simultaneous larval competition in *C. maculatus* on black-eyed beans.

3.3.2. Small host: mung beans

Adult *C. analis* from the two subgroups did not differ in either survival to emergence ($chi^2 = 1.07$, df = 1, $P > 0.05$) or adult size (t = 0.16, df = 41, $P = 0.87$), so the two subgroups were pooled for the following analysis. Once again second larvae

Table 3.1. Mean elytron lengths (mm) for adult *C. maculatus* and *C. analis* from a) the sequential experiment where larvae share a bean one after the other and b) the simultaneous experiment where larvae share the bean at the same time.

a) sequential experiment

	1st adults mean elytron length (± se)	2nd adults mean elytron length (± se)
black-eyed beans		
C. analis	2.07 (0.01)	2.02 (0.01)
C. maculatus	2.44 (0.01)	2.38 (0.02)
mung beans		
C. analis	2.04 (0.01)	1.87 (0.02)
C. maculatus	2.39 (0.02)	1.91 (0.03)

b) simultaneous experiment

	Mean elytron length (se) of adults raised in simultaneous competition
C. maculatus	
black-eyed beans	2.39 (0.01)
mung beans	2.29 (0.02)

Table 3.2. Percentage survival of *C. maculatus* and *C. analis* larvae from a) the sequential experiment where larvae share a bean one after another and b) the simultaneous experiment where larvae share beans at the same time.

a) sequential experiment

	percentage survival (se)	
	first larva	second larva
black-eyed beans		
C. analis	86.5 (3.2)	82.4 (3.2)
C. maculatus	91.7 (2.2)	93.7 (2.2)
Mung beans		
C. analis	74.7 (3.2)	41.7 (4.5)
C. maculatus	72.1 (3.4)	65.3 (2.2)

b) simultaneous experiment

	percentage survival (se)
C. maculatus	
black-eyed beans	88.1 (2.1)
mung beans	56.2 (2.8)

through a bean produced smaller adults than first larvae (Table 3.1a: two-way anova: larval sequence $F_{1,282} = 319.4$, $P < 0.0001$), suggesting that they are suffering due to reduced resource. However, in this case the reduction in size of second larvae in *C. maculatus* was significantly greater than the reduction in size of second larvae in *C. analis* (Table 3.1a: two-way anova: species by larval sequence interaction: $F_{1,282} = 80.4$, $P < 0.0001$) suggesting that the cost of exploitation competition, in terms of its effect on adult size, may actually be greater in *C. maculatus*. *C. analis* showed a greater reduction in survival to emergence of second larvae than *C. maculatus* (Table 3.2a: $G = 9.29$, $df = 1$, $P = 0.002$) suggesting that in terms of survival *C. maculatus* suffers a lower cost of exploitation competition in mung beans. Second *C. maculatus* larvae survived as well as those raised in simultaneous competition (Table 3.2b: $chi^2 = 3.06$, $df = 1$, $P > 0.05$). However, the adults that emerged from the second larvae were smaller than those from larvae raised in simultaneous competition (Table 3.1b: $t = 11.68$, $df = 123$, $P < 0.0001$); they appear to suffer a greater reduction in fitness when in sequential competition.

3.4. Discussion

The results of the sequential development experiments described in this paper suggest that when using black-eyed beans as a host the cost of exploitation competition for the two species is very similar. The fact that both the sequential and simultaneous experiments give comparable estimates of the relative cost of exploitation competition in *C. maculatus* on black-eyed beans suggests that the values obtained in the sequential experiment for *C. analis* are probably a reliable indicator of the values that would be obtained if larvae did share beans simultaneously, without competing aggressively. However, if mung beans are used as a host the situation becomes more complex. In terms of survival to emergence *C. maculatus* seems to suffer less due to exploitation competition than *C. analis*, but in terms of the size of surviving adults the situation is reversed, with *C. maculatus* showing a greater reduction in size of adults than *C. analis*. Also, whilst the estimates of the cost of exploitation competition in terms of survival to adulthood agree for the *C. maculatus* sequential and simultaneous development experiments, the greater reduction in size of second adults from the sequential experiment suggest that on mung beans the sequential method may actually give an overestimate of the cost of exploitation competition.

The results of these experiments also provide estimates of the value of the cost of exploitation competition parameter used by Smith and Lessells (1985) in their model. The cost of exploitation competition parameter (E) used in the model represented the reduction in fitness of a larva due to exploitation competition compared to a fitness of 1 if the larva had been alone in the bean. As lifetime fecundity is directly proportional to female size in both species (see chapter 2) the measures of fitness used in this experiment can be combined by multiplying the mean size of emergent adults by their percentage survival. If the fitness value of larvae raised in competition (either sequentially or simultaneously) is then divided by the fitness value of larvae raised without exploitation competition, then a value of the relative fitness of the competing larvae is obtained. This value can then be subtracted from 1 to give an estimate of the cost of exploitation competition parameter (E).

Estimates of this parameter (E) obtained from the sequential experiments are shown in Table 3.3, along with the estimates obtained for *C. maculatus* competing simultaneously. The model predicts that if there is no *Attack* larval superiority (W=0.5) and E is greater than 0.5 then *Attack* will be the only stable strategy, while if E is less than 0.5 *Avoid* becomes a possible ESS. The values for both species competing on black-eyed beans are not only very similar (*C. maculatus* E=0.01, *C. analis* E= 0.06), but are also well within the range where *Avoid* is expected as a possible evolutionary outcome. When using mung bean as a host the cost of exploitation competition in *C. analis* (E = 0.49) does appear to be higher than in *C. maculatus* (E=0.28), and is also very close to the 0.5 value above which *Attack* is the only stable evolutionary outcome. In a situation where *Attack* larvae are actually better fighters than *Avoid* larvae

Table 3.3. Estimates of the cost of exploitation competition parameter (E) from both the sequential and simultaneous experiments.

	host species	
	black-eyed beans	mung beans
C. maculatus		
Simultaneous	0.06	0.24
Sequential	0.01	0.28
C. analis		
Sequential	0.08	0.49

(W>0.5) the Smith and Lessells model requires that the cost of exploitation competition is reduced further if *Avoid* is to be an ESS (as E<1-W). In this case a small *Attack* larval superiority could put *C. analis* within the conditions in which *Attack* is the only ESS on mung beans. It would require a very large increase in *Attack* larval superiority to stop *Avoid* being an ESS for *C. analis* on black-eyed beans and *C. maculatus* on both hosts.

Thus it appears that on black-eyed beans differing costs of exploitation competition cannot be invoked to explain the disparate larval competition strategies of the two species. It seems that *C. analis* larvae would actually show an increase in individual fitness if they showed the *Avoid* behaviour used by *C. maculatus*. However on the smaller host, mung beans, the two species may indeed be using the appropriate behaviour that maximises individual fitness given their differing cost of exploitation competition on this host. It may be that *C. analis* originally evolved in a host similar to mung bean and has only recently moved to using black-eyed beans as an alternative host. If *Attack* larvae are superior fighters to *Avoid* larvae then once *C. analis* had evolved the *Attack* strategy it would be very difficult for mutant *Avoid* larvae to invade the population even if the cost of exploitation competition reduced, because they would almost always be sharing beans with *Attack* larvae that would often kill them. The population would be stuck at the *Attack* ESS. This is similar to the situation that is thought to occur in parasitoid insects, where the larvae of some species fight over a host even though there is enough resource in a single host to support the development of several larvae (Godfray 1987a, b).

The notion that the costs of exploitation competition are higher in smaller beans, and promotes the evolution of *Attack* type strategies on these hosts is in agreement with the observation that wild bruchid species in Japan (Kiritani 1957 cited in Toquenaga and Fujii 1990), which feed on small wild beans rather than on larger stored products, usually show an *Attack* larval competition strategy. Thanthianga and Mitchell (1987) have also shown that a strain of *C. maculatus*, that was isolated from mung beans in south India shows an *Attack* type of larval competition, even when allowed to develop in larger host beans in the laboratory.

It might be expected that larvae of an *Avoid* species, which may have to share a bean with one or several other larvae, will encounter far more variation in resource availability than larvae of an *Attack* species, which essentially obtain all or none of the resource. Thus *Avoid* species might evolve a greater degree of plasticity in adult emergence size compared to *Attack* species, with each individual modifying its emergence size to suit the resources available. The variance of the first and second larvae through the beans can be pooled to give an idea of the degree of variation in adult size when larvae share different hosts. On the black-eyed beans there was no difference between the variances of *C. analis* and *C. maculatus* (variance *C. analis* = 0.101, variance *C. maculatus* = 0.109: $F_{124,248}=1.08$ $P>0.05$). However on mung bean, the smaller host, *C. maculatus* showed a greater variance than *C. analis* (variance *C. analis* = 0.081, variance *C. maculatus* = 0.181: $F_{105,177} = 2.235$, $P < 0.01$) suggesting that *C. maculatus* larvae may indeed be able to tailor their size at emergence to suit the level of resource to a greater degree than *C. analis* larvae. The fact that second *C. maculatus* larvae show a greater reduction in size than second *C. analis* larvae whilst second *C. analis* show a much higher reduction in survival when developing on mung beans is also consistent with this idea. It may be that when resources are limited *C. maculatus* larvae can respond plastically and produce smaller adults while *C. analis* larvae are unable to respond and so, if resources are significantly reduced, die.

The fact that selection pressures may change between the evolutionary origin of a character and the present day creates problems with making inferences about the evolutionary origins of a behavioural strategy from contemporary experiments. There may have been alterations in the physiology of the species since the larval competition strategy evolved. For example, a species that evolves an *Avoid* type strategy may then also evolve a greater degree of plasticity in its response to resource availability. This could make the currently measured cost of exploitation competition a poor indicator of what it was at the time when the strategy evolved. Nevertheless, the use of theoretical models, along with the experimental testing of the model's predictions is an extremely powerful tool in demonstrating which evolutionary scenarios are consistent with what is observed today.

Thus, it seems that differing cost of exploitation competition for the two species is not the reason for the different larval competition strategies when developing in black-eyed beans (the host on which the cultures used in this experiment has been cultured for at least the last 18 years; C. M. Lessells pers. comm.). However, the higher cost of exploitation competition shown by *C. analis* on mung beans, does suggest that if they originally evolved on a host similar to mung this could explain the origin of their *Attack* strategy. What forces maintain this strategy now is still open to question.

Chapter 4. The effect of host size on the cost of exploitation competition in *Callosobruchus maculatus*

4.1. Introduction

When two organisms compete to exploit the same patch of resource each will, in the absence of an Allee effect (Allee 1931), have a lower fitness than if they had sole access to the resource. Even if the organisms do not actively interfere with each other and compete simply by exploiting the resource in a scramble process (*sensu* Nicholson 1954), each will suffer a cost because the resource must be split between the two of them (Begon et al. 1986). Previous authors have shown that the larvae of *Callosobruchus* beetles suffer a reduction in fitness if they have to compete with other larvae whilst developing within a bean, compared to the fitness of larvae which do not have to compete. Larvae which have to share beans show a lower survival to emergence, and also emerge as smaller adults and hence have lower fecundity (Mitchell 1975, Smith & Lessells 1985, Credland et al. 1986, Giga & Smith 1991, Messina 1991), than larvae which develop alone within beans.

Smith and Lessells (1985, see also Smith 1990) suggested that the size of this reduction in fitness, suffered by larvae due to exploitation competition, could have important consequences for the type of larval competition strategy that a species evolves. In their game theory model of larval competition, Smith and Lessells defined the cost of exploitation competition as the reduction in fitness of a larva which suffers exploitation competition during development, compared to its expected fitness if it had developed without competition (defined as a maximum fitness of 1). The results of the model suggested that the greater the cost of exploitation competition, the more likely a species is to evolve an *Attack* type of competition strategy, such as the strategy used by *C. analis* (Umeya et al. 1975), with larvae fighting to the death within the bean.

However, as the cost of exploitation competition decreases, species are more likely to evolve an *Avoid* type of strategy, such as the strategy used by *C. maculatus* (Mitchell 1975), with larvae competing by exploiting the resource without directly interfering with each other. Smith and Lessells (1985) suggested that disparate larval competition strategies used by *C. maculatus* and *C. analis* could be explained if the two species evolved under conditions in which the cost of exploitation competition experienced by the larvae differed.

One factor that will be expected to affect the cost of exploitation competition is the size of the host on which larvae develop (Smith & Lessells 1985, Smith 1990). Smaller hosts contain less resource and so the costs of sharing these hosts are likely to be higher. The aim of this chapter is to investigate the effect of host size on the cost of exploitation competition in *C. maculatus*. Experiments are described in which the fitness of larvae raised in competition with other larvae are compared to the fitness of larvae raised without competition, on hosts of different sizes. Two approaches were used to produce hosts of different sizes. In the first experiment the seeds of four different species of legume, black-eyed bean (*Vigna unguiculata*), adzuki bean (*V. angularis*), mung bean (*V. radiata*) and brown lentil (*Lens culinaris*) were used as hosts. These four species of bean differ in size and are all known to be suitable hosts for the development of *C. maculatus* larvae (Southgate 1979 and pers. obs.). However, whilst different species of bean differ in weight, they will also differ in other ways. In particular, legume beans are known to contain toxins, and the amount and type of toxin varies between beans of different species (Janzen 1977). Thus a second experiment was carried out using hosts of a single species (black-eyed beans). In this experiment bean weight was manipulated in two ways; first naturally small (<200mg) black-eyed beans were selected, and second the weight of standard black-eyed beans was reduced by allowing a single larva to develop within and emerge from beans before they were used in the experiment. In both experiments the fitness of larvae raised alone within beans was compared to the fitness of larvae that shared beans. Two components of fitness were measured in each experiment; female emergence size, measured as left elytron length, was used, since this is a good indicator of a females lifetime fecundity (Credland et al. 1991, Colegrave 1993, see also chapter 2 of this thesis), and survival of larvae to emergence. The amount of host consumed by larvae was also determined to allow the expected cost of exploitation competition on hosts of different sizes to be estimated, based on the amount of available resource. The effect of competition on emergence size of males was ignored as the relationship between emergence size and fitness in males of this species is unknown.

4.2. Methods

4.2.1. Different host species

The following procedure was used to set up beans of all four species (black-eyed beans, adzuki beans, mung beans and brown lentils) carrying either one or two eggs. 100 adult *C. maculatus* (less than 12h since emergence) were allowed to oviposit on 200 host beans for 12h. The beetles were then removed and the beans examined. Any beans that did not carry at least one egg were returned to the beetles for a further 6h oviposition. This was repeated until all beans carried at least one egg. The beans then had their egg loads modified to exactly one by removal of excess eggs with a scalpel. The same procedure was used to produce host beans with egg loads of two eggs per bean, except that oviposition continued until all beans carried at least two eggs. Female *C. maculatus* are expected to modify the number of eggs that they lay on a bean in response to differences in bean quality (Mitchell 1975), this procedure of forcing females to lay at least the treatment number of eggs on all beans and then manipulating eggs loads, removes any systematic differences in bean quality between the one egg and two egg treatments that could be caused by females laying fewer eggs on poorer quality hosts. The beans were then placed in conditions suitable for larval development (30°C, 70% rh). After one week the beans were examined and any carrying unhatched eggs were removed from the experiment. After a further two weeks the beans were monitored daily and adult beetles were removed on their day of emergence and sexed. The left elytron of each female beetle was then removed and measured. 50 of each host species were weighed before oviposition to provide an estimate of the amount of resource available in each host species. These weighed beans were then used in the one egg per bean treatments, and re-weighed at the end of the experiment to provide an estimate of the amount of resource used by a single larva developing in each of the host species.

4.2.2. Single host species.

Host beans of different species, differ not only in weight but also in other ways (e.g. toxin content; Janzen 1977). To examine the effect of host size, whilst minimising chemical differences between hosts of different sizes, the following experiment was carried out using hosts of a single species (black-eyed bean). Groups of 100 adult *C. maculatus* (less than 12h since emergence) were allowed to oviposit on 200 host beans of each treatment type (standard black-eyed beans weighing approximately 240mg, selected black-eyed beans less than 200mg, and standard black-eyed beans which had been used previously for the development of a single larva) for 24h. The beetles were then removed and the beans examined. Any beans not carrying at least two eggs were returned to the beetles for a further 2h of oviposition. This was repeated until all beans carried at least two eggs. The beans were then randomly allocated to two groups. One group then had their egg loads modified to one egg per bean, the other to two eggs per bean, by removal of any excess eggs with a scalpel. The beans were then placed in conditions suitable for larval development (30°C, 35 ± 5%rh). After one week the beans were examined and any carrying unhatched eggs were removed from the experiment. After a further two weeks the remaining beans were examined daily and any emergent beetles removed and sexed. The left elytron of each female beetle was then measured. The beans in each treatment were also weighed before the experiment.

4.3. Results

4.3.1. Different host species.

The different host species used in the experiment differed in weight (mean weight ± se for black-eyed bean: 232mg ± 0.7; adzuki bean: 89mg ± 0.2; mung bean: 63mg ± 0.4 and lentil 33mg ± 0.1, n = 50 for all hosts: anova $F_{3,196} = 957.5$, $P < 0.0001$), and so do represent different amount of resource available to beetle larvae. However, there was no difference in the amount of a bean consumed by a single larva during development on the four hosts (mean weight loss ± se for black-eyed beans (n = 41): 24.1mg ± 0.8, adzuki beans (n = 34): 23.3mg ± 0.9; mung beans (n = 32): 24.7mg ± 1.0 and lentil (n = 19): 22.8mg ± 1.3: anova: $F_{3,125} = 0.69$, $P = 0.56$). Beetles which had to compete over a bean as larvae, emerged smaller than those that had sole access to a bean (Table 4.1a: 2 way-anova: eggs per bean $F_{1,551} = 12.74$, $P < 0.0001$) suggesting that beetles suffer a reduction in fitness due to exploitation competition. The emergence size of beetles also differed for different host species (Table 4.1a: two-way anova: species $F_{3,551} = 108.25$, $P < 0.0001$.), and so beans of different species seem to provide different amount or different quality of resources. However, the reduction in size of beetles raised with competition compared to those raised alone, did not differ on the different host bean species (two-way anova: egg per bean by species interaction $F_{3,551} = 1.68$, $P = 0.169$). However, this only shows that there is no difference in the absolute reduction in elytron length, whereas the cost of exploitation competition depends on the proportional reduction in fecundity. Therefore a second two-way anova was carried out on log fecundity of females, with fecundity being estimated using the relationship fecundity = -127+101.0(elytron length) (see chapter

Table 4.1. a) Mean elytron length (mm) and b) estimated lifetime fecundity (eggs) of female *C. maculatus* raised with and without competition on the four different host species.

a)

	mean left elytron length ± se (n)	
Host species	1 egg per bean	2 eggs per bean
black-eyed bean	2.44 ± 0.01 (68)	2.39 ± 0.01 (105)
adzuki bean	2.23 ± 0.02 (63)	2.18 ± 0.02 (94)
mung bean	2.39 ± 0.02 (73)	2.29 ± 0.02 (91)
lentil	2.05 ± 0.02 (26)	2.04 ± 0.02 (39)

b)

	mean estimated fecundity ± se (n)	
Host species	1 egg per bean	2 eggs per bean
black-eyed bean	119.4 ± 1.16 (68)	114.4 ± 0.93 (105)
adzuki bean	98.2 ± 2.38 (63)	93.2 ± 2.19 (94)
mung bean	114.4 ± 2.18 (73)	104.3 ± 1.68 (91)
lentil	80.1 ± 2.25 (26)	79.0 ± 2.04 (39)

2). Whilst the egg per bean by species interaction was not significant (Table 4.1b: two-way anova: egg per bean by species interaction $F_{3,551} = 2.07$, $P = 0.10$), the associated probability was low enough to at least be suggestive that such an effect may be occurring. The effect of host species and competition on survival to emergence were analysed using a Logit model (Sokal & Rohlf 1981). Although survival to emergence was lower in beetles raised in competition (Table 4.2: Logit model: eggs per bean: G = 10.4, df = 1, $P = 0.001$) and survival differed on the different hosts (Table 4.2: Logit model: species: G = 325.1, df = 3, $P < 0.0001$), there was no difference in survival to emergence when comparing larvae raised with or without competition on different hosts (Table 4.2: Logit model: egg per bean by species interaction G = 3.59, df = 3, $P = 0.302$). Thus, the reduction in fitness due to competition appears to be of a similar size on all four host species, whether it is measured in terms of absolute reduction in female emergence size, relative reduction in estimated fecundity or relative reduction in survival to emergence.

4.3.2. Single host species

The beans in the three treatments used in this experiment differed in initial weight (mean weight ± se for standard black-eyed beans: 219.3mg ± 3.99; beans less than 200 mg: 147.5mg ± 2.17 and beans previously used by a single larva: 195.3mg ± 4.55. n = 100 for all hosts. one-way anova: $F_{2,297} = 97.1$, $P < 0.0001$). Beetles that had to compete over a bean as larvae emerged smaller than those that had sole access to the bean, (Table 4.3a: two-way anova: egg per bean $F_{1,232} = 4.42$, $P = 0.037$), so again larvae appear to suffer a reduction in fitness due to exploitation competition. The emergence size of beetles also differed for the different host types (Table 4.3a: two-way anova: treatment $F_{2,232} = 14.8$, $P < 0.0001$) due to the smaller size of beetles emerging from the used beans. However, the absolute reduction in size of beetles raised with competition compared to those raised alone did not differ for the different host types (Table 4.3a: two-way anova: eggs per bean by treatment interaction $F_{2,232}$ =

Table 4.2. Percentage survival to emergence of *C. maculatus* larvae raised with and without competition on the four different host species.

	Percentage survival ± se (n)	
Host species	1 egg per bean	2 eggs per bean
black-eyed bean	92% ± 2.2 (156)	88% ± 2.1 (244)
adzuki bean	69% ± 3.4 (179)	65% ± 2.7 (310)
mung bean	72% ± 3.3 (179)	56% ± 2.8 (308)
lentil	35% ± 3.7 (165)	28% ± 2.5 (316)

Table 4.3. a) Mean elytron length (mm) and b) estimated lifetime fecundity (eggs) of female *C. maculatus* raised with and without competition on the three different types of black-eyed bean. Numbers in brackets are standered errors of the mean.

a)

	mean left elytron length ± se (n)	
Host type	1 egg per bean	2 eggs per bean
standard	2.42 ± 0.01 (29)	2.40 ± 0.02 (33)
used	2.35 ± 0.02 (40)	2.33 ± 0.02 (43)
< 200mg	2.46 ± 0.02 (39)	2.41 ± 0.02 (54)

b)

	estimated fecundity ± se (n)	
Host type	1 egg per bean	2 eggs per bean
standard	117.4 ± (29)	115.4 ± (33)
used	110.4 ± (40)	108.3 ± (43)
< 200 mg	121.4 ± (39)	116.4 ± (54)

0.52, $P = 0.593$), and neither did the relative reduction in estimated fecundities (Table 4.3b. two-way anova egg per bean by treatment interaction $F_{2,232} = 0.02$, $P = 0.568$) obtained from an analysis of log fecundities. There was also no difference in survival to emergence for larvae raised with or without competition (Table 4.4: Logit model: eggs per bean $G = 3.02$, df = 1, $P = 0.082$) or larvae raised on different host types (Table 4.4: Logit model: treatment $G = 5.15$, df = 2, $P = 0.076$). It appears that the reduction in fitness, measured in terms of survival to emergence, female emergence size and female fecundity is of similar magnitude on black-eyed beans containing different amounts of resource.

4.4. Discussion

The results of these experiments suggest that there is no difference in the reduction in fitness experienced by *C. maculatus* larvae, whether they compete on hosts of different species, or on hosts of the same species but of different sizes. This is true whether fitness is assessed as survival to emergence, female emergence size, or estimated female fecundity. Although larvae suffered a reduction in all three measures of fitness due to competition on all host, and the fitness components of larvae differed between hosts, the size of this reduction in fitness was the same on hosts of different sizes.

This result is slightly surprising. The hosts used in these experiments represented a large range of host sizes and so presumably a large range of available resource. To estimate the cost that would be expected for larvae competing on the hosts used in these experiments a simple model was constructed. Using the reduction in weight caused by the development of a single larva (about 24 mg) as an estimate of the amount of resource required for the full development of a larva, the amount of resource that a bean must contain if two larvae are to both develop without suffering any cost of exploitation competition can be estimated as being at least 48mg. If the

Table 4.4. Percentage survival to emergence of *C. maculatus* larvae raised with and without competition on the three different types of black-eyed bean.

	percentage survival ± se (n)	
Host type	1 egg per bean	2 eggs per bean
standard	85% ± 4.0 (81)	82% ± 4.6 (107)
used	87% ± 3.6 (85)	85% ± 3.1 (131)
< 200 mg	87% ± 3.8 (77)	86% ± 3.0 (129)

amount of resource obtained by a larva is assumed to directly affect its fitness, the relative fitness of larvae that share beans can be calculated as the amount of resource available to each of the larvae (i.e. the total amount of resource available within the bean divided by two) divided by the 24mg required to attain full fitness. This relative fitness can then be subtracted from 1 to give the expected cost of exploitation competition for larvae sharing hosts of different sizes. However, the weight of a bean is probably an overestimate of the amount of resource it contains; some of the bean will be unavailable for consumption by larvae. By continually allowing *C. maculatus* larvae to develop on a sample of mung beans, for several generations, until no more adults emerged, Mitchell (1975) estimated that at least 9 mg of a mung bean is unavailable for consumption by larvae. This represents about 16% of the weight of the mung beans used in his experiments. If this percentage is assumed to be constant for hosts of different sizes then the true amount of resource present in beans of different sizes can be estimated by reducing their weight by 16%. This assumption is unlikely to be valid for black-eyed beans that have already had one larva develop within them as larval feeding will reduce the amount of resource, whilst not altering the amount of bean that is unavailable for consumption. Thus, these beans were assumed to contain 18% unavailable material (this value was obtained by calculating 16% of the mean mass of standard black-eyed beans, and determining what percentage of the mean mass of a used black-eyed bean this represented). To take into account variation in bean size within a species, 20 random beans of each species were weighed, and the expected cost of exploitation competition for each bean calculated as described above. The individual values were then combined to give a mean value for the expected cost of exploitation competition for the bean species used in these experiments (Table 4.5.).

These estimates of the cost of exploitation competition, based solely on the amount of resource present in a bean, suggest that there should be no cost of exploitation competition on both black-eyed beans (from both of the experiments) and adzuki beans, as both these species seem to contain enough resource for the

Table 4.5. Estimates of the cost of exploitation competition on a) host beans of different species and b) black-eyed beans of different weights. The theoretical estimates are based on the amount of resource in the bean, the experimental estimates are based on the survival to emergence and estimated female fecundity of larvae from the experiments. Numbers in brackets are the standard errors of the means.

a) different host species

	cost of exploitation competition	
Host species	theoretical	experimental ± se (n)
black-eyed bean	0	0.08 ± 0.03 (120)
adzuki bean	0	0.13 ± 0.06 (161)
mung bean	0.03	0.29 ± 0.06 (146)
lentil	0.39	0.31 ± 0.10 (153)

b) single host species

	cost of exploitation competition	
Host type	theoretical	experimental
standard	0	0.10 (0.08) n = 43
used	0	0.06 (0.06) n = 63
< 200mg	0	0.05 (0.05) n = 62

development of two larvae. On mung beans a small cost is predicted as some of the beans do not contain enough resource for the development of two larvae, whilst on lentil, the smallest host, a large cost of exploitation competition is predicted as none of the beans contained enough resource for the full development of two larvae. Thus it does appear that the range of host sizes used in these experiments should be large enough to produce a measurable difference in the cost of exploitation competition.

One possible reason that no differences were found could be due to the way in which fitness was measured in the experiments. The total fitness of larvae was measured as two separate components, survival to emergence and female fecundity (estimated from elytron length), and the effect of competition on these two components was analysed separately. The fact that no difference in the size of the reduction in fitness was detected on either of the two components of fitness, does not necessarily mean that there was no effect on total fitness. To investigate this possibility that the relative reduction in total fitness (survival and fecundity combined) may differ on beans of different sizes the following analysis was carried out on the data from the two experiments.

First the two separate measures of fitness were combined for female larvae raised without competition by multiplying the mean estimated fecundity by the proportion of larvae that survived to emergence. This gives an estimate of total fitness of female larvae raised without competition on each host. The relative fitnesses of female larvae that survived to emergence raised in competition on each host were then determined by dividing the fecundity estimate for each female from the two egg treatments, by the mean total fitness of female larvae raised without competition on the same host. Half of the larvae that failed to emerge were assumed to be female and included in the analysis as female larva with a relative fitness of zero. Finally these relative fitness values were all subtracted from one to give the cost of exploitation competition suffered by each larva.

The mean cost of exploitation competition (Table 4.5), measured in this way, differs on the different host species (Kruskall Wallis; H = 26.7, df = 3, $P < 0.0001$). Thus, even though the relative reduction of both larval survival and female fecundity do not differ on different hosts when analysed separately, the cost of exploitation competition does appear to differ on different host species when the two components are combined into a single measure of total fitness. Furthermore, the size of the relative reduction in fitness varies in the way that would be predicted on the basis of host size, being highest in the smallest host (lentil) and decreasing as host size increases. However, a similar analysis shows that the cost of exploitation does not differ significantly on the three types of black-eyed beans from the second experiment (Kruskall Wallis H = 5.22, df = 2, $P = 0.074$).

