THE EVOLUTION OF INSECT LIFE HISTORY STRATEGIES IN A SOCIAL CONTEXT

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All cold-blooded animals spend an unexpectedly large
proportion of their time doing nothing at all, or at any rate, nothing in particular.

C. Elton in "Animal ecology", 1927

Für Uschi

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Chapter 1

Introduction

The analysis of life histories is essentially aiming for an understanding of the evolution of the temporal sequence of decisions between behavioural alternatives during an organism's entire life-time. Conspicuous behavioural characteristics of an organism's life history are transitions between activity and inactivity, such as between diapause and development, between sleeping and being awake, and plainest between life and death. Certainly choices between other alternatives are of interest, too: the transition from growth to reproduction, the number and timing of reproductive events, the number of offspring, or the choice of a suitable habitat for foraging or oviposition. These and many other characteristics of life vary both between species and between individuals of the same species and their evolution has been addressed in numerable life history studies (Roff, 1992; Stearns, 1992).

Sociobiology and theory of social evolution expanded classical life history analysis from solitary to social organisms. Hamilton's rule (1964) and Triver's (1971) concept of reciprocal altruism paved the way for explaining the evolution of social behaviours such as altruism, aggression, brood care and nourishment. However, since then the relevance of kin selection in the context of social evolution has gradually been downplayed and partly been substituted by explanations based on ecological factors. The temporal variability in life history decisions of social insects due to ecological and demographic factors has been investigated only in a few classical modelling studies (Macevicz & Oster, 1976; Oster & Wilson, 1978). As in evolutionary life history analysis in general, the mathematical formalisation of the biological system and the behavioural alternatives played a key role in these studies. Astonishingly, the original approach has hardly been continued since then (but see Karsai *et al.*, 1996; Beekman *et al.*, 1998a).

This thesis extends the classical work of Macevicz and Oster (1976, expanded by Oster and Wilson, 1978). It focuses on the evolution of dynamic behavioural patterns in social insects as a consequence of optimal allocation of energy and time resources. It is based on detailed empirical observations in the model species *Lasioglossum malachurum* (Halictidae; Hymenoptera, see figure 1.1). The main topics of this thesis are optimisation models for eusocial life histories, temporal variation in life history decisions, and annual colony cycles of eusocial insects. These aspects will be introduced in the next sections.

1.1 COLONY CYCLE IN ANNUAL, PRIMITIVELY EUSOCIAL BEES AND WASPS

The best studied groups of insects with primitively eusocial colony organisation and annual nest cycles are halictid bees (Halictidae; Hymenoptera), vespid wasps (Vespidae; Hymenoptera) and bumble bees (Bombini; Apidae; Hymenoptera). Although the empirical work of our studies focused on the halictid bee *Lasioglossum malachurum*, most of the theoretical results can also be applied to any other species sharing specific characteristics of their nest cycles with halictids (see also figure 1.2). Thus, classifying the species under consideration by their taxonomic subsumption is only possible at a very coarse level.

The halictid bees show nearly all levels of social organisation, from solitary, to subsocial, communal, quasisocial, semisocial, and primitively eusocial species (Michener, 1974; Sakagami, 1974; Michener, 2000). Phylogenetic analyses revealed that eusociality in halictids has evolved independently several times and has been lost even more often (Wcislo & Danforth, 1997; Danforth, 1999; Danforth *et al.*, 1999; Danforth, 2002; Danforth *et al.*, 2003). Most species have an annual life-cycle (due to annual variation between cold and warm or dry and wet season) but this does not need to be so. There is at least one perennial halictid species (*Lasioglossum marginatum*, Packer (1991)), and several tropical species do not exhibit a diapause, i.e. nest founding occurs throughout the whole year (Wcislo, 1997a).

Vespid wasps mainly include solitary and eusocial species. Both, paper wasps (Polistinae; Vespidae) and yellowjackets (Vespinae; Vespidae) are subfamilies with exclusively eusocial species. Although the typical colony cycle is annual, occasionally nests in sheltered sites or during mild winters are not abandoned. Then a perennial colony cycle may be maintained by the queen and the workers from the previous year. Perennial colonies are generally larger than annual colonies (Spradbery, 1973; Ross & Mathews, 1991; Yoshiaki, 1993).

Beside the highly eusocial honeybees (Apini) and stingless bees (Meliponini) the Apidae family also includes several tribi and genera with species exclusively (bumble bees (Bombini, see Goulson, 2003), orchid bees (Euglossini, see Dressler, 1982)) or partly primitively eusocial (carpenter bees (Xylocopa, e.g. Steen & Schwarz, 2000)), allo-

Figure 1.1: Example species with annual, primitively eusocial nest cycle. Upper row, left: *Lasioglossum malachurum* (Halictidae; Hymenoptera), photo by Eric Dufrêne; upper row, right: *Polistes dominulus* (Vespidae; Hymenoptera), photo by Yvan Barbier; lower row, left: *Vespula germanica* (Vespidae; Hymenoptera), photo by Yvan Barbier; lower row, right: *Bombus terrestris* (Apidae; Hymenoptera), photo by Alan Pauly; photos reprinted with friendly permission of "Atlas Hymenoptera" at http://zoologie.umh.ac.be/hymenoptera/

dapine bees (Allodapini, e.g. Cronin, 2001)). Bumble bees are the only species within this list which are widely distributed in central Europe and any further reference to annual, primitively eusocial Apidae will be restricted to this group.

Despite plenty of differences within the specific patterns of hibernation, nest founding, brood care and reproduction, the annual nest dynamics can be described within a general framework that must have been evolved independently many times (Oster & Wilson, 1978).

1.1.1 Nest founding

The typical annual colony cycle in the temperate zone starts with solitary nests founded in spring by mated and hibernated queens. The founding females search for a suitable nesting site and start nest construction. New nests are usually constructed every year, often in the same area where nests were built the previous season (but see Packer, 1990; Kukuk, 2002).

Halictids usually build nests in the ground (but see Wcislo, 1997a) and nest architecture varies considerably between genera (Michener, 1974). Brood cells are excavated adjacent to the main burrow and clustered in comb-like arrangements in a cavity. During the founding phase nest usurpation by conspecific females can be observed in several species (e.g. Field, 1992; Kaitala *et al.*, 1990). Each brood cell is provisioned with a portion of nectar and pollen sufficient for the complete development of a single egg (mass provisioning, see also Knerer, 1992).

Paper wasps build their nests from chewed wood fibres. The comb is attached to a single filament, usually oriented downwards and consists of a single tier of hexagonal-shaped cells for single eggs (Yoshiaki, 1993). While single females sometimes start a colony, more often a group of females will found a colony together. A dominance hierarchy is established among this group of females after several fights. The female at the top of the hierarchy becomes the queen, while the rest of the foundresses start to function as workers (Ross & Mathews, 1991). The ovaries of the queen become well developed and she becomes the main egg layer. The ovaries of the rest of the foundresses start to decrease in size as they attend the dangerous tasks of collecting water, plant fibres to construct the nest, and nectar and caterpillars to feed the queen and her offspring (progressive provisioning Field, 2005).

Yellowjackets are primarily groundnesters, but they also construct aerial nests (Greene *et al.*, 1976). Similar to paper wasps they construct their nests of a paper-like material consisting of wood fibre. However, unlike paper wasp nests, they are completely enclosed in an envelope except for the entrance. When the larvae hatch, the queens feed them for about 18 to 20 days (usually progressive provisioning).

When bumble bee females have left their hibernation sites in the soil, they feed on spring flowers and search for a suitable location for the new colony, often in former burrows of rodents. The females collect pollen, forming it into a tiny clump upon which they lay their first brood of several fertilised eggs. The larvae hatch soon after, and begin feeding on the pollen clump, and on additional pollen and nectar collected by the queen (Goulson, 2003).

1.1.2 Ergonomic phase

The development time from egg to adult in primitively eusocial insects is approximately three weeks, but can vary considerably between species (e.g. Kamm, 1974; Duchateau & Velthuis, 1988; Abrams *et al.*, 1996). The first adults are usually workers. Caste determination occurs to a large extent pre-imaginally, according to the amount of nutrition provided (Roseler, 1970; O'Donnell, 1998). Both, the initial amount and continuous supply of provisions can be adjusted to produce either workers or female sexuals. However, mechanisms of adult caste determination in halictids have also been proposed (Yanega, 1997).

With the emergence of the first workers the eusocial colony enters its second stage, the "ergonomic period" of colony development (Oster & Wilson, 1978). The queen now devotes herself to egg-laying while the newly emerged workers forage, expand the nest, care for the larvae, and protect the colony against enemies. This period lasts for several weeks. A typical mature paper wasp nest contains 20 to 30 adults and hardly more than 200 cells. Yellowjacket nest size may grow up to 20,000 adult workers. Individual numbers in large halictid nests can exceed 100, but will rarely reach 200. In bumble bees typical worker number is about 20 to 100 individuals (depending on the species Goulson, 2003). Especially in bumble bees the ergonomic growth of the colony seems to be limited by the egg laying rate of the queen (Brian, 1951; Beekman *et al.*, 1998a). Yellowjacket workers predominantly forage to feed their larvae insects and spiders while paper wasps, bumble bees and halictids mainly gather nectar and pollen.

1.1.3 Reproductive phase

During late summer and fall, colonies begin to produce male and female sexuals. The timing of the transition from worker production to the production of sexuals varies among species but is crucial for overall fitness achieved during the season (Oster & Wilson, 1978). Males develop from unfertilised, haploid eggs, while females develop from fertilised eggs. Males and females usually mate outside the nest. At the end of the season the old queen and the males die, and the inseminated young females enter sheltered locations for hibernation.

1.1.4 Hibernation

Halictid queens hibernate both within and outside their natal nest (Sakagami, 1974). Yellowjacket and paper wasp queens usually abandon the nest and seek sheltered places to hibernate. Abandoned nests rapidly decompose and are not reused the next year. Overwintering paper wasp queens may join together, sometimes in large groups and preferentially in high structures, such as trees and tall buildings (Reeve, 1991). The hibernated queens emerge the following spring and begin the cycle again.

1.2 OPTIMISATION MODELS IN EVOLUTIONARY ECOLOGY

The prototype of an annual, eusocial colony cycle includes prominent behavioural transitions (see above) which can be analysed from two main perspectives. First, the temporal pattern of worker and sexual production during the season can be investigated with respect to the underlying proximate mechanisms, such as photoperiod or resource availability. However, a proximate approach (alone) will hardly answer the more general question, whether a specific behavioural pattern can be understood as an adaptive result of evolution, until it can be tracked down to the dynamics of its underlying genetic mechanisms. This seems to be impossible at the organismic level.

Although most of his work was dedicated to the microscopic (genetic) perspective on evolution, Fisher (1930) emphasised the basic relevance of optimal resource allocation as the alternative, macroscopic perspective:

> *"It would be instructive to know not only by what physiological mechanism a just apportionment is made between the nutriment devoted to the gonads and that devoted to the rest of the parental organism, but also what circumstances in the life history and environment would render profitable the diversion of a greater or lesser share of the available resources towards reproduction."*

For any individual, available resources in any particular environment are finite. Time and energy spent for one purpose reduce the time and energy available for others. How should resource investment be distributed throughout the life-time to maximise the organism's evolutionary success given the limitations of its evolutionary history? The analysis of the optimal sequence of life history decisions against the background of limited resources (of any kind) represents the general life history problem (Gadgil & Bossert, 1970; Schaffer, 1983; Bulmer, 1994) and outlines the second major research program in the study of life history and has been realised in innumerable studies (for review see Stearns, 1992; Roff, 1992). It has especially led to the introduction of optimisation models in the analysis of life history evolution.

The goal of optimisation models is to determine the best strategy to allocate a limited resource among various alternatives. In order to employ mathematics as a quantitative language, precise definitions of the terms "limited resource" (see subsection 1.2.4 "Constraints") and "best strategy" must be given. The comparison between alternative strategies requires both the determination of a plausible range of alternatives (see subsection 1.2.2 "Strategies") and a criterion of the evolutionary success of a specific alternative (see subsection 1.2.3 "What is maximised?"). The effect of any decision about resource allocation will also depend on the actual state of the biological system (subsection 1.2.1 "System state"). All models have to consider such influences. For example, in the early stage of a colony's development exclusive investment in workers might be beneficial, but this is not the case if worker number has already reached a level that considerably reduces worker efficiency. Although each modelling approach has a particular way of incorporating these mechanisms, a general concept can be presented without mathematical details. This concept can be based on the arguments of Oster & Wilson (1978), and Mangel & Clark (1989).

In general any optimisation model consists of four parts: (1) a state space (representing the state of the biological system during the entire time-span under consideration), (2) a set of strategy variables (representing the possible alternatives of resource allocation, in general as a function of time), (3) a fitness function (the optimisation criterion) that might depend on both state and strategy variables, and (4) a set of constraints (which represent natural constraints, trade-offs and the dynamic properties of the system). Consequently, the optimisation problem is stated as follows: Find the strategy from the set of possible alternatives (2) that maximises fitness (3) and satisfies all of the constraints (4).

1.2.1 System state

In this work every model represents an abstract imagination of a biological system. The system must be described as complete as possible with respect to the question under consideration. If the system is characterised by a collection of measurements $\vec{y}(t') = (y_1(t'), y_2(t'), ..., y_n(t'))$ at some time t' and these measurements are sufficient to calculate all future values of $\vec{y}(t)$ then the vector $(y_1(t), y_2(t), ..., y_n(t))$ is called a state description. In simple, single-species population models for example, the state description is represented by a scalar, the number of individuals $N(t)$ within the population. Models of two interacting species require at least two state variables. Two state variables will also be sufficient for a simple description of eusocial colony dynamics with two different castes, when one variable represents the number of workers ($W(t)$) and the second the number of sexuals ($S(t)$, see section 1.4). However, it is obvious, that a census alone is usually not sufficient to predict the future growth of the population. Age structure, nutritional state, sex ratio, and many other aspects might be crucial for a precise population projection, too.

In physics a general agreement about a set of suitable state descriptions has been developed over centuries based on the empirical evidence collected over generations. In ecology the situation is different, both because the experimental data are too sketchy and the complexity of the system is much greater due to the evolutionary (historical) effects leaving their specific mark in any individual system. Therefore, ecologists are forced to rely more on intuition and personal experience in selecting suitable descriptors. In ecology, models are inevitably provisional. They are at best imprecise and will certainly have to be revised when further empirical evidence is available. However, the main goal of strategic models is a causal analysis providing the logical link between demography, ecology and optimal behaviour. This can be achieved best by keeping a model, i.e. the state description, as simple as possible (Stearns & Hoekstra, 2000).

1.2.2 Strategies

The optimisation of an ecological system always operates within the limits of the behavioural alternatives specified as a set of possible strategies $\vec{u}$. All sections of this thesis use only a single strategy variable ($\vec{u} = u$), but this includes considerable behavioural plasticity, as the strategy might be time dependent ($u = u(t)$). For example, a suitable ratio of the investment in workers and in sexuals must be found in a eusocial insect colony for each point in time during the whole season. As in the case of the state variables, the set of strategies must be as complete as possible.

In a study of the optimal age at maturity when an organism switches from growth to reproduction, the possible strategies might be represented by the sequence of possible ages from $u = 0$ (when the individual is born) until the end of its life ($u = T$). Selecting the most beneficial strategy u^* by simple mathematical optimisation is not necessarily a projection of the real evolutionary process. The main source of new adaptive strategies is mutation and recombination while natural selection deletes the least "fit" individuals. It is nearly impossible (due to the innumerable combinatoric possibilities) to track the sequence of strategies generated by the genetic processes, especially at the organismic level. The innovative nature of evolution essentially precludes to specify an exhausting list of allowed strategies. Nevertheless, optimisation models can not be applied without providing a set of possibilities.

The only way to anticipate the possible strategies is to consider natural history (the change of behavioural options in the past) and to compare options between closely related species to get an impression of a plausible range of strategies. Thus, animal or plant families with large numbers of comparable species and wide behavioural plasticity are best suited for the use of optimality models.

The proximate mechanisms responsible for the implementation of a specific strategy are not necessarily within the scope of an optimality model. The major goal is to answer the evolutionary question why and not how a specific strategy is established (Yodiz, 1989). However, each optimisation model implicitly assumes that there are suitable external or internal cues which trigger behavioural decisions, such as photoperiod for entering diapause or a physiological clock for maturation (see next section).

1.2.3 What is maximised?

Any optimisation model requires a quantity to be maximised. In ecology the optimisation criterion is "fitness". In general, fitness is the number of genes projected into further generations. However, computing this microscopic quantity is often impossible and replaced by a macroscopic measure of fitness. The adequacy of a specific measure of fitness depends on the ecological conditions E. The classical measure of fitness considered is the per capita growth rate of a population resulting from a specific behavioural strategy. This is applicable only in the case of deterministic environments and unlimited resources leading to an exponential growth of population size (Roff, 1992). The growth rate can be implicitly linked to the organism's life history (expressed as age dependent survival rate and age dependent fecundity) via the Euler-Lotka equation (for a detailed derivation see Stearns, 1992).

When the mean population size is constant and the growth rate is approximatively 1, fitness can be measured by the organism's life-time reproductive success. This approach decouples the mechanisms of density regulation from the life history analysis and is only feasibly, when the strategies under consideration do not interact with the regulation mechanisms (Geritz *et al.*, 1998). Life-time reproductive success is the simplest measure of fitness and often used when the analysis focuses on fine-scale dynamics of life history decisions (Macevicz & Oster, 1976; this work). However, this requires a careful verification of the corresponding assumptions.

It is convenient to express life-time reproductive success ($F(E)$) in a specific environment (E) by the rate of fitness increase (I) during the whole time span under consideration ranging from 0 to a finite time horizon (T) (Roff, 2001).

$$F(E) = \int_0^T I(\vec{y}(E,t), \vec{u}(E,t), t)dt \tag{1.1}$$

The terminal time (T) itself might depend on the environment (E). (Remark: An infinite time horizon requires several modifications of the method, but can easily be included in this concept (Klein, 1998)).
When fitness itself can be expressed by a state variable (e.g. the number of sexuals, see subsection 1.2.4), overall fitness as formulated above is equivalent to the terminal value of the corresponding state variable (e.g. the number of sexual offspring produced by an eusocial colony over its life-time, see subsection 1.4.1). This would yield a simpler form of the fitness function, because the integration above can be calculated explicitly.

Measuring fitness in a deterministic environment seems to imply that all individuals are exposed to identical environmental conditions resulting in identical growth and mortality rates. However, this is not necessarily so. When all individuals of a population are exposed to different and unpredictable environmental fluctuations the optimal (unique) strategy maximises the arithmetic mean of the fitness values achieved in specific realisations of the environment (Roff, 1992). As different individuals suffer from e.g. different mortalities, it is possible to calculate the mean fitness value as the average over the whole population. Even more, if the random effect enters the model in a linear way, the optimal strategy can be computed as if the complete population would just be exposed to the mean value of the effect. This often simplifies a modelling approach, because the influence of (simple) stochasticity can be treated in a deterministic way (Yodiz, 1989).

Coarse-grained environmental fluctuations (sensu Yodiz, 1989) require a different approach. When all individuals of a population are exposed to the same realisation of a random environment, the geometric mean of specific fitness values is the appropriate measure of fitness. The typical example of such a scenario is a random season length (e.g. King & Roughgarden, 1982a). For example, all individuals of a population may suffer from a short or benefit from an extended season, but averaging over different realisations of season length is not possible, as a specific season length always affects all individuals simultaneously. Thus, the multiplicative structure of population growth cannot be represented by the arithmetic mean of fitness values. The first order approximation of the geometric mean is the difference of the arithmetic mean and the variance (multiplied with a factor). Thus, geometric and arithmetic mean are equal, only if environmental variance is 0.

The time continuous formalisation of fitness in coarse-grained random environments requires a logarithmic transformation to represent the geometric mean in an additive way (as an integral).

$$\ln F = \int_E \Phi(E) \ln(F(E)) dE \tag{1.2}$$

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The transformation does not change the optimal strategy $u^*(t)$. Each realisation of a specific environment E is weighted according to its probability $\Phi(E)$ (Roff, 1992; Stearns, 1992).

1.2.4 Constraints

Every biological system is constrained. Constraints can refer to both state variables and strategies. The simplest constraints reflect the biological necessity that state variables such as individual numbers, gene frequencies or amounts of resources have to be positive. Constraints can be classified as demographic, genetic and resource constraints. Resource constraints typically represent the fact that only 100% of a resource can be distributed between different demands but the total amount of resources available is limited. This aspect seems to be trivial, but makes it impossible to apply Calculus of Variation (Kamien & Schwartz, 1991) as a standard dynamic optimisation method (see subsection 1.3.2).

The dynamic character of an optimisation model is usually formalised by demographic constraints. For example, the analysis of an optimal harvesting strategy has always to include the population dynamics as a demographic constraint. Demographic constraints are usually expressed by difference or differential equations relating the current change in the state variable y_i to the current state by a specific function $f_i(.)$.

$$D(y_i(t)) = f_i(\vec{y}(t), u(t)) \text{ for all state variables } i \tag{1.3}$$

In the case of differential equations, $D(y_i(t))$ is the time derivative $\frac{dy_i(t)}{dt}$ and in the case of difference equations it is the difference operator $D(y_i(t)) = y_i(t+1) - y_i(t)$. Examples of specific realisations of dynamic constraints can be found in (Macevicz & Oster, 1976; King & Roughgarden, 1982b; Kozlowski & Teriokhin, 1999; chapter 4, chapter 7).