Whilst these experimental estimates of the cost of exploitation competition show qualitative agreement with the theoretical estimates, based on the amount of resource within a bean, there are some interesting quantitative differences between experimental and theoretical values. On the basis of bean weight, there should be no cost of exploitation competition on either black-eyed beans or adzuki beans. However, the experimental results suggest that larvae suffer a cost of exploitation competition on all hosts. This suggests that the cost of exploitation competition measured on these two host species may not be due to a reduction in available resources. Parker (1982) has shown that when organisms compete over a resource in a scramble process they are expected to alter their behaviour due to the presence of competitors. An organism that has sole access to a resource will invest the minimum amount of effort required to gain the resource that it needs. However, in the presence of competitors the organism will increase the amount of effort invested in obtaining the resource, even though this may reduce the efficiency with which it exploits the resource. The net result is that individuals that have to compete will have a lower fitness than an individual with sole access to the resource, even if they obtain the same amount of resource, because the competing individuals invest more to obtain the resource required. *C. maculatus* larvae appear to be able to detect the presence of other larvae within a bean due to the vibrations produced by larval feeding (Thanthianga & Mitchell 1987). If larvae that detect the presence of another larvae alter their feeding behaviour, for example by increasing feeding rate at the expense of feeding efficiency, to ensure that they obtain as much of the bean as possible before it is eaten by the other lava, this could produce a cost of competition even though each larva obtains the same amount of resource as if it had developed alone within a bean. Whether *C. maculatus* larvae do alter their behaviour in this way is at present unknown. A cost of exploitation competition is predicted for larvae competing on mung beans, however the predicted value is much lower than the value obtained experimentally. Again this may be due to some effect of competition other than a simple effect of reduced resources.

The prediction that the cost of exploitation competition suffered by larvae competing on lentils should suffer a large cost is supported, but the measured cost appears to be smaller than the cost that would be predicted on the basis of the size of lentils. The survival of larvae on lentil was very low, even without the presence of a competitor, probably due to high concentrations of toxin within lentils (Smith 1990). This high level of competition independent mortality may mean that although all of the beans in the competition treatment began with two larvae, many of these larvae may have died before using much of the resource, and so many of the emerging adults from the competition treatment may have completed most of their development alone in the bean without competition. This may mean that the cost of exploitation competition measured on lentils is an underestimate of the true cost of competition on this host.

Thus, even though the amount of resource within a bean does appear to have some effect on the cost of exploitation competition suffered by larvae, the poor qualitative fit between the experimental estimates and theoretical estimates based on the amount of resource within beans of different species, suggests that the cost of exploitation competition actually suffered by larvae is also affected by other factors.

There was no difference in the cost of exploitation competition suffered by larvae on the three types of black-eyed bean used in the second experiment, although the probability from the analysis of survival and fecundity combined was low enough to be suggestive that with a larger sample size an effect might be found. If this is the case it suggests the paradoxical result that the cost of exploitation competition is highest on the largest host (standard black-eyed beans). The three types of bean used in this experiment all appear to contain ample resources for the full development of two larvae and so any differences in costs are unlikely to be caused by the amount of resource available to larvae. An interesting possibility is that the presence of two larvae feeding within a bean improves the quality of the host in some way making it easier for larvae to feed on it. Such an effect would be likely to be greater on small hosts and so larvae sharing the smaller black-eyed beans may could suffer less from competition than those in larger beans. Giga and Smith (1981) suggested that such an effect might occur in *C. maculatus*, although their data set was not large enough to demonstrate this unequivocally. However, even if such an effect does occur it is likely to be limited to a small range of host sizes, as once hosts become very small, the reduction in resource quantity will outweigh any improvement in quality.

Previous authors (Smith & Lessells 1985, Smith 1990, Toquenaga & Fujii 1990) have suggested that the interspecific differences in larval competition strategies observed in bruchid beetles may be due to the species evolving on host beans of different sizes, the assumption being that the cost of exploitation competition will be higher on smaller hosts making the evolution of *Attack* type larval competition strategies more likely on smaller hosts. This has been used to explain why most *Callosobruchus* species, which live on large cultivated legumes, use the *Avoid* type of strategy as larvae whilst most wild bruchid species, living on the much smaller wild legumes, generally use an *Attack* type of larval competition strategy (Kiritani 1987 cited in Toquenaga & Fujii 1990). The results discussed here lend support to the idea that the cost of exploitation competition does increase as host size decreases.

However, as differences were only found between hosts of different species of bean, which will differ in ways other than size, it cannot be argued with certainty that the size of the host is the factor affecting the cost of exploitation competition. Further experiments, manipulating the amount of resources within beans, or even using artificial beans, which differ only in size, are required to show unequivocally that host size is the important factor affecting the cost of exploitation competition.

Chapter 5. The cost of having fought in *Callosobruchus analis*

5.1. Introduction

It is generally agreed by ecologists that when organisms compete over resources all competitors pay a cost due to the competition (Begon et al. 1986). The type of cost paid will depend on the mechanism by which competition occurs. If organisms compete without directly interfering with competitors in a scramble process (*sensu* Nicholson 1954), each competitor will have a reduced fitness, either because they obtain less of the resource due to depletion by other individuals (Begon et al. 1986) or because they have to invest more time and energy into obtaining the same amount of resource as they would if there were no competitors present (Parker 1982). If organisms compete actively by attempting to exclude other individuals from the resource, in a contest process (*sensu* Nicholson 1954), the costs to the loser are obvious. As well as the time and energy invested in competition, losers will be excluded from the resource and may be injured or even killed in the process. However, the winners will pay costs too. Successful competitors will also have invested time and energy in excluding individuals and may also occasionally be injured if competition involves active aggression. This means that even though the successful competitors have sole access to the resource, their fitness will be lower than if they had not had to compete in the first place.

In their model of larval competition, Smith and Lessells (1985) highlighted the importance that the cost of competing over a resource will have on whether a species evolves an *Attack* competition strategy, with larvae fighting to the death over the resource, or an *Avoid* strategy, with larvae competing passively, exploiting the resource without directly intefering with each other. They assumed that when two *Avoid* larvae compete in a scramble type of process, each suffers a reduction in fitness due to exploitation competition, relative to the fitness of a larva that develops without competition. This cost of exploitation competition parameter has major consequences for the outcome of the model; the higher the cost of exploitation competition, the more likely that the *Attack* strategy, with larvae fighting to the death within the bean, will be the predicted evolutionary outcome. However, when considering the fitness of larvae that fight over a bean, Smith and Lessells assumed that only the larva that loses the contest pays a cost. The larva that wins was assumed to have the same fitness as a larva that develops without competition, effectively suffering no reduction in fitness due to having fought. If winning larvae actually do suffer a cost of having fought, this would be expected to reduce the range of conditions in which *Attack* behaviour is expected to evolve; the greater the cost of having fought, the more likely that a species will evolve an *Avoid* type of larval competition strategy and compete passively over the resource without interfering with each other.

Smith and Lessells' assumption that larvae that fight over beans suffer no cost of having fought may be largely due to the lack of available data for this cost in bruchid beetles. Whilst there have been several studies measuring the effect of larval competition on fitness in species such as *C. maculatus* and *C. rhodensianus* (Credland et al.. 1986, Giga & Smith 1991, Messina 1991), where larvae compete using the *Avoid* strategy, there has been relatively little work investigating the effects of competition on species such as *C. analis*, whose larvae compete using an *Attack* strategy (Umeya et al. 1975). Umeya and co-workers (1975) found no evidence for a cost of having fought for *C. analis* larvae raised at a range of host densities, but their results were limited to the effect on larval survival to emergence, and did not include any measure of adult fecundity. Toquenaga and Fujii (1990) did measure the effect of different initial larval densities on survival to emergence, beetle emergence size and development time, but the small number of beans per treatment in their experiments coupled with the fact that the beans used in the different treatments carried naturally generated egg loads rather than experimentally manipulated egg loads, make it difficult to draw firm conclusions from their results.

In this chapter experiments are described that were designed to measure the cost of having fought over a bean to the larva that survives the competition, by comparing the fitness of larvae raised alone within beans to the fitness of larvae that develop in beans initially containing one to three other larvae.

5.2. Methods

To obtain host beans with differing egg loads (either one, two, three or four eggs per bean) adult *C. analis* were allowed to oviposit on four groups of 120 host beans for 12h. The number of adult beetles was varied for each group depending on the required number of eggs per bean, with 50, 60, 75 and 100 adults used in the one, two, three and four egg per bean treatments. After 12h the beetles were removed and the beans examined. Any beans not carrying at least the number of eggs required for their treatment were returned to the beetles for a further 6h of oviposition. This was repeated until all beans in a treatment carried at least the required number of eggs. All eggs were laid within 24h. The beans had their egg loads manipulated to the treatment number by removal of excess eggs with a scalpel and were then placed in conditions suitable for larval development (30°C, 70%rh). Female beetles are expected to vary the number of eggs they lay on a bean in response to differences in bean quality. If beans were selected for treatments on the basis of the number of eggs that they carried there could be differences in the quality of the beans in the one and two egg treatments due to females only laying two eggs on better quality beans. This procedure of forcing females to lay at least the treatment number of eggs on all beans, and then manipulating egg loads reduces the possibility of systematic differences in bean quality between treatments which might occur if beans with naturally generated egg loads were used.

After seven days the beans were examined and any carrying unhatched eggs were discarded. After a further 14 days the beans were monitored daily and any adults removed on their day of emergence. The left elytron of each adult was removed and measured as an indicator of body size, which is known to be a good indicator of a female's lifetime fecundity in this species (see chapter 2), and the beetles were then dissected to determine sex.

Because any cost of having fought may depend on the size of the host bean, the experiment was carried out twice using two hosts of different sizes. Black-eyed beans (*Vigna unguiculata*: mean weight = 232mg ± 0.8se, n = 20) were used as the large host and mung beans (*Vigna radiata*: mean weight = 65mg ± 0.4se, n = 20) as the smaller host.

5.3. Results

5.3.1. Large host: black-eyed beans

The emergence size of both male and female beetles was affected by the initial number of larvae in a bean (Table 5.1a: two-way anova: treatment $F_{3,266} = 3.36$, $P = 0.019$), with beetles from treatments with higher initial numbers of larvae within beans emerging smaller than beetles from the one egg per bean treatment. Males and females did not differ in emergence size (Table 5.1a: two-way anova: sex $F_{1,266} = 0.86$, $P = 0.354$), and the effect of the number of eggs per bean on emergence size did not differ for males and females (Table 5.1a: two-way anova: treatment by sex interaction $F_{3,266} = 1.21$, $P = 0.307$). Thus, having to fight for a bean appears to reduce the emergence size of the surviving larvae, and the size of the reduction is the same for both male and female beetles.

Development time was highly skewed, therefore violating the assumptions for parametric statistics. Since there is no suitable nonparametric equivalent to a 2-way

Table 5.1. Mean elytron lengths for male and female *C. analis* that developed at different larval densities on a) black-eyed beans and b) mung beans.

a) black-eyed beans

	mean elytron length (mm) ± se (n)	
eggs per bean	males	females
1	1.92 ± 0.01 (43)	1.92 ± 0.01 (51)
2	1.92 ± 0.01 (43)	1.90 ± 0.01 (35)
3	1.90 ± 0.02 (23)	1.86 ± 0.02 (26)
4	1.89 ± 0.02 (24)	1.90 ± 0.02 (29)

b) mung beans

	mean elytron length (mm) ± se (n)	
eggs per bean	males	females
1	1.82 ± 0.01 (39)	1.83 ± 0.01 (47)
2	1.87 ± 0.01 (40)	1.89 ± 0.01 (39)
3	1.88 ± 0.01 (37)	1.89 ± 0.01 (43)
4	1.92 ± 0.01 (50)	1.90 ± 0.02 (35)

anova for unbalanced designs, development time was analysed separately for males and females. The time taken for larvae to develop from eggs to emergence also differed between the treatments (Table 5.2a: males: Kruskal Wallis $chi^2 = 16.52$, $df = 3$, $P < 0.001$; females: Kruskal Wallis $chi^2 = 21.11$, $df = 3$, $P < 0.001$), with adults that had to compete as larvae emerging later than adults that did not have to compete. Thus, fighting over a bean appears to increase the development time of a larva.

The number of adult beetles emerging per bean did not differ between the four treatments (Table 5.3a: $chi^2 = 6.526$, $df = 3$, $P > 0.05$) because generally only a single adult emerged from each bean. This also suggests that the survival to emergence of the larva that wins the contest within a bean is not reduced by having fought.

5.3.2. Small host: mung beans

The emergence size of both male and female beetles was again affected by the initial number of larvae in the bean (Table 5.1b: two-way anova: treatment $F_{3,322} = 23.34$, $P < 0.001$) but this time beetles that developed in competition with other larvae emerged larger than those that developed alone within a bean: the largest beetles emerged from the beans with the highest initial number of larvae. Males and females did not differ in size (Table 5.1b: two-way anova: sex $F_{1,322} = 0.96$, $P = 0.329$) and the increase in size due to the number of eggs per bean was the same for both males and females (Table 5.1b: two-way anova: treatment by sex interaction $F_{3,322} = 0.82$, $P = 0.484$). Thus having to fight for a bean appears to increase the emergence size of the surviving larvae, and the size of the increase is the same for both males and females.

The time taken for adults to develop from egg to emergence also differed between treatments for both males and females (Table 5.2b: males: Kruskal Wallis $chi^2 = 15.30$, $df = 3$, $P < 0.001$; females: Kruskall Wallis $chi^2 = 19.79$, $df = 3$, $P < 0.001$). However in this case the effect was the same as on black-eyed beans, with larvae that had to fight over a bean taking longer to develop. Again, competition appears to slow

Table 5.2. Development time (days) for male and female *C. analis* that developed at different larval densities on a) black-eyed beans and b) mung beans. Numbers in brackets are standard errors of the means.

a) black-eyed beans

	mean development time ± se (n)	
eggs per bean	male	female
1	29.5 ± 0.24 (43)	29.5 ± 0.20 (52)
2	29.9 ± 0.27 (43)	29.7 ± 0.21 (35)
3	31.1 ± 0.55 (23)	31.0 ± 0.47 (26)
4	31.0 ± 0.45 (24)	30.9 ± 0.46 (29)

b) mung beans

	mean development time ± se (n)	
eggs per bean	male	female
1	31.3 ± 0.19 (39)	31.2 ± 0.16 (47)
2	31.7 ± 0.25 (40)	31.3 ± 0.23 (39)
3	32.1 ± 0.28 (37)	32.2 ± 0.28 (43)
4	33.0 ± 0.31 (50)	33.0 ± 0.39 (35)

Table 5.3. Number of adult *C. analis* emerging per bean on a) black-eyed beans and b) mung beans.

a) black-eyed beans

eggs per bean	emergence per bean ± se (n)
1	0.86 ± 0.03 (101)
2	0.76 ± 0.04 (103)
3	0.71 ± 0.05 (65)
4	0.77 ± 0.05 (69)

b) mung beans

eggs per bean	emergence per bean ± se (n)
1	0.84 ± 0.03 (102)
2	0.88 ± 0.03 (90)
3	0.85 + 0.03 (94)
4	0.83 ± 0.03 (102)

the development of the larvae. The number of emerging adults per bean did not differ between treatments (Table 5.3b: $\text{chi}^2 = 0.807$, $df = 3$, $P > 0.05$), so on this host too, fighting for the resource does not appear to reduce the survival of the larva that wins.

5.4. Discussion

The results on the large host (black-eyed beans) suggest that larvae that fight for access to a bean and win do suffer a cost of having fought. Larvae that have survived contest competition emerge smaller than larvae that do not have to compete and, as emergence size is an indicator of lifetime fecundity for females, this will translate into a reduction in lifetime fecundity for beetles that had to compete as larvae. This reduction in size may be due to the larvae having to divert energy into fighting that could be used for growth, or due to having to spend time fighting which could have been spent feeding. Larvae that have to compete for a bean also emerge later than larvae that do not and again this may be due either to the larvae having to feed for longer after fighting to build up their energy reserves before emergence, or may simply reflect the time spent fighting. The fitness consequences of an increase in development time is not as obvious as the reduction in lifetime fecundity. As a stored product pest, *C. analis* probably experiences periods of rapid population growth, for example when a new bean store or field is first colonised, followed by population crashes when the resource is exhausted. During these periods of rapid increase a fast development time will be an advantage enabling beetles to produce more generations before the hosts become seriously depleted.

However, there does not appear to be any cost in terms of survival to emergence for larvae that have fought over a bean, because the number of beetles emerging per bean does not differ between treatments. Godfray (1987b) has suggested that when the larvae of parasitoid insects, which develop within the body of other insect larvae, fight over a host there is a risk of even the larva that wins the contest suffering injuries that cause it to die before adulthood. The fact that a *C. analis* larva that survives the contest within the bean is no less likely to successfully emerge than a larva that develops without competition suggests that serious injury to the victor is not a major cost in this species.

The results from the small host, mung beans, are slightly more surprising. As on black-eyed beans, fighting over a bean appears to increase the development time of the victor, but not reduce its survival to emergence. However, in contrast to the results on black-eyed beans there appears to be no cost of fighting in terms of reduced lifetime fecundity on this host. Indeed, beetles that had to compete as larvae appear to have increased lifetime fecundity, as they emerge larger than beetles that developed alone. This implies that there may actually be some benefit to larvae of having fought for the bean. This result agrees with that of Toquenaga and Fujii (1990) who also found an increase in emergence size of beetles with increasing number of eggs per bean when developing on mung beans.

This increase in emergence size with increased number of eggs may not be due to any effect of competition on fitness. If there are inherent differences in the size of larvae before competition occurs, caused either by genetic differences or maternal affects, and larger larvae tend to beat smaller larvae when they fight, the beetles that emerge from beans after winning a fight will be a biased sample of the larvae that entered beans. If inherently larger larvae produce larger adults then the beetles that emerge after fighting will tend to be larger on average than beetles that did not compete as larvae. There is evidence that in *C. maculatus* there is variation in egg size between females, and also that the size of eggs varies during the lifetime of the female (Fox 1993). Furthermore, this variation in egg size has been shown to affect the fitness of larvae, with larger eggs producing fitter beetles (Fox 1993). If the same occurs in *C. analis*, this could give rise to the increase in emergence size observed in the experiment.

To investigate the importance of this effect, the following analysis of the mung bean data was carried out. Pseudo pairs, trios and quads of larvae were generated by drawing two, three or four elytron length values at random from the one egg per bean treatment. The largest elytron length from each pair, trio or quad was taken as the elytron length of the surviving larva from each bean. The mean elytron length for these surviving beetles provides an estimate of the sizes of beetles that would be expected from the two, three and four egg per bean treatments if the differences are due simply to the largest larva winning in larval competition. The means generated in this way do increase in size as the number of eggs per bean increases (Table 5.4) as in the experiment. However, the experimental results are still larger than the predictions (Table 5.4: 2-way anova: experimental vs. theoretical $F_{1,332} = 7.93$, $P = 0.005$: comparisons based on the two, three and four egg per bean results) and so the increase in size observed in the experiment is probably not due to a sampling effect. Furthermore, if the increase is simply due to the largest larva winning in competition it is surprising that the same effect was not found on black-eyed beans as well.

Another possibility is that, even though larvae that have fought for a bean emerge larger than those that have not, this increase in size may not translate into an increase in lifetime fecundity. Although there is known to be a relationship between female lifetime fecundity and female size at emergence in *C. analis*, it is not known whether this relationship is the same for larvae raised with and without competition. It is plausible that if the size of a larva affects its success in contest competition, a larva that detects the presence of a competitor within the bean might divert energy into growth which would otherwise have been used for reproduction after emergence. This would result in larvae raised in competition having a lower fecundity for their size than larvae raised alone. If such an effect of competition on lifetime fecundity does exist, then larva raised in competition might still show a reduction in lifetime fecundity even though they emerge larger. However there are two reasons to doubt that this explains the observed size increase in the experiments; first, it is known that in *C. maculatus* there is no effect of larval competition on female fecundity independent of its effect on

Table 5.4. The mean elytron lengths (mm) for *C. analis* emerging from mung beans carrying different number of eggs, along with the predicted elytron lengths if there is no cost of competition and the increase in size is due to larger larvae winning contests. As males and females did not differ in size within treatments, the experimental values, and the predicted values calculated from them using both the male and female data combined.

	mean elytron length (mm) ± se (n)	
eggs per bean	experimental	predicted
1	1.83 + 0.01 (86)	1.83 + 0.01 (86)
2	1.87 + 0.01 (79)	1.86 + 0.04 (43)
3	1.89 + 0.02 (80)	1.87 + 0.04 (28)
4	1.91 + 0.02 (85)	1.88 + 0.05 (21)

female emergence weight (Colegrave 1993), and second, if larvae did react plastically in this way they should be expected to do the same on black-eyed beans.

Thus it seems that larvae which have fought successfully for access to mung beans may indeed show an increase in emergence size, which will translate into an increase in lifetime fecundity. Why might this be? It is possible that the presence of larvae feeding within a bean affects the quality of the resource in some way so that its quality as a food source improves. For example, developing larvae produce moisture which may soften the bean tissue making it easier to ingest and assimilate: such an effect would be likely to increase as the number of larvae within the bean increases. If this is the case then the larva that wins the contest for the bean may have access to a better quality resource, due to the effect of several larvae within the bean before competition occurred, and the benefit of this improved quality resource may outweigh the cost of having fought for it. Such an affect has been reported in the larvae of solitary parasitoid insects, where the presence of several larvae within a host before contest competition occurs reduces the effect of the hosts immune system on the larvae. As a consequence, the larva that wins the contest has a higher fitness than a larva that has sole access to the host for the whole of its development (Waage and Godfray 1985, Askew 1968, Puttler 1974). A similar effect has also been reported in another species of bruchid beetle, *Zabrotes subfasciatus* (Utida 1967). In this species larvae compete using a scramble process of competition, and the survival of an individual larva that shares a bean with one other larva, is higher than for larvae that develop alone within a bean (Utida 1967). If such an effect is responsible for the increase in size observed on mung beans then the reason that it does not occur on black-eyed beans may simply be a consequence of the difference in host size: a few larvae feeding on a small host like mung bean could have a large effect on its quality, but little effect on a large host such as black-eyed bean. However, without detailed information of the way in which larval feeding alters the physical and chemical nature of the bean it is impossible to comment further on the likelihood of this.

The results of these experiments suggest that there is a cost to *C. analis* developing on black-eyed beans in terms of development time and emergence size whilst on mung beans larvae seem to pay a cost in terms of increased development time, but seem to benefit in terms of increased emergence size. Whether the combination of these two effects translates into a net benefit to larvae that have fought over mung beans or simply a smaller cost than they suffer on black-eyed beans depends on their combined effect on overall fitness. While the effect of an increase in emergence size on fitness, due to its effect on lifetime fecundity of females, can be estimated, the effect of increased development time depends on details of the population dynamics of this species that are unknown. However, even if these results do show a cost of having fought on black-eyed beans, and a net benefit on mung beans, the effect of having fought on the fitness of the surviving larva is very small. The reduction in size of females that have fought one other larva for access to a black-eyed bean, compared to the size of females that develop without competition (Table 5.1a) represents only about a 2% reduction in fecundity, whilst the increase in size on mung beans represents a 2% increase. Thus, even though having fought over a bean does appear to affect the fitness of the surviving larvae, the effect is so small in *C. analis* at the densities used in these experiments that it has probably had little effect on the evolution of the larval competition strategy in this species.

Chapter 6. Extending the Smith and Lessells model: asymmetries in fighting and competitive ability

(Based on Colegrave 1994)

6.1. Introduction

The Smith and Lessells (1985) model provided an insight into the types of factors which could be important in determining the way in which organisms compete in closed systems (figure 6.1). If the cost of sharing the resource is high then organisms will evolve a contest strategy and fight over the resource, whilst if the cost of sharing is low a scramble strategy may evolve. These two strategies were called *Attack* and *Avoid* respectively. If *Attack* strategists are also inherently better fighters than *Avoid* strategists this also increases the chance that *Attack* behaviour evolves.

However, this model assumed that competition was symmetric; that if two larvae shared a bean each would gain the same amount of the resource. In nature competition is rarely totally symmetric (Begon 1984, see also Lawton & Hassell 1981 for interspecific competition), with one competitor often doing much better than another. Wilbur and Collins (1973) have described how competition can generate a skewed size distribution in amphibian larvae, due to some larvae competing more strongly than others and so getting more of the resource, and the same phenomenon has been shown to occur in young pygmy sunfish (Rubenstein 1981). Both of these studies also suggest that the degree of asymmetry increases with the intensity of competition. Although previous authors have modelled effects of asymmetries on the evolution of competition (Maynard Smith & Parker 1976, Hammerstein 1981), these models have generally been for open systems. This chapter takes the Smith and Lessells model as a starting point and describes a game theory model addressing the question: What effect does asymmetric competition have on the evolution of competition strategies in a closed system?

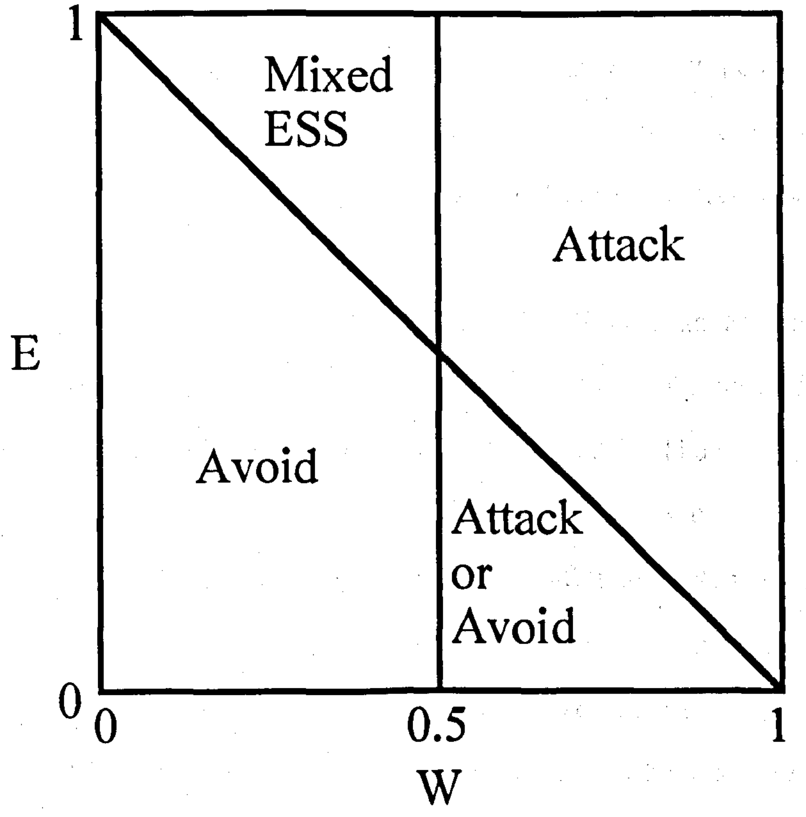

Figure 6.1. The Smith and Lessells model: The x-axis represents W, the probability that an *Attack* larva beats an *Avoid* larva in a fight. The y-axis represents E, the relative cost to an *Avoid* larva of sharing a bean with another *Avoid* larva. The zones represent different ESSs. N.B Although the original Smith and Lessells model only considered Values of W of 0.5 or greater, for completeness this figure includes all possible values of W from 0 to 1. However, values of W less than 0.5 mean that *Attack* larvae are worse fighters than *Avoid* larvae; a situation which is unlikely to occur in nature.

6.2. The asymmetric game

The model I describe is for a two larval game, that is each bean contains two larvae. I use the same basic strategies, *Attack* (attempt to find and kill other larvae within a bean) and *Avoid* (avoid other larvae within the bean and compete passively over the resource), as used in the Smith and Lessells model, but the use of asymmetries in the model also allows for the incorporation of conditional strategies based on detected asymmetries.

I assume two possible asymmetries. The first is an asymmetry of fighting ability, with one larva (the "Superior larva") being a better fighter and thus more likely to win an aggressive encounter (with the "Inferior larva"). The second is an asymmetry in passive competitivness, that is if two *Avoid* larvae share a bean, one is likely to be a better passive competitor than the other and so suffer less from the competition than the other. There could be many reasons for these asymmetries. In the case of *Callosobruchus* beetles the most plausible cause is different arrival time of larvae within the bean. A larva which arrives first in a bean may have a growth head start and so be larger when the two larvae meet, thus which is the superior larva depends on which arrived first in the bean.

The two asymmetries (fighting ability and passive competitive ability) are independent in the model. The labels superior and inferior refer only to the asymmetry in fighting ability. Thus the superior larva (fighting ability) may be a better or worse passive competitor than the inferior larva.

Finally, I assume that both asymmetries are produced by chance effects (such as order of arrival in the bean) not by any inherent difference in the competitive ability of the strategies. In contrast to the Smith and Lessells model, where *Attack* larvae are always equal or better fighters to *Avoid* larvae, in this model *Attack* larvae are not inherently better fighters than *Avoid* larvae. This means that all larvae, independent of the strategy that they use, have a 50% chance of being a superior larva. If the asymmetries are caused by order of arrival in the bean, then the strategy that a larva will use does not affect its probability of being the first larva in the bean. Whilst this may not represent the most biologically realistic situation, it does allow for the effect of asymmetries caused by chance effects to be looked at without the confounding effect of determined asymmetries between strategies.

I consider four strategies, two of which are simple strategies, and two of which are conditional strategies. The two simple strategies are *Attack* and *Avoid.* The conditional strategies are "*Attack* if you are the superior larva and *Avoid* if inferior", which I call *Tyrant*, and "Avoid if you are the superior larva and Attack if inferior", which I call *Martyr*. The strategies are assumed to be determined genetically, but the conditional strategies allow for flexible behaviour dependent on the conditions in which the individual finds itself. Thus two larvae could have the same genetic strategy (eg they may both be *Martyr*), but show different behaviour (*Attack* or *Avoid*), dependent on conditions (eg depending on whether they are the first or second larva to arrive in the bean).

Payoffs are defined relative to the payoff to a larva developing alone within a bean (=1). If two larvae meet and fight for possession of the bean I assign a probability (F) that the superior larva wins. This will occur whenever both larvae show *Attack* behaviour, and also whenever one larva adopts *Attack* behaviour the other *Avoid* behaviour and the *Avoid* larva does not successfully avoid the *Attack* larva. The variable F can take values from 0.5 to 1 depending on the advantage of the superior larva in a fight. If two larvae coexist within a bean then each will pay a cost incurred by sharing the resource. I have used E_1 to represent the cost to the superior larva and E_2 the cost to the inferior larva. These values are calculated as reductions to a maximum fitness of 1, and can thus take values of 0-1. Finally I have used q to represent the probability that an *Avoid* larva successfully avoids an *Attack* larva within a bean. The payoff matrix for this game is shown in Table 6.1, payoffs being calculated assuming that a larva has a probability of 0.5 of being the superior larva. For example if an *Avoid* larva finds itself in a bean with another *Avoid* larva, then with probability of 0.5 it will be the superior larva and so suffer the E_1 cost of passive competition (and so gain a

Table 6.1. Pay-off matrix for the asymmetric game. F is the probability of a superior larva beating an inferior larva in a fight , E_1 and E_2 are the relative costs due to passive competition of the superior and inferior larva respectively. q is the probability of an *Avoid* larva successfully evading an *Attack* larva. Payoffs represent the payoff to larva A in competition with larva B.

	larva B			
larva A	*Attack*	*Avoid*	*Tyrant*	*Martyr*
Attack	0.5	$\frac{1+q-qE1-qE2}{2}$	$\frac{1+q-qE1-Fq}{2}$	$\frac{1+Fq-qE2}{2}$
Avoid	$\frac{1+q-qE1-qE2}{2}$	$\frac{2-E1-E2}{2}$	$\frac{2-F+Fq-E1-qE2}{2}$	$\frac{1+F-Fq+q-qE1-E2}{2}$
Tyrant	$\frac{1+Fq-qE2}{2}$	$\frac{1+F-Fq+q-qE1-E2}{2}$	$\frac{1+q-qE1-qE2}{2}$	$\frac{1+F-E2}{2}$
Martyr	$\frac{1+q-Fq-qE1}{2}$	$\frac{2-F+Fq-E1-qE2}{2}$	$\frac{2-F-E1}{2}$	$\frac{1+q-qE1-qE2}{2}$

pay off of $(1-E_1)/2)$ otherwise it will be the inferior larva (and so gain a payoff of $(1-E_2)/2)$. So the mean payoff to the larva will be $(2-E_1-E_2)/2$.

6.3. Results

Figure 6.2 shows diagrammatically the results of the game under various conditions. The axes of each graph represent the relative cost of passive competition to either the superior (y-axis) or the inferior (x-axis) larvae. Zones can then be delimited onto these figures indicating the evolutionarily stable strategies (ESS; Maynard Smith 1982) under different conditions. Figure 6.2a represents a situation where the asymmetries are undetected, whilst 6.2b and 6.2c represent situations where asymmetry is detected by the larvae.

6.3.1 Asymmetries not detected

If larvae are unable to detect asymmetries (i.e they cannot tell whether they are the superior or inferior larva) then the predicted ESS's are the same as those produced by the Smith and Lessells model, depending only on the average costs to the two larvae of sharing the bean. In the Smith and Lessells model, if two larvae sharing a bean have individual fitnesses of greater than 0.5 of the fitness of a larva alone in a bean ($E < 0.5$), and *Attack* larvae are not better fighters than *Avoid* larvae ($W= 0.5$) then *Avoid* is the stable strategy. In the undetected asymmetry model presented here *Avoid* is the stable strategy if the mean fitness of two larvae sharing a bean is greater than 0.5 of the fitness of a larva alone within a bean. It does not matter whether the passive competition is symmetric, with larvae having equal E values, or whether competition is highly asymmetric, for instance with one larva with an E value of 0.1, the other with an E value of 0.9. The degree of asymmetry in fighting ability also has no effect on which strategy is stable when the asymmetry is undetected. Thus in this situation asymmetry in competitive ability does not affect the evolutionary outcome if the larvae are unable to detect the asymmetry.

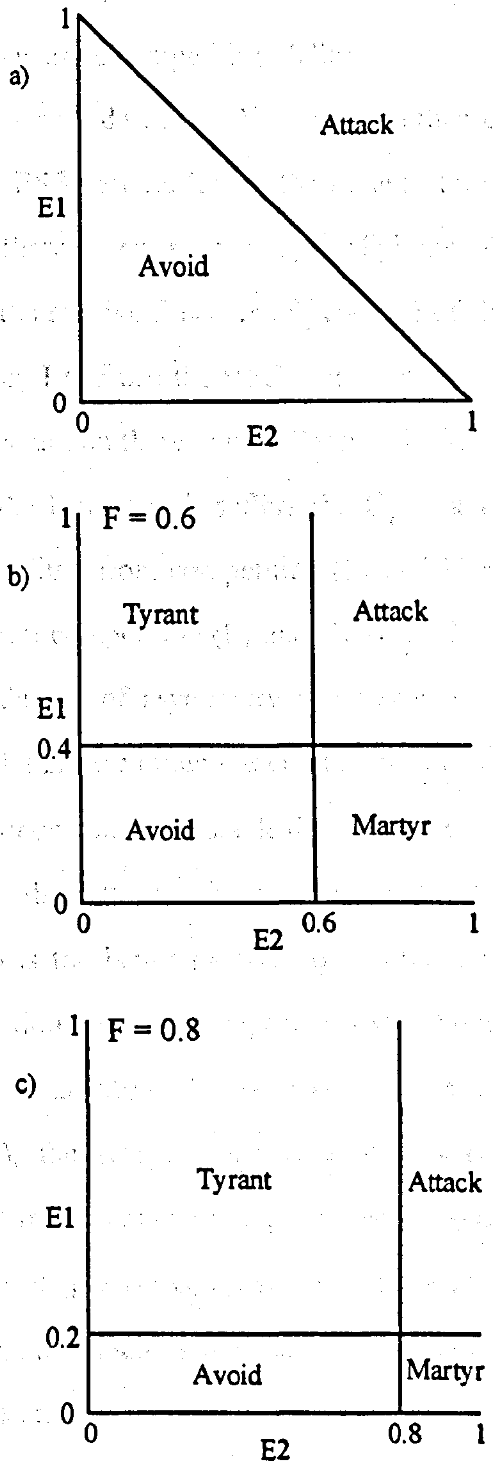

Figure 6.2. The asymmetric game: The x-axis represents E_1, The relative cost due to passive competition to the superior larva, whilst the y-axis represents E_2, the cost to the inferior larva. a) represents the situation where asymmetries are undetected by the larvae whilst b) and c) represent two situations where the larvae are able to detect the asymmetries. F is the probability that a superior larva beats an inferior larva in a fight. The zones represent different ESSs.

6.3.2. Asymmetry in passive competitive ability

If the asymmetry is detectable by the larvae then conditional strategies become a possibility and the ESS's are no longer the same as those predicted by the Smith and Lessells model. If there is no asymmetry in fighting ability ($F=0.5$) then the ESS depends simply on the relative fitnesses (E_1 and E_2) of the two larvae when sharing a bean. For consistency I still use the labels superior and inferior to describe the larvae even though in this situation there is no difference in fighting ability, the superior larva is then defined as the larva which suffers the E_1 cost of passive competition in the model. If both suffer little from competition (E_1 and $E_2 < 0.5$) then *Avoid* is stable. If both suffer badly from competition (E_1 and $E_2 > 0.5$) then *Attack* is the ESS. However if there is a high degree of asymmetry in passive competitive ability ($E_1 < 0.5$ and $E_2 > 0.5$ or $E_1 > 0.5$ and $E_2 < 0.5$) then the conditional strategies become stable. Which of the strategies, *Tyrant* or *Martyr*, is stable depends on the direction of the asymmetry; if the superior larva is the better passive competitor ($E_1 < E_2$) then *Martyr* is stable, while if the inferior larva is the better passive competitor then *Tyrant* is stable. However, because in this situation there is no asymmetry in fighting ability the labels of superior and inferior are just arbritrary labels (they do not imply anything about passive competitive ability), the two conditional strategies are better viewed as a single strategy of "Attack if you suffer the higher cost of passive competition Avoid if you suffer the lower cost of passive competition". This makes sense because a larva that is going to suffer a great reduction in fitness due to passive competition does better by fighting for access to the whole bean and risking dying in the process.

6.3.3. Asymmetry in fighting ability

At the other extreme, if there is no asymmetry in passive competitive ability of superior and inferior larvae ($E_1=E_2$) but there is asymmetry in fighting ability, then *Martyr* is no longer a possible ESS. If the cost to the larvae of sharing a bean is low (E_1 & E_2 are low) then *Avoid* is stable and if it is high (E_1 & E_2 are high) then *Attack* is the ESS. At intermediate values of E_1 and E_2 *Tyrant* is the stable strategy. The exact range of conditions over which *Tyrant* is the ESS depends on the asymmetry in fighting ability. For example, if a superior larva beats an inferior larva in a fight with a probability of 0.6 (F=0.6) then *Tyrant* will be stable when the individual fitnesses of two larvae competing passively within a bean are between 0.4 and 0.6 of the fitness of a larva alone in a bean ($0.4 < E_1, E_2 < 0.6$). If the degree of asymmetry in fighting ability is higher so that a superior larva beats an inferior larvae with a probability of 0.8, *Tyrant* is stable for values of E_1 and E_2 of between 0.2 and 0.8. Thus, increasing the degree of asymmetry in fighting ability increases the range of condition over which *Tyrant* is the ESS.

6.3.4. Asymmetries in both fighting and passive competitive ability

If there are asymmetries in both fighting and competitive ability then which strategy is the ESS depends on the exact values of the asymmetries. In general as asymmetries in passive competitive ability increase the conditional strategies become more likely as the ESS, and as the asymmetry in fighting ability increases the range of conditions over which *Tyrant* is stable increases at the expense of the other three strategies. The formal ESS conditions for each of the strategies are shown in Table 6.2.

The probability of an *Avoid* strategist avoiding an *Attack* strategist (q) has no effect on which strategy is the ESS as long as this probability is not 0 or 1. However computer simulation suggests that the value of q does affect the speed at which a mutant strategy can invade a population (Figure 6.3.).

6.4. Discussion

If asymmetries are present in fighting ability or competitive ability, but cannot be detected by the larvae then they have no effect on the evolutionary outcome of this

Table 6.2. ESS conditions for the asymmetric game. F is the probability of a superior larva beating an inferior larva in a fight, E_1 and E_2 are the relative costs due to passive competition of the superior and inferior larva respectively.

asymmetries undetected

Strategy	ESS Conditions
Attack	$E_1 < 1-E_2$
Avoid	$E_1 > 1-E_2$

asymmetries detected

Strategy	ESS Conditions
Attack	$E_1 > 1-F$ & $E_2 > F$
Avoid	$E_1 < 1-F$ & $E_2 < F$
Martyr	$E_1 < 1-F$ & $E_2 > F$
Tyrant	$E_1 > 1-F$ & $E_2 < F$

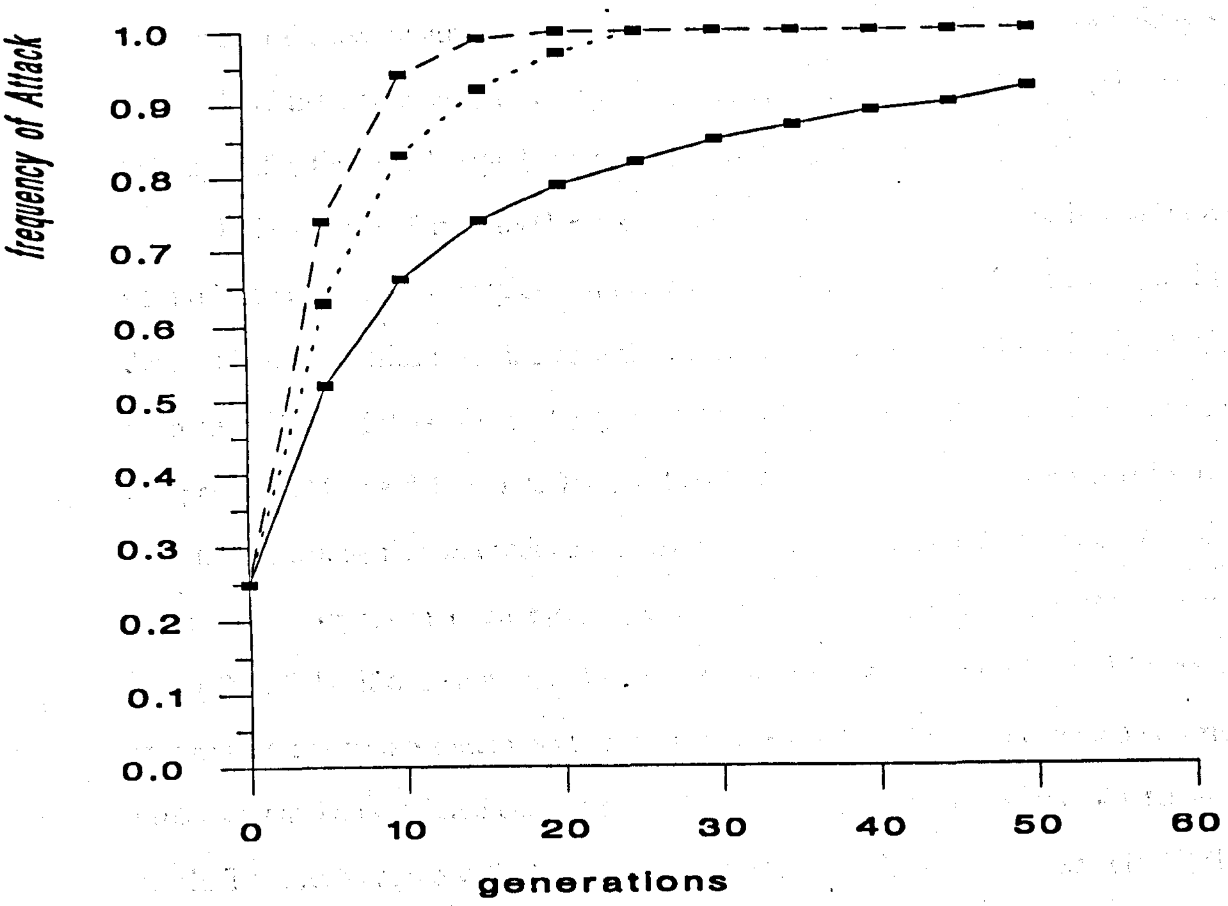

Figure 6.3. The effect of altering the probability, q, that a larva using *Avoid* behaviour successfully avoids a larva using *Attack* behaviour within a bean. The lines show the frequency of *Attack* strategists every five generations, for a population initially containing all four strategies at equal frequencies (0.25). The conditions are such that *Attack* is the ESS (E_1 = 0.9, E_2 = 0.9, F = 0.6). The three lines are for three different value of q (large dashed line; q = 0.8, small dashed line; q = 0.5, solid line q = 0.1). The value of q does not effect the ESS but alters the speed at which it is reached.

game. However, if the asymmetries are detectable by the larvae then conditional strategies become possible and the stable strategy depends on the level of the asymmetry. However, it is unlikely that there would be an asymmetry in passive competitive ability without there being some asymmetry in fighting ability and if both factors are included then the situation becomes more complex. Furthermore it is likely that there would be a relationship between the degree of asymmetry in competitive ability and fighting ability. If this is the case then the possible strategies depend on the relationship between these two asymmetries. If the asymmetry in fighting ability is greater than the asymmetry in competitive ability then *Tyrant* becomes more likely as the ESS. If the asymmetry in competitive ability is greater than the asymmetry in fighting ability then the *Martyr* becomes more likely as the stable strategy.

If the chance of an *Avoid* larva evading an *Attack* larva is small (q is small) then both of the conditional strategies will produce what look like *Attack* outcomes, and so detectable asymmetries may increase the observed frequency of Attack like strategies in nature. This differs from the predictions of previous models of asymmetric competition (Maynard Smith & Parker 1976). In general these models predict that detectable asymmetries will reduce the severity of contests. This discrepancy arises as these models represent open systems where one contestant can leave the resource rather than fight: if one contestant leaves the fight cannot escalate. My model assumes that as long as one larva attempts to fight then the two larvae will meet with a non zero probability and an escalated contest occur; in effect neither larva can leave the resource patch. The results agree with the prediction of Maynard Smith and Parker (1976) that escalated contests are expected when the pay-off for winning is large compared to the loss due to injury; the model predicts fighting when the benefit to one of the larvae of winning a fight is greater than the risk of dying in a fight. This also agrees with the predictions of Enquist and Leimar (1990) that fatal fights are expected when the value of the future to an individual if it does not fight is small compared to the value of the resource over which it is fighting; a larva which will suffer a great reduction in fitness due to sharing a resource (a low future fitness without fighting) will be expected to fight over the resource.

The model assumes that larvae have only two options, to attempt to kill the other competitor or to accept a share of the resource determined by their passive competitive ability. However, it can easily be extended to include the possibility of dominance, with the superior larva forcing the inferior larva to accept a reduced share of the resource. If E_1 is viewed as the cost to the superior larva of being dominant, and E_2 as the cost to the inferior larva of being denied access to the resource, then figure 6.2 can be used to predict the ESS under different conditions. In this situation the *avoid* strategy can be viewed as the *dominant/subdominant* strategy, and any conditions under which avoid is stable can be viewed as conditions under which a system of dominance would be stable, indeed from outside the bean these two strategies would be impossible to distinguish. In general the ESS depends on the way the resource is partitioned between the two larvae; it does not matter if this is determined by passive competitive ability or some system of dominance.

Whilst the conclusions of this model do not disagree with those of the Smith and Lessells model (*Attack* strategies are still more likely when the costs of sharing a seed are high) it does allow for the existence of conditional strategies. There is some evidence that the south Indian strain of *C. maculatus* shows a conditional strategy very similar to the *Tyrant* strategy described here (Thanthianga & Mitchell 1987), with one larva developing normally while the other holds back its development. Thanthianga and Mitchell (1987) suggest that the larvae may be using the vibrations, caused by larval feeding, to asses the presence and size of another larva in the bean. If the two larvae meet then a contest occurs and the smaller larva dies, although active killing by the larger larva has not been demonstrated. Experiments are required to determine whether the *Attack* strategies of other species such as *C. analis* are true *Attack* strategies or in fact conditional strategies.

The model presented here was framed with *Callosobruchus* beetles in mind where the asymmetry is likely to be caused by arrival time at the bean. A larva which arrives first will have a growth head start and so be bigger than the second larva, probably making it a superior fighter. This growth headstart may also make it a stronger passive competitor (Bellows 1982a). However the model will equally apply to larval competition in other species, and even to other types of competition where the competitors are unable to move to another area. In other species the asymmetry in fighting ability could be caused by any number of factors and an individual with a higher fighting ability may not always have a higher passive competitive ability. In fact a trade-off between investment in fighting equipment and feeding equipment could mean that the superior fighter is an inferior passive competitor.

However, although the results of the model will apply to many other competitive situations, the model does not take into account inclusive fitness because in *Callosobruchus* beetles the larvae within a bean are rarely related. The model would need to be extended to apply to situations where competitors are related (ie siblicide in birds).

Whilst previous models of asymmetric competition (Maynard Smith & Parker 1976, Hammerstein 1981) suggested that detected asymmetries should reduce the amount of fighting over resources, the results of the model presented here suggest that in closed systems detected asymmetries may actually increase the likelihood of fighting as a competition strategy. This adds asymmetry in competition to a list of factors (including those of population genetics such as hysteresis) that make *Attack* type behaviour a more likely observed outcome than the simplest models of larval competition suggest.

Chapter 7. Extending the Smith and Lessells model: the effect of population structure on the evolution of competition strategies

(submitted)

7.1. Introduction

Early models of evolution tended to assume that organisms live in large panmictic populations in homogeneous environments. More recently biologists have realised that this idealised view of organisms in structured environments does not apply to many species (Wilson 1977). Moreover, population structure may have profound consequences for the evolution of organisms (Wright 1945, Maynard Smith 1964, Matessi & Jayakar 1976, Cohen & Eshel 1976, Wilson 1977). One population structure that has been shown to have important consequences on evolution is one in which the global population periodically splits into a number of isolated subpopulations for one or more generations. This type of population structure corresponds to the structured deme model of population genetics (Uyenoyama & Feldman 1980).

Structured deme models can produce different evolutionary outcomes from equivalent models with no population structure. For example, in a single panmictic population organisms are generally expected to invest equally in male and female offspring (Fisher 1958). However, if organisms produce offspring in isolated patches of resource, and offspring mate within their natal patch before dispersal, organisms may evolve to invest more heavily in females than in males (Hamilton 1967, Wilson & Colwell 1981, Colwell 1981, Harvey 1985). This difference in outcome arises because in the structured deme there are two selective forces affecting allele frequencies. Within all mixed patches (i.e. patches containing both alleles) female biasing alleles are less fit than equal investment alleles and so decrease in frequency every generation just as they would in a single population; each patch moves towards the Fisherian equal investment outcome. However, patches with relatively high frequencies of female biasing alleles produce a greater number of dispersers. Thus, even though the female biasing allele decreases in frequency in all mixed patches, the greater productivity of patches with a female biased sex ratio may allow the female biasing allele to spread in the global population. Wilson and Colwell (1981) refer to the change in allele frequency within each patch as "individual selection" and the productivity effect as "group selection". However, the use of the term individual selection in this context can be misleading (Grafen 1984) so in this chapter the change in allele frequencies within patches is termed "within patch selection" and the productivity differences between patches as "between patch selection". Structured deme models have also been shown more generally to make the evolution of altruistic traits possible in patchy populations when they could not evolve in a single population (Wright 1945, Maynard Smith 1964, Matessi & Jayakar 1976, Cohen & Eshel 1976). Again, this is because even though altruistic individuals have a lower relative fitness than selfish individuals within all mixed patches, patches with a high relative frequency of altruistic individuals will have a higher productivity and the within patch selection against the altruistic individuals may be outweighed by the between patch selection favouring patches of altruistic individuals.

For a patchy population structure to produce a different evolutionary outcome to a single undivided population there are two general requirements. Firstly, the productivity of patches must vary depending on the frequency of alleles within patches producing between patches selection. Secondly, within patch selection and between patch selection must work in different directions, with one of the selective forces favouring one of the alleles whilst the other selective force favours the alternative allele.

One situation in which a patchy environment might have important evolutionary consequences is on the evolution of competition behaviour. Organisms typically compete in one of two ways; they may compete actively over the resource, attempting to exclude or even kill other competitors in a contest type process (*sensu* Nicholson 1954), or they may compete in a scramble of process (*sensu* Nicholson 1954) with each individual attempting to gain as much of the resource as possible without directly interfering with other competitors. However, a set amount of resource may support a different number of contest and scramble individuals. For example larvae of different species of parasitoid wasps show either a contest or scramble strategy when competing over their host (Godfray 1987a, b). In solitary species the larvae fight and typically only one adult emerges from each host, but if diflubezuron, which stops larvae developing their fighting mouthparts, is added to the host, several adults can emerge from each host (Khoo et al 1985). Thus, each host can support a single contest strategist or several scramble strategists. If larval hosts were patchily distributed this would lead to differential productivity between patches depending on the frequency of the two strategists within a patch.

A similar situation is found in insects such as bruchid beetles whose larvae complete development within seeds or beans. In many of these species larvae are confined to a single host for the whole of their development and, as several eggs can be laid on a single host, larval competition can be intense. The larvae of these beetles show a similar dichotomy of competition behaviour (Smith & Lessells 1985); in some species larvae fight within the host and only a single adult emerges, whilst in others several larvae develop to adulthood within a single bean and apparently compete in a scramble type process. Even closely related species can show disparate competition strategies; whilst most species within the genus *Callosobruchus* use scramble competition behaviour as larvae, the larvae of *C.analis* use contest competition behaviour (Umeya et al 1975). What types of selective forces can cause different species to evolve different competition strategies? Previous authors (e.g. Godfray 1987b for parasitoids, Smith & Lessells 1985 for internally feeding granivorous insects) have used mathematical models to attempt to answer this question, but all of these models have assumed that organisms live in a single undivided population. This chapter describes a series of models of the evolution of competition strategies in a patchy environment. The models were developed with *Callosobruchus* beetles in mind, and are based on a genetic version of the original Smith and Lessells (Smith 1990) model. Initially the results of a model with a patchy population structure are compared to the same model in a single undivided population (the Smith and Lessells model) to determine the general effects of a patchy population structure. Then the results of several patchy models with differing population structures are compared to determine the effects of different aspects of the population structure on the evolutionary outcome.

7.2. The Model

In the model, individuals can adopt one of two alternative competitive strategies. "*Attack*" strategists compete over the resource by fighting to the death, whilst "*Avoid*" strategists compete passively without directly interfering with each other. The behaviour of each individual is controlled by a single diploid locus with two alternative alleles, with the *Avoid* allele dominant. The population goes through two phases (figure 7.1). In the patchy phase individuals reproduce for a set number of generations within isolated patches and competition occurs between the offspring every generation, affecting their survival to adulthood and so causing changes in allele frequencies in the next generation of adults. During the dispersal phase adults leave the patches and form a single population. No reproduction occurs during dispersal and at the end of this phase a new generation of patches is founded by a set number of random females from this dispersal population. The model is then used to follow changes in allele frequency from one dispersal population to the next.

In a structured population such as this the change in allele frequency in the population as a whole depends on three things: i) the change in allele frequency within

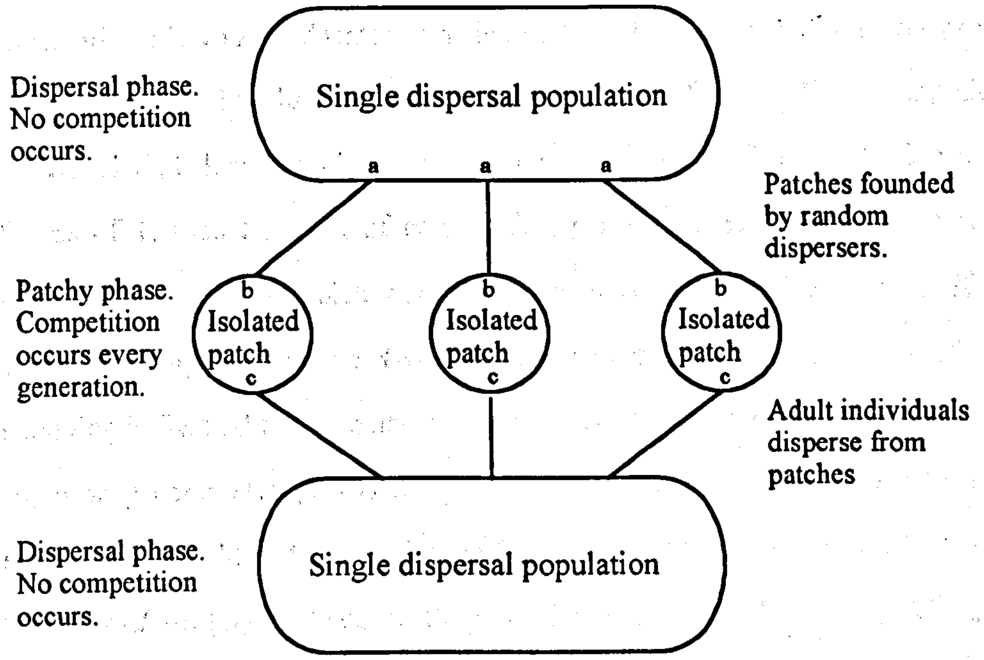

Figure 7.1. The population structure. Individuals begin in a single dispersal population (the dispersal phase). Isolated patches are then founded by random individuals from the dispersal population. Individuals spend a set number of generations within patches and competition occurs every generation. Adult individuals then disperse from the patches and form a single population again. Females that found patches can mate during dispersal (point a), or within patches either after (point b) or before (point c) dispersal.

each patch, ii) the number of adults dispersing from each patch and iii) the number of patches with different initial allele frequencies.