The approach gets more complicated, when the equations of the dynamic system contain time delays ($D(y_i(t)) = f_i(\vec{y}(t), u(t), \vec{y}(t-\tau), u(t-\tau))$, see chapter 4). Typically, only the time consuming aspects of an ecological mechanism are accounted for in the model equations (e.g. the development time of an individual from egg to adult) but without any further details. In this case an extended version of Pontryagin's Maximum Principle can be applied (see later and Malek-Zavarei & Jamshidi, 1987). A time discrete delay equation can also be transformed into an equation system without delay (Malek-Zavarei & Jamshidi, 1987) to allow for a dynamic programming analysis (see subsection 1.3.3). In this thesis a (pseudo-)static approach (see subsection 1.3.1 "Parameter reduction") provides a suitable alternative.

Optimality approaches have been criticised for several reasons. As mathematical formalisation requires fractionalising the biological system into several distinct traits one is tempted to optimise each trait independently and neglect interdependencies, especially genetic ones. The genetic mechanisms do not usually allow traits (which might be defined independently in the model) to evolve independently. Thus, optimisation of a single trait might be inconsistent with the optimisation of another one genetically linked to the first. Trade-offs have to be considered, which reflect the complete phylogenetic history of correlated traits. Formally this could be implemented by genetic constraints. However, if one in fact would be able to express all genetic constraints (including genetic dynamics), the corresponding model would no longer be an optimisation model, but just a model of genetic dynamics that only needs to be observed in the course of time to reveal the evolutionary result. Thus, the optimisation criterion can be interpreted as a substitute for the lack of knowledge about the relationship between genotype and phenotype. Microscopic constraints are substituted by a macroscopic fitness function.

The method of replacing microscopic dynamics by macroscopic extremal principles is yet in the beginning in theoretical biology, but has successfully applied in physics and chemistry (Sieniutycz & Farkas, 2005). However, as long as the link between the microscopic and macroscopic level is not analysed in general (which seems impossible or at least extremely difficult for biological systems), one can only rely on biological intuition and comparative studies to argue for sufficient genetic flexibility within the system.

The assumptions of an evolutionary analysis via fitness maximisation (which a major part of this thesis is based on) can be summarised as follows (Mangel & Clark, 1989):

1. Any significant adaptive advantage that is physically and genetically feasible is selected for.
2. Organisms have some way of getting near to optimal solutions of behavioural problems in situations that they normally encounter.

These assumptions imply a key role of selection and adaptation as evolutionary forces which are not doubted even by the critics of the adaptionist's paradigm (Gould & Lewontin, 1979).

1.2.5 A generalisation

Simple optimisation models assume that the fitness of an individual depends only on the individual's phenotype within a given environment. However, an individual's fitness is often also determined by the phenotypes of other individuals in the population (Day, 2005). The introduction of game-theoretic ideas addresses this complexity, and allows modelling the evolution of social interactions for which optimality models are simply not tenable (Maynard Smith & Price, 1973; Maynard Smith, 1982). The fitness consequences of a certain social interaction for a specific individual depends on the behaviour of all individuals involved; consequently, the focus moves from optimal phenotypes to evolutionarily stable phenotypes (Maynard Smith, 1982). An "evolutionarily stable strategy" (ESS) is one such that if all individuals are using this strategy, then no single individual can do better by altering its phenotype (Maynard Smith, 1982; Bulmer, 1994). Optimality models are just special cases of such game-theoretic models in which the fitness of an individual depends only on its own phenotype. Like other optimality models, original game-theory focused on the end point (equilibrium) of evolution. The underlying idea is that new mutations arise randomly, and either get fixed or die out. Thus, the population is imagined as being monomorphic with the rare introduction of a new genotype by random mutation. Eventually, after a series of new mutations and random allelic replacements, one might expect the population to arrive at a phenotype that is evolutionarily stable. For this thesis' purposes (see chapter 2), it is important to note that the approach is equally useful for modelling ecological interactions. For example, the resources available to an individual do not only depend on its phenotype but also on the phenotypes of other individuals in the population - the fitness consequences of a certain strategy may thus be frequency dependent.

The game-theoretic approach has been extended to other situations involving different roles played by different individuals (e.g., female versus male) and the possibility that the ESS not necessarily consists of a single phenotype, but that a polymorphism is maintained. In addition, although the approach was often used to model the evolution of social interactions, it was soon appreciated that its utility extended well beyond this (e.g. Lawlor & Maynard Smith, 1976; Reed & Stenseth, 1984).

1.3 DYNAMIC ANALYSIS

After the above insight into the general structure of optimisation models in evolutionary ecology and before proceeding to the prominent characteristics of the biological systems under consideration, I first deal with possible ways to find the solutions (the optimal strategy $u^*(t)$) for the optimisation models used in this thesis. Characterising resource allocation strategies (see subsection 1.2.2 from above) as "dynamic" emphasises the central place of temporal variability of behaviour, i.e. the fact that optimal resource allocation patterns might vary during an organism's life-time. However, this does not imply that only advanced mathematical techniques summarised as dynamic optimisation can be implemented to find solutions for such dynamic resource allocation problems. In several cases models can be simplified to a (formally) static system. Then algebraic manipulations and basic calculus are sufficient to find the solution.

1.3.1 Parameter reduction

In the (pseudo-)static case an organism's strategy can be expressed by a few variables which do not change over the course of time – in contrast, the general eusocial investment pattern in workers and sexuals might take different values for each point in time. Cole's work on semelparity versus iteroparity (1954) is often cited as the first example of the application of optimal allocation theory in evolutionary ecology (Mangel & Clark, 1989; Bulmer, 1994) and is a good example in the context of parameter reduction. His analysis is a comparison of two extreme life cycles: a short life ending with a single reproductive event versus an infinite lifespan with repeated reproductive events at a constant rate. He surprisingly found that an infinite life-span should be abandoned when reproduction can be increased by a single offspring per reproductive event instead. Although reproduction rate in general might be a time dependent trait, Cole's analysis got by with two parameters, the life-span and the number of offspring per reproductive event. Even more, one of these parameter could only take two values (life-span $\hat{=}$ one or infinite reproductive events).

Subsequent theoretical effort on the reproductive pattern assumed two major phases of life history: growth and reproduction. However, at that time it has not been shown that only a single period of growth followed by a single period of reproduction yields maximum fitness (Stearns, 1992) and that any alternative pattern, e.g. several switches between reproduction and growth, performs worse. The key quantity of this analysis is the age at maturity when growth should be replaced by reproduction. Again, for the most simple approach a single life history parameter is sufficient to describe the behavioural alternatives (Roff, 2001). However, there is a general precondition of this analysis allowing for strategy representation by a single parameter: The life cycle must be organised in the simple way mentioned above: a single period of growth followed by a single period of reproduction. Thus, the corresponding model cannot be used to evaluate the evolutionary benefit of this simple (and often observed) pattern as such. Consequently, the model cannot predict whether multiple switches between growth and reproduction or simultaneous growth and reproduction can yield a higher fitness.

This goal has not been achieved, until fine-scaled dynamic strategies have been considered explicitly and optimal reproductive effort has been computed for each point in time during an entire life. This has in fact shown that the original assumption of two distinct phases of "exclusive growth before exclusive reproduction" is the optimal investment pattern in most cases (King & Roughgarden, 1982b), but also provides the evolutionary explanation for the many exceptions observed in nature (King & Roughgarden, 1982a). The price for the analysis of dynamic strategies is high computational and analytical effort (see below, and chapter 7), this might restrict the application of the methods in ecology and also restrict the distribution of the corresponding results. Thus, expressing dynamic strategies by a few parameters is desirable (see chapters 4 and 6), but might be an oversimplification. In this thesis I try to overcome this dilemma by hierarchical modelling: We first show the evolution of a general pattern by a dynamic approach, and then proceed to a detailed analysis with an appropriate parameterisation neglecting dynamic aspects that can be excluded according to the preceding analyses (transition from chapters 4 and 5 to chapter 6).

1.3.2 Pontryagin's Maximum Principle

If the biological system can or should not be represented with only a single or few strategy variables, the dynamic allocation problem can be tackled by mathematical techniques borrowed from Optimal Control Theory. If all constraints are binding and continuous, the problem can be solved by classical methods like the "Calculus of Variation" and Lagrangian Mechanics developed in the nineteenth century (Sieniutycz & Farkas, 2005). However, if these conditions are not fulfilled (as it typically occurs in optimal resource allocation problems), these methods cannot readily be applied (Perrin *et al.*, 1993). It took until the 1970's, until Pontryagin published his extremal principle applicable for dynamic optimisation of ecological systems (Pontryagin *et al.*, 1962). The Pontryagin Maximum Principle was first applied in engineering sciences (Sieniutycz & Farkas, 2005) and then adopted by national and business economics (Klein, 1998). The key quantity of Pontryagin's idea is called the "Hamilton function" ($H(t)$):

$$H(t) = \sum_{i=1}^{n} z_i f_i(\vec{y}(t), u(t)) + I(\vec{y}(E,t), \vec{u}(E,t), t) \tag{1.4}$$

Defining the Hamilton function requires to associate each state variable $y_i(t)$ with a costate variable $z_i(t)$

$$\frac{dz_i}{dt} = -\frac{\partial H}{\partial y_i} \text{ for all state variables } i \tag{1.5}$$

with boundary conditions at terminal time T

$$z_i(T) = 0 \text{ for all state variables } i \tag{1.6}$$

The solution of the optimal control problem can now be found by maximising the Hamilton function with respect to $u(t)$. This seems to transform the dynamic problem into a static problem at each point in time. However, the introduction of the costate variables has added a new technical challenge. Costate variables can be calculated (by backwards integration) only for specific conditions, but then provide the possibility of an analytical solution.

Analytical solutions immediately reveal the dependency of optimal strategies on model parameters and thus, are the most convenient and desirable presentation form of theoretical results. The Hamilton function also allows for classifying the potential solution of optimal control problems (Perrin *et al.*, 1993). If the Hamiltonian function depends linearly on the strategy variable, one can conclude that maximum fitness is achieved only for strategy values at the margins of the possible strategy range. However, this only holds, if the Hamilton function is not equal 0. When the Hamilton function vanishes for a finite time span, it cannot be used as a maximisation criterion,

but it is still helpful, especially to identify periods in which strategies are realised which do not lie on the margins of the range of possible alternatives but in the inner region.
Examples of the application of this technique can be found in Perrin *et al.* (1993), Kozlowski & Teriokhin (1999), and Iwasa (2000). Especially case studies from economics provide exhaustive insight into different applications and variations of the general principle (Klein, 1998).

Although restricted to particular cases, Pontryagin's Maximum Principle has been applied successfully for many problems in evolutionary ecology (reviewed in Perrin *et al.*, 1993). It was the basic method for the first dynamic analysis of life histories in social insects by Macevicz and Oster (1978). The mathematical difficulties related to the method might be a major obstacle, why their "bang-bang principle" for social insect reproduction has not led to consecutive theoretical effort, even though it is a well-known and often cited result.

Pontryagin's Maximum Principle provides valuable additional perspectives for dynamic life history analysis. Similar to the "shadow price" interpretation in economics there is a biological meaning of the costate variables (Klein, 1998). The costate variables indicate the priority of changing the value of the corresponding state variables. A high value of the costate variable will force a high proportion of resources to be spent promoting the corresponding state. Thus, costate variables indicate the potential fitness effects of changes in the state variable. As age-specific effects of the state variables on fitness change, so should the priorities of allocating resources to conflicting demands. It can be shown mathematically, that each costate variable is in fact proportional (not necessarily equal) to the residual fitness value of its state variable.

This makes obvious that the Pontryagin's Maximum Principle has entered evolutionary ecology from two main directions: (1) The application of a general mathematical principle to solve specific evolutionary problems which require techniques with high temporal resolution, and (2) the distinction between current and future reproductive value established by theoretical ecologists in the middle of the 20th century (Stearns, 1992; Roff, 1992).
After recognising the interpretation of costate variables as residual fitness values the technical approach (1) meets a substantial development of theoretical life history analysis (2). A milestone of evolutionary life history analysis since the first optimisation approaches by Lack (1947) and Cole (1954) has been achieved by the distinction between current and future reproductive success (for a historical outline see Bulmer, 1994). This provides a biological characterisation of dynamic optimisation methods. At the same time the mathematical generality has demonstrated the limitations of the

biologically approach. The originally biological approach was based on the obvious temporal structure of an organism's life history. Distinguishable developmental stages like the egg, larval, or adult stage provide a natural structure of life history that can serve as a general modelling framework. In contrast, the neutral view of fine-scale dynamic optimisation models on temporal structures (1) is not based on a sequence of typical stages, and therefore allows for the evolutionary analysis of the temporal pattern itself.

1.3.3 Dynamic programming (Bellman)

When an analytical solution is out of reach, a dynamic optimisation problem is usually solved by dynamic programming based on Bellman's Optimality Principle (Houston *et al.*, 1988; Mangel & Clark, 1989). The term "dynamic programming" was originally used to emphasise the technical relationship to "linear programming", a well-known algorithmical (not necessarily computer-based) method to solve static linear optimisation problems, e.g. by the simplex-method (Stoer & Burlish, 2005).

Dynamic programming is based on the mathematical insight that specific dynamic optimisation problems can be divided into subproblems which can be solved independently from each other. Thus, time discrete models are the typical framework of the application of dynamic programming. The suitable choice of subproblems is again orientated by the concept of the residual fitness value (see above), however, this interpretation is not part of the mathematical core of the method. The key quantity of the method is the fitness gain achieved within an interval starting at time (t) and ending at the terminal time (T) under consideration.

$$\begin{aligned} G(\vec{Y}, u(t), u(t+1), ..., u(T-1), t) = \\ I(\vec{y}(t), u(t), t | \vec{y}(t) = \vec{Y}) + \sum_{j=t+1}^{T-1} I(\vec{y}(j), u(j), j | \vec{y}(j) = f(\vec{y}(j-1))) \\ \text{for } t = 0, 1, ..., T-1. \end{aligned} \tag{1.7}$$

The quantity $I(\vec{y}(t), u(t), t|\vec{Y})$ is the time step specific amount of fitness increase: the fitness gain during a single time step, when state $\vec{y}(t) = \vec{Y}$ is transformed into state $\vec{y}(t+1)$ by decision $u(t)$ under the dynamic constraints f (see subsection 1.2.4). The residual overall fitness gain ($G(\vec{y}, u(t), u(t+1), ..., u(T-1), t)$) is just the sum of every particular increase in fitness achieved during all future time steps. It does not only depend on t but also on the state $\vec{Y}$ of the system at time t and all future strategy decisions which determine the sequence of future states. When $t = 0$ and $\vec{Y} = \vec{y}(0)$ this is a discrete version of the fitness function defined in subsection 1.2.3 ("What is maximised?"). Thus, the quantity to be maximised in this context is $G(\vec{y}(0), u(0), u(1), ..., u(T-1), t), 0)$. The crucial point is that it is not necessary to explicitly calculate the sum in equa-

tion 1.7 as the optimum (not necessarily maximum) sequence of residual fitness gains as $G(.,t)$ for $t = 0, 1, .., T$ satisfies a recurrence equation and can be computed by a simple backward iteration method (see equation 1.9).
The iteration starts at the end of the time interval under consideration $[0;T]$. A final value of the residual fitness gain ($G(\vec{y},T)$, after the last time step) cannot be provided with equation 1.7. However, as long as no additional fitness gain after the time interval under consideration is considered (but see Mangel & Clark, 1989), it is obvious that $G(\vec{y},T) = 0$. Thus, the final decision at most depends on the pre-final state of the system and it is possible to calculate the optimum final decision for all possible pre-final states ($\vec{y}$) by maximising the final increase in fitness:

$$G(\vec{y},u^*(T-1),T-1) = \max_{u(T-1)} \{I(\vec{y},u(T-1),T-1)\} \tag{1.8}$$

Actually the final decision does not even depend on the system state. At the end of the time span under consideration (e.g. just before the death of an organism, when the season ends) further investment in growth will always be less beneficial than a last bout of reproduction. However, one step further back in time the decision might be less clear, and the optimal strategy might depend on the current state of the organism: If the individual is already very weak, a pre-terminal period of growth could be beneficial, if it is in good condition, reproduction might be advisable.
Technically the vital point here is that the final value $G(\vec{y},T) = 0$ is known as a closure condition for the equation system below and the first step of the recurrence procedure (equation 1.8) can be extended to cover the complete time interval (equation 1.9).

It can be shown that the sequence of $G(\vec{y},.,t)$ which leads to maximum fitness ($G(\vec{y},u^*(0),u^*(1),...,u^*(T-1),t),0)$) satisfies a recurrence equation (for $t = T, T-1, \ldots, 0$) involving the current increase in fitness due to the current decision and the future gain in fitness:

$$\begin{aligned} &G(\vec{y},u^*(t),u^*(t+1),...,u^*(T-1),t) = \\ &\max_{u(t)}\{I(\vec{y},u(t),t) + G(f(\vec{y},u(t),t),u^*(t+1),...,u^*(T-1),t+1)\} \end{aligned} \tag{1.9}$$

Hereby each possible state is related to a specific state in the time step before by the dynamic constraints $f(.)$. The backwards iteration method has still a degree of freedom which must be considered during the numerical realisation: As the method proceeds backwards in time, it is not clear, which state is displayed by the system in the preceding time step. However, as long as the number of state variables is sufficiently low, the iteration sequence can be computed for all possible preceding states.

Note, that this does not lead to an exponential increase of computational effort (with increasing number of time steps), because system states in subsequent time steps are interrelated by the dynamic equations $f(.)$.

The equation above has also an intuitive "forward" interpretation. An individual has to decide about its current behaviour. The immediate reward of any decision is $I(\vec{y}(t), u(t), t)$. However, a beneficial current decision might also have a negative effect on the future. Thus expected future reproductive success should also be considered. Future reproductive success is (by definition) $G(\vec{y}(t+1), ., t+1) = G(f(\vec{y}(t), u(t), t), ., t+1)$. The optimal strategy is always achieved by following the rule "Maximise life-time fitness from now on" and Bellman's Optimality Principle ensures mathematically that the strategy which is optimal from t to T is also optimal from $t+1$ to T, whatever decision has been taken at time t.

Again, the sequence of arguments is based on the crucial distinction between current and future reproductive value (see subsection 1.3.2 above).

1.4 EVOLUTIONARY ANALYSIS OF THE COLONY CYCLE

The last two sections provide a toolbox for the construction (section 1.2) and analysis (section 1.3) of dynamic life history models. The methods have been widely applied in evolutionary ecology (Mangel & Clark, 1989; Perrin *et al.*, 1993) and are the basic techniques of dynamic life history analysis in social insects.

The prototype of an annual, eusocial colony cycle (see section 1.1) shows several prominent peculiarities in the temporal structure of behaviour which can be analysed with these techniques (figure 1.2). The next sections present the main questions of former studies as well as of current research in a unique modelling context.

1.4.1 *Optimal resource allocation in deterministic environments*

The evolutionary analysis of dynamic life history patterns in annual social insects began with the work of Macevicz and Oster (1976) reprinted and extended in Oster and Wilson's text book "Caste and ecology in the social insects" (1978). The authors focused on the optimal ratio between worker and sexual production within the course of an annual eusocial colony cycle. Macevicz and Oster (1976) formalised the colony dynamics by two differential equations (see "dynamic constraints" in subsection 1.2.4) representing the temporal change in worker number $W(t)$ and sexual number $S(t)$ ($W(t)$ and $S(t)$ are the state variables).

$$\frac{\partial W(t)}{\partial t} = u(t)R(W(t)) - \mu W(t) \tag{1.10}$$

$$\frac{\partial S(t)}{\partial t} = (1-u(t))R(W(t)) - \nu S(t) \tag{1.11}$$

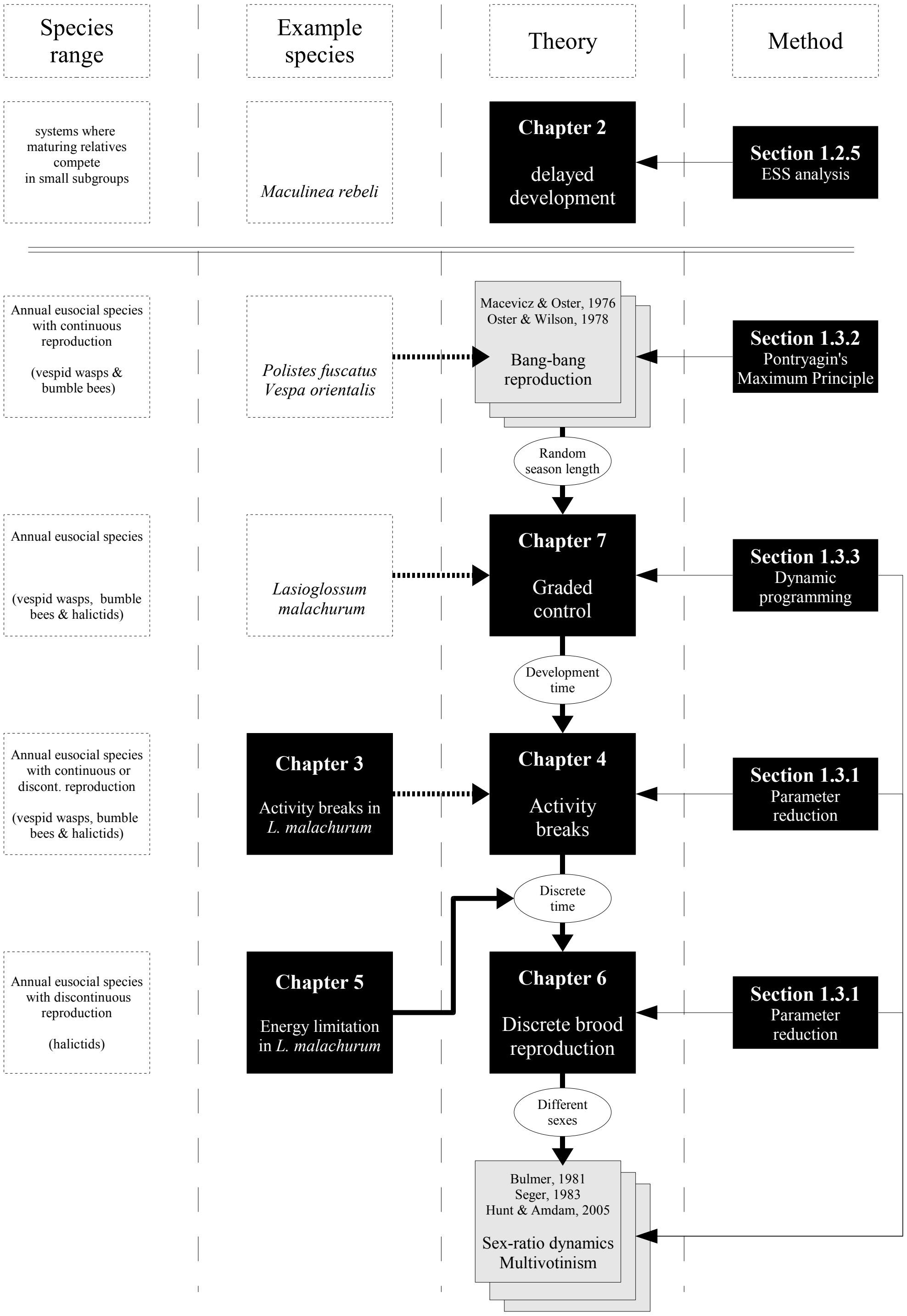

Figure 1.2: Schematic illustration of the methods and topics of this thesis. The specific realisation of the general methods is exemplified in the corresponding chapters.

$$\text{for } t \in [0;T]; W(0) = 1; S(0) = 0; u(t) \in [0;1]$$

Workers and sexuals suffer from mortality rates μ and ν respectively and the colony cycle starts with the presence of a single worker (i.e. the founding female, $W(0) = 1$) and without young sexuals ($S(0) = 0$)). Available resources R are a function of the worker number ($R = R(W(t))$) and divided into two possible parts. A fraction $u(t)$ is invested into new workers and $1 - u(t)$ into new sexuals (resource constraint, see subsection 1.2.4).