Competition within a patch is modelled by assuming that the resource is divided up into a large number of discrete units. Adult females deposit their offspring within these resource units, and the offspring are restricted to a single resource unit where they develop into adults. Each unit contains exactly two individuals and they compete over the resource during development. This competition during development affects the survival of the individuals to adults. The expected fitness of an adult after competition depends on two variables, the cost of competition and *Attack* larval superiority. If two *Avoid* strategists share a bean they each have a lower probability of survival than if they had developed alone within a bean without competition. If an individual that develops alone without competition is defined as having an expected fitness of 1, then the cost of competition parameter (E) is simply the reduction in fitness of individuals which compete over resources relative to this. If an *Attack* strategist competes with an *Avoid* strategist over a resource unit, they fight and the surviving individual has sole access to the resource and gains a fitness of 1. The *Attack* superiority parameter (W) is the probability that an *Attack* strategist beats an *Avoid* strategist in a fight and allows for the fact that *Attack* strategists may be better fighters than *Avoid* strategists, because they specialise in *Attack* behaviour. W can take any value from 0.5, when *Attack* and *Avoid* strategists are equally good fighters, to 1 where *Attack* strategists always kill *Avoid* strategists. If two *Attack* strategists compete over a resource unit, each has an equal chance of killing the other and gaining sole access to the resource and a fitness of 1.

The *Avoid* allele is represented by v and the *Attack* allele by t, so the genotypes of individuals can be represented as [vv], [tt], and [vt] denoting *Avoid* homozygotes, *Attack* homozygote and heterozygotes respectively. If Pvv, Ptt and Pvt are the frequencies of these three genotypes in young individuals before competition occurs, and individuals are assumed to compete with one other random individual, the frequencies of the three genotypes in the adults after competition (denoted P'vv, P'vt and P'tt) can be determined using the following relationships. For *Avoid* homozygotes

$$P'vv = \frac{((1\text{-}E)(2Pvv^2+2Pvv.Pvt)+2(1\text{-}W)Pvv.Pvt)}{(2(1\text{-}E)(Pvv^2+2Pvv.Pvt+Pvt^2)+2Pvv.Ptt+2Pvt.Ptt+Ptt^2)} \qquad \text{i}$$

for *Attack* homozygotes

$$P'tt = \frac{W(2Pvv.Ptt+2Pvt.Ptt)+Ptt^2}{(2(1\text{-}E)(Pvv^2+2Pvv.Pvt+Pvt^2)+2Pvv.Ptt+2Pvt.Ptt+Ptt^2)} \qquad \text{ii}$$

The frequency of heterozygotes is then simply

$$P'vt = 1 - (Pvv+Ptt) \qquad \text{iii}$$

Similarly, the number of adult beetles produced in each generation (N') can be calculated in terms of the number of females in the previous generation (N_f), their fecundity (R) and the frequencies and fitnesses of the three genotypes in their larvae using

$$N' = N_f.R(2(1-E)(Pvv^2+2Pvv.Pvt+Pvt^2)+2Pvv.Ptt+2Pvt.Ptt+Ptt^2) \qquad \text{iv}$$

The absolute population size within a patch will depend on the fecundity of females, but the change in allele frequency in the global population depends only on the relative number of dispersers produced in each patch rather than the absolute number, and this is independant of the fecundity of females. Thus the value of R used will not alter the outcome of simulations.

In general, the population within a patch was assumed to be large enough to be in Hardy-Weinberg equilibrium; genotype frequencies before competition occurred were the same as in the previous generation of adults. However, because each patch is founded by a small number of individuals, this assumption will not hold for the first generation of offspring within a patch. Instead genotype frequencies were calculated separately for each mated female within a patch and then combined to give the overall genotype frequencies in the first generation of offspring.

The deterministic nature of these equations means that patches of the same type (i.e. patches with the same initial genotype frequencies) will produce the same number and frequency of dispersing adults. Thus, to determine the genotype frequencies in the next dispersal population it is necessary to know the number of each patch type. In models in which females mate before or during dispersal, each mated female can be viewed as having a tetraploid genotype, made up of the females diploid genotype as well as the genotype of her mate. This mated female genotype can be represented as [vv/tt], with the females genotype before the slash and the males after. If Fvv/tt is the frequency of [vv/tt] females in the dispersal population, Fvt/vt the frequency of [vt/vt] females, Patch[vv/tt,vv/tt] the frequency of patches founded by two [vv/tt] females, Patch[vv/tt,vt/vt] the frequency of patches founded by one [vv/tt] female and one [vt/vt] female, and it is assumed that an infinite number of patches are founded , then

$$\text{Patch}[vv/tt,vv/tt] = \text{Fvv/tt}^2 \qquad \text{v}$$

and

$$\text{Patch}[vv/tt,vt/vt] = 2\text{Fvv/tt.Fvt/vt.} \qquad \text{vi}$$

The frequency of other patch types with all possible combinations of mated female genotypes can be calculated in the same way.

If females mate within patches after dispersal, patch frequencies cannot be calculated in terms of mated female genotypes in the dispersal population. Instead, a slightly different procedure is used. The frequency of patches with different combinations of unmated males and females are determined in terms of the frequency of the three genotypes in the dispersal population. For example, if Fvv, Fvt and Ftt are the frequencies of the three genotypes in the dispersal population, and genotype frequencies are the same for both males and females and Patch[vv,tt][vt,tt] represents the frequency of patches founded by one [vv] female, one [tt] female, one [vt] male and one [tt] male, the frequency of patches with this mix of unmated individuals can then be calculated as

$$\text{Patch}[vv,tt][vt,tt] = 4\text{Fvv.Ftt.Fvt.Ftt.} \qquad \text{vii}$$

However, within a patch of this type there are four possible mating combinations which can give rise to different mated female patch types. If mating is random within the patches and both females can mate with the same male the four possible combinations are; both females mating with the [vt] male, both with the [tt] male, the [vv] female mating with the [vt] male and the [tt] female with the [tt] male or the [vv] female mating with the tt male and the [tt] female with the [vt] male. In terms of mated females this will give rise to the four mated female patch types [vv/vt,tt/vt], [vv/tt,tt/tt], [vv/vt,tt/tt] and [vv/tt,tt/vt] with each with a frequency of Fvv.Ftt.Fvt.Ftt. This same procedure can be carried out for all possible combinations of unmated male and female genotypes to give the frequencies of patch types with all possible combinations of mated female genotypes.

Once the frequency of each patch type, the number of dispersers from each patch type and the frequency of genotypes within these dispersers are known, the frequency of each genotype in the next dispersal population can be determined. This is simply the sum of that genotype's frequency within dispersers from each patch type, weighted by both the relative number of dispersers produced by that patch type, and the frequency of that patch type in the population.

For a behavioural strategy to be an evolutionarily stable strategy (ESS, Maynard Smith 1982), a population fixed for the appropriate allele must be stable against invasion by rare mutant alleles for the alternative behaviour. To see if this is the case for *Attack* or *Avoid* the model was begun with the allele for the other behaviour at low frequency (0.00001) in the initial dispersal population. The change in allele frequencies were then followed for 30 cycles of patchy and dispersal phases. If the rare allele decreased in frequency the behaviour determined by the common allele was deemed to be an ESS. The genotypes in the dispersal population will generally not be in Hardy-Weinberg proportions, and so the way in which an allele is distributed amongst the three genotype in the initial dispersal population might have important consequences for the outcome of the model. To assess the importance of this, separate runs of the model were carried out under a range of conditions, with the rare allele either present only in homozygotes, in Hardy-Weinberg proportions or only in heterozygotes. Whilst the initial conditions occasionally affected the results for the first one or two cycles, these differences were negligible after 10 cycles, and so all runs of the model were begun with the alleles in Hardy-Weinberg proportions.

Initially the model was set up with each patch being founded by 2 females which mated during dispersal, and patches existed for two generations of competition. The ESS's were determined for a range of values of E (0-1) and W (0.5-1: Values of W less than 0.5 are biologically unlikely and have not been considered here.) and compared to the results of the model with an undivided population structure. There are several components of the population structure which may affect the outcome of the model; the spread of an allele may depend on i) the number of females that found each patch, ii) the number of generations that individuals spend within a patch and iii) the point at which founding females mate (before, during or after dispersal; see figure 7.1). Consequently further runs of the model were carried out with each of these parameters altered in turn to asses their effect on the predictions of the model.

7.3. Results

The effect of the patchy population structure can be seen by comparing the outcome of the basic patchy model, in which patches are founded by two females that mate during dispersal and spend two generations within patches before dispersing, to the model with an undivided population structure, which is exactly equivalent to the genetic version of the Smith and Lessells model with the *Avoid* allele dominant (Smith 1990). If the cost of competition is high (E >0.5) *Attack* is the only ESS in both models. Similarly, if the cost of competition is low (E < 0.5) and there is no *Attack* superiority, *Avoid* is the only ESS in both models. Thus under these two sets of conditions, the structured population has no effect on the model's outcome. However, if there is some level of *Attack* superiority (W >0.5) and the cost of competition is also low (E<0.5) the outcomes of the two models differ.

The ESS's for this range of conditions are shown in figure 7.2. If there is any level of *Attack* superiority (i.e.W>0.5) then *Attack* is always a possible ESS in the undivided model, but this is not the case in the patchy population model. If the cost of competition is low enough then *Avoid* alleles are able to invade a population fixed for the *Attack* allele, even if there is some level of *Attack* superiority. *Avoid* becomes the only ESS for a range of conditions in which both *Attack* and *Avoid* were possible ESS's in the undivided population model. As both *Attack* superiority and the cost of competition increase a boundary is reached (E<1-W) above which *Attack* becomes the only ESS in the undivided population model. In the patchy model this boundary is shifted to higher values of E and W, and *Avoid* continues to be a possible ESS for a range of values where E >1-W. *Avoid* continues to be a possible ESS in the patchy model under conditions in which *Attack* is the only ESS in the undivided population. Thus, the patchy population structure increases the range of conditions in which *Avoid* is a possible ESS, and reduces the range in which *Attack* is a possible ESS.

The reason for this change in outcome is that, as with other structured population models, there are two selective forces which affect allele frequencies in a patchy population; within patch selection acting on the relative fitness of the two alleles within patches, and between patch selection acting on the differential productivity of patches with different initial genotype frequencies. Within patch selection operates within each patch in exactly the same way as it would do in an single undivided population. If conditions are such that *Attack* is the only ESS in an undivided population then *Attack* alleles will be replacing *Avoid* alleles within all mixed patches, whatever the initial frequencies of the two alleles (figure 7.3a), whilst if *Avoid* is the only ESS in an undivided population, *Avoid* alleles will be replacing *Attack* alleles within all mixed patches (figure 7.3b). If both *Attack* and *Avoid* are alternative

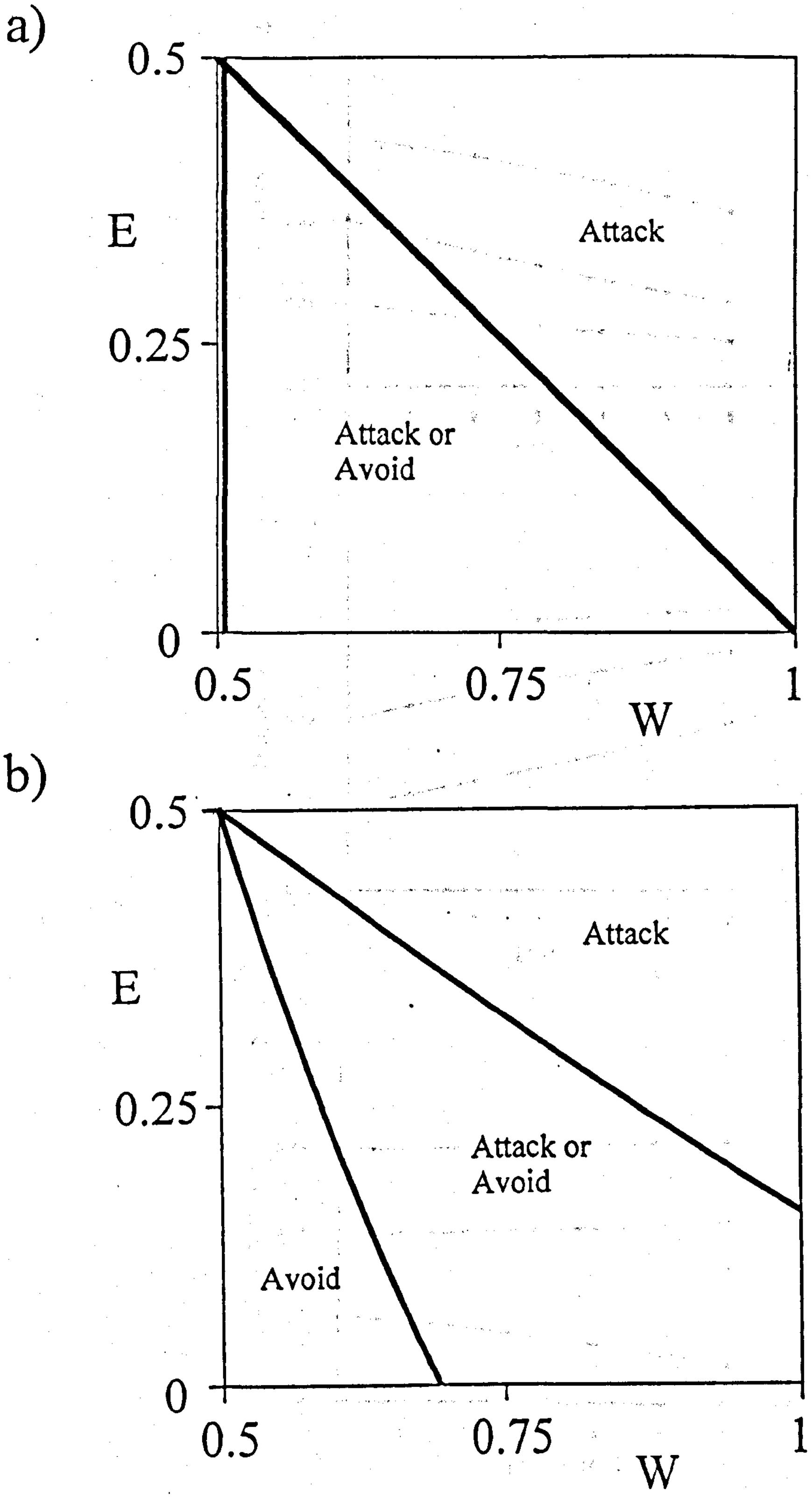

Figure 7.2. Predicted ESS's for a) the undivided population model (the Smith and Lessells model) and b) the basic patchy model with patches founded by two females which mated during dispersal and two generations of competition within patches. E is the cost of competition and W the level of *Attack* superiority. Lines represent boundaries between conditions with different ESS's. Values of W below 0.5 are biologically unlikely and so not shown on figures, values of E above 0.5 are also not shown as *Attack* is the only ESS under these conditions, and does not change in any of the models. There is a zone (unlabelled on figure) corresponding to the y axis in the undivided population figure, for which *Avoid* is the only ESS.

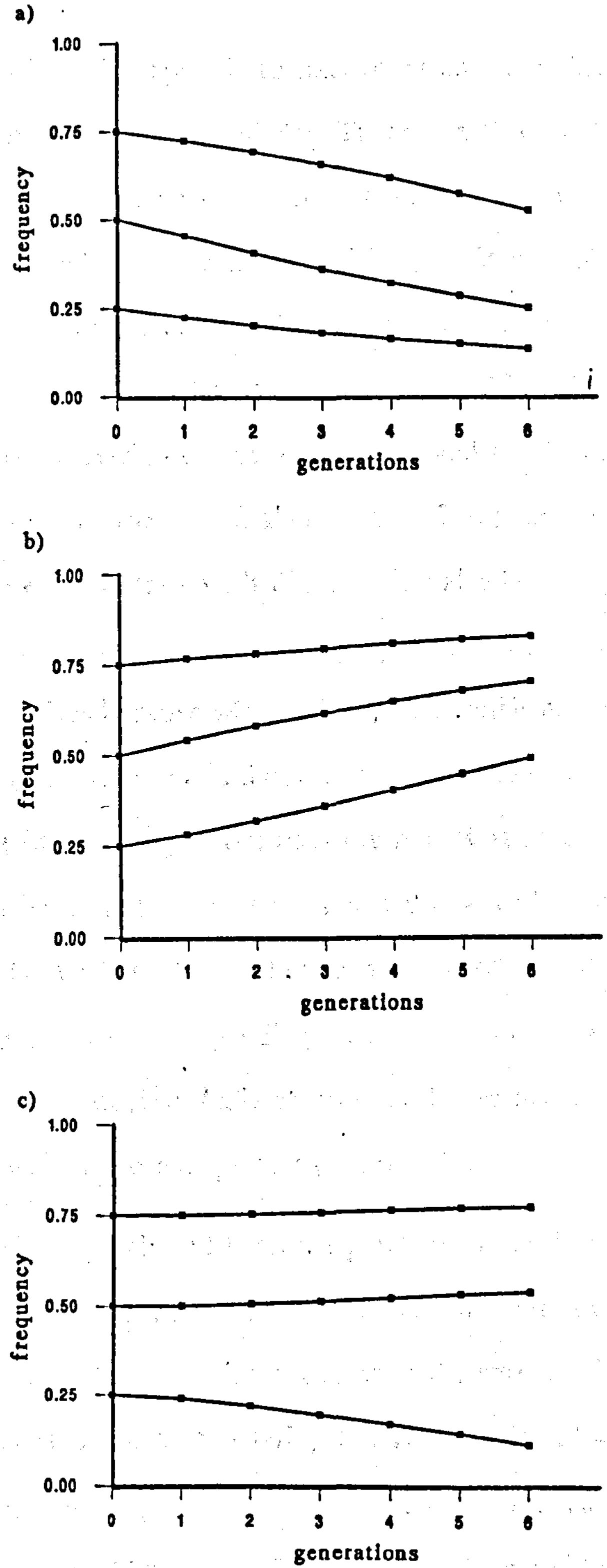

Figure 7.3. Within patch change in *Avoid* allele frequency under conditions in which a) *Attack* is the only ESS (E=0.6, W=0.5), b) *Avoid* is the only ESS (E=0.2,W=0.5) and c) *Attack* and *Avoid* are both possible ESS's (E=0.1, W=0.75) in the undivided population model. Each graph shows the frequency of the *Avoid* allele after one to six generations of competition within patches. The three lines represent patches with different initial frequencies of the *Avoid* allele (0.25, 0.5, 0.75).

ESS's the allele which spreads to fixation in an undivided population depends on the initial frequencies of the two alleles. There is a threshold frequency above which the *Avoid* allele will spread to fixation and below which it will decrease in frequency. Under these conditions the allele which spreads within each patch depends on the initial frequency of the alleles when the patch is founded; patches initially above the threshold frequency for the spread of the *Avoid* allele in an undivided population moving towards fixation of the *Avoid* allele and patches below this threshold moving towards fixation of the *Attack* allele (figure 7.3c). On the other hand, between patch selection, due to patches with different initial allele frequencies producing different numbers of dispersing adults, can only operate in a patchy population. The differential productivity arises because when pairs of individuals compete over a resource unit, the number which survive to adulthood depends on the strategy of the two competitors. If at least one of the competitors uses the *Attack* strategy, only a single individual will survive, whilst if both competitors use the *Avoid* strategy, the resource unit will produce 2(1-E) adults. Hence between patch selection can favour either the *Attack* allele or the *Avoid* allele depending on the cost of competition; if $E > 0.5$ patches with a high frequency of *Avoid* alleles produce fewer dispersers (figure 7.4a), whilst if $E < 0.5$ they produce more dispersers (figure 7.4b).

If within patch and between patch selection both favour the same allele, the population structure does not affect the outcome of the model. If the cost of competition is high then both forces favour the spread of the *Attack* allele and the ESS in both models is *Attack*. Similarly, if there is no *Attack* larval superiority and the cost of competition is low, both forces favour the *Avoid* allele and the ESS is *Avoid* in both models. However, if the two selective forces favour different alleles the predictions of the two models may differ. If *Attack* is the only ESS in the single population model, within patch selection favours the spread of the *Attack* allele, but if the cost of competition is also low between patch selection favours the spread of the *Avoid* allele. If between patch selection is strong enough, the *Avoid* allele is able to spread in the

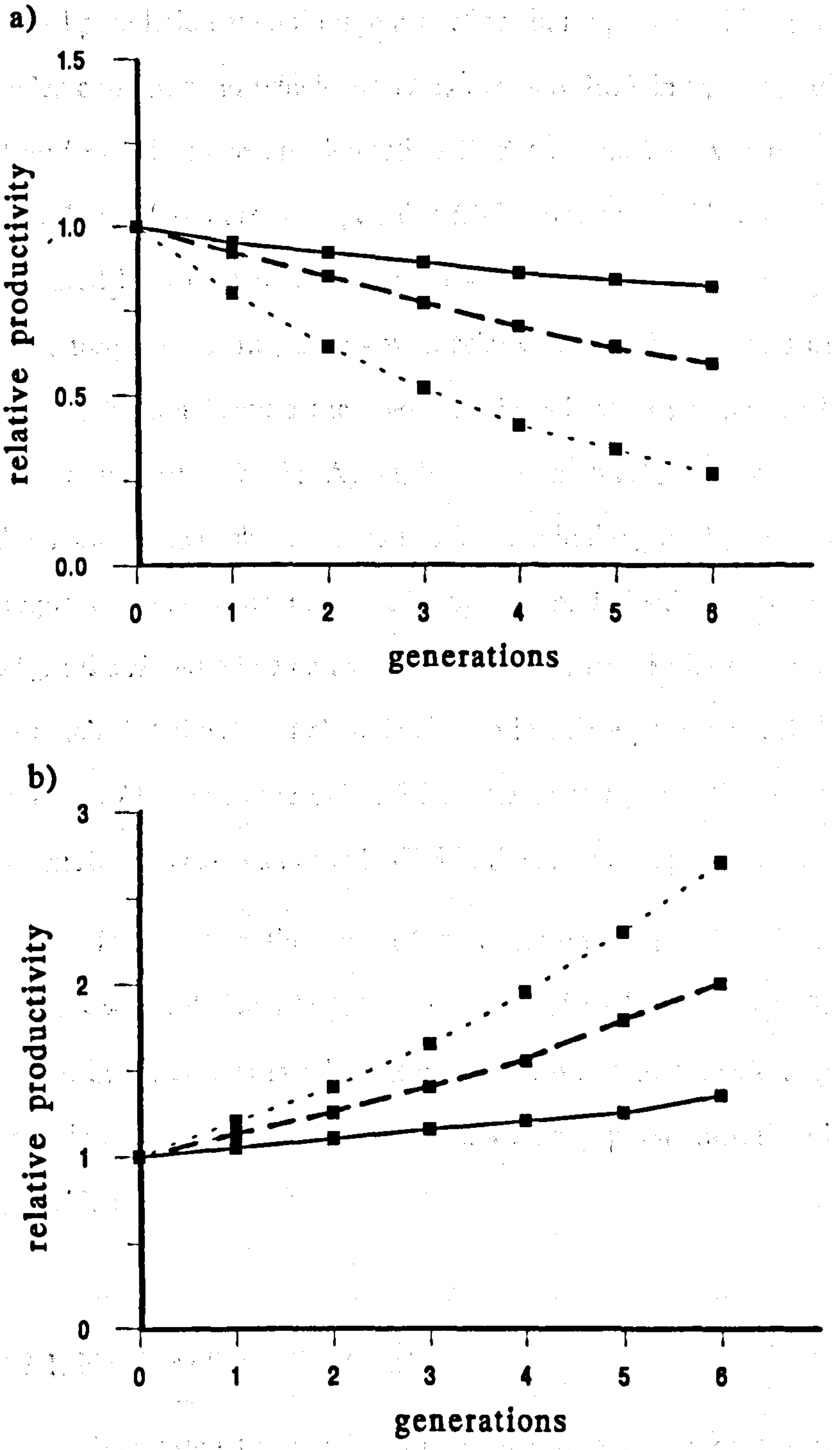

Figure 7.4. Relative productivity of patches with different initial frequencies of *Avoid* alleles. The graphs show the productivity of patches with different initial frequencies of *Avoid* alleles, relative to the productivity of a patch fixed for the *Attack* allele. Value are shown for one to six generations of competition, under conditions in which a) the cost of competition is high (E = 0.6, W=0.5) and b) low (E = 0.4, W=0.5). The three lines represent patches with initial *Avoid* allele frequencies of 0.25 (solid line), 0.5 (large dashed line) and 0.75 (small dashed line).

global population even though it declines in frequency within every mixed patch. Thus, under conditions in which *Attack* is the only ESS in the undivided population model, *Avoid* may become an alternative ESS to *Attack* in a patchy population model. If *Attack* and *Avoid* are both possible ESS's in the undivided population model, the allele favoured by within patch selection varies between patches depending on their initial allele frequencies. In patches with relatively high frequencies of *Avoid* alleles, within patch selection favours the *Avoid* allele, whilst in patches with lower frequencies it favours the *Attack* allele. Again, between patch selection favours the *Avoid* allele, and the *Avoid* allele is able to spread to fixation in the global population from a lower initial frequency than in an undivided population. Indeed, the threshold frequency above which the *Avoid* allele can spread to fixation in the global population may be reduced so much that the *Avoid* allele is able to invade a population fixed for the *Attack* allele and *Avoid* becomes the only ESS in the patchy population model under conditions in which *Attack* is also a possible ESS in the undivided population model.

Thus, when the cost of competition is low, the increased productivity of patches with relatively high frequencies of *Avoid* alleles may allow the *Avoid* allele to spread in conditions in which it could not do so in a single population, and so *Avoid* behaviour is more likely to evolve in a patchy population than in a population that is undivided.

7.3.1. Number of founding females

Increasing the number of females that found each patch from two to three reduces the effect of the population structure on the spread of the *Avoid* allele (figure 7.5). The zone in which *Avoid* is the only ESS is reduced and the zone in which *Attack* is the only ESS is increased. This occurs because the strength of between patch selection depends on the initial variation in allele frequencies between patches which is caused by sampling effects when the patches are founded. The smaller the number of founding females, the greater the variation between patches. As the number of females

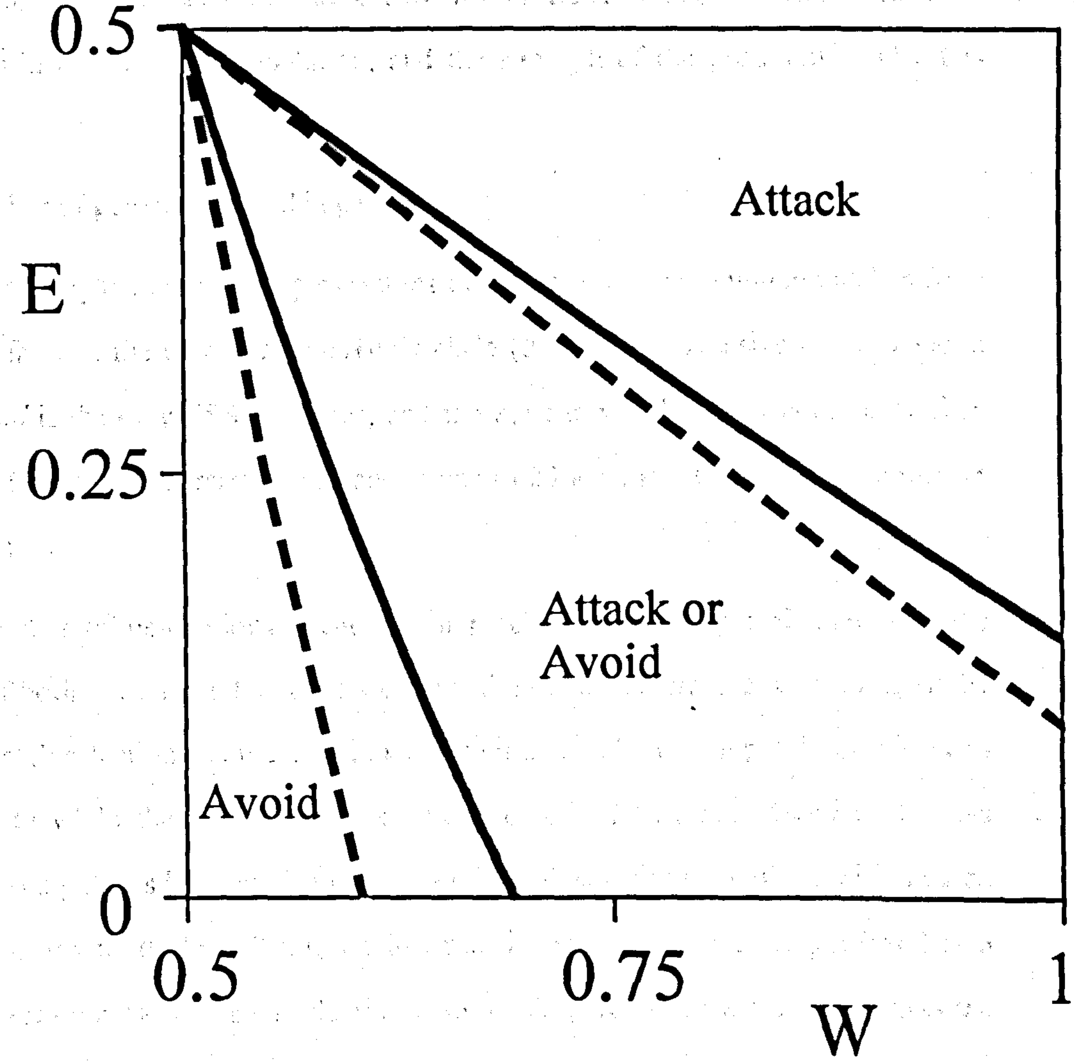

Figure 7.5. Effect of the number of founding females. E is the cost of competition and W is the level of *Attack* superiority. Lines represent boundaries between conditions with different ESS's. Boundaries are shown for models in which patches are founded by two females (solid lines) or three females (broken lines).

is increased, the frequency of the alleles within patches become closer to their frequencies in the dispersal population, and the strength of the productivity effect is reduced.

7.3.2. Number of generations within patches

Increasing the number of generations that organisms spend within patches from two to 10 favours the spread of the *Avoid* allele (figure 7.6). The size of the zone in which *Avoid* is the only ESS increases, and the zone in which *Attack* is the only ESS decreases. Increasing the number of generations to 20 increases this effect even further (figure 7.6).

As the number of generations spent within patches before dispersal increases, the strength of both within patch and between patch selection increases. However, whilst between patch selection can increase in strength indefinitely, within patch selection can only operate while there are patches containing both *Attack* and *Avoid* alleles. As initially mixed patches become fixed for one of the alleles, the strength of within patch selection begins to decline. Thus, an increase in generations within patches has a greater effect on between patch selection than within patch selection and increases the range of conditions in which the *Avoid* allele is able to spread.

7.3.3. Point at which founding females mate

In the basic model founding females mate in the single population during dispersal. If instead, mating occurs within patches either before or after dispersal, *Avoid* becomes more likely as an ESS (figure 7.7). The zone in which *Avoid* is the only ESS increases in size and the zone in which *Attack* is the only ESS decreases in size. The effect of moving the point at which founding females mate to either before or after dispersal is to increase the variation in allele frequencies between patches. This will increase the differences in productivity between patches and thus favour the spread of the *Avoid* allele. If founding females mate during dispersal they can mate with any male

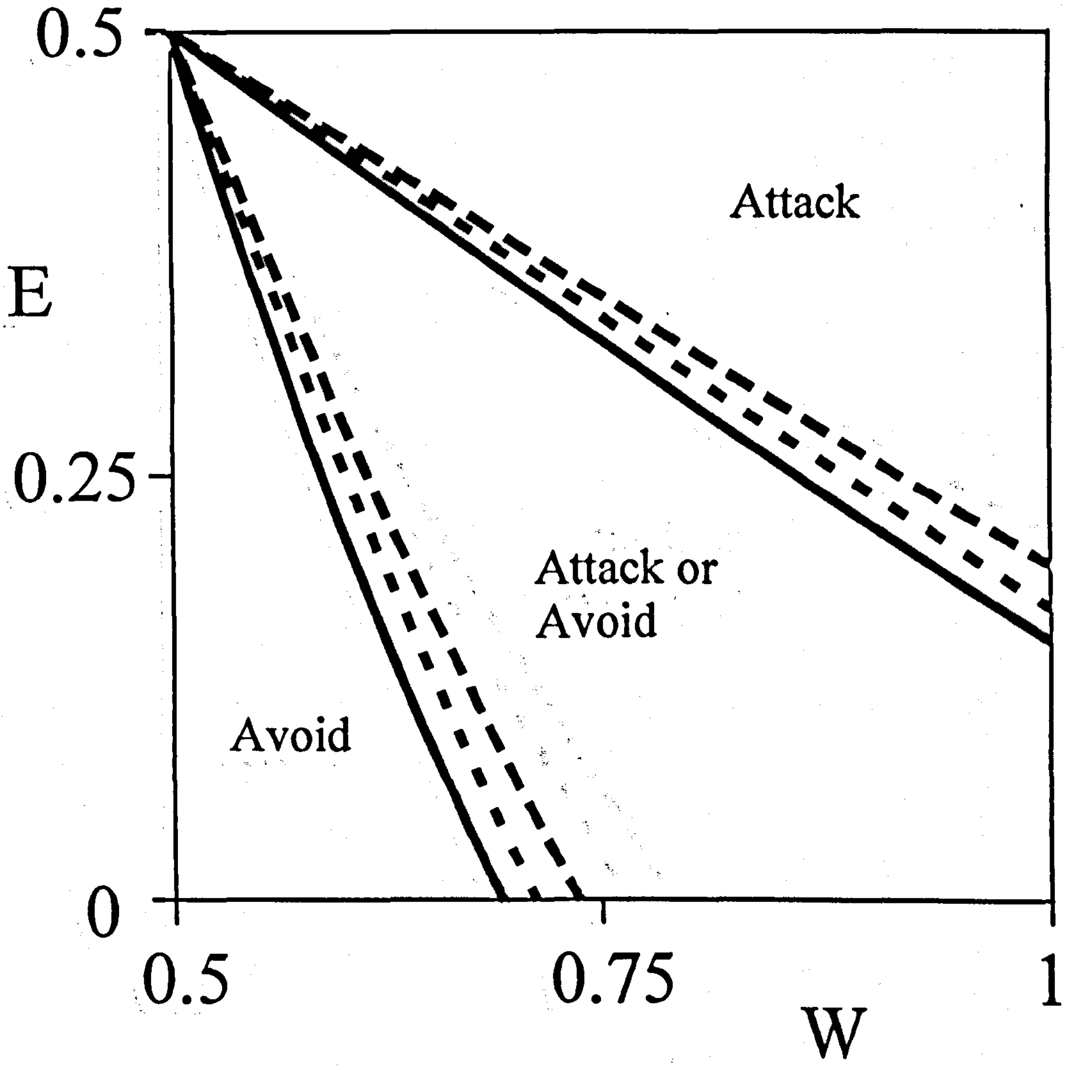

Figure 7.6. Effect of number of generations of competition within patches. E is the cost of competition and W the level of *Attack* superiority. Lines represent boundaries between conditions with different ESS's. Boundaries are shown for models in which individuals compete for two generations (solid lines) 10 generation (small dashed lines) and 20 generation (large dashed lines).

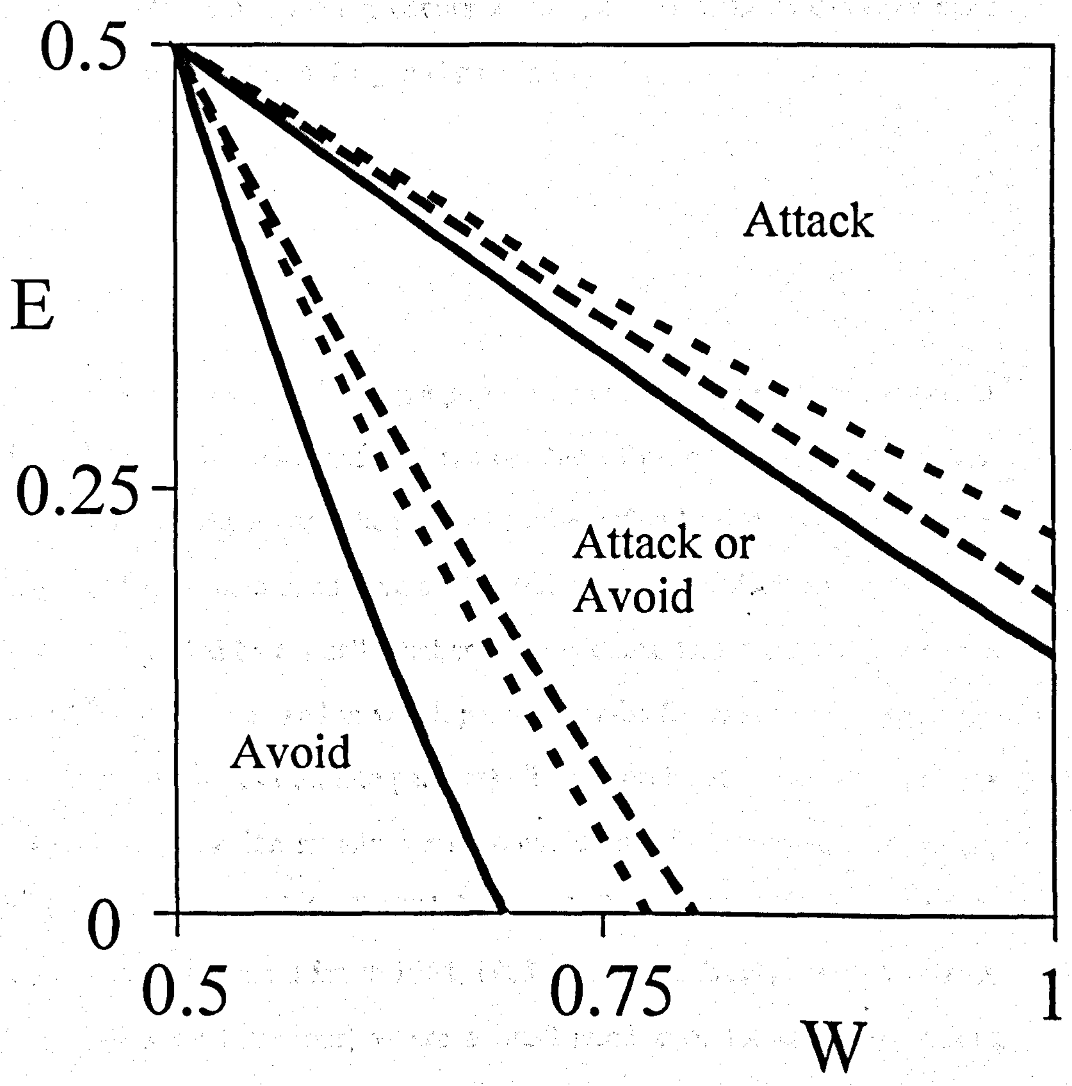

Figure 7.7. Effect of altering the point of mating. E is the cost of competition and W the level of *Attack* superiority. Lines represent boundaries between conditions with different ESS's. Boundaries are shown for models in which females mate before (small dashed lines), during (solid lines) or after (large dashed lines) dispersal.

in the entire population, but if mating occurs within patches, females can only mate with a small subset of the males in the global population.

7.4. Discussion

The model shows that subdividing a population into isolated patches can favour the evolution of *Avoid* behaviour and that the number of generations within patches, the number of founding females and the point of mating affect how strong this effect is. The population structure most conducive to the evolution of *Avoid* behaviour is one in which patches are founded by a small number of individuals, that mate within patches either before or after dispersal and in which patches persist for many generations (but see below for possible effect of infinite patches). These results are consistent with the effects of a patchy population structure on the evolution of other traits such as sex ratio and altruistic behaviour (Colwell 1981, Wilson & Colwell 1981, Harvey 1985 for sex ratio, Wilson 1977, Maynard Smith 1964, 1983, Matessi & Jayakar 1976, Cohen & Eshel 1976 for altruistic behaviour) where a small number of founders and mating within patches also increased the effect of the population structure on the evolutionary outcome.

The model makes assumptions that may not necessarily be true of natural populations. In the model each patch is founded by the same number of females. However patches certainly vary in the number of founders. If the variance in allele frequency is determined for patches founded by exactly two mated females, and also for patches founded by a mean of two mated females but with the exact number varying from one to six in Poisson frequencies, the variance is higher for the latter case. Thus variation in the number of founders per patch may further increase the spread of the *Avoid* allele. The mean number of females founding patches is also expected to vary in relation to the size of the dispersal population. This introduces an interesting dynamic, because as the frequency of the *Avoid* allele increases the dispersal population size will also increase. This will then increase the mean number of founders which will work against the spread of the *Avoid* allele. Thus, an increase in the frequency of the *Avoid* allele may actually alter conditions so that it is no longer able to spread. The exact effect will depend on the conditions but could include long term cycling of allele frequencies or even a stable polymorphism.

In the model the number of competitors per resource unit is assumed constant throughout the lifetime of the patch, whereas it would probably increase as the population within the patch becomes larger. This increase in the number of competitors per resource unit with time will differ between patches depending on their relative growth rates. It is hard to predict the effect of this, but Smith and Lessells showed that the results of their game theory model were qualitatively, but not quantitatively the same with different number of larvae per bean. It seems likely that the same will be true of the patchy model; the effect will still be to favour the spread of the *Avoid* allele although the strength of this effect may differ.

In the model an infinite number of patches are founded at the beginning of each patchy phase allowing the frequency of different patch types to be calculated deterministically in terms of the frequency of alleles in the previous dispersal population. In the real world the number of patches will be finite which will add an element of stochasticity to the frequencies of patch types. This may have important consequences for the spread of the *Avoid* allele when rare, particularly when beetles spend a large number of generations within patches. In the deterministic model some patches will always begin fixed for the *Avoid* allele, no matter how rare the allele is in the population as a whole. Even if conditions are such that the *Attack* allele is able to spread in all other patches, these patches will remain fixed for the *Avoid* allele. In a population with a finite number of patches, chance events may lead to no patches beginning fixed for the *Avoid* allele, and if the number of generations within patches is high enough, all patches could become fixed for the *Attack* allele, and the *Avoid* allele be lost from the population. So although in theory a large number of generations within patches increases the range of conditions in which the *Avoid* allele can spread when rare, in practice, if the number of generations is too high, it may be very difficult for the *Avoid* allele to spread , as chance events will frequently result in it disappearing from the population. To examine this effect the model was set up with a finite number of patches, each founded by two mated females whose genotype was selected at random from the dispersal population. Individuals spent 10 generations competing within patches and conditions were such that *Avoid* alleles could spread when rare in the infinite patch version of the model (E=0.67, W=1). If 10 000 patches were founded, only 16 out of 100 replicate runs went to fixation for the *Avoid* allele, whilst if 100 000 patches were founded, 93 out of 100 went to fixation.

Whilst the model should be generally applicable to the evolution of competition strategies in patchy population structures, it was developed with *Callosobruchus* beetles in mind. *Callosobruchus* beetles are stored product pests of various legumes cultivated by man, and as such their environment is made up of many isolated bean stores. Initial infection occurs in the field, and the beetles are then transported as larvae within the beans into large bean stores (Southgate 1979, Hagstrum 1985, Germaine et al 1987). Infestation levels in the field are low and so only a small number of beetles emerge within the store. Hagstrum (1985) has reported *C. maculatus* infestation in the field at a level of about one larva in every 100 000 beans. The founding beetles then emerge and mate within the store, before reproducing rapidly on the abundant resource. After several generations within the store the resource becomes depleted and the beetles enter a dispersal phase leaving the store in search of new beans to infect. Lefevre (1950 cited in Taylor 1981) reports 48-70% damage of beans within 8 months of bruchid infestation. In the laboratory the generation time of *Callosobruchus* beetles is about one month but is likely to be slower in the field. This suggests that *C.maculatus* may destroy most of the beans within a store within 10 generations. This population structure, with a low number of founders mating after dispersal within the store, and several generations of reproduction before dispersal is the type of structure which should favour the evolution of *Avoid* type competition strategies. Most *Callosobruchus* species use an *Avoid* type competition strategy as larvae, whilst other bruchid beetles, which exploit wild legumes, tend to show *Attack* behaviour (Kiritani 1957 cited in Toquenaga & Fujii 1990). The results of this model support the idea that moving from a wild host to a stored product, and the associated change in population structure, may have been an important step in the evolution of the *Avoid* competition strategy in this genus (Smith and Lessells 1985, Smith 1990). However wild legumes are smaller than cultivated ones, and this could also favour *Attack* behaviour in the wild and *Avoid* behaviour in stored products. A detailed comparative study examining the relationship between the two competition strategies and factors such as host size, and population structure across different species of bruchids would be required to determine whether either or both of these factors have been important. Also while most *Callosobruchus* species use *Avoid* behaviour, *C. analis* uses *Attack* behaviour (Umeya et al 1975); a comparison of the exact population structure of this species to other *Callosobruchus* species might provide clues to the reason for its larval competition strategy.

The similarities between the effects of a patchy population structure on the evolution of competition strategies shown by this model, and the effect shown by other authors on the evolution of female biased sex ratios and altruistic traits are not surprising as the systems have many common features. In all three cases the population structure has an effect because the allele which has the greater relative fitness within a patch is not the allele which maximises the absolute fitness of individuals within the patch. Indeed, Wilson and Colwell (1981) regarded females producing a female biased sex ratio as behaving altruistically because the trait lowered their relative fitness within a patch whilst increasing the absolute fitness of all members of the patch. Using this same definition, the *Avoid* behaviour in this model could also potentially be described as an altruistic trait. This redefining of the term altruism, to refer to a trait which reduces individuals relative fitness within its group rather than its absolute fitness compared to the global population, has been criticised by Grafen (1984), but whatever term is used, there is no doubt that the same processes that make the evolution of female biased sex ratios and altruistic traits more likely in a subdivided population also make the evolution of scramble competition strategies more likely too. This model adds the way in which organisms compete over resources to the list of traits whose evolution can be affected by the population structure in which they evolve, so any attempt to understand why different species compete in different ways cannot ignore the population structure of the organisms concerned.

Chapter 8. General discussion

8.1. Introduction

The two species of bruchid beetle, *Callosobruchus analis* and *C. maculatus* present an interesting problem to evolutionary biologists. The larvae of both species develop within legume seeds, such as black-eyed beans and mung beans, but the larvae of the two species compete in very different ways. The larvae of *C. analis* adopt an extreme contest type behaviour (the *Attack* strategy) and fight to the death within the bean, so that normally only a single adult emerges from each bean, no matter how many initially entered the bean. In contrast, the larvae of *C. maculatus* adopt a scramble competition strategy (the *Avoid* strategy), and compete passively by exploiting the resource, as a result several *C. maculatus* adults may emerge from a single bean. The aim of this study was to investigate the types of selective forces that can cause two closely related species to evolve such different larval competition strategies when competing over identical hosts.

The main factors likely to affect the competition strategy that a species evolves in a closed system are summarised in Table 8.1. In this chapter I will discuss each of these factors in relation to the results of this study, and also discuss some of the implications of these factors to competition in general.

8.2. Factors affecting competition in closed systems

8.2.1. The cost of sharing resources

One factor that the Smith and Lessells model suggests may have important consequences for the type of competition strategy that a species evolves is the cost of exploitation competition. This represents the relative reduction in fitness of a larva that shares a bean compared to the fitness of a larva that develops alone within a bean. The higher the cost of exploitation competition, the more likely that the *Attack* larval

Table 8.1. Factors that affect the competition strategy that a species evolves in a closed system

Factor	**Effect**	**References**
Cost of sharing the resource (the cost of exploitation competition).	The higher this cost the more likely that contest strategies will evolve.	Smith & Lessells(1985) Godfray (1987b) Smith (1990) Chapters 3 and 4
Cost of fighting	Any cost of fighting over the resource will reduce the likelihood that contest competition strategies will evolve	Godfray (1987b) Chapter 5
Asymmetries in fighting and passive competitive abilities	Detected asymmetries make the evolution of conditional strategies possible. Increased asymmetries make the evolution of contest strategies, either pure or conditional, more likely.	Chapter 6
Historical constraints on evolution	Models of competition suggest that species may often be constrained to using a contest competition strategy, once they have evolved it, even if conditions change so that a scramble strategy would have higher fitness	Smith & Lessells (1985) Godfray (1987b) Godfray & Harper (1990)
Population structure.	A subdivided population structure makes the evolution of scramble competition strategies more likely.	Smith & Lessells (1985) Smith (1990) Chapter 7

competition strategy (the contest strategy) will be the evolutionarily stable strategy (ESS: Maynard Smith 1982). The results described in chapters 3 and 4 suggest that one factor determining the cost of exploitation competition in bruchid beetles is the size of the host bean, or more precisely the amount and quality of the resource within the host bean, in which the larvae develop. This idea is also supported by the work of Toquenaga and Fujii (1990, 1991a, b) on interspecific competition between *C. analis* and *C. phaseoli* (another *Avoid* species). They found that the *Attack* species, *C. analis*, was favoured in competition over small hosts, but that the *Avoid* species, *C. phaseoli*, was favoured on large hosts. This is likely to be generally true for the evolution of competition strategies in many other closed systems. Godfray's model (Godfray 1987b) of the evolution of larval competition strategies in parasitic wasps predicted that contest competition strategies would be likely to evolve when the optimum clutch size per host is small. The optimum clutch size per host is likely to depend in a large part on the amount of resource within the host (Klomp & Teerink 1967, Waage & Godfray 1985). Thus, it seems that in these types of closed systems the size of the host probably does play an important role in the type of competition strategy that a species evolves.

However, current differences in the cost of exploitation competition caused by differences in host size cannot be the sole reason for the different larval competition strategies used by these two species of beetle, because both species are known to occur on beans of the same species (Southgate 1978) both in nature and in the laboratory. One possible explanation is that there are inherent differences in the cost of exploitation competition suffered by the two species so that although they both use the same hosts, *C. analis* larvae suffer a greater cost of exploitation competition than *C. maculatus* larvae. There do indeed appear to be differences in the cost suffered by the two species when they compete on small hosts, such as mung beans, but on larger hosts such as black-eyed bean this does not appear to be the case; both species suffer a similar cost of exploitation. Moreover, the cost is low, so that the larvae of both species would appear to have higher individual fitness if they shared beans rather than fighting over them. Thus, in terms of individual fitness, *C. analis* larvae appear to be using a maladaptive strategy on black-eyed beans. A similar problem has been observed with the larvae of parasitoid insects, with the larvae of some solitary species fighting over hosts that are large enough to support the development of several larvae of gregarious species of a similar size (Godfray 1987a,b). Why should some species contest over resources when they would appear to show greater individual fitness if they scrambled for the resources? One possible explanation is that a species may be constrained to using a strategy that was evolved under different conditions. The importance of such historical constraints in limiting the evolution of a species are discussed below.

8.2.2. The cost of fighting

In chapter 5 it was suggested that if larvae that fight over a bean and win suffer some cost of having fought this will reduce the conditions in which *Attack* behaviour will evolve. Similar conclusions apply to both the parasitoid model (Godfray 1987b) and also the siblicide models (Dickens & Clark 1987, Godfray & Harper 1990). The experiments in chapter 5 show that in *C. analis* there seems to be very little effect of fighting over a bean on the fitness of the winner, so in this system costs of fighting would appear to have been of little importance in the evolution of competition strategies. How general this conclusion is to other systems is difficult to assess. Salt (1961) reported cases in which the larvae of solitary parasitoids would kill each other within a host, but it is not clear how often this occurs. Dickens and Clark (1987) suggest that the ease with which a siblicidal kittiwake chick can dispose of a sibling, simply by pushing it from the nest over the cliff, may make it more likely that siblicide will evolve in cliff nesting species. However, it seems unlikely that fighting will always have very little cost for the victor, thus in some cases the cost of fighting probably does increase the chance that a species will evolve a scramble competition strategy.

8.2.3. Asymmetries in fighting and passive competitive abilities

The major effect of adding asymmetries in fighting and competitive ability to the Smith and Lessells model of larval competition, is that they allow the evolution of more complex conditional strategies, in which the behaviour of the individual depends on whether it is the inferior or superior competitor. It is difficult to assess the importance of this to the evolution of competition strategies because it is often difficult in a closed system to tell whether the competitive outcome observed arose from individuals using conditional or pure strategies. In the case of siblicide in birds it is common for asymmetries to mean that the larger chick kills the smaller chick, but it is impossible to tell whether this is a result of the chicks using a pure, "attempt to kill your nest mate" strategy or a conditional "if you are the big chick attempt to kill your nest mate, otherwise keep out of your nest mates way", because unless small chicks are very good at keeping out of the way, the outcome will look the same; the big chick kills the smaller chick.

The model in chapter 6 shows that as the degree of asymmetries increases, the conditional strategies become more likely to evolve, thus in closed systems asymmetries appear to increase the chance that individuals will compete aggressively, whether this is as part of a conditional strategy, or is a pure contest strategy.

8.2.4. Historical constraints on evolution

The results of the Smith and Lessells model show that a species may not always be free to evolve the competition strategy that maximises individual fitness, but instead may be constrained by its history. Under conditions in which *Attack* and *Avoid* are alternative ESS's in the Smith and Lessells model, the ESS that the population evolves to will depend on the relative frequencies of the two strategies in the initial population. If a species originally evolved an *Attack* larval competition strategy on a small host, it may be unable to escape from this ESS, even if host size increases so that *Avoid* becomes an alternative ESS. The species may be limited to using a strategy which, although evolutionarily stable, is of lower individual fitness than the alternative *Avoid* behaviour. It is generally accepted that the ancestral strategy of bruchid beetles is the *Attack* strategy, evolved on small wild legumes, and that selective breeding by man for larger seed size, may have resulted in conditions altering so that *Avoid* became a possible ESS. *C. analis* may be constrained to using the *Attack* strategy on black-eyed beans, even though individuals would be fitter if they used the *Avoid* strategy. However although historical constraints may explain why *C. analis* still uses the *Attack* strategy on hosts where the *Avoid* strategy would apparently have higher fitness, the fact that most other *Callosobruchus* species do use the *Avoid* strategy on large hosts suggests that there must be ways to escape this constraint. One possible mechanism, the effect of a patchy population structure is discussed below.

The results of other models suggest that historical constraints may be quite a common factor in limiting a species to using a contest competition strategy under conditions in which a scramble strategy would give individuals a higher fitness. The models of larval competition in parasitoid insects (Godfray 1987b) and siblicide in birds (Godfray & Harper 1990) both suggest that it is often hard for a species that has evolved a contest competition strategy to subsequently evolve a scramble competition strategy, even if conditions change so that individuals using the scramble competition strategy would have higher fitness. This may explain why some species of parasitoid larvae fight over hosts that are large enough to support several similarly sized larvae of gregarious species (Godfray 1987b) and also the fact that some species of eagle practice siblicide, even when resources are plentiful (Godfray & Harper 1990 discussing the results of Meyburg 1974).

Historical constraints mean that it may often not be possible to understand the competition strategy used by a species in terms of current selective pressures, without some knowledge of how selection pressures operated in the past.

8.2.5. Population structure

In chapter 7 it was argued that scramble competition strategies are more likely to evolve in a population that periodically divides into isolated patches, each founded by a small number of random individuals, than in a single undivided population. This effect can be thought of as an example of kin selection; the *Avoid* allele is able to spread because even though it has a lower relative fitness within each patch, it increases the absolute fitness of all individuals within the patch. As patches are founded by a small number of individuals, larvae within a patch will be more closely related to each other than to a random individual drawn from the global population. Thus an allele that increases the absolute fitness of all individuals within the patch will be increasing the fitness of relatives, and this allows it to spread in the population as a whole even if it is reduced in frequency within every patch.

Models of this type have been criticised because the conditions required for the population structure to significantly alter the evolutionary outcome are stringent (e.g. Maynard Smith 1964). In particular the number of individuals that found each patch must be small. However, this may be the case for stored product pests such as *Callosobruchus* beetles. The natural environment of *Callosobruchus* beetles is made up of many temporary grain stores, and each of these is originally colonised by a small number of individuals. This is exactly the type of population structure that should be expected to favour the evolution of scramble competition strategies. Thus population structure may well have had an important effect on the evolution of competition strategies in this genus.

A patchy population structure provides one way for a species to escape the constraints of its evolutionary history. When discussing historical constraints above it was suggested that the ancestral strategy of *Callosobruchus* beetles was probably the *Attack* strategy. The Smith and Lessells model shows that if there is any level of *Attack* larval superiority a species that evolves the *Attack* larval competition strategy will be unable to evolve the *Avoid* strategy, even if conditions change. However, in a patchy population structure this is not the case, it becomes possible to evolve from *Attack* to *Avoid* even if there is some level of *Attack* larval superiority. This may explain how many species of *Callosobruchus* beetles, including *C. maculatus*, appear to have been able to escape their ancestral *Attack* strategy as bean size increased.

Thus organisms living in a patchy environment should be more likely to evolve scramble competition strategies than similar species living in undivided populations. However, it is probably true that few organisms live in an environment that is as patchy as that of *Callosobruchus* beetles. So although population structure may have had an important effect on the evolution of competitive strategies in this genus, its importance to the evolution of competitive strategies more generally is likely to be limited.

8.3. Extension to competition in open systems

This thesis, and other studies cited in table 8.1 have investigated competition in closed systems, in which individuals have the option of how to compete over the resource, but not of leaving the resource patch in search of another. The advantages of studying competition in closed systems are obvious; the limited behavioural options open to individuals make it potentially easier to understand the factors that affect individuals behaving in different ways. How applicable are the conclusions to the open systems typical of many competitive interactions?

A high cost of sharing the resource, probably increases the chance that a species will evolve a contest competition strategy in all competitive systems. If a territory contains enough food to support one individual, but not two, the individuals should fight over the territory rather than sharing it. Davies and Houston's (1981) work on territoriality in pied wagtails shows how the amount of food within a territory affects how individuals compete over it. A territorial individual normally excludes all other individuals from a stretch of river, but if the amount of food within the territory increases, the territorial individual may allow another individual to share the resource. If the amount of food increases further, as it does in the spring when a rapid supply of insects emerge, territorial individuals give up territories completely. Thus this species seems to have evolved a plastic response allowing individuals to change their competitive strategy in response to changing levels of resource.