Fitness is measured by the life-time reproductive success of the colony, thus, the rate of fitness increase is $I(t) = \frac{\partial S(t)}{\partial t}$ and overall fitness is $F(E) = \int_0^T I(t)dt = S(T)$, the number of sexuals at the end of the season (see subsection 1.2.3).

The major result of Macevicz and Oster's optimisation analysis based on Pontryagin's Maximum Principle (see subsection 1.3.2) was, that the optimal allocation pattern is a so called "bang-bang strategy" (for technical details see Macevicz & Oster, 1976; Oster & Wilson, 1978). The colony cycle should start with the exclusive production of workers and then switch to the exclusive production of sexuals at an optimal point in time. In the case of constant resource availability and linear dependency of resource allocation on worker number ($R(t) = cW(t)$) the optimal switching time can be predicted as an analytical function of the season length (T), the productivity rate of the workers (c) and the mortality rates of workers and sexuals (μ and ν).

Although the theoretical studies of Macevicz and Oster (1976) as well as of Oster and Wilson (1978) have yielded a fundamental result in life history analysis of social insects, their work has not been continued and expanded until now. The authors suggested several modifications of the model system and gave predictions for the corresponding results, but it will turn out, that these were not always apt (chapter 7).

1.4.2 A bet-hedging hypothesis for graded control

One of their predictions concerns deviations from the pure bang-bang strategy. Field observations in bumble bees (Roseler, 1970; Müller & Schmid-Hempel, 1992), wasps (Smith, 1956; Blackith & Stevenson, 1958; Greene *et al.*, 1976; Haggard & Gamboa, 1980; Greene, 1984; Kolmes, 1986; Martin, 1991) and halictid species (Yanega, 1988, 1993; Strohm & Bordon-Hauser, 2003; Hirata *et al.*, 2005) indicate that gradual strategies with an intermediate reproductive period of simultaneous production of workers and sexuals are a common alternative to the predicted dichotomous strategy transition between exclusive worker and exclusive sexual production. Oster and Wilson (1978) suggested that this kind of strategy is an evolutionary response to unpredictable, coarse-scale variations in environmental conditions. When complete populations suffer from identical fluctuations the geometric mean is the appropriate measure of fitness (see subsection 1.2.3). As the geometric mean decreases with increasing variance in fitness, strategies which buffer fitness variations are favoured in stochastic environments. Such strategies are typically **gradual** strategies and the corresponding evolutionary principle is called "bet-hedging" or "spreading of risk" (Slatkin, 1974). This principle has been applied widely to explain gradual behaviour in animals and plants, however, often ignoring the details of life history dynamics. In solitary insects, it turned out several times that the sensitivity against environmental fluctuations is astonishing low (Hopper, 1999). Thus, a corresponding studies in social organisms are required (see chapter 7 of this work).

1.4.3 Nest founding

Oster and Wilson also pointed out that solitary nest founding in social insects plays a crucial role for colony success. Their arguments were mainly based on examples from ants, but also the ground nesting halictids spend considerable effort in solitary nest construction. Prominent changes in behaviour accompany the transition from nest founding to the ergonomic stage (e.g. the exclusive devotion of the queen to egg production). However, they are not considered by the original model of the colony cycle by Macevicz and Oster (1976) who treated the complete colony development exclusively based on worker ergonomics.

Kaitala *et al.* (1990) investigated nest usurpation as a specific aspect of nest founding with a dynamic programming approach (see subsection 1.3.3) and predicted the temporal course of the optimal number of floater females trying to take over a foreign nest. However, neither empirical evidence for the crucial role of nest founding in halictids nor a modelling approach for the complete nest cycle with specific account for the founding phase have yet been proposed (see chapter 5 and chapter 6).

1.4.4 Activity breaks during the nest cycle

The annual nest cycle of most halictids is – in contrast to wasps and bumble bees – not a continuous period of activity (Sakagami, 1974; but see Richards, 2004), but a sequence of active and inactive phases (figure 1.3). After the founding phase, when a halictid queen has provisioned several brood cells, she closes the nest for a few weeks and no activity can be observed outside the nest. With the emergence of the first workers the nest is reopened. However, the activity period of the first workers is limited, too. After two or three weeks the nest is closed again. Depending on the geographical location the switch between activity and inactivity can be repeated for

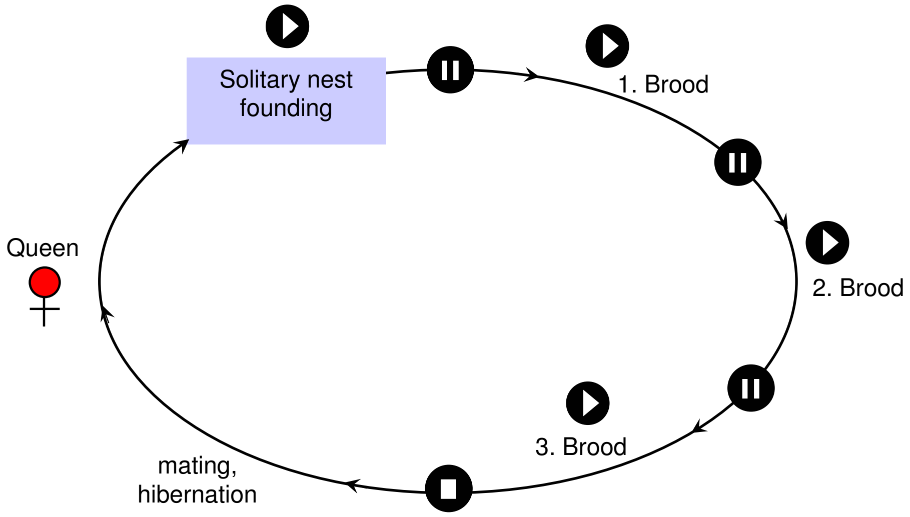

Figure 1.3: Schematic illustration of an halictid's nest cycle

several times until the sexuals emerge (Yanega, 1997; Wyman & Richards, 2003). In *Lasioglossum malachurum* only a single worker brood can be observed in northern Germany, but up to four broods in southern Greece. Some other species even switch to solitary nesting when season length is very short, e.g. in high altitudes (Eickwort *et al.*, 1996; Miyanaga *et al.*, 1999). The prominent activity pattern of halictids has not yet been described quantitatively (but see chapter 3). However, this is the precondition for a modelling analysis linking the activity pattern to the classical analysis of colony dynamics by Macevicz and Oster (1976) (see chapter 4) and providing an evolutionary investigation.

Up to now the analysis of temporal patterns in the nest cycle of eusocial insects is restricted to bumble bees where oscillations in brood production have been investigated theoretically as a emergent characteristic of colony dynamics but not against the background of evolution (Karsai *et al.*, 1996).

1.4.5 Dynamic sex ratios

Alternative models of colony dynamics have been proposed to analyse the variations in sex ratio during the nest cycle. Sex ratios in social insects are usually male-biased in early broods while female production is favoured at the end of the season. However, in many halictids early broods are female-biased (Strohm & Bordon-Hauser, 2003).

Bulmer (1981) and Seger (1983) developed models based on discrete brood dynamics to investigate the conditions favouring biased sex allocation. Their analyses considered the conflict of interest over the sex ratio between the queen and the workers. Sex ratios are not in the scope of this thesis, but our sequence of modelling approaches demonstrates a possible hierarchy and the structural transitions between model alternatives developed independently from each other and culminating at the level of discrete brood models.

1.5 SCOPE AND OUTLINE OF THE THESIS

As indicated above there are several possibilities to arrange the single chapters of this work, but the most general possibility is based on the classification of the behavioural alternatives under question. The two major parts of the work represent two pairs of behavioural alternatives. The first part (chapters 2, 3 and 4) focuses on the choice between activity and inactivity. In contrast to the remaining sections chapter 2 deals not with life history strategies in eusocial insects itself, but with the development strategy of a social parasite, the butterfly *Maculinea rebeli* whose larvae develop and feed within ant nests. The chapter links this work to a classical question of (solitary) life history theory, but also considers the dynamics of the social host. The major part of the larvae of *M. rebeli* (75%) delays development for a whole season, while the rest directly develops within a year, after the corresponding eggs were brought into the ant nest. We present an analytical model including all mechanisms known from field observations and predict the evolutionary stable fraction of fast-developing larvae (sensu subsection 1.2.5).

Inactivity on the level of the eusocial colony itself is analysed in the following two chapters (chapters 3 and 4). Other than in bumble bees and wasps the activity pattern of most eusocial halictid colonies is organised as a sequence of extended periods of activity and inactivity. We first present quantitative data on the entire temporal course of colony activity in the annual, primitively eusocial halictid *Lasioglossum malachurum* (chapter 3) to provide an empirical fundament for a theoretical analysis (chapter 4). We have observed the daily activity state of about 1200 nests in 2003 at 13 different sites. Several sites have been located near heating pipes at the Hubland campus of the University of Wuerzburg. Thus, it was possible to study the nest cycle in different temperature regimes.

These empirical data allowed for a corresponding ultimate modelling analysis (chapter 4). In the original version of Macevicz and Oster's model of eusocial colony development, switches between active and inactive colony states can only be explained by assuming an external trigger, such as specific variability in resource availability or in predation risk. However, several simple modifications of the model provide the possibility to analyse the potential evolution of expanded inactive periods as an emergent characteristic of colony dynamics itself. The key modification is the introduction of finite development rates of the brood instead of the implicit assumption of instantaneous development in the model by Macevicz and Oster.

Part II (chapters 5, 6 and 7) investigates the choice between growth and reproduction in social insects. At the level of a eusocial colony this choice arises as the question about the optimal investment in workers and sexuals during the annual nest cycle. This is exactly what has been analysed by Macevicz and Oster (1976). However, their approach was based on a single constraint of the system, the limited season length. Chapter 5 demonstrates that in the ground nesting halictid species *L. malachurum* queens suffer from high energy loss during the solitary nest founding phase. Thus, energy limitation is likely to be an additional factor influencing the optimal investment pattern.

The combination of the results of chapter 4 (stability of the temporal activity pattern with respect to variation in the productivity and mortality rates of the individuals) and chapter 5 (energy limitation of the queen) leads to an alternative modelling approach for the annual eusocial colony cycle. As a consequence, the advanced mathematical methods required to analyse the optimal control system by Macevicz and Oster (1976) can be replaced by simple algebraic equations representing the discrete brood structure of colony development.

The last manuscript (chapter 7) directly ties to Macevicz and Oster's classical work (1976) on optimal resource allocation. Based on a short remark about the effect of risk spreading on dynamic resource allocation in annual eusocial insects, gradual investment patterns have widely been considered as bet-hedging response to environmental variations. However, the causal relationship has never been analysed in detail within the framework of colony dynamics. Our investigation bridges that gap and explicitly states the conditions under which environmental fluctuations are sufficient to promote graded strategies and which are not. Therefore we could directly use Macevicz and Oster's (1976) formalisation of the colony dynamics, but had to add some random variability in season length and to apply stochastic optimisation methods.

Part I

Activity versus inactivity

from www.macman-project.de

Chapter 2

An ESS model for the evolution of dimorphic development strategies in the butterfly *Maculinea rebeli*, a social parasite of *Myrmica* ant colonies

with Thomas Hovestadt (first author), Graham W. Elmes, Jeremy A. Thomas and Michael E. Hochberg

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Abstract. Larvae of the butterfly *Maculinea rebeli* develop as parasites inside ant colonies. In intensely studied French populations about 25% of larvae mature within one year ("fast-developing larvae" FDL), the others after two years ("slow-developing larvae", SDL); this ratio is predetermined, presumably genetically. We present an analytical model to predict the evolutionary-stable fraction of FDL (p_{ESS}). The model accounts for added winter mortality of SDL, general and sibling competition among larvae, a competitive advantage of SDL over newly entering FDL ("priority effect"), and avoidance of renewed infection of ant nests by butterflies in the coming season ("segregation"). We come to the following conclusions: (i) all factors listed above can promote the evolution of delayed development. (ii) Kin-competition and segregation stabilises p_{ESS} near 0.5. (iii) A priority effect is the only mechanism potentially selecting for $p_{ESS} < 0.5$. However, given the empirical data p_{ESS} is predicted to fall closer to 0.5 than the 0.25 that has been observed. Presumably, previously unsuspected fitness benefits for SDL also contribute to the evolution of delayed development. The model presented here may be of general applicability for systems where maturing relatives compete in small subgroups.

2.1 INTRODUCTION

The social parasite of ants, *Maculinea rebeli* (Lycanidae) (Elmes *et al.*, 1991a; Thomas *et al.*, 1998b) and its congeners (Als *et al.*, 2002; Schönrogge *et al.*, 2000; Witek *et al.*, in press) are remarkable and rare examples of the presence of a fixed larval growth dimorphism with annual and biennial development. The time taken to develop into a mature individual is a critical life history component of an individual's fitness with delayed development being almost universally associated with added costs, e.g. an increased mortality risk during the prolonged time of development or an increase in generation time. Nonetheless, polymorphism in developmental time has been described for a number of other insect species (Danks, 2002). A straightforward explanation for the existence of polymorphic developmental times is that some individuals are constrained by the lack of critical resources to complete development within a certain time span (e.g. Peck & Walton, 2005). However, a number of arguments have been brought forward to explain developmental polymorphism on the basis of adaptive arguments, e.g. the avoidance of kin-competition (Ellner, 1985) and the spread of risk in fluctuating environments ("bet-hedging"; Cohen, 1966; Hopper, 1999; Menu *et al.*, 2000; van Dooren & Metz, 1998; Venable & Brown, 1993).

In the case of *M. rebeli*, the most studied of the cuckoo *Maculinea*, all larvae feed briefly on the flower buds of an initial food-plant, but further development depends on their adoption, as very small final instar larvae (Elmes *et al.*, 2001) into a specific host ant's nest, where they might compete with other larvae for resources provided by the nurse ants (for a complete description of life history see Elmes *et al.*, 1991a,b; Hochberg *et al.*, 1994, 1992; Thomas *et al.*, 1998a, 1993, 2005; Thomas & Wardlaw, 1992). Some larvae grow rapidly following adoption, overwinter as half-grown larvae, complete growth in the following spring, and eclose in early summer to complete the life-cycle. Others grow little in the first summer, overwinter as small larvae but grow considerable during the early part of the second summer; they survive a second winter inside the ant colonies and complete their growth in spring – nearly two years after entering the ant colony (Elmes *et al.* (1991b), especially see Thomas *et al.* (1998b), figure 3 for growth trajectories). Initial laboratory rearing experiments indicate that the decision to take the "fast" (one year) or "slow" (two years) growth trajectory is not dependent on rearing conditions such as amount of food available to the larvae or competition with other larvae (Elmes *et al.*, 1991b), as has been reported in other instances (Edgerly & Livdahl, 1992). Also, the initial weight of a larva when adopted into ant nest (affected by early growth on the food-plant) does not determine subsequent growth strategy in the ant nest - a heavy larva is as likely to grow slowly as a light one (Thomas *et al.* (1998b) based on unpublished results of detailed laboratory rearing experiments). The laboratory data strongly indicate that the fraction of larvae following the fast or slow growth trajectories is either genetically predetermined or in some way controlled by the mother during oviposition (Elmes *et al.*, 1991b; Thomas *et al.*, 1998b). The proportion of larvae taking either trajectory seems to be stable across two isolated but locally widespread populations of *M. rebeli* from the Spanish Pyrenees and the French Alps. Overall 0.74 (± 0.02 SE) of all larvae followed the slow-developing path. This did not vary when the larvae were reared by a non-host species (poorer rearing conditions, Thomas *et al.* (1998b)).

Schönrogge *et al.* conclude that a dimorphic development might be a more general consequence of parasitising ant nests presenting data for a *Microdon* hoverfly and other *Maculinea* species (see also Als *et al.* (2002); Witek *et al.* (in press)); in particular they showed that the phenomena was present in three distinct geographic races of *Maculinea alcon*. These data suggest that in *M. alcon* the ratio of fast-developers:slow-developers might be near 1:1; however, this and other studies have not yet repeated the large scale rearing tests that gave the 3:1 estimate for *M. rebeli*.

Due to the peculiar life history of this species, standard explanations (Hopper, 1999) for the evolution of diapause cannot easily be applied, because several factors are likely to be involved. First, the number of larvae entering an ant-colony is typically larger than the number of larvae which can successfully be raised (Hochberg *et al.*, 1994, 1992; Thomas *et al.*, 1998a). Avoidance of competition may thus be a fundamental benefit of delayed development.

Second, there is evidence that the larvae adopted into a nest are in part siblings (cf. Elmes *et al.* (1996), Thomas unpub.). This is mainly a consequence of only a small proportion of all gentian buds being at a suitable developmental stage for oviposition, during the 1-3 days that a typical female lays eggs, combined with a shortage of gentians on many, often small, sites (Thomas & Elmes, 2001). Consequently the eggs of any particular female tend to be more clustered than the overall distribution of eggs on the site would imply. Larvae from eggs laid on the same day on the same clump of gentians generally become available for adoption at the same time and are likely to be adopted in the same nest. As competition among and within cohorts of sibling larvae is often intense, it appears reasonable that avoidance of kin-competition is an important factor driving the evolution of the dimorphic growth strategy (Ellner, 1985).

Third, if nests are infected over several years, slow-developing larvae grow under a different competitive regime than fast-developing larvae: the latter must compete with both the fast growing cohort and the larger resident slow-developers for all but the last few weeks of development (slow-developers tend to pupate slightly earlier than competing fast-developers). Slow-developers avoid competition by growing little until the previous year's slow-developers and their contemporary fast-developers near pupation. Subsequently they tend to be larger than any of the new larvae taken into the

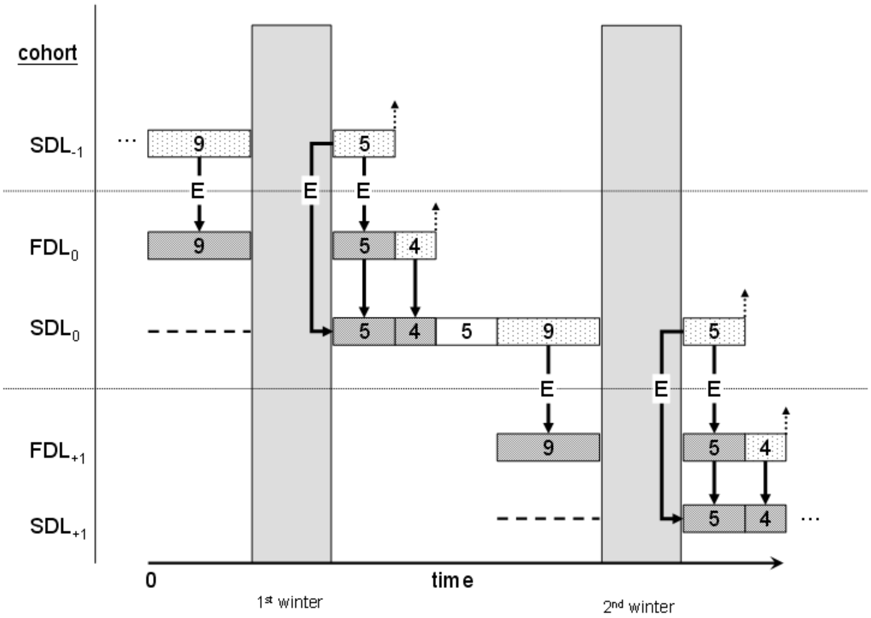

Figure 2.1: Schematic presentation of life-cycle of *M. rebeli* within host-ant colonies (after Thomas *et al.* (1998b)). Fast- (FDL_0) and slow-developing larvae (SDL_0) of the focal cohort enter the colony at time 0. FDL_0 start to grow immediately for ca. 9 weeks, SDL_0 remain dormant until the next spring. Depending on the situation, the larvae have to compete with larvae which already entered the nest in the previous year (SDL_{-1}) and/or with larvae which will enter the nest in the following season (FDL_{+1} and SDL_{+1}). Short dotted arrows indicate time of pupation. Heavy arrows indicate the competition between larger and smaller sized cohorts. The bars indicate different phases in development with the numbers indicating (average) duration in weeks. Bars are dark hatched if the cohort (potentially) suffers from competition by larger larvae, lightly hatched, if cohort competes with smaller larvae, and not filled, if cohort does not compete with larvae from any other cohort. Competition arrows marked with "E" do not apply if larvae enter an ant nest which was not infected in the previous season (mostly to the benefit of FDL_0) or if the colony segregates in the coming season and thus avoids immigration of new larvae in the following season (to the benefit of SDL_0).

nest (figure 2.1).

Elmes *et al.* (1991a) show that large (half-grown) larvae are 5 times more likely to get attention (grooming and feeding) from worker ants than small larvae ($<\frac{1}{4}$ grown). After living one year in an ant nest, the SDL are so closely integrated with their host's society that the newly adopted FDL are neglected after retrieval by foragers and deposition in the ant brood chamber, especially in societies where the ratio of SDL or ant brood to nurse ants is high (e.g. Elmes *et al.*, 2004; Schönrogge *et al.*, 2004). There is thus evidence that resident slow-developing larvae have competitive advantage over newly arriving fast-developers in the second summer, especially when the nest is near its rearing capacity (cf. Thomas *et al.* (1998b), Thomas unpub.): we term this effect "priority effect". The presence of such a priority effect has been documented in some cross-species examinations (Blaustein & Margalit, 1996; Shorrocks & Bingley, 1994) but also within species, e.g. salamanders (Eitam *et al.*, 2005). Fourth, ant nests can in principle be infected by new *M. rebeli* larvae year after year. However, plant turnover and, especially, the tendency of infected ant colonies to move to nests in new locations (taking along the *Maculinea* larvae already in the nest!) removes a fraction of ant colonies into refuges where they are not at risk of a new infection in the coming year (Hochberg *et al.*, 1994; Thomas *et al.*, 1998a; Thomas & Elmes, 1998; Thomas *et al.*, 1997). Such "ergonomic segregation" leads to a separation of this year's slow-developing from next year's fast-developing larvae and reduces competition between the two cohorts of larvae and occurs quite frequently (Thomas *et al.*, 1998b; figure 1). The above arguments are non-exclusive, making it difficult to assess their quantitative contribution to and interaction in the evolution of delayed development of *M. rebeli* larvae. A quantitative evaluation can thus only be based on a formal and quantitative model considering the effect of all of these factors. Here, we present an ESS-model incorporating all the above parameters. We will demonstrate that the evolution of delayed development is in fact adaptive in a wide range of conditions but that only the priority effect can explain why more than 50% of the larvae postpone development into the second year. However, empirical parameter estimates and model predictions are not in exact agreement, and we consider additional factors that potentially contribute to the evolution of delayed development.

2.2 MODEL AND RESULTS

Taking account of the above considerations we develop a general analytical model to predict the evolutionary stable fraction of larvae developing in the first year (p_{ESS} – see table 2.1 for a summary of symbols used throughout the text). We currently have a fairly accurate knowledge of the fraction of larvae delaying development (i.e. in the range 0.25-0.35) but not of the values of all the parameters likely to affect the ESS. Thus, a future test of our model requires estimating these unknown parameters and comparing them with model predictions.

2.2.1 Expected number of offspring

In the model, we estimate the expected number of offspring to emerge from single ant nest for a focal female following a given strategy (p) in a model that accounts for (i) the role of added density-independent winter survival (μ) of those larvae delaying development into the second year, (ii) the effect of overall competition between larvae (ε), (iii) the effect of relatedness between larvae, i.e. the fraction of all larvae which are offspring of the female under consideration (f), (iv) the consequence of an existing competitive advantage, or priority effect (α) of second year larvae over those newly entering an ant colony in the following summer, and (v) the consequences of competitive segregation (E) between fast- and slow-developing larvae due to nest relocation. We assume that the number of adult butterflies (A) emerging from an ant colony can be scaled to the colonies capacity as

$$A = \frac{K \cdot L}{K + L} \tag{2.1}$$

with

$$L = \varepsilon \cdot K \tag{2.2}$$

where L is the number of butterfly larvae competing in an ant colony and K is the capacity of an ant nest to successfully raise butterfly larvae. This equation is convenient and at least qualitatively catches the observed asymptotic relationship between the number of *M. rebeli* larvae entering a nest and the number of butterflies successfully emerging from it (Hochberg *et al.*, 1994, 1992). The average capacity K clearly affects overall production of adult butterflies on any particular site but has, as we will see, no effect on the evolution of the ESS. In the graphics we thus scale, without loss of

Table 2.1: List of symbols used in text and equations. Throughout the text, a suffix "R" at any symbol indicates values for the resident strategy, the suffix "M" values for the mutant (invading) strategy. The suffix "1" relates to values derived in the first year (FDL) and the suffix "2" to values derived for the second year (SDL). Finally, the suffix "F" is used if a value only relates to FDL and the suffix "S" if it only relates to SDL.

Symbol	Definition	Comment [parameter range]
p	fraction of larvae developing in first year	evolving strategy parameter [0 .. 1]
L	number of larvae competing in ant colony	$L = \varepsilon K$
K	carrying capacity of ant colonies	no effect on evolution of ESS [0 .. 8]
μ	winter survival in second winter	only for SDL [0 .. 1]
ε, ε'	intensity of overall competition between larvae. Hyphen indicates values adjusted for feedback effect of resident strategy on competition.	[0 .. 8]
f, f'	fraction of larvae entering colony which are offspring of focal female. Hyphen indicates values adjusted for feedback effect of resident strategy on competition.	[0 .. 1]
α	competitive advantage of SDL over newly arriving FDL (see text)	[0 .. 1]; 0=symmetric competion; 1= complete dominance of SDL
E	segregation index, i.e. fraction of infected colonies moving away from host plant neighbourhood (see text)	[0 .. 1]; 0=no segregation; 1=complete segregation
c	added fitness benefits for SDL after emergence, e.g. higher survival, fecundity	multiplier for SDL fitness calculated from model; [1..∞[
A	number of adults emerging	number of larvea surviving till pupation
g	fraction of emerging adults which are offspring of focal female	
O	number of offspring for focal female	$O = A \cdot g$

generality, all results to a value of $K = 1$.

It is further convenient to scale the number of larvae entering an ant nest to the colony's carrying capacity (equation 2.2). The parameter ε thus defines the general level of competition between larvae inside the ant colonies and site-specific differences in K and ε can be expressed as differences in ε when K is fixed at unity. Field data collected for *M. rebeli* typically gives $K \approx 8$ and $\varepsilon \approx 3.2$ (estimates based on information in Hochberg *et al.* 1994; Hochberg *et al.* 1992; Thomas and Elmes 1998). However these field data also indicate a systematic difference between sites where $\varepsilon \approx 2.2$ in those having low densities of gentian food-plants (about 100/ha) and $\varepsilon \approx 6$ in sites with high plant densities (about 2000 plants/ha). This is on the one hand due to small differences in the clumping parameters for gentian distribution and the distribution of eggs on gentians resulting in higher values of L on high density sites. On the other hand, the average carrying capacity (K) of nests being greater on low density sites (see Elmes *et al.*, 1996) because more host-nests live in enemy free space (this only affects ε when segregation $E > 0$).

Without loss of generality, we next focus on the reproductive output of a specific female following either the resident (p_R) or a mutant strategy (p_M). We assume that a fraction f of all the larvae entering an ant colony is descended from this focal female (see introduction). It is difficult to estimate f accurately. However, field data (Elmes *et al.*, 1996; unpublished) suggest that f may fall into a range of 0.05 to 0.25, with higher values occurring on sites with low food-plant densities.

As a reference, we assume that the population originally consists of fast-developing larvae (FDL) only and that nests do not segregate ($E = 0$). It is straightforward to calculate the expected number of offspring emerging from this ant colony and for the specified (as any other) female in such a population of pure FDL (the term O_R will be used to indicate the expected fitness of the resident strategy throughout the paper):

$$O_R = f\frac{KL}{K+L} = f\frac{\varepsilon K^2}{K(1+\varepsilon)} = f\varepsilon K\frac{1}{1+\varepsilon} \tag{2.3}$$

An ESS strategy can resist invasion by any other strategy (Bulmer, 1994; Geritz *et al.*, 1998; Maynard Smith & Price, 1973). To find it, we first address the question under which conditions a mutant female allocating a fraction $p_M < 1$ of its larvae to FDL and consequently $1 - p_M$ larvae to slow-developing larvae (SDL) could successfully invade a resident population of pure FDL ($p_R = 1$). As we assume a population at stable equilibrium, life-time reproductive success (R_0) is an appropriate fitness measure and a criterion for mutant invasability (Benton & Grant, 1999; Heino *et al.*, 1997; Mylius & Diekmann, 1995; van Dooren & Metz, 1998) (see also Brommer *et al.*, 2004). Consequently, a resident strategy can resist invasion if the expected number of offspring for a mutant female (O_M) is smaller than that of females following the resident strategy. If otherwise, the mutant strategy will invade.

Obviously, a mutant female can expect some offspring to emerge from both years, i.e.

$$O_M = O_{M,1} + O_{M,2} \tag{2.4}$$

In the appendix (subsection 2.4.1) we derive the equations which allow the magnitude of the two fitness components $O_{M,1}$ and $O_{M,2}$ to be estimated. Combining equation 2.3 and equation 2.21 the condition for invasion is $O_R < O_M$, that is:

$$\begin{aligned} f\varepsilon K \frac{1}{1+\varepsilon} &< f\varepsilon K \left(\frac{p_M}{1+\varepsilon(1-f+fp_M)} + \frac{a_{M,2}(1-p_M)\mu}{1+\varepsilon(1+f(1-p_M)\mu)} \right) \\ 0 &< (1+\varepsilon) \left(\frac{p_M}{1+\varepsilon(1-f+fp_M)} + \frac{a_{M,2}(1-p_M)\mu}{1+\varepsilon(1+f(1-p_M)\mu)} \right) - 1 \end{aligned} \tag{2.5}$$

Note that the right side of this inequalities collapses to the left side if we set $p_M = 1$, the resident strategy. The parameter μ accounts for the added mortality risk the SDL experience in the second winter. At least under laboratory conditions, winter survival is very high in *M. rebeli* (Thomas *et al.*, 1998b), i.e. μ is typically between 0.9 and 0.95, but it may be lower (say 0.8) under natural conditions. In addition, from the second autumn onwards, newly adopted FDL will compete with the SDL from the previous season, requiring us to account for the priority effect, i.e. the competitive dominance of SDL over the new cohort of FDL. This is achieved by introducing the model parameter α contained in the term $a_{M,2}$ (see equation 2.18 and equation 2.19 for its derivation). α is constrained to fall into the interval $0 \leq \alpha \leq 1$: a value of "0" implies complete competitive symmetry between FDL and SDL, a value of "1" complete competitive dominance of SDL over FDL. In figure 2.2 we show how the overall fitness O_M compares to O_R. The figure illustrates that under competitive symmetry it might be possible for a mutant with p_M in range 0.7-1.0 to invade a population of pure FDL and that already a fairly weak priority effect (α) greatly increases the range of mutants p_M capable of invading a pure FDL population.

2.2.2 Finding the ESS

We now turn to the problem of finding the ESS strategy, i.e. a resident strategy p_R that cannot be invaded by any other mutant strategy. First, we need drop the assumption that the resident strategy is $p_R = 1$; instead, p_R can take any value between 0 and 1. From the point of view of any female ovipositing in year 0 and following the resident strategy p_R, there are now four different "types" of adults emerging over a two year period: Adults from FDL and SDL in the first year ($A_{1,F}$ and $A_{1,S}$) and the second year ($A_{2,F}$ and $A_{2,S}$). The expected fitness for a female (O_R, the total number of emerging offspring) thus depends on the number of these emerging adults and her "relatedness"

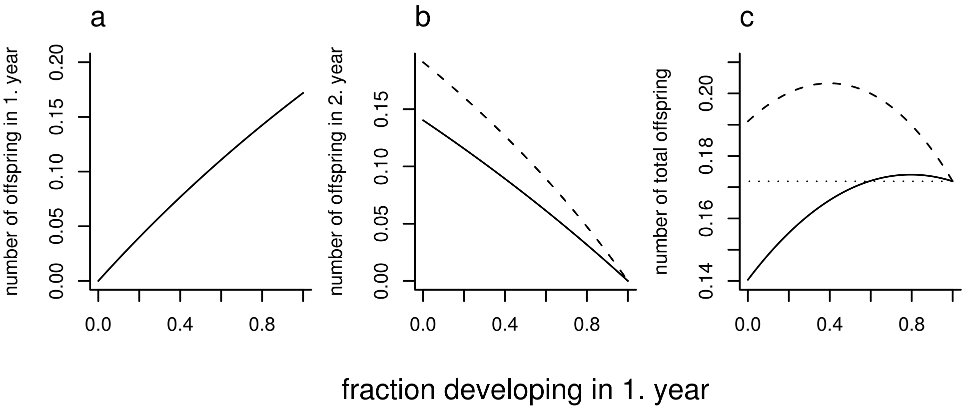

Figure 2.2: Relationship between the fraction of larvae developing in the first year (p_M) and the expected number of offspring for a mutant female invading a population of fast-developers (FDL, p_R=1.0) with parameters K=1, ε=2.2, $f = 0.25$, $E = 0$, and $\mu = 0.95$ (realistic parameters estimated for sites with low host plant density). Panel (a) shows the expected number in the first year, panel (b) in the second year, and panel (c) the total number over both years. The solid lines in (b) and (c) give expected number under the assumption of competitive symmetry between FDL and SDL ($\alpha = 0$), the hatched lines under the assumption of a moderate competitive advantage ($\alpha = 0.25$) of SDL over FDL (see text). The dotted line indicates expected offspring number for the resident FDL-strategy. Any mutant with an expected fitness above this threshold line can invade a population of pure FDL.

($g_{.,.}$) to them. Clearly, the female is neither related to the $A_{1,S}$ nor to $A_{2,F}$, i.e. $g_{1,S} = g_{2,F} = 0$. The females expected fitness can thus be calculated by summation of the following terms:

$$O_R = O_{R,1} + O_{R,2} = A_{1,F}g_{1,F} + A_{2,S}g_{2,S} \tag{2.6}$$

where $g_{1,F}$, and $g_{2,S}$ measure her relatedness to adults emerging from the FDL and SDL in years 1 and 2, respectively.

In the appendix (subsection 2.4.2 and subsection 2.4.3) we derive the equation which gives the expected number of offspring for a female following the resident strategy p_R including also the effect of segregation (E; see introduction). In addition, we need to adjust the environmental parameters ε and f to ε' and f' to account for the "feedback" effect the resident strategy itself has on the values of these environmental parameters (Metz *et al.* (1996); Mylius & Diekmann (1995), see appendix (subsection 2.4.5) for details). They remain unchanged only for the "reference strategy" $p_R = 1$.

In the special case of no segregation ($E = 0$) summation of equation 2.27 and equation 2.28 yields

$$O_R = O_{R,1} + O_{R,2} = f'\varepsilon' K \frac{p_R - (a_{R,1} - 1)(1 - p_R)\mu + a_{R,2}(1 - p_R)\mu}{1 + \varepsilon'[p_R + (1 - p_R)\mu]} \tag{2.7}$$

When the resident population is not a pure FDL population, we must also consider the competition between FDL and SDL from the previous year in the first season, and need an additional term $a_{R,1}$ to account for this effect as well as $a_{R,2}$, which accounts for the priority effect of SDL over new FDL entering in the next season. Their derivation is based on the same rationale introduced in equation 2.18 and equation 2.19 for the calculation of $a_{M,2}$, but is based on different quantities (cf. equation 2.25). However, for the case of a homogeneous population $a_{R,1} = a_{R,2}$ (equation 2.25 ff.). We can thus multiply through equation 2.7 and recognise that it collapses to (assuming $E = 0$):

$$O_R = f'\varepsilon' K \frac{p_R + (1-p_R)\mu}{1+\varepsilon'[p_R + (1-p_R)\mu]} \tag{2.8}$$

i.e. in a homogeneous population the expected number of offspring is not affected by the existence of a priority effect. It is possible to show (appendix subsection 2.4.5, equation 2.43 ff.) that in a homogeneous population the optimal strategy in the absence of segregation ($E = 0$) is always $p_R = 1$ and may thus be different from the ESS. If segregation occurs, an analytical solution for the optimal strategy can still be found but it is too complex to be useful. The resident strategy p_R will prevail in the population if its expected number of offspring is larger than that of any mutant strategy p_M. To estimate the expected fitness of a mutant female whose larvae enter a colony to compete with larvae following the resident strategy, we again need to separate between the four different adult compartments. However, in a nest with a mutant female, different equations apply (appendix subsection 2.4.4) than in a nest that contains only females that follow the resident strategy. The simplified equation 2.40 for the case of no segregation ($E = 0$) is:

$$\begin{aligned}
O_M &= A_{M,1,F} \cdot g_{M,1,F} + A_{M,2,S} \cdot g_{M,2,S} \qquad (2.9)\\
&= \varepsilon' K f' \frac{(1-f')p_R + f'p_M - (a_{M,1}-1)(1-p_R)\mu}{1+\varepsilon'[(1-f')p_R + f'p_M + (1-p_R)\mu]} \cdot \frac{p_M}{(1-f')p_R + f'p_M}\\
&+ a_{M,2}\varepsilon' K f' \frac{(1-p_M)\mu}{1+\varepsilon'[p_R + (1-f')(1-p_R)\mu + f'(1-p_M)\mu]}
\end{aligned}$$

To clearly separate the estimates for this situation from the "standard" situation with resident strategies only, we introduce the terms $a_{M,.}$, $A_{M,.,.}$ and $g_{M,.,.}$ respectively. A strategy fulfilling the ESS-stability criterion (Geritz *et al.*, 1998) meets the following condition (Bulmer, 1994) defined for the special case $E = 0$ by equation 2.8 and equation 2.9:

$$O_R > O_M \text{ for all } p_M \neq p_R, \text{ respectively all } \Delta \neq 0 \tag{2.10}$$

Unfortunately, it is not possible to find a general analytical solution (but see below) to this equation and we thus had to rely on numerical approaches to find the ESS (all done with MATHEMATICA 4.0, Wolfram Research 1999). As equation 2.9 gives an implicit and highly nonlinear relationship between p_R and p_M, we need to scan the

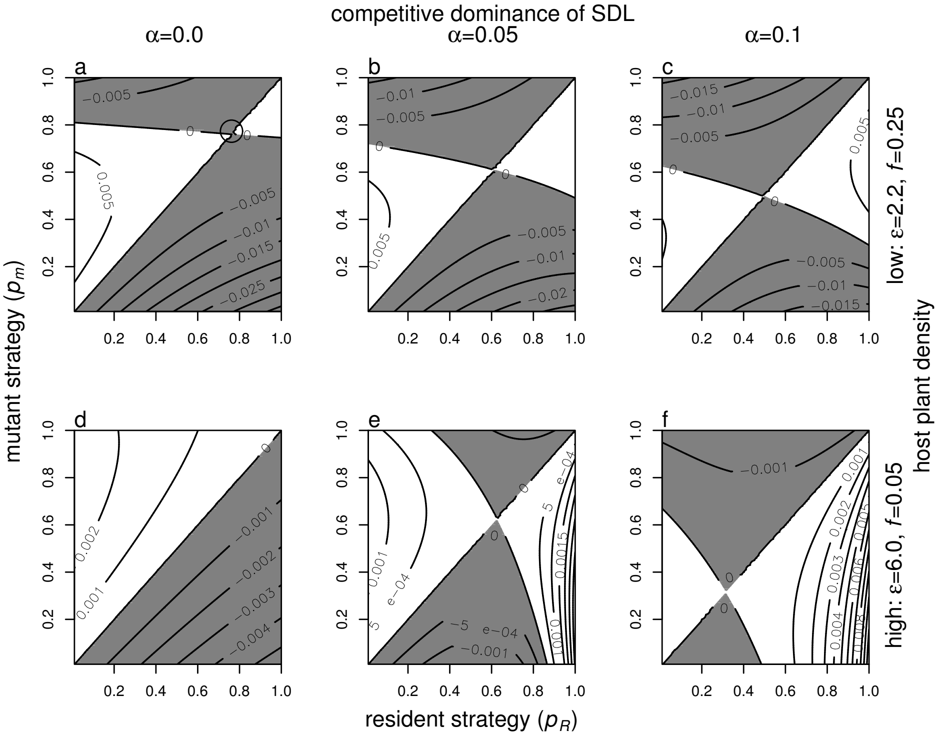

Figure 2.3: Difference between expected fitness of resident and mutant strategy for K=1, and $\mu = 0.95$. In the top row (a-c), we set $f = 0.25$ and $\varepsilon = 2.2$ values characteristic for sites with low host plant density; in the bottom row (d-f) $f = 0.05$ and $\varepsilon = 6$, values more typical for high density sites. Values for competitive dominance of SDL over FDL increase from $\alpha = 0$ (a,d) to $\alpha = 0.05$ (b,e), and $\alpha = 0.1$ (c,f). Grey areas indicate regions where the resident strategy is superior to the mutant strategy; in white areas the reverse statement is true. An ESS is thus indicated by a point with grey above an below the main diagonal. In panel (a) the ESS is exemplarily marked by a circle. If the whole upper triangle appears in white (as in d), the ESS is $p_{ESS} = 1$, if the whole lower triangle is white, $p_{ESS} = 0$. According to the criteria outlined by Geritz *et al.* (1998) the ESS strategies not equal 0 or 1 are in fact "ESS-stable", "convergence stable" and can also invade other close strategies, i.e. the strategies are "continuous stable strategies".

complete p_R-p_M-parameter space to find those resident strategies p_R which satisfy the ESS condition. Figure 2.3 gives an example of the effect of differing levels of competitive dominance α, larval relatedness f, and overall competition ε on the ESS. Intermediate strategies ($0 < p_{ESS} < 1$) can exist over quite a wide range of values of α when f is high (as in sites with low gentian density) but only over a small range of α when f is low (as in high gentian density sites). With this procedure we test for local ESS-stability as well as "convergence stability" sensu Geritz *et al.* (1998), i.e. all ESS strategies $0 < p_{ESS} < 1$ are also continuously stable strategies (CSS).