The cost of fighting will almost certainly have an effect in open as well as closed systems. It has long been appreciated that high costs of defending a territory will make it less likely that a species will evolve territorial behaviour. The pied wagtail study discussed above (Davies & Houston 1981) also showed this effect; as prey density in a territory increased, the cost of defending the resource also increased as more individuals attempted to use the territory. Davies and Houston (1981) suggested that the reduction in the costs of sharing the resource coupled with the increased cost of defending the resource could explain why, as prey density increased, territorial individuals would allow a second individual to use the territory as well.

The effect of asymmetries in allowing the evolution of conditional strategies will also apply to open systems as well as to closed systems. The models of asymmetric competition produced by Maynard Smith and Parker (1976) and also by Hammerstein (1981) both show how asymmetries allow conditional competition strategies to evolve. However, the effect of asymmetries on increasing the amount of aggressive contests that occur in closed systems will not be the same in open systems. In a closed system if one individual wants to fight for the resource it is very difficult for the other to avoid the contest, whilst in an open system a competitor that does not want to fight can simply leave the resource. Models of asymmetric competition in open systems (Maynard Smith & Parker 1976, Hammerstein 1981) suggest that asymmetries will actually decrease the amount of active aggression, as the asymmetries can be used to settle contests without fighting.

Historical constraints will occur in any competitive system in which there are alternative ESS's. There is no obvious reason to suppose that they will be more likely to occur in closed systems than in open systems. Similarly, the effects of genetic relatedness caused by a patchy population structure would appear to be just as likely to apply in open systems as in closed systems. Scramble competition strategies will still be more likely to evolve in subdivided populations than in undivided populations.

Thus although the work in this study was carried out specifically with *Callosobruchus* beetles in mind, the results have implications to the evolution of competition strategies in general.

8.4. Problems with inferring evolutionary origins from contemporary data

This study illustrates some of the problems associated with making inferences about the evolutionary origins of behavioural strategies from contemporary experiments. The importance of historical constraints in limiting the ability of a species to adapt to new conditions mean that it may often be difficult to explain strategies observed today in terms of current selective pressures. For example, it would be very difficult to explain the different strategies of *C. analis* and *C. maculatus* when competing over black-eyed beans in terms of current differences in the cost of exploitation competition on this host. *C. analis* appears to be using a maladaptive strategy. It is only by making assumptions about the evolutionary history of the species, and assuming that *C. analis* originally evolved on a smaller host and then became stuck at the *Attack* ESS, that it becomes possible to understand the contemporary situation. Although there are fairly good reasons for thinking that this assumption may be valid, it can never be tested as the original hosts of the two species are unknown. Thus, when investigating the effects of selective pressures in the past the researcher must be satisfied with producing plausible explanations that fit with contemporary observations and consequently provide further testable predictions, rather than producing a definite answer.

A second problem that will often arise is that the values of such factors as the cost of exploitation competition measured now may not be a good indicator of their value at the time when the strategies originally evolved. In chapter 3 it was argued that although there seem to be inherent differences in the effect of host size on the larvae of *C. analis* and *C. maculatus* now, this does not mean that this was the case when the two species evolved their competition strategy. It is possible that the reason *C.*

maculatus is less affected by reductions in host size than *C. analis* is an effect of the different competition strategies that the two species use rather than the cause. *C. maculatus* may have evolved a more plastic response to host size, simply because its *Avoid* competition strategy means larvae will often be sharing beans with variable numbers of other larvae.

8.5. Possible extensions to this work and the limits of the system

Whilst this study provides an insight into some of the factors that may affect the evolution of competition strategies, there are still areas in which further work could yield much useful information. The Smith and Lessells (1985) model suggests that *Avoid* behaviour should only be found in species that live on large hosts, whilst *Attack* behaviour should be found in species living on small hosts and also, due to historical constraints, species living on large hosts. Although there is some information suggesting that this expected relationship between larval competition strategy and size of host does exist across different species of bruchids, this evidence is largely anecdotal. The same is true of parasitoid insects (Godfray 1987b). It was hoped to carry out a more rigorous analysis of the available data to investigate this relationship using the statistical techniques that are now available to correct for the confounding effects of phylogenetic relationship (Harvey & Pagel 1991) as part of this study. However, the lack of an accurate phylogeny for bruchids (C.H.C. Lyal pers. com.) along with difficulty obtaining high enough quality data from the literature, meant such an analysis could not be carried out. As better quality data becomes available such a comparative study could provide a strong test for the effect of host size on larval competition strategies. Such a study could also provide information on the relationship between population structure and competitive strategy as well.

To answer the question of why a species behaves in one way rather than another it is necessary to measure the costs and benefits associated with each of the possible behaviours. There are many difficulties in measuring the fitness consequences of a behaviour that a species does not normally use. In chapter 3 the cost of exploitation competition was estimated for *C. analis* by forcing two larvae to share the same bean one after another. The reduction in fitness of the second larva through the bean was used to estimate the cost that larvae would pay if they shared a bean simultaneously. However, the fitness consequences of sharing a bean sequentially may be very different to the consequences of sharing simultaneously. For example, mung beans that have had a single larva pass through them, show a marked change in colour soon after the adult emerges (pers. obs.), suggesting that the damage caused by the first larva causes changes to the chemistry of the bean. Thus the quality of the resource available to the second larva may be very different to the quality available to the first, leading to an over- or under-estimate of the cost of exploitation competition. However, comparisons of the cost of exploitation competition in *C. maculatus*, measured both directly and using the sequential development method, suggest that the sequential development method does provide a fairly good estimate of the cost of sharing beans simultaneously.

There are other possible ways in which these costs and benefits could be measured. Godfray (1987a) discusses how certain insecticides can stop the larvae of some species of solitary parasitoid larvae developing the fighting mouthparts. They are then unable to fight within the host, and several adults can emerge from a single host. If such a chemical could be used for the same purpose in *C. analis* it would then be possible to measure the fitness consequences of *C. analis* larvae developing simultaneously within a bean. Alternatively, current advances in the field of molecular genetics may one day allow the development of genetically altered *C. analis* larvae, that do not fight within hosts and these could also be used to measure the fitness of larvae that share beans. However, techniques such as these also have problems; a chemical that stops larvae developing fighting jaws will almost certainly affect other aspects of development, and even genetic manipulations may alter traits not directly linked to the competition behaviour.

This outlines a common problem found in most studies that attempt to manipulate the way in which an organisms behaves, and assess the fitness consequences. It is impossible to be certain that the manipulation only affects that trait of interest, and thus that the fitness measured is a true indication of the fitness that would be measured if the organism actually used the behavioural strategy normally. However, as long as manipulations are carefully chosen, and if possible calibrated by carrying them out on another species where the fitness can be measured using the manipulation and also directly, these type of techniques provide a powerful tool in investigations of the adaptive nature of behaviours.

8.6. Conclusions

The way in which an individual competes over resources will have a major effect on its fitness, and ultimately on the population dynamics and stability of the species. Despite the limitations discussed above, *Callosobruchus* beetles provide a good model system for studying the evolution of competition strategies. The work described in this thesis shows that the competition strategy a species uses may depend on a few simple factors. However, the results also show that the previous evolutionary history of a species may be critical in determining whether the species can evolve the behavioural strategy that maximises individual fitness under current ecological conditions; differences observed between species now may depend on differences in the past rather than differences in current conditions.

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Appendix 1. Publications.

Ecological Entomology (1993) **18**, 275–277

SHORT COMMUNICATION

Does larval competition affect fecundity independently of its effect on adult weight?

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Key words. *Callosobruchus maculatus*, bruchid, larval competition, oviposition.

Introduction

One of the most successful areas of life history theory has been the modelling of insect oviposition behaviour (Parker & Courtney, 1984; Charnov & Skinner, 1985; Godfray, 1987; Wilson & Lessells, 1993). The first models estimated the optimal clutch size by measuring the effect of larval competition on the survival of larvae from different sized clutches (Mitchell, 1975). However, it was soon realized that, as well as reducing the survival of larvae to maturity, larval competition also affects the fecundity of surviving adults. More recent optimal clutch size models have been based on measurements of the survival of larvae and the fecundity of adults from clutches of different sizes (Smith & Lessells, 1985; Charnov & Skinner, 1985). Because of the difficulty in measuring fecundity in relation to larval competition it has generally been done in two steps; first the effect of competition on adult weight, then the effect of adult weight on fecundity (Waage & Ng, 1984; Wilson, 1993; see also Charnov & Skinner, 1985, using results from Klomp & Teerink, 1967). This two-step method makes the implicit assumption that the only effect of larval competition is via its effect on emergent adult weight (solid lines, Fig. 1a) and that there is no independent effect of competition on fecundity (dashed lines, Fig. 1a).

This paper tests the assumption that competition has no effect on fecundity independent of its effect on adult weight in the bruchid beetle *Callosobruchus maculatus*. By comparing the regression of fecundity on adult emergence weight in larvae, raised alone or in competition with another larva in a bean, it is possible to test whether competition does (Fig. 1b) or does not (Fig. 1c) have an independent effect on fecundity. *C.maculatus* does not feed as an adult and exhibits a strong correlation between fecundity and adult emergence weight (Smith & Lessells, 1985; Credland *et al.*, 1986; Messina, 1991). Previous models of optimal oviposition behaviour have made the assumption that there is no effect of larval competition independent of its effect on adult emergence weight. It is essential that this assumption is tested if these models are to be based on solid foundations.

Methods

Two hundred adult *C.maculatus* (less than 24 h old) were allowed to oviposit on 500 mung beans (*Vigna radiata*) for 1 h. Mung beans were used as they are small enough for competition to have a detectable effect at densities of two larvae per bean (Mitchell, 1975). Because females would be expected to lay fewer eggs on poor quality beans, 170 beans carrying at least two eggs were selected (Thanthianga & Mitchell, 1990). Seventy of these beans had their egg load reduced to one egg and 100 to two eggs by removal of excess eggs. A greater number of beans was used for the two-egg treatment as the chance of both eggs hatching was lower than the chance of the single eggs hatching in the one-egg treatment. The beans were then placed in individual cells in a partitioned petri dish, and incubated at 30°C, 70% humidity. After 10 days the beans were examined and any with unhatched eggs were discarded. After a further 10 days the beans were monitored daily and any adults removed on their day of emergence. Females were anaesthetized with CO_2, weighed and paired with a male drawn randomly from a stock culture. The pair were then placed in a container with at least 150 black-eyed beans (*V.unguiculata*), ensuring an excess of oviposition sites (Messina, 1991). The females were allowed to oviposit until they died and the number of eggs laid by each female counted. A total of thirty pairs was set up from the one-egg treatment and thirty-two pairs from the two-egg treatment.

Results

Adult females raised in competition with another larva were lighter than those raised alone (weights of females

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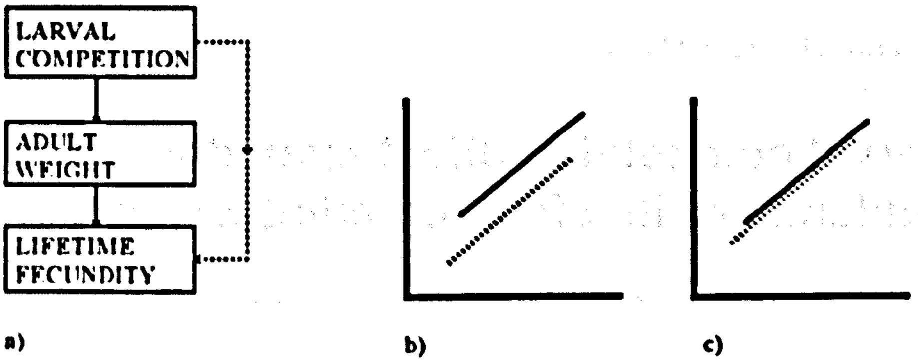

Fig. 1. The alternative effects of larval competition on female fecundity. (a) Larval competition could affect female fecundity via an effect on female emergence weight (solid arrows) and also directly, independent of its effect on female weight (dashed arrow). (b) If there is an independent effect of larval competition on fecundity, then the regression lines of fecundity on emergence weight for the no competition treatment (solid line) and the competition treatment (dashed line) would have different slope or elevation. (c) If there is no independent effect of larval competition on fecundity then the regression lines for the two treatments should have the same slope and elevation.

raised in competition = 6.59 ± 0.20 mg (standard error), $N = 32$; raised alone = 7.16 ± 0.17 mg, $N = 30$; Mann-Whitney $U = 320$, $P = 0.024$). Thus even at larval densities of two larvae per bean, competition reduces adult emergence weight.

The weights of adult females ranged from 3.70 to 8.68 mg across the two treatments. When the data from the two treatments were combined, fecundity was correlated with emergence weight (Fig. 2; $r = 0.47$, $N = 62$, $P < 0.001$).

Analysis of covariance was used to determine whether the slopes and the elevations of the regression of fecundity on weight differed between treatments. In an analysis using competition as a factor and weight as a covariate, the interaction between competition and weight did not explain a significant amount of the variance in fecundity ($F_{1,58} = 0.88$, $P = 0.35$) showing that there was no difference between the slopes of the regression lines. The interaction term was then omitted from the analysis, and competition did not explain a significant amount of the remaining variance ($F_{1,59} = 0.31$, $P = 0.58$) showing that there was no between treatment difference in the elevations of the regression lines. Thus competition appears to have no effect on fecundity independent of its effect on adult emergence weight.

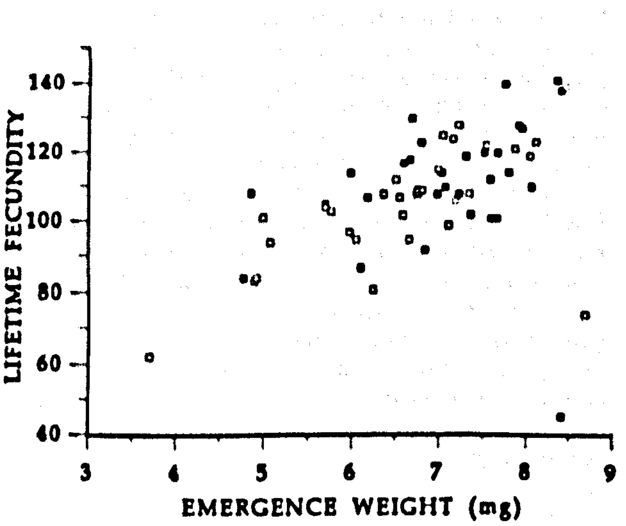

Fig. 2. The relationship between adult emergence weight and lifetime fecundity. Solid squares represent females raised without competition, open squares represent females raised in competition with a second larva.

Discussion

The results of this experiment show, that in *C.maculatus* at least, there is no effect of larval competition on adult fecundity independent of its effect on adult weight. This means that the work done by previous authors based on this assumption is safe (e.g. Credland *et al.*, 1986; Wilson, 1993).

The result is slightly surprising. It is easy to see that competition will reduce adult weight due to reduced resource intake, and that this will reduce adult fecundity. However, it is quite conceivable that competition could reduce fecundity in other ways which do not reduce adult weight. A limited supply of some micronutrient within the bean which is essential for egg production but not growth, could result in competing beetles emerging from the bean at full size but with a reduced capacity to produce eggs. Alternatively, a phenotypic response to the presence of another larva within the bean could cause the larva to develop faster to avoid competition, but at the expense of some reproductive potential.

The result is likely to also apply to other bruchid beetles of the genus *Callosobruchus*, such as *C.chinensis* and *C.phaseoli* which have a very similar ecology to *C.maculatus*, although whether the result will apply to *C.analis*, which shows a more active form of larval competition, is by no means certain. Even less obvious is whether this result will apply to species outside this genus (e.g. parasitoid wasps) whose larvae compete in similar ways but for completely different types of resource. Further experiments, similar to those reported here, are needed to judge the generality of the findings reported in this paper.

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Game theory models of competition in closed systems: asymmetries in fighting and competitive ability

N. Colegrave

Colegrave, N. 1994. Game theory models of competition in closed systems: asymmetries in fighting and competitive ability. – Oikos 71: 499–505.

A game theory model is presented which investigates the effect of asymmetries on the evolution of competition strategies in a closed system. The system of larval competition in *Callosobruchus* beetles is used as a basis and two asymmetries are considered; an asymmetry in fighting ability and an asymmetry in passive competitive ability. If the asymmetries are not detected by the larvae then the predictions of the model are the same as those of simpler models without asymmetry. If the asymmetries are detected then the model allows for the possibility of conditional strategies. In contrast to the situation in open systems, the results of this model suggest that detectable asymmetry in fighting or passive competitive ability may make the evolution of contest competition strategies more likely than is suggested by simple models without asymmetries.

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Competition by organisms for scarce resources is a major driving force of evolution, thus organisms are expected to compete efficiently over resources. Much competition takes place in 'open' systems, where individuals have the choice of either competing over the resource or of leaving the resource patch and going elsewhere. Competitions of this type have been extensively modelled (Maynard-Smith and Parker 1976). However, some competition occurs in a 'closed' system in which competitors have the choice of how to compete over the resource but not of leaving the resource patch and going elsewhere (e.g. parasitoid wasps; Godfray 1987, Leaf miners; Faeth 1990, sawflies; Craig et al. 1990). For instance, in many species, young organisms have limited mobility, and are thus unable to avoid competition with conspecifics by moving to another area to feed. Intraspecific competition for food is also likely to be intense between juveniles: young organisms have a high requirement for food as they are growing, and the amount of food they get when young may have a very large effect on their lifetime fitness. In beetles of the genus *Callosobruchus*, for example, adult females lay eggs on the surfaces of various leguminous beans (Southgate 1979). On hatching the larvae burrow into the bean where they feed until pupation. As several eggs may be laid on a single bean and larvae cannot move between beans, larval competition may be intense.

When faced with intense intraspecific competition in a closed system an organism has two possible strategies open to it, to accept the presence of conspecifics and compete passively (scramble competition sensu Nicholson 1954), or to actively try to exclude conspecifics (contest competition sensu Nicholson 1954) and even kill them. Both strategies can be found throughout the animal kingdom. For instance, although the nestlings of many birds exhibit scramble competition, the nestlings of some species, particularly of large raptors fight over food and may commit siblicide (Meyburg 1974, Mock 1984). Similarly, in parasitoid insects there is a dichotomy between gregarious parasitoids which show scramble competition, with several larvae sharing a host, and solitary parasitoids which show contest competition with larvae fighting

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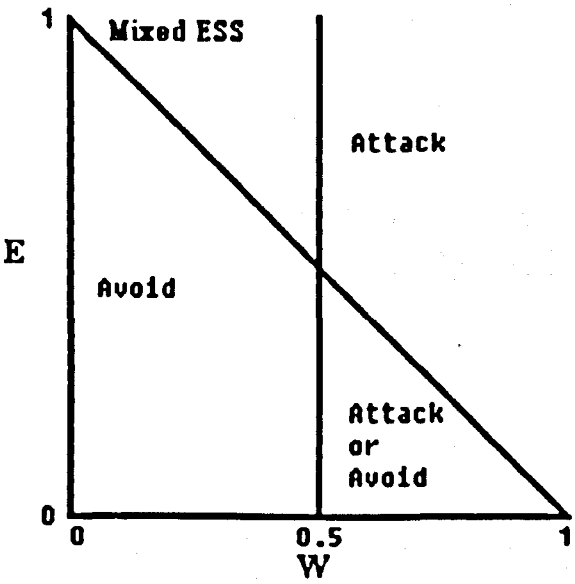

Fig. 1. The Smith and Lessells model: The x-axis represents W, the probability that an *Attack* larva beats an *Avoid* larva in a fight. The y-axis represents E, the relative cost to an *Avoid* larva of sharing a bean with another *Avoid* larva. The zones represent different ESSs. N.B. Although the original Smith and Lessells model only considered values of W of 0.5 or greater, for completeness this figure includes all possible values of W from 0 to 1. However, values of W less than 0.5 mean that *Attack* larvae are worse fighters than *Avoid* larvae; a situation which is unlikely to occur in nature.

within the host until all are dead except for one (Godfray 1987). In *Callosobruchus* beetles different species within the genus exhibit different competitive strategies (Smith and Lessells 1985): larvae of *C. maculatus* coexist within a bean and compete passively by exploiting the resource, with several adults emerging from the same bean. In contrast larvae of *C. analis* show an extreme form of interference competition, with larvae fighting within a bean until all are dead except one. What kinds of selective forces can determine whether a species evolves a contest or scramble strategy?

In an effort to investigate this problem previous authors have produced both phenotypic and genetic models. The question of siblicide in birds has probably received the most attention (O'Connor 1978, Dickens and Clark 1987, Godfray and Harper 1990); however, Godfray (1987) has also modelled the evolution of the solitary and gregarious strategies in parasitoid insects. Although the models differ in detail their conclusions are similar: contest competition is most likely to evolve when the benefits to the individual of excluding or killing a conspecific competitor outweighs the costs and risks associated with the interference. If the competitor is a relative (as is usually the case for chicks in a nest) the reduction in inclusive fitness due to loss of a relative must also be taken into account. For these conditions to be met requires that the fitness of the remaining individuals is large compared to what it would have been had it shared the resources with the dead individual, a situation which is most likely to occur when food is very scarce. However, genetic models suggest that once a contest strategy has evolved it is very difficult for scrambling individuals to invade, even if conditions change and scrambling individuals would actually be fitter (a hysteresis effect; Godfray 1987). Both the bird and the parasitoid models also point to the possibility of parent-offspring conflict (Macnair and Parker 1979) over whether young should adopt a contest or scramble strategy.

The evolution of larval competition strategies in *Callosobruchus* beetles has been modelled by Smith and Lessells (1985) who produced a game theory model, later extended to a genetic model by Smith (1990), which looked at the effect that differing costs of sharing a bean would have on the competition strategies adopted by larvae. The results of the model suggested that if the cost of sharing a bean is high then a contest strategy is evolutionarily stable, whilst if the cost of sharing a bean is low then a scramble strategy will evolve. However, this model assumed that competition was symmetric; that if two larvae shared a bean each would utilise half of the resource. In nature, competition is rarely totally symmetric (Begon 1984, see also Lawton and Hassell 1981 for interspecific competition), with one competitor often doing much better than another. Wilbur and Collins (1973) have described how competition can generate a skewed size distribution in amphibian larvae, due to some larvae competing more strongly than others and so getting more of the resource; the same phenomenon has been shown to occur in young pygmy sunfish (Rubenstein 1981). Both of these studies also suggest that the degree of asymmetry increases with the intensity of competition. Although previous authors have modelled effects of asymmetries on the evolution of competition, these models have generally been for open systems. This paper takes the Smith and Lessells model as a starting point and describes a game theory model addressing the question: What effect does asymmetric competition have on the evolution of competition strategies in a closed system?

The Smith and Lessells model

The Smith and Lessells model assumes that larvae can adopt one of two strategies. An "*Attack*" larva seeks out other larvae within the bean and fights until either all other larvae are dead or it dies itself; this strategy therefore represents an extreme contest strategy. An "*Avoid*" larva avoids other larvae within a bean and competes by using the resource; this represents a scramble strategy. The fitness payoffs of larvae adopting different strategies are defined relative to that of an *Avoid* larva which is the sole occupant of a bean (= 1). If an *Avoid* larva shares a bean with another *Avoid* larva both suffer a reduction in fitness due to limited resources. This reduction in fitness

Table 1. Payoff matrix for the asymmetric game. F is the probability of a superior larva beating an inferior larva in a fight, E_1 and E_2 are the relative costs due to passive competition of the superior and inferior larva respectively. q is the probability of an *Avoid* larva successfully evading an *Attack* larva. Payoffs represent the payoff to larva A in competition with larva B.

Larva A	Larva B			
	Attack	*Avoid*	*Tyrant*	*Martyr*
Attack	0.5	$\frac{1+q-qE_1-qE_2}{2}$	$\frac{1+q-qE_1-Fq}{2}$	$\frac{1+Fq-qE_2}{2}$
Avoid	$\frac{1+q-qE_1-qE_2}{2}$	$\frac{2-E_1-E_2}{2}$	$\frac{2-F+Fq-E_1-qE_2}{2}$	$\frac{1+F-Fq+q-qE_1-E_2}{2}$
Tyrant	$\frac{1+Fq-qE_2}{2}$	$\frac{1+F-Fq+q-qE_1-E_2}{2}$	$\frac{1+q-qE_1-qE_2}{2}$	$\frac{1+F-E_2}{2}$
Martyr	$\frac{1+q-Fq-qE_1}{2}$	$\frac{2-F+Fq-E_1-qE_2}{2}$	$\frac{2-F-E_1}{2}$	$\frac{1+q-qE_1-qE_2}{2}$

relative to the fitness of the larva alone in a bean is called E and can vary in value from 0 to 1. If two *Attack* larvae occur within a bean then they fight until one is dead. A larva survives with a probability of 0.5 and if it does so has sole access to the resource and a fitness of one (assuming there is no cost of having fought to the larva that wins the fight), so the expected payoff to an *Attack* larva in this situation is 0.5 (i.e. fitness of 1 multiplied by survival probability of 0.5). If an *Attack* and *Avoid* larva occur in the same bean they will fight and the *Attack* larva will kill the *Avoid* larva with a probability of W ($0.5 \leq W \leq 1$), otherwise the *Avoid* larva kills the *Attack* larva. The results of the game under different conditions are summarised in Fig. 1. If $W > 0.5$ then *Attack* is always a possible Evolutionary stable strategy (ESS; Maynard-Smith 1982). IF $(1-E) > W$ then *Avoid* is an ESS and if both conditions are true then attack and avoid are alternative ESSs. Smith and Lessells also extended the model to a multilarval game. However, the results of this are qualitatively the same as for the two larval game.

The asymmetric game

The model I describe is for a two-larval game, that is, each bean contains two larvae. I use the same basic strategies, *Attack* (attempt to find and kill other larvae within a bean) and *Avoid* (avoid other larvae within the bean and compete passively over the resource), as used in the Smith and Lessells model, but the use of asymmetries in the model also allows for the incorporation of conditional strategies based on detected asymmetries.

I assume two possible asymmetries. The first is an asymmetry of fighting ability, with one larva (the "Superior larva") being a better fighter and thus more likely to win an aggressive encounter (with the "Inferior larva"). The second is an asymmetry in passive competitivness, that is, if two *Avoid* larvae share a bean, one is likely to be a better passive competitor than the other and so suffer less from the competition than the other. There could be many reasons for these asymmetries. In the case of *Callosobruchus* beetles the most plausable cause is different arrival time of larvae within the bean. A larva which arrives first in a bean may have a growth head start and so be larger when the two larvae meet, thus which is the superior larva depends on which arrived first in the bean.

The two asymmetries (fighting ability and passive competitive ability) are independant. The labels superior and inferior refer only to the asymmetry in fighting ability. Thus the superior larva (fighting ability) may be a better or worse passive competitor than the inferior larva.

Finally I assume that both asymmetries are produced by chance effects (such as order of arrival in the bean) not by any inherent difference in the competitive ability of the strategies. In contrast to the Smith and Lessells model, where *Attack* larvae are always equal or better fighters to *Avoid* larvae, in this model *Attack* larvae are not inherently better fighters than *Avoid* larvae. This means that all larvae, independent of the strategy that they use, have a 50% chance of being a superior larva. If the asymmetries are caused by order of arrival in the bean, then the strategy that a larva will use does not affect its probability of being the first larva in the bean. Whilst this may not represent the most biologically realistic situation, it does allow for the effect of asymmetries caused by chance effects to be looked at without the confounding effect of determined asymmetries between strategies.

I consider 4 strategies, two of which are simple strategies, two of which are conditional strategies. The two simple strategies are *Attack* and *Avoid*. The conditional strategies are "*Attack* if you are the superior larva and *Avoid* if inferior", which I call *Tyrant*, and "Avoid if you are the superior larva and Attack if inferior", which I call *Martyr*. The strategies are assumed to be determined genetically, however the conditional strategies allow for flexible behaviour dependent on the conditions in which the individual finds itself, thus two larvae could have the same genetic strategy (e.g. they may both be *Martyr*), but show different behaviour (attack or avoid), dependent on conditions (e.g. depending on whether they are the first or second larva to arrive in the bean).

Payoffs are defined relative to the payoff to a larva developing alone within a bean (= 1). If two larvae meet and fight for possession of the bean I assign a probability (F) that the superior larva wins. This will occur whenever both larvae show *Attack* behaviour, and also whenever one larva adopts *Attack* behaviour, the other *Avoid* behaviour and the *Avoid* larva does not successfully avoid the *Attack* larva. The variable F can take values from 0.5 to 1 depending on the advantage of the superior larva in a fight. If two larvae coexist within a bean then each will pay a cost incurred by sharing the resource. I have used E_1 to represent the cost to the superior larva and E_2 to represent the cost to the inferior larva. These values are calculated as reductions to a maximum fitness of 1, and can thus take values of 0–1. Finally, I have used q to represent the probability that an *Avoid* larva successfully avoids an *Attack* larva within a bean. The payoff matrix for this game is shown in Table 1, payoffs being calculated assuming that a larva has a probability of 0.5 of being the superior larva. For example if an *Avoid* larva finds itself in a bean with another *Avoid* larva, then with probability of 0.5 it will be the superior larva and so suffer the E_1 cost of passive competition (and so gain a pay off of $(1-E_1)/2$), otherwise it will be the inferior larva (and so gain a payoff of $(1-E_2)/2$). So the mean payoff to the larva will be $(2-E_1-E_2)/2$.