If both strategy values are equal ($p_R = p_M$), equation 2.9 collapses into equation 2.8, therefore an ESS resident strategy $0 \leq p_{ESS} \leq 1$ can only exist if the root at $p_R = p_M$ is of even order. This fact serves to simplify numerical straightforward searching, as it provides a suitable initial point and an exclusion criterion to reject a given resident strategy without checking the whole possible strategy range.

For the special case of $\alpha = 0$ and $E = 0$, i.e. the absence of a priority effect and segregation, an explicit solution for the ESS does in fact exist – however, the equation is fairly complicated and of little practical use. Evaluation of this equation reveals that the ESS approaches values $p_{ESS} = 0.5$ as winter survival μ approaches values of 1, but that it never falls below this values whatever the values for ε or f.

For the more general case of $\alpha > 0$ we can plot the numerically derived ESS in a two-dimensional plane defined by α and f (figure 2.4). The rationale for presenting results in this way is that (i) the empirical estimates for these two parameters are less reliable than those for μ, ε, and K, (ii) they have the strongest effect on the ESS, and (iii) they show an interesting interaction in their effect on the ESS. Figure 2.4 shows that p_{ESS} is highly sensitive to the presence of a priority effect (α) especially on sites where gentian density is high; in other word, when winter survival μ is high and the fraction f of larvae derived from a single female is low, a small change in α can dramatically change the ESS.

However, this sensitivity declines as f becomes larger and the ESS (potentially) covers a wider range as winter mortality (μ) declines. Evidently, the ESS shifts closer to 0.5 if the fraction f of larvae expected to derive from a single female increases. This is due to the fact that delaying too many larvae also enhances the level of kin-competition between siblings in the second season and is thus not favoured by selection. The best estimates for f (ca. 0.25) in low gentian density sites as well as the laboratory estimates for winter survival ($\mu = 0.95$) are in fact of the appropriate magnitude to stabilise the ESS in the range observed in empirical studies. However, for high density sites (which are much rarer than small ones in the field, Elmes *et al.* 1996), f values seem to be too low to bring the predicted ESS into the range actually observed: the model predicts that an even smaller fraction of larvae should develop in the first year. Assuming lower values for winter mortality, which may be more realistic for natural conditions, the situation "improves" slightly. However, the ESS should nonetheless be highly sensitive to changes in either winter survival (μ) or the strength of the priority effect (α) – a result not in agreement with the observed stability of the fraction of larvae delaying their development (Thomas *et al.*, 1998b).

So far we have not yet accounted for the effect of segregation due to mobile ant colonies (see introduction). Field observations indicate that a fraction E as large as 0.6 of infected colonies succeed in moving their nest away from the domain of influence of host-plants (Elmes *et al.*, 1996; Thomas *et al.*, 1997). Evidently, the SDL larvae carried along with such a colony will not have to compete at all with new FDL larvae in the following season. A first, naive consideration may thus lead to the conclusion that segregation benefits the SDL only and should strengthen the selection for delayed

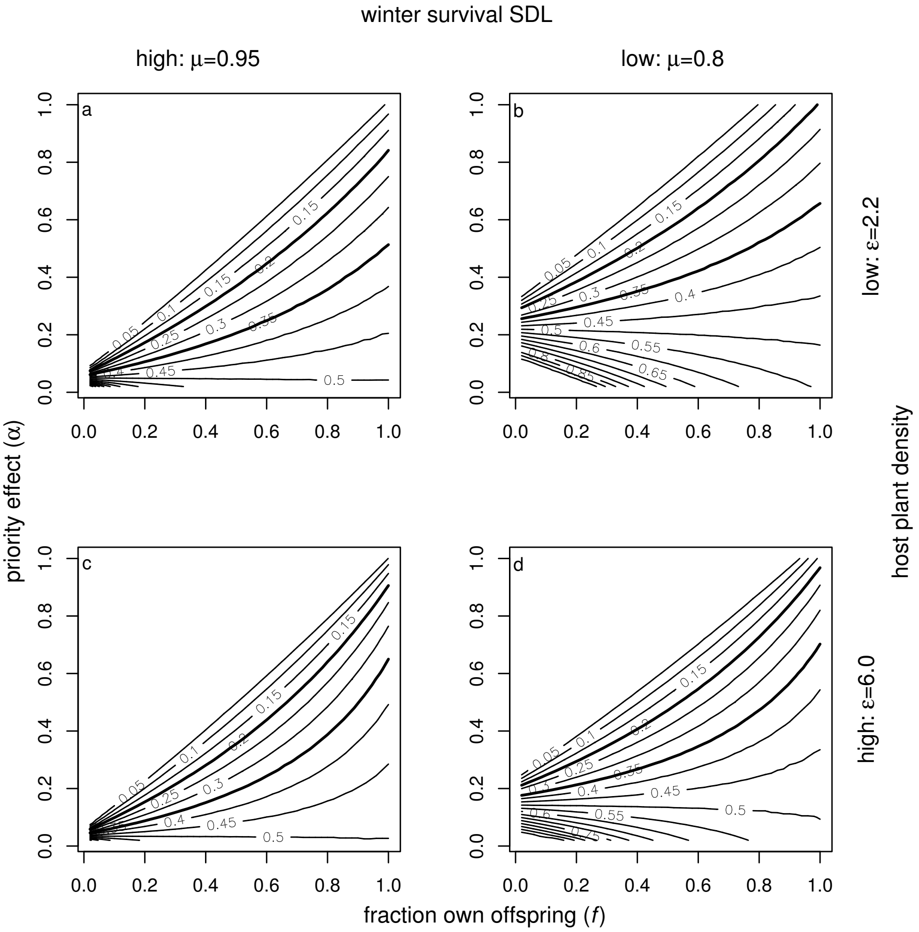

Figure 2.4: Contour lines for the ESS strategy (p_{ESS}) and dependence of the intensity of competitive dominance of SDL over FDL (priority effect, α) and changes in the fraction of larvae which are an individual female's offspring (f). In the top panels (a,b) overall competition $\varepsilon = 2.2$, a value typical for sites with low host plant (gentian) density; in the bottom panels (c,d), $\varepsilon = 6$, a value typical for high density sites. On the left side (a,c), winter survival for SDL is $\mu = 0.95$, on the right side (b,d), it is $\mu = 0.8$. Note that p_{ESS} tends to increase with increasing f if α is large, but to decline with f if α is small. The heavy contour lines envelope the range of p_R observed in the empirical studies.

development. However, segregation implies – if the whole population is in a steady state – that the number of ant colonies removed due to emigration into safe areas must be replaced by a similar number of uninfected colonies (Thomas *et al.*, 1997). These colonies will provide valuable opportunities for FDL to develop free of competition from SDL from the previous year (cf. figure 2.1). This is especially true if the priority effect (α) is strong because the SDL do not profit much from segregation if they can dominate the FDL anyways.

Thus, with segregation, FDL and SDL both only compete in a fraction $1 - E$ of colonies while they develop in a fraction E of colonies independently of competition

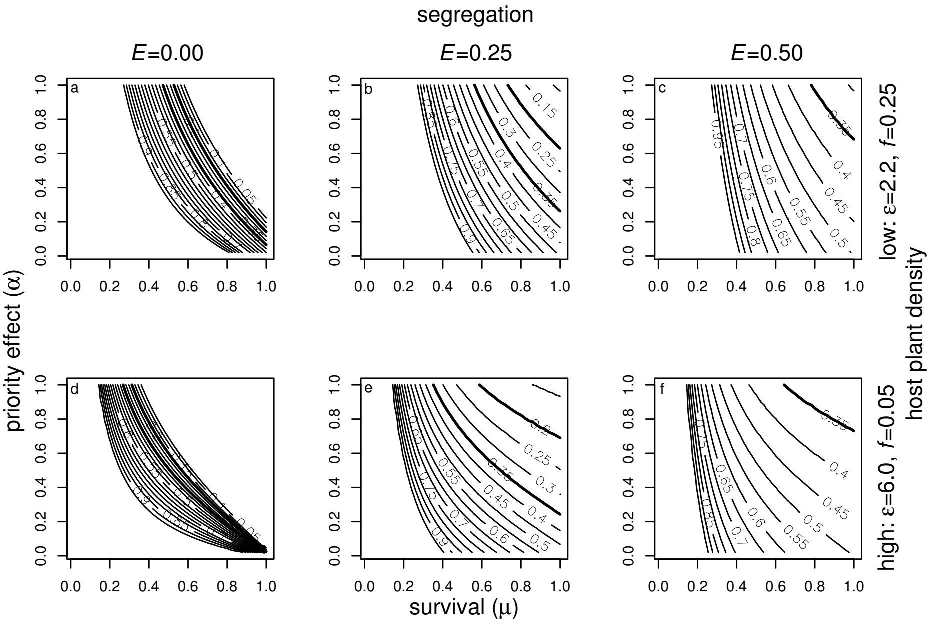

Figure 2.5: Effect of a segregation effect (E) on the ESS strategy under a parameter combination typical for small sites ($\varepsilon = 2.2$ and $f = 0.25$; a,b,c) and a combination more characteristic for large sites ($\varepsilon = 6$, $f = 0.05$; d,e,f). Left column: segregation $E = 0.0$, middle column $E = 0.25$, right column $E = 0.5$. The heavy contour lines envelope the range of p_R observed in the empirical studies.

from the other cohort (cf. appendix section 2.4 equation 2.27, equation 2.28, and equation 2.40). We have visualised the effect of segregation on the ESS in figure 2.5. It is obvious that increased segregation tends to stabilise the ESS at values closer to 0.5 and diminishes sensitivity against changes in α – a result that evidently makes sense: as both cohorts benefit from segregation, the optimal strategy in the case of complete segregation would clearly be 0.5 (if $\mu = 1$) no matter what the priority effect is. The latter in fact becomes irrelevant with complete segregation as the FDL and SDL from different seasons would never compete. The important message from figure 2.5 is that – given the empirical evidence for segregation – the priority effect would need to be stronger than currently plausible to obtain an ESS in the range actually observed.

2.3 CONCLUSIONS

The model presented here accounts for a number of factors which are all likely to affect the evolution of delayed development in *M. rebeli*. It demonstrates that combinations of parameter values for α, f, μ, and E can account for any observable fraction of SDL in the range between 0 and 1. Interestingly, changes in overall competition ε are of minor influence when $\varepsilon > 2$ which is the minimum value estimated for any site. In principal, this result is in itself quite important because we need not assume that time or energy constraints are responsible for the delayed development of larvae. However, the main problem is that realistic combinations of parameters do not fix the ESS in the region of 0.25, the observed value. General competition and kin-competition alone cannot drive p_R below 0.5. In the presence of sibling competition natural selection will favour strategies that increase the overall success of all larvae and not just the success of an individual larva. This tends to be maximised when p_R is close to 0.5 even if the winter mortality (μ) of SDL is very low. A similar conclusion holds for the effect of segregation which strongly selects for delayed development but never for $p_{ESS} < 0.5$ (see figures 2.4 and 2.5 for $\alpha = 0$). Thus, among all the parameters included in our model the priority effect α is the only mechanism that theoretically allows for the evolution of p_{ESS} values lower than 0.5.

Unfortunately, empirical information on parameter values in *M. rebeli* is limited. Estimates of ε, μ, and E are probably fairly reliable but that for f was only crudely and indirectly derived. Current field estimates indicate a high probability of segregation (E nearly 0.6). Natural values might be lower, especially on sites with lower gentian densities, but E is probably always > 0.25. At these levels of segregation only a very large priority effect (high α) could bring predicted values for the ESS into the range observed by Thomas *et al.* (1998b), i.e. a ratio of 3:1 in favor of SDL (figure 2.5 b, c, e, f). There are no field estimates of α but the data obtained from one laboratory experiment suggests that the priority effect is quite small. However it is not unreasonable to assume that under (severe) field conditions resident half-grown SDL might have considerable competitive advantages over newly adopted FDL. An attempt to estimate this parameter in wild populations of *M. rebeli* is therefore key to future research on this system. However, in light of the current empirical evidence, we thus have to admit that the fit between our model's prediction and the empirical observation is not satisfactory. Although the model incorporates four different mechanisms (overall competition, kin-competition, the priority effect, and segregation) that singly or jointly can select for delayed development, there could nonetheless be other factors involved. One might be the effect of environmental variability, for example, catastrophes affecting the whole adult butterfly or egg population. Such catastrophes or strong environmental variability favor the "dilution" of reproductive investment in space and/or time. Bet-hedging has been the primary argument brought forward to explain the evolution of dormancy in seeds (Cohen, 1966; Ellner, 1985; Ellner & Shmida, 1981), crustaceans (Maffei *et al.*, 2005) and insects (Menu & Desouhant, 2002; Soula & Menu, 2003). It is an alternative to dispersal in space (Hanski, 1988; Hopper, 1999) and has recently been cited as an important factor driving the evolution of delayed development in *Maculinea nausithous* and *teleius* (Witek *et al.*, in press). However, in the case of *M. rebeli*, risk spreading is unlikely to be an important explanation for delayed development. First, *Maculinea rebeli* populations are known for their remarkable stability (Elmes *et al.*, 1996; Nowicki *et al.*, 2005; Thomas *et al.*, 1998a) compared to other butterfly species. More importantly, it is not compatible with the observation that there are only one- and two-year-developers but no larvae delaying development for more than one season (Thomas *et al.*, 1998b) despite laboratory rearing of many hundreds of larvae. Under a bet-hedging hypothesis, a large fraction of SDL would indicate a massive risk of environmental catastrophes (there is no empirical evidence of this), and one would expect a substantial proportion of larvae to delay development for even longer time spans (Maffei *et al.* (2005); results on three-stage model in Menu *et al.* (2000); Philippi (1993)). If, on the other hand, larvae for some reason cannot delay development for more than one winter, the fraction of SDL should obviously not surpass a 1:1 ratio if risk spreading were the primary reason for the evolution of delayed development. Thus, while the benefit of bet-hedging may contribute to the evolution of delayed development it cannot alone explain the evolution of values of p_{ESS} below 0.5. Besides the priority effect the SDL may gain three additional benefits: (i) the specialist parasitoid *Ichneumon eumerus*, which kills up to 50% of *M. rebeli* larvae, and selects its host inside ant nests using size, odour and possibly sound cues, which may make the more active FDL more vulnerable (Thomas & Elmes, 1993; Thomas *et al.*, 2002, 2005). (ii) After emergence from the ant's nest, adults from slow-developing larvae are somewhat heavier, and hence presumably more fecund, than those from FDL (Thomas & Elmes, 1998). (iii) Adults from SDL apparently emerge earlier in the season than the FDL (cf. figure 2.1). These differences combined may give SDL an advantage in survival, mating opportunities, or the number of eggs they can produce, suggesting a trade-off between growth rate and reproductive capability (Abrams *et al.*, 1996; cf.). Accounting for such a benefit in our model does not introduce any complications as we simply need to multiply the fitness contribution from SDL by some constant $c > 1$. Obviously, with an appropriate value of c, the fitness landscapes presented in the figures could be shifted into a range that better corresponds with the empirical observation. However, introducing such a "magic number" into the model without good empirical evidence would be a dishonest way to resolve the conflict between model prediction and field evidence. Nonetheless, testing whether such benefits do exist is a priority for future studies. In figure 2.6 we show which combinations of a priority effect and such added benefits would lead to the evolution of p_{ESS} in the observed range.

We cannot rule out the possibility that some subtle constraints prevent larvae from developing within a single season, although the empirical evidence and existing experiments strongly indicate against this. As outlined above, the mechanisms included in the model provide us with good arguments to expect a SDL:FDL ratio of approximately 50:50 to be adaptive, the deviation from this fraction in favor of SDL may

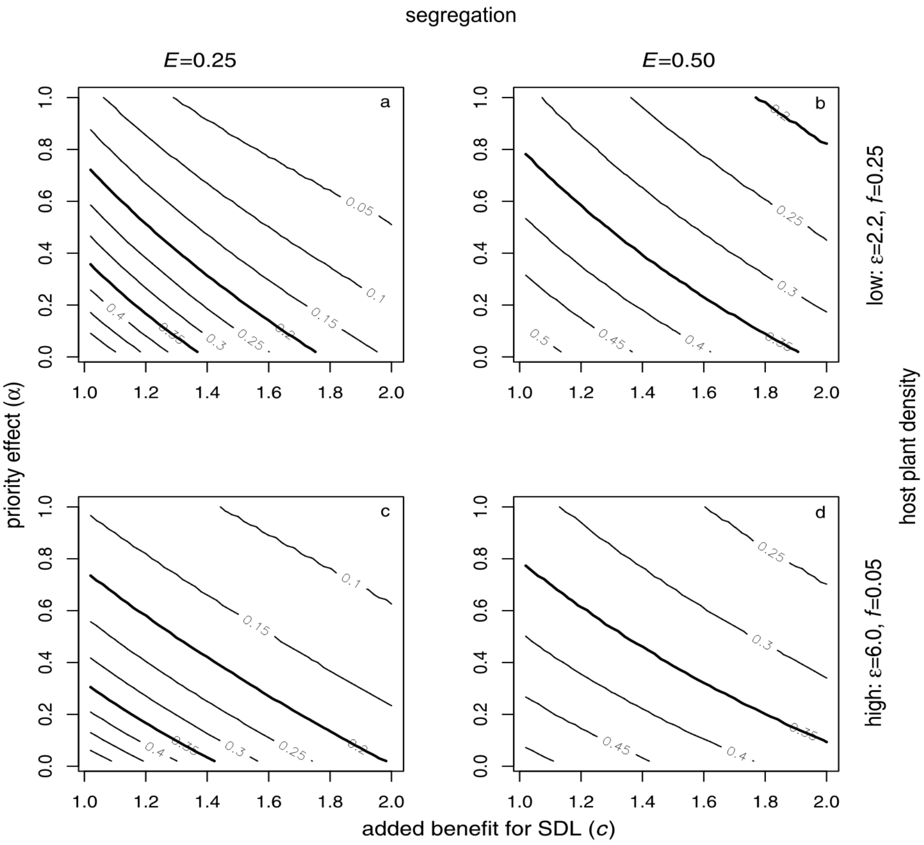

Figure 2.6: Visualisation of the exchangeability of the priority effect (α) by some added benefit (c) for SDL emerging after enclosure. Winter survival for SDL (μ) is 0.9 in all graphs. Top row situation low density sites, bottom row for high density sites. Values for two levels of segregation are given. The heavy contour lines envelope the range of p_R observed in the empirical studies.

indicate that at least a fraction of larvae do, for some unknown reason, not manage to complete development within a single season.

Finally, although our empirical evidence for a fairly robust 3:1 ratio is based on two distinct geographic populations of *M. rebeli*, they have many features in common. They use the same food plants, live on montane meadows at about the same altitude, where seasonal climate is fairly predictable, and they use the same host-ant species. There is mounting evidence (Schönrogge *et al.*, 2000) that while SDL are also present in other lowland populations of *M. rebeli* and in the closely related *M. alcon* they may occur at ratios nearer 1:1, as also seems to be the case in other *Maculinea* species (and Witek *et al.*, in press). Furthermore, recent taxonomic evidence suggests that the populations considered here may just be special cases of a complex of cryptic sibling sub-species comprising the *M. alcon/rebeli* complex. (Als *et al.*, 2004). Thus, the trait for SDL might have evolved generally with an ESS in the region of 0.5 (as suggested by this study) and the skew towards SDL observed in the southern montane populations of *M. rebeli* might be due to local additional influences such as those considered above. This should become clearer when the ratios observed in other populations of the *M. alcon/rebeli* complex are accurately determined and good local estimates of the key parameters included in our model are obtained. However, as fractions of SDL close to or smaller than 0.5 probably occur in other populations (see above), it would be desirable to additionally account for the benefits of bet-hedging in an extended model. Unfortunately, in variable environmental conditions life-time reproductive success is not an appropriate measure of fitness anymore (Heino *et al.*, 1997; van Dooren & Metz, 1998; e.g.). Finding an ESS in such an extended version of the model will presumably only be possible by performing simulation experiments.

In conclusion we consider that this investigation of an ESS for the ratio of FDL:SDL has been worthwhile. The result that quite unlikely combinations of parameters are required to produce the observed ratio has led us to consider other mechanisms that might also be involved and has helped to prioritise future research efforts on the *Maculinea alcon/rebeli* system. Furthermore, while our model has been designed for a specific situation occurring in that host-parasite system it is structurally quite general; especially the effect of kin-competition on the evolution of delayed development may be of broader applicability. We can expect to find delayed development (dispersal in time) to evolve whenever close relatives compete over limited resources within a single season, but not across seasons. In addition, the model may apply to situations were competition occurs in small groups on resources which are not always accessible. However, delayed development is especially likely to evolve, when slowly maturing individuals gain a competitive benefit over fast-developers.

2.4 APPENDIX: MATHEMATICAL DERIVATIONS

2.4.1 Fitness components for a mutant $p_M < 1$ invading a resident population with $p_R = 1$.

The sizes of the two compartments $O_{M,1}$ and $O_{M,2}$ depend on the number of offspring raised successfully in the first respectively the second year and the fraction $g_{M,1}$ and $g_{M,2}$ of theses to be offspring of the female under consideration. Clearly, this depends on the fraction p_M of larvae developing in the first and consequently $1 - p_M$ delaying development to the second year.

$$L_1 = L(1-f) + Lfp_M = \varepsilon K(1-f+fp_M) \tag{2.11}$$

Of these the fraction

$$g_{M,1} = \frac{Lfp_M}{L_1} = \frac{Lfp_M}{L(1-f+fp_M)} = \frac{fp_M}{1-f+fp_M} \tag{2.12}$$

is the female's own progeny. The expected number of adult offspring to successfully emerge from the ant nest in the first year is thus (replacing L in equation 2.1 by L_1 from equation 2.11 and multiplying by $g_{M,1}$

$$\begin{aligned} O_{M,1} &= g_{M,1} \cdot A_{M,1} = \frac{fp_M}{1-f+fp_M} \cdot \frac{\varepsilon K[1-f+fp_M]}{1+\varepsilon(1-f+fp_M)} \\ &= \frac{f\varepsilon Kp_M}{1+\varepsilon[1-f+fp_M]} \end{aligned} \tag{2.13}$$

This equation converges to equation 2.3 if $p_M = 1$, i.e. for a non-mutant female.

When estimating the magnitude of $O_{M,2}$ matters become more complicated as we need to account for the potential effect of (partial) competitive dominance of (this year's) SDL over next year's FDL. We expect that again L larvae will enter the colony which will all be FDL (the mutant is still rare!) and compete with the fraction μ of the SDL that survive the second winter. In the second year, the fitness component $O_{M,2}$ of the female will only derive from the SDL as it is not related to the new FDL. We consequently need to separate the number of larvae falling into the group of SDL ($L_{2,S}$) respectively FDL ($L_{2,F}$):

$$L_2 = L_{2,F} + L_{2,S} = \varepsilon K + \varepsilon Kf(1-p_M)\mu = \varepsilon K[1+f(1-p_M)\mu] \tag{2.14}$$

In total, the following number of adults $A_{M,2}$ will emerge from these larvae:

$$A_{M,2} = \frac{KL_2}{K+L_2} = \frac{\varepsilon K[1+f(1-p_M)\mu]}{1+\varepsilon[1+f(1-p_M)\mu]} \tag{2.15}$$

However, as we need to account for the consequences of competitive superiority of SDL in the second year ("priority effect") over the newly arriving FDL it is necessary to separately account for the adults emerging from SDL respectively FDL.

To do so, it is convenient to first consider the two extreme scenarios with respect to dominance. In the first case the SDL do not dominate the FDL and thus they will produce adults in the exact proportion of $L_{2,S}$ to L_2:

$$A_{M,2,S} = \frac{L_{2,S}}{L_2} \cdot \frac{KL_2}{K+L_2} = \frac{KL_{2,S}}{K+L_2}$$

and similarly for the fast-developers

$$A_{M,2,F} = \frac{L_{2,F}}{L_2} \cdot \frac{KL_2}{K+L_2} = \frac{KL_{2,F}}{K+L_2} \tag{2.16}$$

At the other extreme, SDL compete only among each other leaving the non-utilised "rest-capacity" for the FDL.

In this case $A_{M,2,S}$ becomes:

$$A_{M,2,S} = \frac{KL_{2,S}}{K+L_{2,S}}$$

and consequently $A_{M,2,F}$ is

$$A_{M,2,F} = A_{M,2} - A_{M,2,S} = \frac{KL_2}{K+L_2} - \frac{KL_{2,S}}{K+L_{2,S}} \tag{2.17}$$

We thus know the two possible extreme values for $A_{M,2,S}$ and can write

$$\begin{aligned} \frac{KL_{2,S}}{K+L_2} &\leq A_{M,2,S} \leq \frac{KL_{2,S}}{K+L_{2,S}} \text{ or} \\ \frac{KL_{2,S}}{K+L_2} &\leq a_{M,2}\frac{KL_{2,S}}{K+L_2} \leq \frac{KL_{2,S}}{K+L_{2,S}} \text{ with} \\ 1 &\leq a_{M,2} \leq \frac{K+L_2}{K+L_{2,S}} \end{aligned} \tag{2.18}$$

The term $a_{M,2}$ allows – within the limits defined above – gradual accounting for the competitive advantage of SDL over FDL. The potential magnitude of $a_{M,2}$ depends on the ratio of L_2 to $L_{2,S}$. Remembering that $L_{2,S} = \varepsilon K f(1-p_M)\mu$ it is useful to control the priority effect independent from ratio of L_1 to L_2:

$$\begin{aligned} a_{M,2} &= 1+\alpha\left(\frac{K+L_2}{K+L_{2,S}}-1\right) \\ &= 1+\alpha\left(\frac{L_{2,F}}{K+L_{2,S}}\right) = 1+\alpha\left(\frac{\varepsilon}{1+\varepsilon f(1-p_M)\mu}\right) \\ &\quad \text{with } \alpha \in [0;1] \end{aligned} \tag{2.19}$$

$\alpha = 0$ indicates complete competitive symmetry, $\alpha = 1$ complete dominance of the slow-developers. A more general estimator for $a_{M,2}$ will be introduced in equation 2.38 which includes the one given here as a special case for $p_R = 1$.

The number of adults emerging from fast-developing larvae can thus be calculated as:

$$A_{M,2,F} = \frac{KL_2}{K+L_2} - a_{M,2}\frac{KL_{2,S}}{K+L_2} = K\frac{L_2 - a_{M,2}L_{2,S}}{K+L_2} \tag{2.20}$$

In case of invasion into a population with strategy $p_R = 1$ all the $A_{M,2,S}$ are descendants of the female under consideration and none of the $A_{M,2,F}$, i.e. $O_{M,2} = A_{M,2,S}$. Consequently, her expected fitness O_M can be estimated by summing and substituting equation 2.13 and equation 2.18:

$$\begin{aligned} O_M &= O_{M,1} + A_{M,2,S} \\ &= f\varepsilon K\left(\frac{p_M}{1+\varepsilon[1-f+fp_M]} + \frac{a_{M,2}(1-p_M)\mu}{1+\varepsilon(1+f(1-p_M)\mu)}\right) \end{aligned} \tag{2.21}$$

and must be larger than O_R to allow successful invasion.

2.4.2 Expected offspring for a female following the resident strategy p_R

We first consider a homogeneous population, i.e. a population where all individuals follow the same reproductive strategy p_R. Any female can expect offspring to emerge from first year's fast-developers (FDL) and second year's slow-developers (SDL) but evidently not from the first year's SDL and second year's FDL. However, as competition takes place among all larvae we need nonetheless to determine the expected values of all four of these quantities. We additionally need to estimate the fraction of larvae, respectively emerging adults which are the female's own offspring.

For the number of larvae competing we can separate between FDL and SDL for both years:

$$\begin{aligned} L_1 &= L_2 = L_{1,F} + L_{1,S} \\ L_{1,F} &= L_{2,F} = \varepsilon K p_R \\ L_{1,S} &= L_{2,S} = \varepsilon K (1-p_R)\mu \end{aligned} \tag{2.22}$$

$$\begin{aligned} g_{1,F} &= \frac{f \varepsilon K p_R}{\varepsilon K p_R} = f \\ g_{2,S} &= \frac{f \varepsilon K (1-p_R)\mu}{\varepsilon K (1-p_R)\mu} = f \end{aligned} \tag{2.23}$$

The number of adults emerging from the four larval components can be calculated (cf. equation 2.18) as

$$\begin{aligned} A_{1,S} &= a_{R,1} \frac{K L_{1,S}}{K + L_{1,T}} \\ &= a_{R,1} \varepsilon K \frac{(1-p_R)\mu}{1 + \varepsilon[p_R + (1-p_R)\mu]} \end{aligned} \tag{2.24}$$

which are all not related to the female under consideration. However, as we do not assume $p_R = 1$ anymore, we need to account for the fact that first year's FDL will compete with already present SDL which entered the nest in the previous year. We do this by the newly introduced term $a_{R,1}$. Its derivation is based on the same logic we used when calculating $a_{M,2}$ in equation 2.18 and equation 2.19, but we have to replace the terms in the equation by the ones appropriate in this case:

$$a_{R,1} = 1 + \alpha \left(\frac{L_{1,F}}{K + L_{1,S}} \right) = 1 + \alpha \left(\frac{\varepsilon p_R}{1 + \varepsilon(1-p_R)\mu} \right) \tag{2.25}$$

We can thus calculate the number of adults to emerge from the $L_{1,F}$ larvae (cf. equation 2.20):

$$\begin{aligned} A_{1,F} &= K\frac{L_1 - a_{R,1}L_{1,S}}{K+L_1} \\ &= K\frac{L_{1,F} - (a_{R,1}-1)L_{1,S}}{K+L_{1,F}+L_{1,S}} \\ &= \varepsilon K\frac{p_R - (a_{R,1}-1)(1-p_R)\mu}{1+\varepsilon[p_R+(1-p_R)\mu]} \end{aligned} \tag{2.26}$$

As a fraction f of these adults are the female's own progeny we thus get $fA_{1,F}$ as the expected number of offspring emerging from this year's FDL.

Up to this moment we have, however, not accounted for the fact that the resident strategy itself also has an effect on the number of larvae (ε) entering the colonies, i.e. the evolutionary environment in part depends on the resident strategy itself. This has to be so, as the number of butterflies emerging from the colonies clearly affects the number of eggs respectively young larvae deposited for adoption into ant colonies. In addition, we also have to recognise that the resident strategy implicitly affects f because individual females are unlikely to change their egg-laying behaviour. Fortunately, it is rather straightforward to make this adjustment (see appendix subsection 2.4.5) which has no effect on the system of equations as such. We simply need to replace the values for ε and f in the equation 2.22 to equation 2.26 by the strategy-adjusted values ε' and f'. In the following, we will use symbols ε' and f' to account for the fact that the resident strategy will usually not be $p_R = 1$.

2.4.3 The effect of segregation

We assume that a fraction E of freshly infected ant colonies succeeds in moving their colonies out of the vicinity of host plants. This protects them against new infection in the next years. However, in a steady state the ant colonies removed due to their emigration into safe areas must be replaced by a similar number of uninfected colonies which either move into the vicinity of host plants or are newly founded. This implies that some of the FDL will find themselves in colonies where they do not need to compete with former years' SDL. Thus, equation 2.26 only applies to the fraction $1-E$ of colonies which did not move their nest from the vicinity of butterfly host plants, the remaining larvae enter nests where they compete only among each other. In the following, the fraction $E \in [0;1]$ is called segregation index. $E = 0$ implies no segregation and $E = 1$ corresponds to complete segregation.

The overall number of fast-developing offspring can consequently be calculated as:

$$\begin{aligned} O_{R,1} &= f' A_{1,F}(1-E) + f' \frac{K L_{1,F}}{K + L_{1,F}} E \\ &= f' \varepsilon' K \frac{p_R - (a_{R,1} - 1)(1-p_R)\mu}{1+\varepsilon'[p_R + (1-p_R)\mu]}(1-E) + f'\varepsilon' K \frac{p_R}{1+\varepsilon' p_R} E \end{aligned} \tag{2.27}$$

with the second summand derived in direct analogy to equation 2.3.

Evidently, in the homogenous population $L_{1,F} = L_{2,F}$ and $L_{1,S} = L_{2,S}$. Consequently, $a_{R,1}$ is equal to $a_{R,2}$ (equation 2.25) and $A_{2,F} = A_{1,F}$ and $A_{2,S} = A_{1,S}$. We thus can directly estimate the second fitness component for the female under consideration:

$$\begin{aligned} O_{R,2} &= f' A_{2,S}(1-E) + f' \frac{K L_{2,S}}{K + L_{2,S}} E \\ &= f' \varepsilon' K \frac{a_{R,2}(1-p_R)\mu}{1+\varepsilon'[p_R + (1-p_R)\mu]}(1-E) \\ &\quad + f'\varepsilon' K \frac{(1-p_R)\mu}{1+\varepsilon'(1-p_R)\mu} E \end{aligned} \tag{2.28}$$

Summing equation 2.27 and equation 2.28 yields the expected number of emerging adult offspring for a female following the resident strategy p_R. It is important to note that the two terms containing $a_{R,1}$, respectively $a_{R,2}$ as multipliers cancel out as $a_{R,1} = a_{R,2}$.

2.4.4 The expected number of offspring for a mutant female with strategy p_M

We now consider the fitness of a female following strategy $p_M = p_R + \Delta$ with $\Delta \in [-p_R; (1-p_R)]$ introduced into the population. From these calculations we then attempt to define the ESS strategy, i.e. the resident strategy p_R which has a higher expected number of offspring than any potential mutant strategy p_M. We first need to calculate the four different "larval compartments" $L_{M,1,F}$, $L_{M,1,S}$, $L_{M,2,F}$, $L_{M,2,S}$, the number of adults emerging from these larvae ($A_{M,1,F}$, $A_{M,2,S}$) and the fraction among these which are the mutant females offspring ($g_{M,1,F}$, $g_{M,2,S}$). As before, the female cannot have offspring among first year's SDL and second year's FDL, i.e. $g_{M,1,S} = g_{M,2,F} = 0$.

From this information we will be able to estimate the expected fitness for the mutant female,

$$O_M = O_{M,1} + O_{M,2} = A_{M,1,F} \cdot g_{M,1,F} + A_{M,2,S} \cdot g_{M,2,S} \tag{2.29}$$

$$\begin{aligned} L_{M,1,F} &= \varepsilon' K[(1-f')p_R + f' p_M] \equiv \varepsilon' K(p_R + f'\Delta) \\ L_{M,1,S} &= \varepsilon' K[(1-p_R)\mu] \text{ for } 1-E \text{ of all cases and 0 otherwise} \end{aligned} \tag{2.30}$$

$L_{M,1,S}$ is equal to 0 for those uninfected colonies immigrating into the area exposed to butterfly larvae infection (compensating for those lost in the second year due to segregation). In these nests there is no competition between FDL and SDL. The fraction of offspring which are the mutant female's offspring is

$$g_{M,1,F} = \frac{f' p_M}{(1-f')p_R + f' p_M} \equiv f' \frac{p_R + \Delta}{p_R + f'\Delta} \tag{2.31}$$

and is not affected by segregation. From the $L_{M,1,F}$ larvae, which are competing with the (dominant) SDL larvae of the previous year, the following number of adults is expected to emerge in the fraction $1-E$ of colonies which do not segregate (cf. equation 2.26):

$$\begin{aligned} A_{M,1,F} &= K\frac{L_{1,F,M} - (a_{M,1}-1)L_{1,S,M}}{K + L_{1,F,M} + L_{1,S,M}} \\ &= \varepsilon K \frac{(1-f')p_R + f' p_M - (a_{M,1}-1)(1-p_R)\mu}{1+\varepsilon'[(1-f')p_R + f' p_M + (1-p_R)\mu]} \\ &\equiv \varepsilon K \frac{p_R + f'\Delta - (a_{M,1}-1)(1-p_R)\mu}{1+\varepsilon'[p_R + f'\Delta + (1-p_R)\mu]} \end{aligned} \tag{2.32}$$

We need to calculated of the term $a_{M,1}$ accounting for the priority effect in analogy to equation 2.18 and equation 2.19 by inserting the appropriate terms:

$$\begin{aligned} a_{M,1} &= 1+\alpha\left(\frac{L_{M,1,F}}{K + L_{M,1,S}}\right) \\ &= 1+\alpha\left(\frac{\varepsilon' K[(1-f')p_R + f' p_M]}{K + \varepsilon' K[(1-p_R)\mu]}\right) \\ &\equiv 1+\alpha\left(\frac{\varepsilon'(p_R + f'\Delta)}{1+\varepsilon'[1-p_R]\mu}\right) \end{aligned} \tag{2.33}$$

which simplifies to equation 2.25 ($a_{R,1}$) if we set $\Delta = 0$.

We can now calculate the expected number of offspring emerging from the $L_{1,F}$ larvae by multiplying equation 2.31 and equation 2.32:

$$\begin{aligned}
O_{M,1} &= g_{M,1,F} \cdot A_{M,1,F}(1-E) + \frac{KL_{M,1,F}}{K+L_{M,1,F}} g_{M,1,F} E \\
&= f'\varepsilon' K \frac{(1-f')p_R + f'p_M - (a_{M,1}-1)(1-p_R)\mu}{1+\varepsilon'[(1-f')p_R + f'p_M + (1-p_R)\mu]} \frac{p_M}{(1-f')p_R + f'p_M}(1-E) \\
&\quad + \varepsilon' K \frac{[(1-f')p_R + f'p_M]}{1+\varepsilon'[(1-f')p_R + f'p_M]} E \cdot g_{M,1,F} \\
&= f'\varepsilon' K \frac{(1-f')p_R + f'p_M - (a_{M,1}-1)(1-p_R)\mu}{1+\varepsilon'[(1-f')p_R + f'p_M + (1-p_R)\mu]} \frac{p_M}{(1-f')p_R + f'p_M}(1-E) \\
&\quad + f'\varepsilon' KE \frac{p_M}{1+\varepsilon'[(1-f')p_R + f'p_M]} \\
&\equiv f'\varepsilon' K \frac{p_R + f'\Delta - (a_{M,1}-1)(1-p_R)\mu}{1+\varepsilon'[p_R + f'\Delta + (1-p_R)\mu]} \frac{p_R+\Delta}{p_R + f'\Delta}(1-E) \\
&\quad + f'\varepsilon' K \frac{(p_R+\Delta)}{1+\varepsilon'(p_R + f'\Delta)} E \qquad (2.34)
\end{aligned}$$

The equation contains two summands, one for the non-segregating fraction of nests $(1-E)$ another for those immigrating from safe areas (fraction E). For the second year we need to make similar calculations:

$$\begin{aligned}
L_{M,2,F} &= \varepsilon' K p_R \text{ in fraction } 1-E \text{ of all cases and 0 otherwiese} \\
L_{M,2,S} &= \varepsilon' K[(1-f')(1-p_R) + f'(1-p_M)]\mu \\
&\equiv \varepsilon' K(1-p_R-f'\Delta)\mu \qquad (2.35)
\end{aligned}$$

$$\begin{aligned}
g_{M,2,S} &= \frac{f'(1-p_M)\mu}{\mu[(1-f')(1-p_R) + f'(1-p_M)]} = \frac{f'(1-p_M)}{1-p_R+f'(p_R-p_M)} \\
&\equiv \frac{f'(1-p_R-\Delta)}{1-p_R-f'\Delta} \qquad (2.36)
\end{aligned}$$

(not affected by E). The number of adults emerging from the $L_{M,2,S}$ larvae can thus be calculated by (cf. equation 2.18)

$$\begin{aligned}
A_{M,2,S} &= a_{M,2} K \frac{L_{M,2,S}}{K + L_{M,2,F} + L_{M,2,S}} \\
&= a_{M,2}\varepsilon' K \frac{(1-f')(1-p_R)\mu + f'(1-p_M)\mu}{1+\varepsilon'[p_R + (1-f')(1-p_R)\mu + f'(1-p_M)\mu} \\
&\equiv a_{M,2}\varepsilon' K \frac{(1-p_R-f'\Delta)\mu}{1+\varepsilon'[p_R + (1-p_R-f'\Delta)\mu]} \qquad (2.37)
\end{aligned}$$

with the term $a_{M,2}$ defined as:

$$\begin{aligned} a_{M,2} &= 1+\alpha\left(\frac{L_{M,2,F}}{K+L_{M,2,S}}\right) \\ &= 1+\alpha\left(\frac{\varepsilon' K p_R}{K+\varepsilon' K[(1-f')(1-p_R)+f'(1-p_M)]\mu}\right) \\ &\equiv 1+\alpha\left(\frac{\varepsilon' p_R}{1+\varepsilon'[1-p_R-f'\Delta]\mu}\right) \end{aligned} \tag{2.38}$$

This equation becomes identical to equation 2.33 and simplifies to equation 2.25 if we assume $\Delta = 0$.