Results

Fig. 2 shows diagrammatically the results of the game under various conditions. The axes of each graph represent the relative cost of passive competition to either the superior (y-axis) or the inferior (x-axis) larvae. Zones can then be delimited onto these figures indicating the ESSs under different conditions. Fig. 2a represents a situation where the asymmetries are undetected, whilst 2b and 2c represent situations where asymmetry is detected by the larvae.

Asymmetries not detected

If larvae are unable to detect asymmetries (i.e they cannot tell whether they are the superior or inferior larva) then the predicted ESSs are the same as those produced by the Smith and Lessells model, depending only on the average costs to the two larvae of sharing the bean. In the Smith and Lessells model, if two larvae sharing a bean have individual fitnesses of greater than 0.5 of the fitness of a larva alone in a bean ($E < 0.5$), and *Attack* larvae are not better fighters than *Avoid* larvae ($W = 0.5$) then *Avoid* is the stable strategy. In the undetected asymmetry model presented here *Avoid* is the stable strategy if the mean fitness of two larvae sharing a bean is greater than 0.5 of the fitness of a larva alone within a bean. It does not matter whether the passive competition is symmetric, with larvae having equal E values, or whether competition is highly asymmetric, for instance, with one larva with an E value of 0.1, the other with an E value of 0.9. The degree of asymmetry in fighting ability also has no effect on which strategy is stable when the asymmetry is undetected. Thus in this situation, asymmetry in competitive ability does not affect the evolutionary outcome if the larvae are unable to detect the asymmetry.

Asymmetry in passive competitive ability

If the asymmetry is detectable by the larvae then conditional strategies become a possibility and the ESSs are no longer the same as those predicted by the Smith and Lessells model. If there is no asymmetry in fighting ability ($F = 0.5$) then the ESS depends simply on the relative fitnesses (E_1 and E_2) of the two larvae when sharing a bean. For consistency I still use the labels superior and inferior to describe the larvae even though in this situation there is no difference in fighting ability, the superior larva is then defined as the larva which suffers the E_1 cost of passive competition in the model. If both suffer little from competition (E_1 and $E_2 < 0.5$) then *Avoid* is stable. If both suffer badly from competition (E_1 and $E_2 > 0.5$) then *Attack* is the ESS. However if there is a high degree of asymmetry in passive competitive ability ($E_1 < 0.5$ and $E_2 > 0.5$ or $E_1 > 0.5$ and $E_2 < 0.5$) then the conditional strategies become stable. Which of the strategies, *Tyrant* or *Martyr*, is stable depends on the direction of the asymmetry; if the superior larva is the better passive competitor ($E_1 < E_2$) then *Martyr* is stable, while if the inferior larva is the better passive competitor then *Tyrant* is stable. However, because in this situation there is no asymmetry in fighting ability the labels of superior and inferior are just arbitrary lables (they do not imply anything about passive competitive ability), the two conditional strategies are better viewed as a single strategy of "Attack if you suffer the higher cost of passive competition, avoid if you suffer the lower cost of passive competition". This makes sense because a larva that is going to suffer a great reduction in fitness due to passive competition does better by fighting for access to the whole bean and risking dying in the process.

Asymmetry in fighting ability

At the other extreme, if there is no asymmetry in passive competitive ability of superior and inferior larvae ($E_1 = E_2$) but there is asymmetry in fighting ability, then *Martyr* is no longer a possible ESS. If the cost to the larvae of sharing a bean is low (E_1 and E_2 are low) then *Avoid* is stable, if it is high (E_1 and E_2 are high) then *Attack* is the ESS. At intermediate values of E_1 and E_2 *Tyrant* is the stable strategy. The exact range of conditions over which *Tyrant* is the ESS depends on the asymmetry in fighting ability. For example if a superior larva beats an inferior larva in a fight with a probability of 0.6 ($F = 0.6$) then *Tyrant* will be stable when the individual fitnesses of two larvae competing passively within a bean are between 0.4 and 0.6 of the fitness of a larva alone in a bean ($0.4 < E_1$,

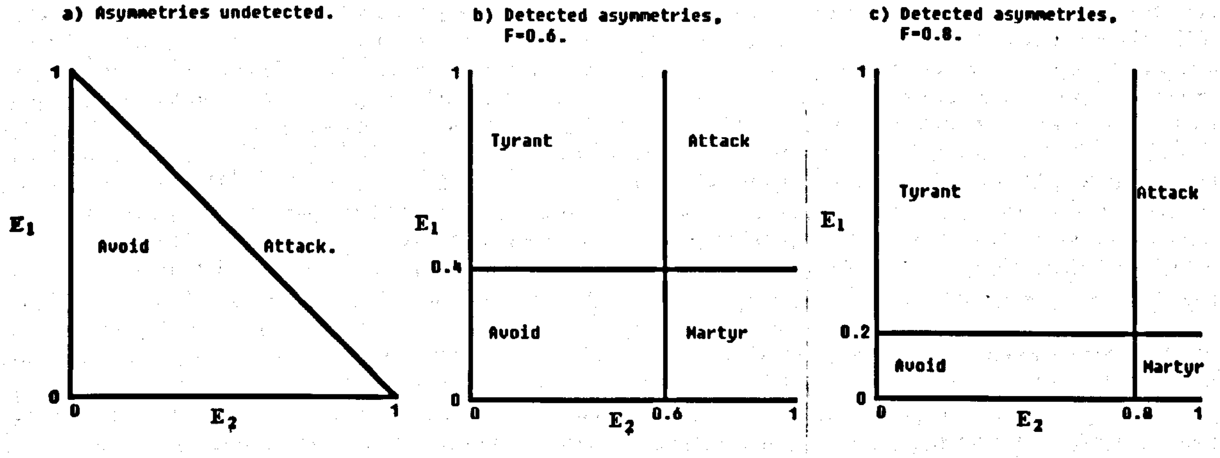

Fig. 2. The asymmetric game: The x-axis represents E_1, the relative cost due to passive competition to the superior larva, whilst the y-axis represents E_2, the cost to the inferior larva. a) represents the situation where asymmetries are undetected by the larvae whilst b) and c) represent two situations where the larvae are able to detect the asymmetries. F is the probability that a superior larva beats an inferior larva in a fight. The zones represent different ESSs.

$E_2 < 0.6$). If the degree of asymmetry in fighting ability is higher so that a superior larva beats an inferior larvae with a probability of 0.8 then the conditional strategy is stable for values of E_1 and E_2 of between 0.2 and 0.8. So increasing the degree of asymmetry in fighting ability increases the range of conditions over which *Tyrant* is the ESS.

Asymmetries in both fighting and passive competitive ability

If there are asymmetries in both fighting and competitive ability then which strategy is the ESS depends on the exact values of the asymmetries. In general as asymmetries in passive competitive ability increase, the conditional strategies become more likely as the ESS, and as the asymmetry in fighting ability increases, the range of conditions over which *Tyrant* is stable increases at the expense of the other three strategies. The formal ESS conditions for each of the strategies are shown in Table 2.

The probability of an *Avoid* strategist avoiding an *Attack* strategist (q) has no effect on which strategy is the ESS as long as this probability is not 0 or 1. However, computer simulation suggests that the value of q does affect the speed at which a mutant strategy can invade a population (unpubl.).

Table 2. ESS Conditions for the asymmetric game. F is the probability of a superior larva beating an inferior larva in a fight, E_1 and E_2 are the relative costs due to passive competition of the superior and inferior larva, respectively.

Asymmetries undetected	
Strategy	ESS conditions
Attack	$E_1 < 1-E_2$
Avoid	$E_1 > 1-E_2$
Asymmetries detected	
Strategy	ESS conditions
Attack	$E_1 > 1-F$ & $E_2 > F$
Avoid	$E_1 < 1-F$ & $E_2 < F$
Martyr	$E_1 < 1-F$ & $E_2 > F$
Tyrant	$E_1 > 1-F$ & $E_2 < F$

Discussion

If asymmetries are present in fighting ability or competitive ability, but cannot be detected by the larvae then they have no effect on the evolutionary outcome of this game. However, if the asymmetries are detectable by the larvae then conditional strategies become possible and the stable strategy depends on the level of the asymmetry. However it is unlikely that there would be an asymmetry in passive competitive ability without there being some asymmetry in fighting ability and if both factors are included then the situation becomes more complex. Furthermore, it is likely that there would be a relationship between the degree of asymmetry in competitive ability and fighting ability. If this is the case then the possible strategies depend on the relationship between these two asymmetries. If the asymmetry in fighting ability is greater than the asymmetry in competitive ability then *Tyrant* becomes more likely as the ESS. If the asymmetry in competitive ability is greater than the asymmetry in fighting ability then the *Martyr* becomes more likely as the stable strategy.

If the chance of an *Avoid* larva evading an *Attack* larva is small (q is small) then both of the conditional strategies will produce what look like *Attack* outcomes, and so detectable asymmetries may increase the observed frequency of *Attack*-like strategies in nature. This differs from the predictions of previous models of asymmetric competition (Maynard-Smith and Parker 1976). In general, these models predict that detectable asymmetries will reduce the severity of contests. This discrepancy arises as these models represent open systems where one contestant can leave the resource rather than fight: if one contestant leaves the fight cannot escalate. My model assumes that as long as one larva attempts to fight then the two larvae will meet with a non-zero probability and an escalated contest occurs; in effect neither larva can leave the resource patch. The results agree with the prediction of Maynard-Smith and Parker (1976) that escalated contests are expected when the pay-off for winning is large compared to the loss due to injury; the model predicts fighting when the benefit to one of the larvae of winning a fight is greater than the risk of dying in a fight. This also agrees with the predictions of Enquist and Leimar (1990) that fatal fights are expected when the value of the future to an individual if it does not fight is small compared to the value of the resource over which it is fighting; a larva which will suffer a great reduction in fitness due to sharing a resource (a low future without fighting) will be expected to fight over the resource.

The model assumes that larvae have only two options, to attempt to kill the other competitor or to accept a share of the resource determined by their passive competitive ability. However, it can easily be extended to include the possibility of dominance, with the superior larva forcing the inferior larva to accept a reduced share of the resource. If E_1 is viewed as the cost to the superior larva of being dominant, and E_2 as the cost to the inferior larva of being denied access to the resource, then Fig. 2 can be used to predict the ESS under different conditions. In this situation the *avoid* strategy can be viewed as the *dominant/subdominant* strategy, and any conditions under which avoid is stable can be viewed as conditions under which a system of dominance would be stable, indeed from outside the bean these two strategies would be impossible to distinguish. In general, the ESS depends on the way the resource is partitioned between the two larvae; it does not matter if this is determined by passive competitive ability or some system of dominance.

Whilst the conclusions of this model do not disagree with those of the Smith and Lessells model (*Attack* strategies are still more likely when the costs of sharing a seed are high) it does allow for the existence of conditional strategies. There is some evidence that the South Indian strain of *C. maculatus* shows a conditional strategy very similar to the *Tyrant* strategy described here (Thanthianga and Mitchell 1987), with one larva developing normally while the other holds back its development. Thanthianga and Mitchell (1987) suggest that the larvae may be using the vibrations, caused by larval feeding, to asses the presence and size of another larva in the bean. If the two larvae meet then a contest occurs and the smaller larva dies, although active killing by the larger larva has not been demonstrated. Experiments are required to determine whether the *Attack* strategies of other species such as *C. analis* are true *Attack* strategies or in fact conditional strategies.

The model presented here was framed with *Callosobruchus* beetles in mind where the asymmetry is likely to be caused by arrival time at the bean. A larva which arrives first will have a growth head start and so be bigger than the second larva, probably making it a superior fighter. This growth head start also makes it a stronger passive competitor (Bellows 1982). However, the model will equally apply to larval competition in other species, and even to other types of competition where the competitors are unable to move to another area. In other species the asymmetry in fighting ability could be caused by any number of factors and an individual with a higher fighting ability may not always have a higher passive competitive ability. In fact a trade-off between investment in fighting equipment and feeding equipment could mean that the superior fighter is an inferior passive competitor.

However, although the results of the model will apply to many other competitive situations, the model does not take into account inclusive fitness because in *Callosobruchus* beetles the larvae within a bean are rarely related. The model would need to be extended to apply to situations where competitors are related (e.g. siblicide in birds).

Whilst previous models of asymmetric competition suggested that detected asymmetries should reduce the amount of fighting over resources, the results of the model presented here suggest that in closed systems detected asymmetries may actually increase the likelihood of fighting as a competition strategy. This adds asymmetry in competition to a list of factors (including those of population genetics such as hysteresis) that make *Attack*-type behaviour a more likely observed outcome than the simplest models of larval competition suggest.

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The cost of exploitation competition in *Callosobruchus* beetles

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Summary

1. The relative cost of intraspecific exploitation competition is determined for the larvae of two species of bruchid beetle, with different larval competition strategies, by allowing two larvae to share host beans one after the other.
2. On the larger host (*Vigna unguiculata*, black-eyed bean, also known as cowpea) there is no difference between the cost of exploitation competition for *Callosobruchus analis* and *C. maculatus*.
3. On the smaller host (*V. radiata*, mung bean) *C. analis* seems to suffer a higher cost of exploitation competition than *C. maculatus*.
4. The experimental results are interpreted using a game theory model of larval competition.
5. The results suggest that a differing cost of exploitation competition is not the selective force maintaining the different larval competition strategies of laboratory populations of the two species now, although it may have been responsible for the origin of the different strategies in the past.

Key-words: Bruchid, *Callosobruchus analis*, *Callosobruchus maculatus*, larval competition, scramble competition

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Introduction

The way in which an organism competes over a scarce resource has a major effect on its lifetime fitness. Thus organisms are expected to evolve to compete over resources efficiently. Intraspecific competition is often intense between young organisms because their limited mobility means that they are unable to move to another area to find food and are dependent on resources provided by their parents (either directly by parental feeding or indirectly via the female producing the young in a suitable patch of resource). For example beetles of the genus *Callosobruchus* lay their eggs on the surfaces of various legumes (Southgate 1979). The larvae burrow into the bean where they feed until pupation. As several larvae may be found within a bean and an individual larva completes its development within a single bean, larval competition can be intense. However different species show different larval competition strategies (Smith & Lessells 1985). Several *Callosobruchus maculatus* Fab. larvae will coexist within a single black-eyed bean (*Vigna unguiculata* (L.) Walp, also known as cowpea) and compete passively in a scramble-type process (*sensu* Nicholson 1954). As a result several adults can emerge from a single bean. However in the same host *C. analis* Fab. larvae compete actively by apparently seeking each other out within the bean and fighting until all are dead except one (Umeya, Kato & Kocha 1975). As a rule, only one *C. analis* adult will emerge from a single black-eyed bean no matter how many larvae entered in the first place. What types of selective forces cause two species, similar in so many ways, to compete in such different ways over identical resources?

In an attempt to answer this question, Smith & Lessells (1985) produced a game theory model of larval competition using two disparate larval strategies. The first was called the Avoid strategy and was analogous to the strategy used by *C. maculatus*, with larvae competing passively by depleting the resource. The second strategy, the Attack strategy, was analogous to that used by *C. analis* larvae, with larvae fighting within a bean until all are dead except one. The model assumed that larvae would show a reduction in fitness due to sharing beans that was represented by the variable E. This cost of exploitation competition was defined as the reduction in fitness of a larva which shares a bean compared to its fitness if it had developed without exploitation competition. The fitness of a larva developing without exploitation competition was defined as 1. The model also allowed for the possibility that an Attack larva may, by

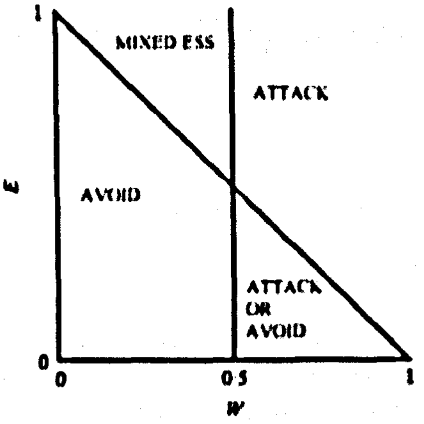

Fig. 1. The Smith & Lessells model, *E* is the cost of competition, *W* is the attack larval superiority. Zones represent the ESS under different conditions.

specializing in aggressive behaviour, be a superior fighter to an Avoid larva. Fighting superiority of Attack was represented by the variable *W*, defined as the probability of an Attack larva beating an Avoid larva in a fight. It was further assumed that one adult would always emerge successfully from a bean such that an Avoid larva would beat an Attack larva with a probability of $1-W$. The model did not take into account inclusive fitness caused by relatedness of larvae within beans because *Callosobruchus* beetles tend to distribute their eggs over the available beans (Messina & Mitchell 1989), so that larvae within beans are rarely related. The model predicted three general outcomes under different conditions (Fig. 1). If there is Attack larval superiority ($W>0{\cdot}5$) then Attack is always an evolutionary stable strategy (ESS; Maynard-Smith 1982). If the cost of exploitation competition is low $[E<(1-W)]$ then Avoid is an ESS. If both conditions are met then the two strategies are alternative ESSs (Maynard-Smith 1982); populations of entirely Attack or Avoid individuals are stable against invasion by mutants using the other strategy and a mixed population can move to either of the ESSs, depending on the initial frequencies of the strategies. In these circumstances individuals need not have the same fitness at the alternative ESSs; indeed the model predicts that individuals in Avoid populations will often be fitter than those in Attack populations. However, once the population has moved to one of the alternative ESS it effectively becomes trapped there because mutants are unable to invade when rare, even if individuals would be fitter at the other ESS.

The Smith & Lessells model is a simple game theory model and suffers from the limitations associated with this type of model, including reduction in the strategy set, in this case to two simple strategies. However models which allow for more complex conditional strategies (Colegrave 1994) give the same qualitative predictions, that Attack type behaviour is more likely to evolve when the cost of exploitation competition is high. Although Smith & Lessells (1985) developed their model for internally feeding seed predators, the model is clearly relevant to many species whose larvae are confined to discrete patches of resource. In particular, insect parasitoids show a parallel dichotomy of life histories, known as 'solitary' and 'gregarious' (Godfray 1987).

A higher cost of exploitation competition in *C. analis* than in *C. maculatus* could thus explain their different larval competition strategies. Previously, authors have successfully measured the cost of exploitation competition in *C. maculatus* (Credland, Dick & Wright 1986; Giga & Smith 1991; Messina 1991) by measuring the relative fitness of larvae raised with and without exploitation competition. However this cannot be done for *C. analis* as the larvae kill each other leaving a single larva to develop without exploitation competition. Nevertheless, it is possible to get two *C. analis* larvae to share a bean sequentially, by allowing one to develop alone within a bean and then, once it has emerged, allowing a second larva to develop in the same bean. The reduction in fitness of the second larva compared to the first can be used as a measure of the cost if the two larvae had shared the bean simultaneously. If the same is done with *C. maculatus* larvae, then the reduction of fitness of second larvae through a bean can be compared for the two species. If the cost of exploitation competition in *C. analis* is higher than in *C. maculatus* then the reduction in fitness of the second *C. analis* larva will be expected to be higher than for the second *C. maculatus* larva. Finally the sequential development method can be calibrated for Avoid competition by comparing the relative fitness of the second *C. maculatus* larva with the fitness of *C. maculatus* larvae raised in simultaneous competition (i.e. sharing the bean with one other larva).

This paper describes a series of experiments designed to answer the question: can differences in the cost of exploitation competition in *C. analis* and *C. maculatus* explain their different larval competition strategies? Sequential competition experiments were carried out on both species of beetle to provide comparable measures of the cost of exploitation competition, and simultaneous competition experiments were carried out on *C. maculatus* to calibrate the sequential experiments. All experiments were carried out on black-eyed beans (mass ± SE, 234 ± 1·19 mg) and also on smaller mung beans (62·5 ± 0·63 mg), to provide two sizes of hosts with differing expected levels of exploitation competition.

Materials and methods

SEQUENTIAL DEVELOPMENT

One hundred adult *C. analis* (within 12-h of emergence) were allowed to oviposit on 200 host beans for

24 h. The beetles were then removed and the beans examined. Any beans that did not carry eggs were returned to the beetles for a further 6 h of oviposition. This was repeated until all beans carried at least one egg. All eggs were laid within a period of 36 h. The beans then had their egg load modified to one by removal of excess eggs with a scalpel and were placed in individual cells of a partitioned Petri dish in conditions suitable for larval development (30 °C, 70% rh). This procedure removes any systematic difference in bean quality caused by females laying fewer eggs on poorer-quality hosts. After 7 days the beans were re-examined and any carrying unhatched eggs were removed from the experiment. After a further 21 days the beans were monitored daily and any emergent adults removed. The length of the left elytron of each adult was measured. Once adults had ceased emerging, all beans from which beetles had emerged were collected for the next stage of the experiment. Any beans from which no beetle had emerged were kept for a further 7 days to ensure no further emergence and then discarded. One hundred *C. analis* adults (less than 12 h old) were then allowed to oviposit on the remaining beans for 24 h, after which the beetles were removed and the beans examined. Any beans not carrying eggs were returned to the beetles for a further 6 h of oviposition and this was repeated until all beans carried at least one egg. As *C. analis* adults showed reduced oviposition on used mung beans, not all beans carried eggs within 36 h. Beans that did carry eggs after 36 h were therefore used as a subgroup. The remaining beans were given to a new set of adults (less than 12 h old) for a further period of oviposition until they also all carried at least one egg. Thus two subgroups were set up, the beans within each subgroup carrying eggs laid within 36 h of each other. All beans in both subgroups were then modified to have an egg load of one and the larvae were allowed to develop exactly as in the previous parts of the experiment. Once again all emergent adults were measured.

The *C. maculatus* sequential experiment was carried out using exactly the same method, but owing to the shorter development time of *C. maculatus* larvae the beans were monitored for emergence daily 21 days (rather than 28) after the eggs were laid. As *C. maculatus* adults showed less aversion to laying on used beans, all second eggs were laid within 36 h and it was not necessary to set up subgroups.

SIMULTANEOUS DEVELOPMENT

One hundred adult *C. maculatus* (less than 12 h old) were allowed to oviposit on 200 host beans for 24 h. The beetles were removed and the beans examined. Any beans that did not carry eggs were returned to the beetles for a further 6 h of oviposition. This was repeated until all beans carried at least two eggs. All eggs were laid within 36 h. Each bean then had its egg load reduced to two by removal of excess eggs with a scalpel. The beans were then placed in individual cells of a partitioned Petri dish and placed in conditions suitable for larval development. After 7 days the beans were re-examined and any carrying unhatched eggs were discarded. After a further 14 days the beans were monitored daily and any emergent adults removed on the day of their emergence. All adults were measured.

ANALYSIS

Both the survival of larvae and the size of emergent adults were used as measures of fitness in the statistical analysis. Size was used as a measure of fitness as lifetime fecundity is strongly correlated with size in both species (Credland *et al.* 1986; Colegrave 1993 for *C. maculatus* and N. Colegrave unpublished data for *C. analis*). As males and females of *C. analis* are impossible to distinguish reliably without dissection, and do not differ in size when raised with or without competition ($F_{1,40}=0{\cdot}79$, $P=0{\cdot}38$), size data for the two sexes were pooled for *C. analis* in the statistical analysis. However as *C. maculatus* shows sexual dimorphism with males smaller than females, and the effect of size on a male's fitness is unknown, only the data on *C. maculatus* female size were used.

Results

LARGE HOST — BLACK-EYED BEANS

In both *C. analis* and *C. maculatus* the second larvae to pass through the beans showed a reduction in the size of emergent adults compared to first larvae (Table 1a; larval sequence, $F_{1,372}=23{\cdot}0$, $P<0{\cdot}0001$) suggesting that they suffered a reduction in fitness owing to reduced resources. However second *C. analis* larvae did not show a greater reduction in size than second *C. maculatus* larvae (species by larval sequence interaction, $F_{1,372}=0{\cdot}18$, $P=0{\cdot}68$). There was no difference between the species in survival to emergence when comparing first larvae to second larvae, as shown by the non-significant three-way interaction in a three-way log-linear model (Table 2a, $G=1{\cdot}17$, df $=1$, $P=0{\cdot}28$; Sokal & Rohlf 1981). Thus it appears that in black-eyed beans the cost of exploitation competition is similar in *C. analis* and *C. maculatus*. Furthermore second *C. maculatus* larvae did not differ in either survival to emergence ($\chi^2=2{\cdot}83$, df $=1$, $P>0{\cdot}05$), or emergent female size ($t=0{\cdot}96$, df $=161$, $P=0{\cdot}34$) when compared to *C. maculatus* larvae raised in simultaneous competition with another larva (Tables 1b and 2b), suggesting that the estimate of the cost of exploitation competition obtained by the sequential development method is a good estimate of the true cost of simultaneous larval competition in *C. maculatus* on black-eyed beans.

Table 1. Mean elytron length of adults from (a) the sequential experiment where larvae share a host one after the other and (b) the simultaneous experiment where larvae share a bean at the same time

(a)	First adults mean ± SE elytron length (mm)	Second adults mean ± SE elytron length (mm)
Black-eyed beans		
C. analis	2·07 ± 0·01	2·02 ± 0·01
C. maculatus	2·44 ± 0·01	2·38 ± 0·02
Mung beans		
C. analis	2·04 ± 0·01	1·87 ± 0·02
C. maculatus	2·39 ± 0·02	1·91 ± 0·03

(b)	Mean ± SE elytron length (mm) adults raised in simultaneous competition
C. maculatus	
Black-eyed beans	2·39 ± 0·01
Mung beans	2·29 ± 0·02

SMALL HOST — MUNG BEANS

Adult *C. analis* from the two subgroups did not differ in either survival to emergence ($\chi^2 = 1{\cdot}07$, df = 1, $P > 0{\cdot}05$) or adult size ($t = 0{\cdot}16$, df = 41, $P = 0{\cdot}87$), so the two subgroups were pooled for the following analysis. Once again second larvae from beans produced smaller adults than first larvae (Table 1a; larval sequence, $F_{1,282} = 319{\cdot}4$, $P < 0{\cdot}0001$), suggesting that they suffered from reduced resources. However in this case the reduction in size of second larvae in *C. maculatus* was significantly greater than the reduction in size of second larvae in *C. analis* (species by larval sequence interaction, $F_{1,282} = 80{\cdot}4$, $P < 0{\cdot}0001$) suggesting that the cost of exploitation competition, in terms of its effect on adult size, may be greater in *C. maculatus*. *Callosobruchus analis* showed a greater reduction in survival to emergence of second larvae than *C. maculatus* (Table 2a; $G = 9{\cdot}29$, df = 1, $P = 0{\cdot}002$) suggesting that in terms of survival *C. maculatus* suffered a lower cost of exploitation competition in mung beans. Second *C. maculatus* larvae survived as well as those raised in simultaneous competition (Table 2b; $\chi^2 = 3{\cdot}06$, df = 1, $P > 0{\cdot}05$). However the adults that emerged from the second larvae were smaller than those from larvae raised in simultaneous competition (Table 1b; $t = 11{\cdot}68$; df = 123, $P < 0{\cdot}0001$); they seemed to suffer a greater reduction in fitness when in sequential competition.

Discussion

The results of the sequential development experiments suggest that when using black-eyed beans as a host the cost of exploitation competition for the two species is very similar. The fact that both the sequential and simultaneous experiments give comparable estimates of the relative cost of exploitation competition in *C. maculatus* on black-eyed beans suggests that the values obtained in the sequential experiment for *C. analis* are probably a reliable indicator of the values that would be obtained if larvae did share beans simultaneously without competing aggressively. However if mung beans are used as the host the situation becomes more complex. In terms of survival to emergence *C. maculatus* seems to suffer less owing to exploitation competition than *C. analis*, but in terms of the size of surviving adults the situation is reversed, with *C. maculatus* showing a greater reduction in size of adults than *C. analis*. Also while the estimates of the cost of exploitation competition in terms of survival to adulthood agree for the *C. maculatus* sequential and simultaneous development experiments, the greater reduction in size of second adults from the sequential experiment suggest that on mung beans the sequential method may give an overestimate of the cost of exploitation competition.

My results also provide estimates of the value of the cost of exploitation competition parameter used by Smith & Lessells (1985). The cost of exploitation competition parameter (E) represented the reduction in fitness of a larva owing to exploitation competition compared to a fitness of 1 if the larva had been alone in the bean. As lifetime fecundity is directly proportional to female size in both species (N. Colegrave, unpublished data) the measures of fitness used in this experiment can be combined by multiplying the mean size of emergent adults by their percentage survival. If the fitness value of larvae raised in competition (either sequentially or simultaneously) is then divided by the fitness value of larvae raised without exploitation competition, then a value of the relative fitness of the competing larvae is obtained. This value can then

Table 2. Percentage survival of larvae from (a) the sequential experiment where larvae share a host one after another and (b) the simultaneous experiment, where larvae share a bean at the same time

	% survival (± SE)	
(a)	First larvae	Second larvae
Black-eyed beans		
C. analis	86·5 (3·2)	82·4 (3·2)
C. maculatus	91·7 (2·2)	93·7 (2·2)
Mung beans		
C. analis	74·7 (3·2)	41·7 (4·5)
C. maculatus	72·1 (3·4)	65·3 (4·3)

(b)	% survival (± SE) of two larvae sharing a bean simultaneously
C. maculatus	
Black-eyed beans	88·1 (2·1)
Mung beans	56·2 (2·8)

Table 3. Estimates of the cost of competition and parameter (E) from both the sequential and simultaneous experiments

	Development on	
	Black-eyed beans	Mung beans
C. maculatus		
Simultaneous	0·06	0·24
Sequential	0·01	0·28
C. analis		
Sequential	0·08	0·49

be subtracted from 1 to give an estimate of the cost of exploitation competition parameter (E).