The expected number of offspring for the mutant female to emerge in the second year can be calculated by multiplying equation 2.36 and equation 2.37 and introducing two separate summands accounting for the effect of segregation as in equation 2.34:

$$\begin{aligned} O_{M,2} &= a_{M,2}\varepsilon' K \frac{(1-f')(1-p_R)\mu+f'(1-p_M)\mu}{1+\varepsilon'[p_R+(1-f')(1-p_R)\mu+f'(1-p_M)\mu]} \\ &\quad \cdot \frac{f'(1-p_M)}{[(1-f')(1-p_R)+f'(1-p_M)]}(1-E) \\ &\quad +\varepsilon' K \frac{[(1-f')(1-p_R)+f'(1-p_M)]\mu}{1+\varepsilon'[(1-f')(1-p_R)+f'(1-p_M)]\mu} \\ &\quad \cdot \frac{f'(1-p_M)\mu}{[(1-f')(1-p_R)+f'(1-p_M)]\mu}E \\ &= a_{M,2}f'\varepsilon' K \frac{(1-p_M)\mu}{1+\varepsilon'[p_R+(1-f')(1-p_R)\mu+f'(1-p_M)\mu]}(1-E) \\ &\quad +f'\varepsilon' K \frac{(1-p_M)\mu}{1+\varepsilon'[(1-f')(1-p_R)+f'(1-p_M)]\mu}E \\ &\equiv a_{M,2}\varepsilon' K \frac{(1-p_R-f'\Delta)\mu}{1+\varepsilon'[p_R+(1-p_R-f'\Delta)\mu]} \cdot \frac{f'(1-p_R-\Delta)}{1-p_R-f'\Delta}(1-E) \\ &\quad +f'\varepsilon' K \frac{(1-p_R-\Delta)\mu}{1+\varepsilon'(1-p_R-f'\Delta)\mu}E \\ &= a_{M,2}f'\varepsilon' K \frac{(1-p_R-\Delta)\mu}{1+\varepsilon'[p_R+(1-p_R-f'\Delta)\mu]}(1-E)+ \\ &\quad \varepsilon' f' K \frac{(1-p_R-\Delta)\mu}{1+\varepsilon'(1-p_R-f'\Delta)\mu}E \end{aligned} \tag{2.39}$$

In total, the number of expected offspring for a mutant female following strategy p_M

can thus be calculated as (sum of equation 2.34 and equation 2.39)

$$\begin{aligned}
O_M &= O_{M,1} + O_{M,2} \\
&= f'\varepsilon' K \frac{(1-f')p_R + f'p_M - (a_{M,1}-1)(1-p_R)\mu}{1+\varepsilon'[(1-f')p_R + f'p_M + (1-p_R)\mu]} \frac{p_M}{(1-f')p_R + f'p_M}(1-E) \\
&\quad + f'\varepsilon' K E \frac{p_M}{1+\varepsilon'[(1-f')p_R + f'p_M]} \\
&\quad + a_{M,2} f'\varepsilon' K \frac{(1-p_M)\mu}{1+\varepsilon'[p_R + (1-f')(1-p_R)\mu + f'(1-p_M)\mu]}(1-E) \\
&\quad + f'\varepsilon' K \frac{(1-p_M)\mu}{1+\varepsilon'[(1-f')(1-p_R) + f'(1-p_M)]\mu} E \\
&\equiv f'\varepsilon' K \frac{p_R + f'\Delta - (a_{M,1}-1)(1-p_R)\mu}{1+\varepsilon'[p_R + f'\Delta + (1-p_R)\mu]} \frac{p_R+\Delta}{p_R + f'\Delta}(1-E) \\
&\quad + f'\varepsilon' K \frac{(p_R+\Delta)}{1+\varepsilon'(p_R + f'\Delta)} E \\
&\quad + a_{M,2}\varepsilon' f' K \frac{(1-p_R-\Delta)\mu}{1+\varepsilon'[p_R + (1-p_R-f'\Delta)\mu]}(1-E) \\
&\quad + f'\varepsilon' K \frac{(1-p_R-\Delta)\mu}{1+\varepsilon'(1-p_R-f'\Delta)\mu} E
\end{aligned} \tag{2.40}$$

with $a_{M,1}$ respectively $a_{M,2}$ as defined by equation 2.33 and equation 2.38.

2.4.5 Adjustment of ε and f for resident strategies $p_R < 1$

The population parameters ε and f are dominantly defined by the environmental conditions prevailing in a butterfly habitat but to some degree also depend on the strategy of the resident population itself. In an equilibrium population the emerging butterflies must ultimately produce sufficient larvae to ensure that ε larvae enter each colony again in the next season, i.e. $\varepsilon = O_R s$ (setting $f = 1$, as we are interested in total population output). The constant s accounts for fertility and density independent survival of emerging butterflies and young larvae outside the nest.

Without loss of generality we can assume that for the "reference strategy" $p_R = 1$, the value of the parameter ε is purely defined by environmentally conditions, i.e. independent of the resident strategy. However, with a change in the resident strategy from $p_R = 1$ to $p_R < 1$, O_R changes as well, i.e. there is a "feedback" of the resident strategy on ε. Yet, whatever the resident strategy the equilibrium condition must still hold. This gives us two equations (ignoring f as we are interested in overall productivity not that of an individual female):

$$\begin{aligned}
\varepsilon &= O_R(p_R = 1, \varepsilon) \cdot s \text{ and} \\
\varepsilon' &= O_R(p_R < 1, \varepsilon') \cdot s
\end{aligned} \tag{2.41}$$

This allows to directly calculate ε' by rearranging:

$$\begin{aligned}\frac{\varepsilon}{O_R(1,\varepsilon)} &= s = \frac{\varepsilon'}{O_R(p_R,\varepsilon')} \text{ and thus} \\ \varepsilon' &= \varepsilon\frac{O_R(p_R,\varepsilon')}{O_R(1,\varepsilon)} \qquad (2.42)\end{aligned}$$

Inserting equation 2.8 (without segregation) as well as equation 2.27 and equation 2.28 (including segregation) for $O_R(1)$ respectively $O_R(p_R)$ yields explicit solutions for ε' (the latter only as long as there is no added benefit for SDL, i.e $c = 1$). If $c > 1$, the equations can numerically be solved for ε'.

In the case of $E = 0$ and $c = 1$ the equation simplifies to:

$$\varepsilon' = 1 + \varepsilon - \frac{1}{p_R + (1 - p_R)\mu} \qquad (2.43)$$

Replacing p_R by $1 - \delta$ and simple algebraic manipulation make clear that ε' is always smaller than ε if $p_R < 1$ (both, δ and μ are ≤ 1). From this we can directly deduce that offspring reproduction in a homogeneous population is always maximal if $p_R = 1$ independent of the values for ε, f, μ, and α!

The egg-laying behaviour of females is (presumably) not affected by changes in the resident strategy but by environmental conditions like host plant density only. Thus, the number of larvae of a certain female (l) entering an ant colony is expected to remain constant. For the reference case $p_R = 1$ we thus can simply state:

$$f = \frac{l}{\varepsilon K} \qquad (2.44)$$

while for the case $p_R < 1$ the following condition must hold:

$$f' = \frac{l}{\varepsilon' K} \qquad (2.45)$$

Combining the two equations and rearranging yields:

$$f' = f\frac{\varepsilon}{\varepsilon'} \qquad (2.46)$$

After setting p_R we thus can adjust ε and f in the way outlined above to derive the appropriate fitness estimates for resident as well as mutant females.

Photo by Alain Pauly

Chapter 3

The influence of soil temperature on the nesting cycle of the halictid bee *Lasioglossum malachurum*

with Norbert Weissel (first author), Jürgen Liebig, Hans-Joachim Poethke and Erhard Strohm

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Abstract. The physiology and behaviour of ectothermic organisms is strongly influenced by temperature. For ground nesting species like the primitively eusocial halictid bee, *Lasioglossum malachurum*, soil temperature might influence the life cycle as well as the complexity of the social group since the number of broods that can be fitted into the flight season might increase with increasing temperature. Our study population of *L. malachurum* at Wuerzburg exhibits a remarkable variability with respect to the number of broods and the pattern of sexual production. Broods are separated by activity pauses during which the larvae develop. In this study we investigate the influence of soil temperature on the pattern of nesting activity (duration of broods and pauses) and on the number of broods in *L. malachurum*. We observed a total of 1138 nests in 13 aggregations near Wuerzburg. As expected, soil temperature shortened the duration of the pauses, resulting in an overall shortening of the nesting cycle. This is most probably due to a physiological effect of soil temperature on the development of the larvae. With regard to the nesting strategies, we hypothesised that a shortening of the nesting cycle within the limited flight season should enhance the success of a strategy with more worker broods. In fact, patches with higher soil temperature showed more broods. However, this effect was rather weak, suggesting that other factors might have a stronger impact on the variability in nesting strategy within our study population of *L. malachurum*.

3.1 INTRODUCTION

Temperature strongly affects the life of insects including numerous behavioural and physiological processes such as flying ability, mating behaviour, and especially the duration of development and survival of larvae (Borrell & Medeiros, 2004; Grafton-Cardwell *et al.*, 2005; Larsson, 1991; Woods *et al.*, 2005). Ground nesting insects like many wasp, bee, and ant species probably depend more on soil temperature than on air temperature with regard to nest-site selection, daily activity patterns, as well as foraging success and sex allocation (e.g. Cameron *et al.*, 1996; Crist & Williams, 1999; Potts & Willmer, 1997; Strohm & Linsenmair, 1998; Vogt *et al.*, 2003; Wuellner, 1999).

Social ground nesting Hymenoptera with an annual life cycle might be particularly dependent on soil temperature since it might influence the duration of development of helpers and the rate of provisioning. This in turn would affect the number of broods that can be produced during the limited flight season and, thus, the colony size and the level of social complexity. Here we focus on the influence of soil temperature on the nesting cycle of a ground nesting social halictid bee, *Lasioglossum (Evylaeus) malachurum* (Kirby 1802). We investigate how temperature affects the different nesting phases and whether it has an influence on the pattern of broods of workers and sexuals.

Bees of the family Halictidae exhibit a great variability with respect to social organisation, both within and among species (Hirata *et al.*, 2005; Packer, 1998; Plateaux-Quenu, 1993; Richards *et al.*, 2003; Yanega, 1988). This extreme social diversity seems to be strongly affected by environmental conditions (for review see Wcislo, 1997a; Yanega, 1997), although a genetic influence on the life strategy is sometimes involved as well (Danforth *et al.*, 2003; Plateaux *et al.*, 2000; Soucy & Danforth, 2002). Our study population of *L. malachurum* at Wuerzburg shows a remarkable plasticity with respect to the pattern of worker and sexual production even within individual nest aggregations (Strohm & Bordon-Hauser, 2003). Mated females hibernate, solitarily found a nest in early spring, and provision a first brood of about four to six workers. After emergence, these workers take over foraging and provision a second brood that consists of either sexuals or workers. Only, if workers are produced, the brood cycle continues with the production of sexuals in the third brood. A third group of nests produces a mixed second brood that consists of both workers and sexuals that is followed by a third brood of only sexuals. There are pauses of mostly one to three weeks between the provisioning of a brood and the emergence of the first individuals. During these pauses, there is no activity outside the nests and nest entrances are usually closed.

We investigated the influence of soil temperature on the duration of the activity phases as well as the pauses of a population of *L. malachurum* at Wuerzburg. We hypothesised that due to the well known effect of temperatures on biological processes

(Cossins & Bowler, 1987; Gilbert & Raworth, 1996; Howe, 1967), higher temperatures will shorten the different phases of the nesting cycle of *L. malachurum*. We expected this effect to be strongest during the early stages of the flight season, when weather conditions are cooler and less predictable. A shortening of the nesting cycle in turn is likely to improve the prospects of a strategy with more worker broods. Taking also into account the known clinal variation in the social behaviour of *L. malachurum*, with more worker broods produced in warmer climates (Knerer, 1992; Richards, 2000), we hypothesised a higher percentage of colonies with three broods at nesting aggregations with higher soil temperature. To test these hypotheses we investigated different nesting aggregations at Wuerzburg. Some of our nest aggregations were located above subterranean heating pipes at the campus of the University of Wuerzburg. The inclusion of these aggregations considerably increased the available range of temperatures and should make any effect of temperature easier to be detected.

3.2 MATERIAL AND METHODS

3.2.1 Study species and nest cycle

The ground nesting halictid bee *L. malachurum* is widely distributed in the Western Palaearctic region and can be found from northern Europe to North Africa and from Iberia to the Caucasus (Amiet *et al.*, 2001; Knerer, 1992; Michener, 1979). Detailed information on the nesting biology of the species can be found in Knerer (1992) and Richards (2000). In the following, the solitary nest founding phase is abbreviated by NF, the different broods are B1 (workers only), B2 (workers, or sexuals, or workers and sexuals), and B3 (sexuals only). The three pauses between the activity periods are abbreviated by P1 (NF-B1), P2 (B1-B2), and P3 (B2-B3).

3.2.2 Study site

We investigated 13 nesting aggregations of *L. malachurum* in the vicinity of the Biocenter of the University of Wuerzburg and in the rural environment in the south of the University in 2004. Within each of these aggregations we selected one observation patch at random leading to 13 observation patches in total. Patches on the university campus were numbered form 1 to 7 and those at the other nesting sites from 8 to 13. All 13 patches were located in an area with a radius of 1 km (figure 3.1). All nests of the aggregations at the Biocenter (patches 1-7) were located on densely overgrown sandy soil and right above subterranean heating pipes. These pipes run in a depth of two to five meters and constantly transport 140 °C hot pressurised water, thereby heating up the surrounding soil. The nesting sites in the rural environment (patches 8-13) in the south of the Biocenter were located on sandy or silty soil with very little vegetation. Patches on top of the subterranean heating pipes (1-7) are referred to as "heated" patches; those in the rural environment (8-13) are called "unheated" patches.

Each of the 13 observation patches measured 0.25 m^2, with a nest density between 96 and 852 nests / m^2 during NF (table 3.1). To facilitate the monitoring of the nest cycle, all nests of an observation patch were marked with numbered nails and the exact position of each nest was mapped. Furthermore, vegetation was cut every two weeks.

3.2.3 Soil temperature

Soil temperature of all 13 patches was recorded during the whole observation period from the beginning of April until the end of September using thermo-loggers (iButton DS1921G-F5, Dallas Semiconductor). In the immediate vicinity of each patch (approx. 10 cm from the edge of a patch) two loggers were buried in depths of 20 and 40 cm. They were programmed to measure the temperature every three hours. One of the 26 thermo-loggers could not be recovered at the end of the observation period, so the temperature data for patch 8 at a depth of 40 cm is missing. A nest may range between depths of 10-15 cm during NF, 25-30 cm during B1, and up to 50 cm or more at the end of B2 (Knerer 1992; Legewie 1925; Noll 1931). Thus, the measurements reflect a relevant area with regard to the location of the brood cells.

For all subsequent analyses we use the mean soil temperature for each patch at a depth of 20 and 40 cm over the whole flight season of *L. malachurum* in Wuerzburg (April 09 - September 19). The mean temperature is a suitable measure since it represents the progression and differences that occur over the season very well.

3.2.4 Nesting activity

In the 13 patches, a total of 1138 nests was checked every other day for nesting activity from the beginning of April until the end of September. We recorded open nest entrances, burrowing activity, and/or the presence of a guarding bee and regarded these as reliable signs for nesting activity. Based on these observations, data on the beginning, end, and duration of the activity periods of the different broods and the respective pauses are available. However, the very first days of the nest founding phase (starting in mid March) were not observed. Therefore, we do not have exact data on the founding of each nest. Some colonies showed no nest closure between B1 and B2 (9 out of 622) or B2 and B3 (24 out of 489), so some data on the end of B1/B2 and the beginning of B2/B3 are missing.

It should be noted that the duration of the nesting activity during B1 depends only on the duration of the foraging activity of workers, whereas during B2 duration of nesting activity means foraging of workers, or the emergence of sexuals, or both. In contrast, duration of activity of B3 exclusively refers to the emergence of sexuals.

3.2.5 Nesting strategy

As a measure of the incidence of either a two or a three brood nesting strategy we calculated the proportion of colonies that showed B3 in relation to the number of active colonies during B2 in a patch. To determine which nests with three broods produced either exclusively workers or workers and sexuals during B2 would have required prolonged observations of the B2 phase as well as catching the emerging bees of B2. The latter might have undesirably affected the nesting cycle. Thus, we only differentiated between nests that showed activity during two or three broods. This procedure has, however, the consequence that colonies that actually had workers in B2 and "tried" to produce a third brood but failed due to whatever reason were counted as nests with a two brood strategy. Therefore, we might somewhat overestimate the number of nests with a two brood strategy.

This procedure might cause biases since patches with low overall success would have a low estimated proportion of a three brood strategy. To check for such a bias we calculated the failure rates between NF and B1 (proportion of B1 nests divided by the number of NF nests) as well as between B1 and B2 (proportion of B2 nests divided by the number of B1 nests) for each patch. Then we tested whether these failure rates correlate with the proportion of nests that show a three brood strategy. No correlation indicates that failure rates do not affect our measure of the nesting strategy.

3.2.6 Data analysis

We checked for normal distributions of our data by histogram plots. All samples showed reasonable approximation to normality. Samples that differed in variance (according to a Levene test) were compared using Welch tests that correct for unequal variances. The data on the proportions of nests with B1, B2, and B3 of the different patches were arcsine-transformed. Data are presented as means ± SD.

A One-way ANOVA was calculated to test for differences between the 13 observation patches with regard to soil temperature. We tested whether the patches differed in the timing of nesting activities (beginning, end, and duration of the broods; duration of the pauses) using a One-way ANOVA with Welch correction for inhomogeneous variances. We used t tests or Welch tests to compare means of soil temperature, nesting activity, and nesting strategy of the "unheated" and "heated" patches. A Spearman rank correlation procedure was used to test for a correlation between the failure rates between NF and B1 as well as B1 and B2 and the proportion of nests with B3. We tested whether soil temperature at depths of 20 and 40 cm had an effect on the duration of different phases of the nesting cycle using Pearson correlation analyses. Since it is reasonable to assume that there can only be an effect of soil temperature on the nesting activity and not vice versa we assume a causal effect of temperature on nesting

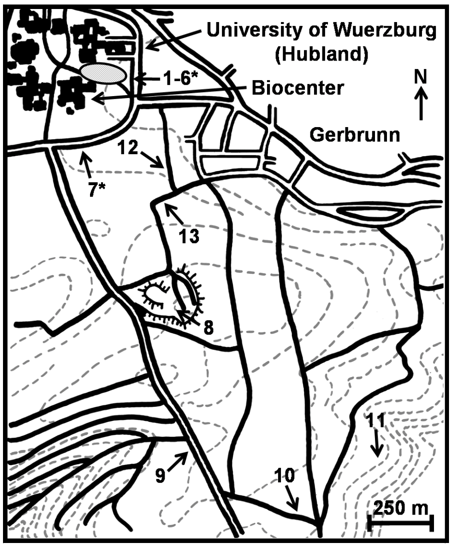


Figure 3.1: Map of the study area showing the location of the 13 observation patches (* heated patches) in the vicinity of the Biocenter of the University of Wuerzburg (1-7) and in the rural environment in the south of the University (8-13).

activity. A χ^2 test was calculated to test whether the patches differed in the proportion of nests with a two versus a three brood strategy. Logistic regression analyses were used to test for an influence of the different measures of nesting activity on the nesting strategy of the colonies. Logistic regression analysis was also used to test for an effect of soil temperature on the proportion of colonies in a patch that produced B3. Nagelkerke's R^2 as well as the area-under-curve (*AUC*) from a receiver-operating characteristic (ROC curve) are used for validation of the calculated logistic regression tests. *AUC* values range from 0.5 (randomly guessing) to 1.0 (perfect test accuracy). Tests were calculated using either SPSS 12.0, BiAS 8.10, or R 2.1.1.

3.3 RESULTS

3.3.1 Soil temperature

During the flight season of *L. malachurum* we measured an overall mean soil temperature of 19.6 ± 1.5 °C (range: 17.9 - 22.0 °C, $n = 13$, table 3.1, figure 3.2) 20 cm below surface and 19.8 ± 3.1 °C (range: 16.9 - 26.2 °C, $n = 12$, table 3.1) 40 cm below surface. The 13 observation patches differed significantly in soil temperature at a depth of 20 (One-way ANOVA: $F_{12,299} = 3.72$, $p < 0.001$) as well as 40 cm ($F_{11,276} = 16.9$, $p < 0.001$). The relatively high temperatures at some patches and the large SD in a depth of 40 cm are caused by the heating pipes. The mean soil temperature 20 cm below surface of the "heated" patches was significantly higher (20.7

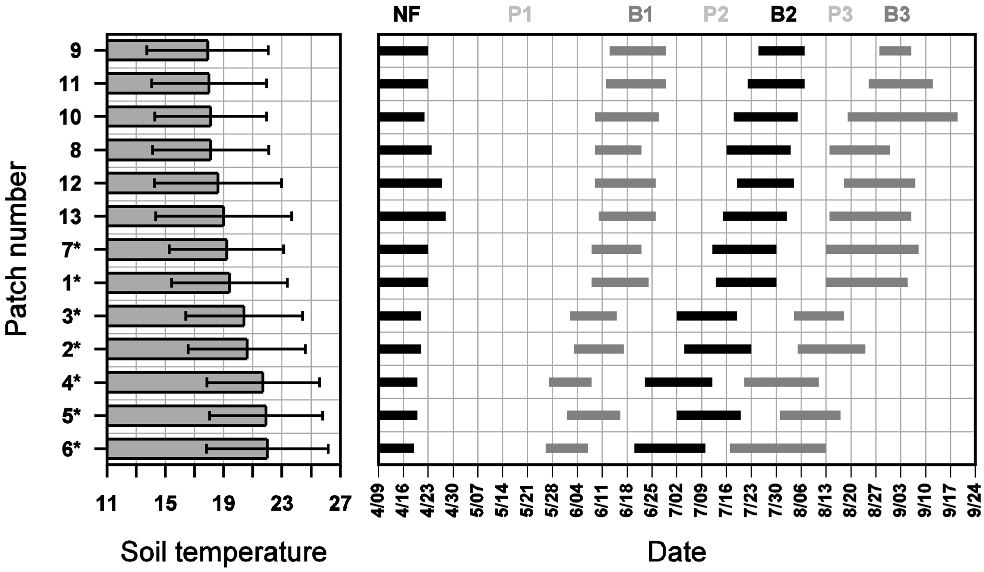


Figure 3.2: Mean temperature (season means) in a patch and position of the activity periods (patch means) within the flight season of *L. malachurum* for the 13 observation patches (* heated patches) ordered according to their mean temperatures 20 cm below surface. The bars mark the position of the nest founding phase, B1, B2, and B3.