Estimates of this parameter (E) obtained from the sequential experiments are shown in Table 3, along with the estimates obtained for *C. maculatus* competing simultaneously. The model predicts that if there is no Attack larval superiority ($W=0{\cdot}5$) and $E>0{\cdot}5$ then Attack will be the only stable strategy; if $E<0{\cdot}5$ Avoid becomes a possible ESS. The values for both species competing on black-eyed beans are not only very similar (*C. maculatus* $E=0{\cdot}01$, *C. analis* $E=0{\cdot}08$), but are also well within the range where Avoid is expected as a possible evolutionary outcome. When using mung bean as a host the cost of exploitation competition in *C. analis* ($E=0{\cdot}49$) does appear to be higher than in *C. maculatus* ($E=0{\cdot}28$), and is also very close to the 0·5 value above which Attack is the only stable evolutionary outcome. In a situation where Attack larvae are actually better fighters than Avoid larvae ($W>0{\cdot}5$) the Smith & Lessells model requires that the cost of exploitation competition is reduced further if Avoid is to be an ESS [as $E<(1-W)$]. In this case a small Attack larval superiority could put *C. analis* within the conditions in which Attack is the only ESS on mung beans. It would require a very large increase in Attack larval superiority to stop Avoid being an ESS for *C. analis* on black-eyed beans and *C. maculatus* on both hosts.

Thus it appears that on black-eyed beans differing costs of exploitation competition cannot be invoked to explain the disparate larval competition strategies of the two species. It seems that *C. analis* larvae would actually show an increase in individual fitness if they showed the Avoid behaviour used by *C. maculatus*. However on the smaller host, mung beans, the two species may indeed use the appropriate behaviour that maximizes individual fitness given their differing cost of exploitation competition on this host. It may be that *C. analis* originally evolved in a host similar to mung bean and has only recently moved to using black-eyed beans as an alternative host. If Attack larvae are superior fighters to Avoid larvae then once *C. analis* had evolved the Attack strategy it would be very difficult for mutant Avoid larvae to invade the population even if the cost of exploitation competition reduced, because they would almost always be sharing beans with Attack larvae that would often kill them. The population would be stuck at the Attack ESS. This is similar to the situation that is thought to occur in parasitoid insects, where the larvae of some species fight over a host even though there is enough resource in a single host to support the development of several larvae (Godfray 1987).

The notion that the costs of exploitation competition are higher in smaller beans, promoting the evolution of Attack-type strategies on these hosts, is in agreement with the observation that the wild bruchid species in Japan (Kiritani 1957 cited in Toquenaga & Fujii 1991), which feed on small wild beans rather than on larger stored products, usually show an Attack larval competition strategy. Thanthianga & Mitchell (1987) have also shown that a strain of *C. maculatus*, which was isolated from mung beans in south India, shows an Attack type of larval competition, even when allowed to develop in larger beans in the laboratory.

It might be expected that larvae of an Avoid species, which may have to share a bean with one or several other larvae, will encounter much more variation in resource availability than larvae of an Attack species, which essentially obtain all or none of the resource. Thus Avoid species might evolve a greater degree of plasticity in adult emergence size compared to Attack species, with each individual modifying its emergence size to suit the resources available. The variance of the first and second larvae through the beans can be pooled to give an idea of the degree of variation in adult size when larvae shift different hosts. On the black-eyed beans there was no difference between the variances of *C. analis* and *C. maculatus* (variance *C. analis* = 0·101, variance *C. maculatus* = 0·109; $F_{124,248}=1{\cdot}08$ $P>0{\cdot}05$). However on mung bean, the smaller host, *C. maculatus* showed a greater variance than *C. analis* (variance *C. analis* = 0·081, variance *C. maculatus* = 0·181; $F_{105,177}=2{\cdot}235$, $P<0{\cdot}01$) suggesting that *C. maculatus* larvae may be able to tailor their size at emergence to suit the level of resource to a greater degree than *C. analis* larvae. The fact that second *C. maculatus* larvae show a greater reduction in size than second *C. analis* larvae while second *C. analis* show a much higher reduction in survival when developing on mung beans is also consistent with this idea. It may be that when resources are limited *C. maculatus* larvae can respond plastically and produce smaller adults while *C. analis* larvae are unable to respond and so, if resources are significantly reduced, die.

The fact that selection pressures may change between the evolutionary origin of a character and the present day creates problems with making inferences about the evolutionary origins of a behavioural strategy from contemporary experiments. There may have been alterations in the physiology of the species since the larval competition strategy evolved. For example, a species that evolves an Avoid-type strategy may then also evolve a greater degree of plasticity in its response to resource availability. This could make the currently measured cost of exploitation competition a poor indicator of what it was at the time when the strategy evolved. Nevertheless the use of theoretical models, along with the experimental testing of their predictions, is an extremely powerful tool in demonstrating which evolutionary scenarios are consistent with observation today.

Thus it seems that differing cost of exploitation competition for the two species is not the reason for the different larval competition strategies when developing in black-eyed beans (the host on which the cultures used in this experiment have been cultured for at least the last 18 years; C. M. Lessells, personal communication). However the higher cost of exploitation competition shown by *C. analis* on mung beans suggests that if they originally evolved on a host similar to mung this could explain the origin of their Attack strategy. The forces that maintain this strategy now are still open to question.

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Sperm precedence in zebra finches does not require special mechanisms of sperm competition

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SUMMARY

Competition between the spermatozoa of different males to fertilize the eggs of a single female acts as a selection pressure on the behaviour of males and females. However, quantitative predictions about behaviour can only be made if the paternity consequences of different patterns of copulation are known. Because exhaustive empirical measurement of these consequences may be impractical, interest has centred on determining the mechanisms by which sperm competition occurs, knowledge of which may allow consequences to be calculated. One method of elucidating mechanisms of sperm competition is to use mathematical models to determine which mechanisms are necessary or sufficient to account for empirical observations. We use this approach for zebra finches *Taeniopygia guttata* and show that empirically measured rates of disappearance of sperm from the reproductive tract, and differences in the number of sperm in the first and subsequent ejaculates of each male, are sufficient to account for observed levels of sperm precedence. Special mechanisms of sperm competition, such as displacement or stratification of sperm, are therefore unnecessary to explain sperm precedence in this species.

1. INTRODUCTION

The recognition that sperm competition – competition between the spermatozoa from different males to fertilize the eggs of a single female (Parker 1970) – may be frequent even in apparently monogamous species has led to considerable advances in the understanding of male and female behaviour during the female's fertile period (Birkhead & Møller 1992). However, a lack of detailed knowledge of the paternity consequences of different patterns of insemination by pair and extra-pair males, particularly in birds, has hindered the making of precise quantitative predictions about optimal behaviour. This deficit has led to increased interest in mechanisms of sperm competition: knowledge of such mechanisms may provide an alternative to empirical measurements in determining the fitness consequences of different copulation strategies (Lessells & Birkhead 1990).

In birds, one of the most intriguing observations in terms of the mechanism of sperm competition is the apparently disproportionate success of extra-pair copulations (EPCs). For example, in several wild bird populations the proportion of extra-pair young is considerably higher than the observed proportion of EPCs (see, for example, Westneat *et al.* 1990; Dixon *et al.* 1994; Mulder *et al.* 1994). Although such a discrepancy might be accounted for by the discreetness, and hence low observability, of EPCs in the wild, studies of caged birds, where all copulations can be observed, reveal a similar inconsistency between the proportion of EPCs and extra-pair young (the single EPC experiment in Birkhead *et al.* 1988*a*). Such observations encourage the provocative suggestions that either the mechanism of sperm competition entails an advantage to the last male to copulate, over and above any advantage from minimizing the loss of sperm through constant disappearance between insemination and fertilization (Lessells & Birkhead 1990), or females are in some way able to influence the outcome of sperm competition and select sperm providing a favourable genetic endowment to their offspring (Birkhead *et al.* 1993*a*). However, before pursuing these possibilities, the alternative explanation that the success of EPCs is due to differences in the number of sperm inseminated, and the relative timing of EPCs in conjunction with constant sperm loss rates, should be evaluated. In particular, Birkhead & Fletcher (1992, 1995; T. R. Birkhead & F. Fletcher, unpublished results) have recently demonstrated that the number of sperm transferred in copulations by zebra finches *Taeniopygia guttata* is considerably larger when the male is 'rested' than when he has inseminated a female within the previous calendar day. If EPCs normally occur after the male has ceased copulating with his own mate (Birkhead *et al.* 1988*b*; Morton *et al.* 1990; Birkhead & Møller 1992), larger ejaculate size may account for the disproportionate success of EPCs.

The aim of this paper is, therefore, to investigate whether levels of sperm precedence in the zebra finch measured in captivity can be accounted for by the number of sperm inseminated in conjunction with a constant disappearance rate of sperm between insemination and fertilization. To do this, we use mathematical models together with empirical measurements of: (i) the number and timing of copulations; (ii) the proportion of copulations that result in insemination; (iii) the number of sperm inseminated; and

(iv) the rate of loss of previously inseminated sperm from the reproductive tract, to make predictions of levels of sperm precedence. We then test these predictions by comparing them with levels of precedence in captivity measured by Birkhead *et al.* (1988*a*), (reanalysed by T. R. Birkhead, unpublished results): (i) a single EPC performed after the last of several copulations by the pair male fertilizes 53.7% (95% confidence limits: 41.6–66.1%) of the potentially fertilizable eggs (allowing for the timing of copulation, fertilization and oviposition) ('EPC experiment'); (ii) when males are switched during the female's fertile period, the second male fertilizes 75.3% (65.2–83.2%) of the potentially fertilizable eggs ('mate-switching experiment'). A fit between the predicted and observed levels of extra-pair paternity (EPP) or second-male precedence would imply that no special mechanism is required to explain the level of sperm precedence observed in the zebra finch.

2. METHODS

We modelled the female's reproductive tract as a single 'compartment' (see Lessells & Birkhead 1990). Sperm are deposited into this compartment at insemination, and then disappear at a constant rate. Any remaining sperm are eventually used for fertilization. We assumed that the probability of each male fertilizing an egg depends only on the proportion of sperm in the reproductive tract that is his at the time of fertilization. This model is the simplest possible linear model, i.e. it embodies a situation in which sperm from different ejaculates experience the same rate of loss from the reproductive tract, and are not favoured or disadvantaged by the order in which they are introduced into the tract (Parker's (1990) 'loaded raffle') or through physiological discrimination by the female. Success of sperm is still affected by the timing of insemination but only because, with a constant loss rate, more sperm from earlier ejaculates will have disappeared by the time of fertilization. More complex linear models are possible (Lessells & Birkhead 1990) but first, empirical measurements of the parameters included in such models are lacking, and second in linear models asymptotic levels of sperm precedence are dominated by the loss rate from only one compartment, and that loss rate will be equal to the observed rate of disappearance in all compartments in the system (Lessells & Birkhead 1990).

Table 1. *The pattern of copulations and number of sperm inseminated by paired male zebra finches*

(The number and timing of copulations is that observed in video trials of ten paired males (Birkhead *et al.* 1988*a* (reanalysed by T. R. Birkhead, unpublished results)). The number of inseminations was estimated by assuming that 67% of copulations transfer sperm (Birkhead *et al.* 1989). The number of sperm inseminated was estimated by assuming that 7.815×10^6 ($\pm 4.035 \times 10^6$ s.d.) sperm are inseminated in the first successful copulation by a male, and 1.699×10^6 ($\pm 1.339 \times 10^6$) in subsequent successful copulations by the same male (*n* = 30 males; Birkhead & Fletcher 1995; T. R. Birkhead, E. J. Pellatt & F. Fletcher, unpublished results).)

day	number of copulations	number of inseminations	number of sperm inseminated $\times 10^6$
−5	2.304	1.544	8.739[a]
−4	1.836	1.230	2.090
−3	1.584	1.061	1.803
−2	2.448	1.640	2.787
−1	2.088	1.399	2.377
0	1.476	0.989	1.680
1	0.804	0.539	0.915
2	0.612	0.410	0.697
3	0.264	0.177	0.300
4	0.168	0.113	0.191
5	0.192	0.129	0.219

[a] $8.739 = 7.815 + 0.544 \times 1.699$.

Within the framework of this model, the pattern of insemination by two (or more) males can be varied in terms of both the timing and size of ejaculates and the probability of fertilization of each egg in the clutch by each of the males predicted. Initially we modelled the paternity of clutches of six eggs (as in domesticated zebra finches) when the pair male made the normal pattern of about 14 copulations between days −5 (relative to the laying of the first egg) and +5 (see table 1), and a different male made a single EPC between days −5 and +3. We then modified the pattern of insemination by each of the two males to predict the expected paternity of chicks in each of Birkhead *et al.*'s experiments (1988*a*).

The first insemination by any male was assumed to transfer about 8 million sperm, subsequent copulations by the same male to transfer about one and a half million sperm (see table 1). When a male was expected to make less than one whole insemination on his first day of copulation, the larger ejaculate size was assumed to apply to the remaining fraction of a 'first insemination' made on subsequent days. The number of sperm inseminated by each male on each day was calculated by summing the amount of sperm transferred in each insemination (see table 1).

Of copulations by zebra finches, 67% result in insemination of the female (Birkhead *et al.* 1989). This creates stochastic variation in the amount of sperm inseminated, which is expected to alter the predicted average paternity. We investigated the magnitude of this effect by carrying out preliminary simulations for single EPC models in which: (i) insemination by both males was deterministic (i.e. each copulation resulted in 0.67 of an insemination); (ii) insemination by the pair male was deterministic, and by the extra-pair male stochastic (i.e. each copulation resulted in insemination with a probability of 0.67; this was determined in the simulations using a random-number generator); and (iii) inseminations by both males were stochastic. These simulations showed that whereas stochasticity in insemination by the extra-pair male had a large effect, stochasticity in insemination by the pair male generally altered the predicted paternity by less than 1%. Similar simulations showed that variation in ejaculate size of first and subsequent ejaculates by either male (ejaculate size chosen from mean − s.d., mean and mean + s.d. with equal probability; see table 1 for means and s.d.s) also had a trivial effect on the predicted paternity. We therefore used models in which insemination by the pair male was deterministic, and by the extra-pair male stochastic. This allowed us to calculate an exact expected mean EPP (= 0.67 × EPP when the extra-pair male does inseminate the female), rather than estimating the expected mean from multiple runs of the simulation. The effect of stochasticity in insemination in simulations of the mate-switching experiment was rather more variable, but because the effect was generally small (about 1–2%) and occurred in both directions, and an overall prediction could only be made by summing separate predictions for each trial (see below), we used deterministic models to make predictions for the mate-switching experiment.

In birds, fertilization of an egg occurs about 30 min after it is ovulated, and about 1 day before it is laid (Howarth 1974). In zebra finches, eggs are laid early in the morning, and copulations are concentrated in the same period of the day (Birkhead *et al.* 1989). Because sperm take time to reach the infundibulum (the site of fertilization at the top of the reproductive tract), we have made the simplifying assumption that all the copulations by the pair or first male on any day occur immediately after fertilization of the egg ovulated on that day. To be consistent with Birkhead *et al.*'s (1988*a*) protocol, we have assumed that EPCs, and copulations made by the second male on the day of mate switching, are made 4 h later. Thus the earliest egg that a copulation (pair or extra-pair) on day 0 (the day that the first egg is laid) can fertilize is that ovulated on day 1 and laid on day 2, i.e. the third egg.

While the sperm is in the reproductive tract we assume that it suffers an instantaneous loss rate of 0.026 ± 0.007 (s.e.) h^{-1}, as estimated from the decline in the number of sperm adhering to the vitelline layer of sequentially oviposited eggs (Birkhead *et al.* 1993*b*). The extent to which this loss rate reflects use in fertilization, death or inactivation in the reproductive tract, or evacuation from the reproductive tract is unknown, but is immaterial to the predictions of the model. The finite survival rate of sperm on day d,

$$D_d = \exp(-t \cdot r), \qquad (1)$$

where r is the hourly instantaneous loss rate and t is the number of hours on day d that the sperm was present in the reproductive tract. Thus for the sperm of an extra-pair male, or of the second male on the day of switching, D_d for the day of insemination is 59.5% (exp (−20 × 0.026)). In all other cases D_d is 53.6% (exp (−24 × 0.026)). If N_i sperm are inseminated on day i, the number of them surviving to be able to take part in fertilization on day f,

$$S_{i,f} = N_i \cdot \prod_{d=i}^{f-1} (D_d). \qquad (2)$$

Thus, the total number of sperm from a given male, available to take part in fertilization on day f,

$$S_{\mathrm{tot},f} = \sum_{i=-5}^{f-1} (S_{i,f}). \qquad (3)$$

The probability of a given male fertilizing an egg ovulated on day f is then his value of $S_{\mathrm{tot},f}$ divided by the sum of the values of $S_{\mathrm{tot},f}$ for all males who have copulated with the female.

3. RESULTS

We used the model to predict levels of sperm precedence. Figure 1 shows the expected probability of EPP for each egg when a single EPC is made between days −5 and +3. The probability of EPP varies through the laying sequence of eggs. Sperm cannot fertilize eggs laid less than 2 days after insemination (see above), so that eggs laid early in the laying sequence may have no EPP. After the last insemination by any male the number of each male's sperm will continue to decrease, but the proportions will not, so that the probability of EPP would then remain constant. Thus when, as in this case, the pair male continues to copulate after the EPC, the predicted EPP drops from an initial peak. In general, the later the EPC, the higher the level of EPP in those eggs that could be fertilized, but the lower the number of eggs that could be fertilized (see figure 1). This is because the amount of the pair male's sperm in the reproductive tract reflects the balance between gains through insemination and losses through constant disappearance. In zebra finches, this balance results in a decline in the amount of pair male's sperm in the reproductive tract over the period when the clutch is being fertilized (although this is not necessarily true for other rates of insemination and disappearance). Thus the later the EPC, the higher the proportion of sperm in the tract that it represents.

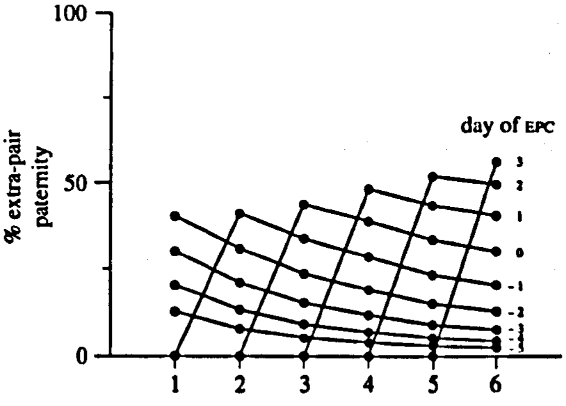

Figure 1. Predicted levels of EPP when pair males make about 14 copulations between days −5 and +5 (see table 1), and there is a single successful EPC between days −5 and +3. The EPC was assumed to occur 4 h after fertilization of the egg ovulated on that day. All other copulations were assumed to take place immediately after fertilization of the egg ovulated on that day. While in the reproductive tract, sperm are assumed to disappear at an instantaneous rate of 0.026 h^{-1}. The probability of paternity was determined by the proportion of sperm in the reproductive tract at the time of fertilization.

Birkhead *et al.*'s (1988*a*) single EPC experiment represents the case where the EPC occurs on day 0, and the pair male achieves the normal pattern of copulations until day −1 (see table 1), and 0.2 copulations on day 0 in the 1 h that he has access to the female (further analysis of video trials (Birkhead *et al.* 1988*a*: T. R. Birkhead, unpublished results)). As a result, the extra-pair male can only fertilize eggs laid on or after day 2, but is then predicted to achieve a constant 49.2% paternity of eggs. This is well within the observed 95% confidence limits of 41.6–66.1% (mean 53.7%).

In Birkhead *et al.*'s (1988*a*; T. R. Birkhead, unpublished results) mate-switching experiment, mate switching in each trial occurred after a variable number of days of copulation by the first male (mean = 3.6; range = 2–5), and a variable number of days before the female began egg laying (2.0; 0–4). We therefore predicted the pattern of copulation by each male from that observed in the separate video trials of mate switching. In these video trials, the number of copulations by the first male did not vary with day number relative either to laying (linear or quadratic terms) or mate switching, nor did it differ between the day of mate switching and other days. We therefore assumed that first males in the paternity trials made the observed mean rate of 1.268 copulations per day. The number of copulations by second males in the video trials varied only relative to the day of laying (number of copulations per day = 0.874–0.266 (day number); $F_{1,61} = 5.98$, $p = 0.017$). We used this relation to estimate the number of copulations made each day by second males in each of the paternity trials. Because of the variation in the timing of mate switching we predicted paternity separately for each paternity trial, and summed over all trials to obtain an overall prediction of paternity by the second male of 77.9%. This is again well within the observed 95% confidence limits of 65.2–83.2% (mean 75.3%).

4. DISCUSSION

Our model has considerable success in predicting levels of sperm precedence: the predictions for both of Birkhead *et al.*'s (1988*a*) experiments lie well within the 95% confidence limits for the observed values. We are thus able to conclude that special mechanisms of sperm competition are not necessary to explain measured sperm precedence in zebra finches. This conclusion is not affected by any difference in parameters such as ejaculate size between captive and wild birds: this is because our main aim was not to predict levels of sperm precedence in the wild, but to use comparisons of observed and predicted levels of sperm precedence in captivity to test ideas about the mechanism of sperm competition. However, we have made several simplifying assumptions and made predictions for only a single value for the loss rate of sperm and for the relative numbers of sperm inseminated at first and subsequent inseminations. We therefore carried out further analysis to determine how sensitive our predictions were to these assumptions.

First, the estimate of instantaneous loss rate has a large standard error. The predicted second male precedence when the model was rerun using values one standard error below or above the mean was 43.5–53.3% for the EPC experiment and 71.4–82.7% for the mate-switching experiment. Moreover, the method used to estimate the disappearance of sperm (counting sperm adhering to the vitelline layer) prevents any estimate of disappearance rate being made for the period before the fertilization of the first egg. Loss rates might be much higher once eggs have begun to be fertilized, for instance if loss-free storage is physiologically incompatible with use of sperm for fertilization. We therefore repeated the calculations with a zero loss rate until the time of fertilization of the first egg. This resulted in lower predicted second male precedence of 31.5% for the EPC experiment and 52.4% for the mate-switching experiment, but did not alter the qualitative pattern of EPP through the laying sequence of eggs. A higher loss rate until the fertilization of the first egg would have the opposite effect on EPP, but is not so likely biologically.

Second, the standard errors for the number of sperm inseminated at first and subsequent copulations are also large. Because it is the ratio of sperm from different males that is used in the model to determine the expected EPP, it is only the ratio of the numbers of sperm at first and subsequent copulations which is important. The standard error of this ratio is approximately 1.41 (Armitage & Berry 1987), and when we reran the model using values one standard error below or above the mean, the predicted second male precedence was 44.5–52.1% for the EPC experiment and 76.1–78.9% for the mate-switching experiment. The general conclusion from these sensitivity analyses is that increased accuracy in the parameter estimates or in the experimentally determined values of second male precedence would increase the power of the model to discriminate between different hypotheses concerning the mechanisms of sperm competition.

Table 2. *The effect of disappearance of sperm and ejaculate size on predicted levels of second male sperm precedence for Birkhead* et al.*'s (1988*a*)* (a) *EPC experiment* (b) *mate-switching experiment*

		sperm disappearance rate/h^{-1}	
		0	0.026
(*a*) EPC experiment			
ratio of sperm in	1	8.4%	26.6%
1st : subsequent ejaculates	4.6	20.3%	49.2%
(*b*) mate-switching experiment			
ratio of sperm in	1	41.6	69.4
1st : subsequent ejaculates	4.6	46.3	77.9

Our model also assumes that all inseminated sperm enters the single compartment in the model, which might not be the case if, for example, females expel sperm from the reproductive tract. This would have no effect on the predictions of the model if the same proportion of all ejaculates are expelled by females (because only relative sperm numbers are important), but would alter the expected level of precedence if females expelled a different proportion of ejaculates from different males, or on different days relative to laying. We have no information on these possibilities. In addition, the single compartment of the model implies that there is essentially only one 'route' by which inseminated sperm can reach the infundibulum. Because it is biologically implausible that sperm storage tubules (STS) do not function in sperm storage, this amounts to assuming that sperm cannot pass directly up the reproductive tract, bypassing the STS. The ability of sperm to exploit any 'fertilization window' (Cheng *et al.* 1983) by moving directly up the reproductive tract would increase the predicted level of last male sperm precedence (Lessells & Birkhead 1990).

Finally, the controlled circumstances under which the number of sperm inseminated were measured in captivity preclude differences in male quality contributing to differences in ejaculate size between pair and extra-pair males. In the wild, females may choose good quality males with whom to perform EPCS (Kempenaers *et al.* 1992; Møller 1994). These males may also have larger ejaculates (Sheldon 1994), thus exaggerating the disproportionate success of EPCS.

In our model, both constant disappearance of sperm and differential ejaculate size may contribute to the disproportionate success of EPCS. To judge their relative importance we also predicted EPP when no sperm disappeared, or when all ejaculates contained the same number of sperm (see table 2). These calculations

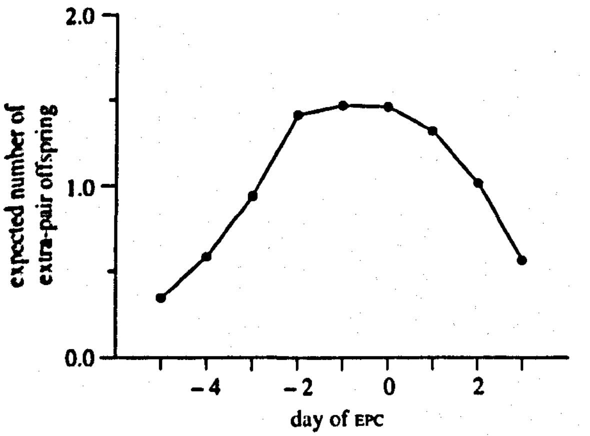

Figure 2. The optimum time for a single EPC. The expected number of extra-pair offspring was determined by summing the expected EPP for each chick in the brood (see figure 1), and reaches a maximum when the single EPC takes place on day −1.

suggest that, in the case of single EPC, both constant disappearance of sperm and differences in ejaculate size have approximately equal effects, and both are needed to achieve high levels of EPP. In the case of mate switching, disappearance of sperm has an important effect relative to that of ejaculate size differences.

Our conclusion that observed levels of sperm precedence in zebra finches do not require any special mechanism of sperm competition contrasts with that of Lessells & Birkhead (1990) for the domestic chicken *Gallus domesticus*. A series of mathematical models similar to that used here suggested that observed levels of sperm precedence measured by Compton *et al.* (1978) could only be explained by a nonlinear model embodying some advantage to the last male, for instance sperm displacement or stratification. Recent failed attempts to replicate the empirically measured value of second-male precedence (T. R. Birkhead & G. J. Wishart, unpublished results) used in these models suggest that unreliability in this value may account for the discrepancy between the conclusions for domestic chickens and zebra finches.

An important motive for studying mechanisms of sperm competition is as a first step in a functional understanding of the copulation behaviour of males and females. Figure 1 suggests that an individual able to achieve a single EPC faces a trade-off, governed by the timing of that EPC, between the number of young that the EPC can potentially father in the brood and the likelihood of paternity of each. By summing the expected EPP over all offspring in the brood (see figure 2), it is possible to predict the optimal timing of an EPC. The model suggests that maximum EPP in the whole brood is achieved when the EPC occurs on day −1, although there is little reduction in EPP if it occurs on day 0 or −2. Mate guarding and extra-pair courtship in the wild and in aviaries do not show a close fit with this prediction of maximum mate guarding and extra-pair courtship on day −1. In the wild, mate guarding (in the form of following) remains at a constant high level throughout the female's fertile period and extra-pair courtship peaks on days 0 and 1 of the female cycle (Birkhead *et al.* 1988*b*). In aviaries, mate guarding (in the form of frequent copulations) does peak on day −1, but extra-pair mounting peaks earlier, on day −3 of the female's cycle (Birkhead *et al.* 1989). The poor fit is not surprising given that the optimal timing of an EPC is an evolutionary game between the pair male, the extra-pair male and the female, in which males may have less than perfect information about the timing of laying. However, our example illustrates the kinds of functional predictions that can be made given a knowledge of the mechanism of sperm competition.

In conclusion, the simple model presented in this paper makes predictions which are in agreement with the observed levels of precedence in zebra finches in captivity. It suggests, therefore, that the outcome of sperm competition in this species may simply be a consequence of the number of sperm inseminated and the constant disappearance of sperm from the reproductive tract, rather than any specialized mechanism. It therefore serves to caution against invoking mechanisms that entail an advantage to the last male to mate (other than constant disappearance of sperm) or the active physiological intervention of the female in determining the outcome of sperm competition. However, the predictions of our model are sensitive to the parameter estimates, so further empirical work making more accurate estimates will increase the power to discriminate between hypotheses: both theoretical models and empirical studies are needed to make progress in understanding mechanisms of sperm competition.

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