± 1.2 °C, $n = 7$) compared to the "unheated" patches (18.3 ± 0.4 °C, $n = 6$, Welch test: $t = 5.19$, $df = 7.78$, $p < 0.001$). This difference was even more pronounced in 40 cm ("heated": 21.5 ± 3.1 °C, $n = 7$; "unheated": 17.5 ± 0.3 °C, $n = 5$; Welch

Table 3.1: Summary for the 13 observation patches (* heated patches). The number of nests during NF, the failure rates between NF and B1 as well as B1-B2, the proportion of nests with B3, and the mean soil temperature (season mean ± SD) at a depth of 20 and 40 cm are given.

Patch number	Number of nests (NF)	Failure rate (%) NF-B1	Failure rate (%) B1-B2	Proportion of nests with B3	Soil temperature (°C) 20 cm	Soil temperature (°C) 40 cm
1*	99	23.2	10.5	89.7	19.4 ± 4.0	18.1 ± 3.5
2*	99	30.3	18.8	85.7	20.6 ± 4.0	19.6 ± 3.8
3*	101	30.7	11.4	83.9	20.4 ± 4.0	21.3 ± 3.8
4*	77	32.5	9.6	78.7	21.7 ± 3.9	25.2 ± 3.5
5*	50	32.0	5.9	71.9	21.9 ± 3.9	21.1 ± 3.6
6*	32	37.5	15.0	76.5	22.0 ± 4.2	26.2 ± 4.0
7*	213	37.6	13.5	89.6	19.2 ± 3.9	19.0 ± 3.7
8	72	23.6	20.0	52.3	18.1 ± 4.0	-
9	158	45.6	88.4	40.0	17.9 ± 4.2	17.5 ± 3.9
10	70	22.9	3.7	90.4	18.1 ± 3.8	16.9 ± 3.1
11	77	15.6	6.2	60.7	18.0 ± 3.9	17.6 ± 3.9
12	24	29.2	5.9	43.8	18.6 ± 4.4	17.6 ± 3.9
13	66	25.8	14.3	81.0	19.0 ± 4.7	17.7 ± 4.2

test: $t = 3.43$, $df = 6.18$, $p = 0.013$). Thus, the heating pipes on the campus of the University significantly increased the temperature of the surrounding ground by 2-4 °C.

3.3.2 Nesting activity

The first queens started nest founding in the middle of March, but provisioning of brood cells did not start until the beginning of April. The duration of P1 (NF-B1) was 43 ± 4 days, whereas P2 (B1-B2) lasted for only 19 ± 5 and P3 (B2-B3) for 13 ± 5 days (means ± SD for 13 patches). Activity of B1 lasted for 16 ± 2, for B2: 18 ± 2, and for B3: 21 ± 6 days (means ± SD for 13 patches). The flight season ceased at the end of September with the last sexuals of B3 emerging on September 19.

Comparing the 13 different patches of *L. malachurum*, there was a great variability with regard to the activity pattern of the different broods despite their spatial proximity (figures 3.1 and 3.2). The 13 observation patches differed significantly in the beginning, end, and duration of the different broods as well as in the duration of the pauses (One-way ANOVA with Welch correction: $p < 0.05$ for all comparisons, table 3.2). For example, we observed a maximum difference of 18 days between the 13 different patches with respect to the beginning of B1 (range: May 26 - June 13, 2004, $n = 13$). These differences add up in the course of the season resulting in a maximum difference of 35 days for the beginning of B2 (range: June 20 - July 25, 2004, $n = 13$) and 42 days for the beginning of B3 (range: July 17 - August 28, 2004, $n = 13$).

Table 3.2: Results of the One-way ANOVA with Welch correction testing for significant differences among the 13 observation patches with regard to the different measures of nesting activity (beginning, end, and duration of the broods; duration of the pauses). The test statistic F, the degrees of freedom df, and the probability p are given.

One-way ANOVA	F	df	p
End of NF	21.1	12, 301	< 0.001
Duration of P1	71.9	12, 209	< 0.001
Beginning of B1	278	12, 210	< 0.001
End of B1	111	12, 206	< 0.001
Duration of B1	7.51	12, 206	< 0.001
Duration of P2	16.2	12, 138	< 0.001
Beginning of B2	246	12, 136	< 0.001
End of B2	157	12, 115	< 0.001
Duration of B2	2.03	12, 115	0.028
Duration of P3	10.3	12, 53.2	< 0.001
Beginning of B3	156	12, 53.0	< 0.001
End of B3	216	12, 71.1	< 0.001
Duration of B3	21.6	12, 54.2	< 0.001

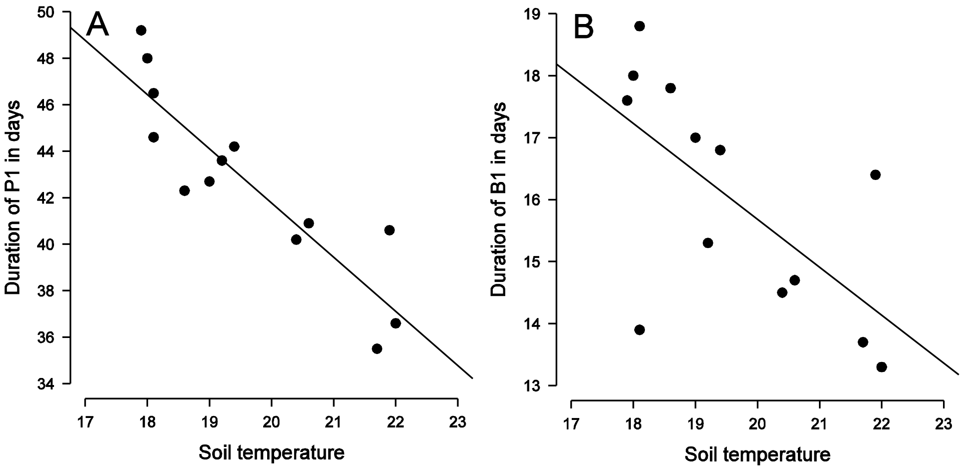


Figure 3.3: Duration of P1 (A) and B1 (B) for the 13 observation patches as a function of the mean soil temperature (season means) 20 cm below surface. Linear regression lines are given.

3.3.3 Influence of soil temperature on nesting activity

The mean soil temperature 20 and 40 cm below surface had a strong negative effect on the end of NF and on the beginning and end of B1-B3 (Pearson correlation: $p < 0.05$ for all correlations, $n_{20cm} = 13$, $n_{40cm} = 12$). Both temperature measures were significantly negatively correlated with the duration of all three pauses as well as the duration of B1 (figure 3.3, table 3.3).

However, soil temperature at a depth of 20 and 40 cm had no effect on the duration of B2 and B3 (table 3.3). The large coefficients for some correlations between temperature and the duration of pauses indicate that soil temperature has a strong effect on the shift in the position of the different broods (earlier beginning and end of B1-B3, figure 3.2).

In "heated" patches activity of the different broods started and ended earlier and showed a reduced duration of P1, P2, and B1 in comparison to the "unheated" patches (t test: $p < 0.05$ for all comparisons, $n_1 = 7$, $n_2 = 6$). The duration of P3, B2, and B3

Table 3.3: Results of the Pearson correlation analyses between the duration of P1-P3 and B1-B3 and the mean soil temperature (season mean) 20 and 40 cm below surface of the 13 observation patches. The correlation coefficient *r*, the sample size *n*, and the probability *p* are given.

Soil temp.		Duration of P1	Duration of P2	Duration of P3	Duration of B1	Duration of B2	Duration of B3
20 cm	*r*	-0.895	-0.839	-0.701	-0.644	0.440	0.023
$n = 13$	*p*	< 0.001	< 0.001	0.008	0.017	0.133	0.941
40 cm	*r*	-0.875	-0.694	-0.590	-0.879	0.344	-0.069
$n = 12$	*p*	< 0.001	0.012	0.043	< 0.001	0.274	0.831

did not differ significantly between the two groups of patches (t test: $p > 0.05$ for all comparisons, $n_1 = 7, n_2 = 6$).

3.3.4 Nesting strategy

In the 13 observation patches we observed NF for 1138 nests; 70.3 ± 7.8% of these showed activity in B1, 59.2 ± 17.5% in B2, and 44.2 ± 16.2% in B3 (means across 13 patches). A total proportion of 72.6 ± 17.7% (range: 40 - 90.4%; $n = 13$, table 3.1) of the nests that were active during B2 showed activity during B3. The 13 patches differed significantly in the proportion of nests with three broods (χ^2 test: $\chi^2 = 71.6$, $df = 12$, $p_{exact} < 0.001$).

The analysis of the failure rates between the different broods (table 3.1) revealed no evidence for a correlation between the proportion of nests with B3 and the proportion of colonies that failed between NF and B1 (Spearman rank correlation: $r = -0.189$, $p = 0.536$, $n = 13$) as well as B1 and B2 ($r = -0.211$, $p = 0.489$, $n = 13$). Thus, the difference in the proportion of nests with a three brood strategy was not the result of differences in failure rate.

3.3.5 Influence of nesting activity pattern on nesting strategy

The proportion of the nests that exhibited B3 was significantly influenced by the beginning of B1 and B2, the end of NF and B2, and the duration of B1, B2, and P2 (table 3.4). Of these, the durations of B1 and B2 were positively correlated whereas the beginning of B1 (figure 3.4 A) and B2, the end of NF and B2, and the duration of P2 were negatively correlated with the proportion of a three brood strategy.

Table 3.4: Results of the logistic regression analyses with the probability of the colonies within a patch to produce B3 as the dependent and the different measures of nesting activity as the independent variables.

independent variable	Wald χ^2	r^2	AUC	effect	p
End of NF	4.93	0.013	0.561	-	0.026
Duration of P1	3.17	0.008	0.549	-	0.075
Beginning of B1	8.9	0.024	0.598	-	0.003
End of B1	0.43	0.001	0.528	-	0.512
Duration of B1	6.58	0.017	0.569	+	0.01
Duration of P2	62.4	0.178	0.737	-	< 0.001
Beginning of B2	37.1	0.109	0.681	-	< 0.001
End of B2	6.28	0.017	0.578	-	0.012
Duration of B2	28	0.075	0.636	+	< 0.001

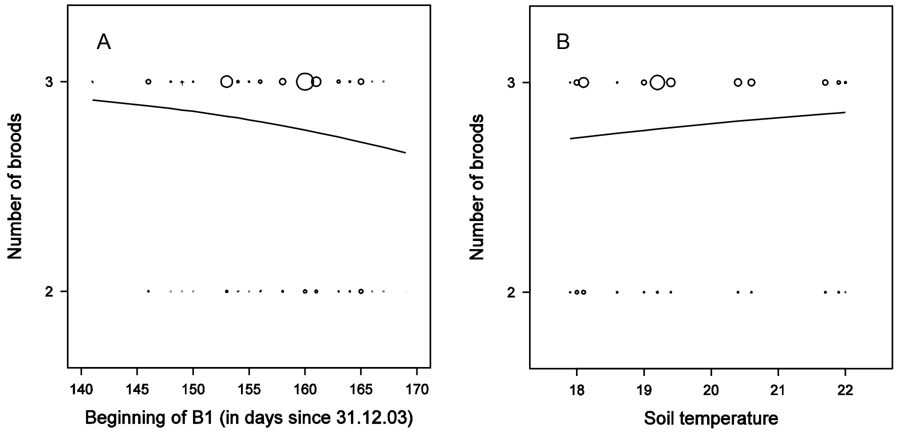


Figure 3.4: A: The number of broods (2 or 3) as a function of the beginning of B1 (in days since 31.12.03). The logistic fit is shown. The frequency of the combinations of x and y values that occur more than once are indicated by the size of the circles (2-123 nests per data point). B: The number of broods (2 or 3) as a function of the mean soil temperature (season mean) at a depth of 20 cm. The logistic fit is shown (4-103 nests per data point).

3.3.6 Influence of soil temperature on nesting strategy

There was a marginally non significant difference in the proportion of a three brood strategy between the "heated" and "unheated" patches: 82.3 ± 6.8% of the B2 nests at the "heated" patches and 61.4 ± 20.4% of the B2 nests at the "unheated" patches had B3 (Welch test: $t = 2.27$, $df = 6.49$, $p = 0.06$, $n_1 = 7$, $n_2 = 6$). Variation in the nesting strategies was significantly higher among the "unheated" as compared to the "heated" patches (Levene test: $F_{5,6} = 5.66$, $p = 0.037$).

Overall, we found a significant effect of the mean temperature 20 cm below surface on the nesting strategy (logistic regression: Wald $W^2 = 5.75$, $p = 0.016$, figure 3.4 B). Nests at patches with a higher soil temperature showed a higher probability of producing three instead of two broods. However, the effect of soil temperature on the number of broods was rather small ($AUC = 0.599$, $R^2 = 0.015$). The odds that the colonies produced three instead of two broods increased by 21.3% with a temperature increase of 1 °C (odds ratio = 1.21). Soil temperature 40 cm below surface had no significant effect on the nesting strategies of the nests (logistic regression: Wald $W^2 = 0.053$, $AUC = 0.554$, $p = 0.82$, $R^2 = 0.0001$).

3.4 DISCUSSION

3.4.1 Influence of soil temperature on nesting activity

Soil temperature mainly affected the duration of the different pauses in the nest cycle of *L. malachurum* in the population at Wuerzburg. Pauses at patches with higher soil temperature were shorter, resulting in an earlier initiation and termination of provisioning activity of the different broods within the flight season. These results are confirmed by the comparison of nesting activities of "heated" and "unheated" patches and provide clear evidence for an accelerating, physiological effect of higher soil temperature on the development of the larvae. This is consistent with numerous studies on the effect of temperature on development (Eliopoulos & Stathas, 2003; Gilbert & Raworth, 1996; Grafton-Cardwell *et al.*, 2005; Howe, 1967; Kamm, 1974; Melville & Schulte, 2001; Porter, 1988; Whitfield & Richards, 1992).

The negative correlation of soil temperature with the duration of provisioning of B1 workers might be due to a longer daily activity of workers at warmer patches, thereby reducing the number of days needed to provision the next brood. Additionally, soil temperature might also accelerate ageing of the workers (Cossins & Bowler, 1987). This might lead to a reduced life span of the bees and, thus, a shorter duration of the foraging activity. Soil temperature had an effect on the duration of B1 but not on B2 and B3. In early spring when weather conditions are less predictable and colder on average soil temperature might be more important than during summer. Then other factors like air temperature, solar radiation, and resource availability might have a larger influence than soil temperature (Richards, 2004).

3.4.2 Influence of nesting activity pattern on nesting strategy

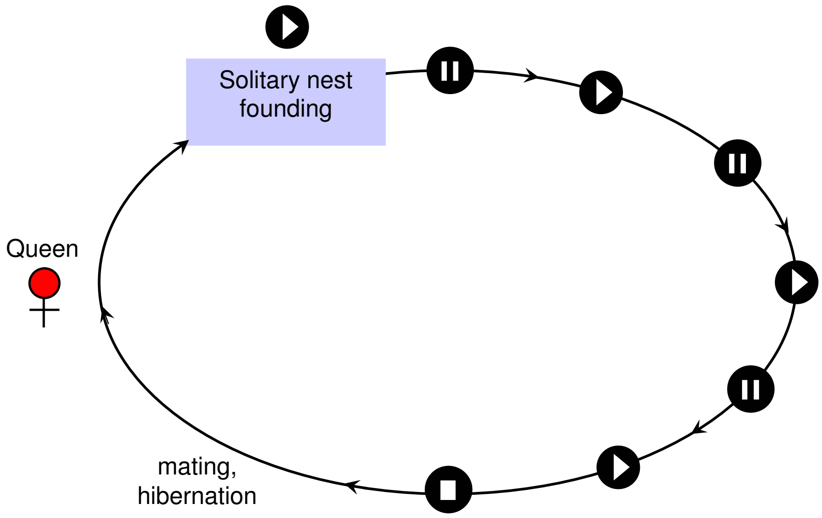
Nearly all measured aspects of nesting activity were significantly negatively correlated with the proportion of nests with B3. However, these effects were rather small with R^2 values ranging from 1 to 19%. Actually, whether a nest produces a third brood depends on whether it had (enough) workers in the second brood, which in turn depends on whether workers were produced during the activity of B1. Thus, whether there is a two or three brood nest cycle can only be influenced during or prior to B1: the end of NF, the duration of P1, and the beginning of B1. Of these three variables, only the end of NF and the beginning of B1 (figure 3.4 A) had a significant and negative influence (the earlier, the more) on the proportion of colonies with B3. Both effects were rather small, however, and can not explain the considerable variability with respect to the different nesting strategies among patches (table 3.1).

All the other measures of nesting activity that were significantly correlated with the proportion of B3 nests have to be interpreted as non-causal relationships. For example, in colonies with a three brood strategy, B2 consists of only workers or workers and sexuals whereas in colonies with a two brood strategy, B2 consists of exclusively sexuals. Since workers are smaller than sexuals (Strohm & Bordon-Hauser, 2003), they develop faster and emerge earlier. Thus, a three brood strategy may result in a reduced duration of P2 and an earlier beginning of B2, which in turn leads to a strong negative correlation between the duration of P2 and the proportion of B3 nests. These considerations show that the duration of P2 does not directly affect the probability of B3, but that both are correlated due to an underlying pattern.

3.4.3 Influence of soil temperature on nesting strategy

We predicted that a reduction in the length of the nesting cycle (maximum difference in the onset of B3: 42 days) would improve the prospects of a strategy with more worker broods. We know that sexuals of *L. malachurum* need at least 22 days for egg to adult development (Weissel and Strohm, unpublished data). Additionally, for sexuals of *L. zephyrum* reared in artificial colonies in the laboratory at a temperature of 26 °C Kamm (1974) reports a development time of at least 21 days. Therefore, taking time for provisioning into account colonies should need at least four weeks to produce a brood of sexuals. In accordance with the clinal variation in the social behaviour of *L. malachurum*, with more worker broods in warmer climates (Knerer, 1992; Richards, 2000), we found a higher percentage of colonies with a three brood strategy at patches with a higher soil temperature 20 cm below surface. Yet, the effect of temperature on the number of broods was rather small. Less than 2% ($R^2 = 0.015$) of the variation in the number of broods could be explained by the influence of soil temperature. The probability for a three brood strategy increased only by 13% over the total range of measured temperatures. Moreover, comparing "heated" and "unheated" patches we found no significant difference in the proportion of nests with B3. Why only the temperature in a depth of 20 cm had a significant effect on the nest strategy is not clear. As explained above, the nesting strategy is determined prior to or during B1. The depth of the nest might be around 20 cm at that time. Thus, the temperature at 40 cm might not have a strong influence on B1.

In conclusion, soil temperature strongly affected the temporal pattern of the nesting activity at different patches of *L. malachurum* at Wuerzburg. However, although the nests under study experienced a much larger range of soil temperatures than would have been available under natural conditions, temperature does not satisfactorily explain the differences in the proportion of a three as opposed to a two brood nesting strategy. Even though there are various examples for the influence of environmental conditions like photoperiod, altitude, or climate on the variability in social behaviour (Eickwort *et al.*, 1996; Knerer, 1992; Miyanaga *et al.*, 1999; Soucy, 2002; Yanega, 1997), at a local scale other extrinsic or intrinsic factors like resource availability, queen quality, or genetic components might have a greater impact on the number of broods in the flight season.


Solitary nest founding
Queen
mating,
hibernation

Chapter 4

The evolution of activity breaks in the nest cycle of annual eusocial bees: a model of delayed exponential growth

with Norbert Weissel, Erhard Strohm and Hans-Joachim Poethke

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Abstract. Background: Social insects show considerable variability not only in social organisation but also in the temporal pattern of nest cycles. In annual eusocial sweat bees, nest cycles typically consist of a sequence of distinct phases of activity (queen or workers collect food, construct, and provision brood cells) and inactivity (nest is closed). Since the flight season is limited to the time of the year with sufficiently high temperatures and resource availability, every break reduces the potential for foraging and, thus, the productivity of a colony. This apparent waste of time has not gained much attention.

Results: We present a model that explains the evolution of activity breaks by assuming differential mortality during active and inactive phases and a limited rate of development of larvae, both reasonable assumptions. The model predicts a systematic temporal structure of breaks at certain times in the season which increase the fitness of a colony. The predicted pattern of these breaks is in excellent accordance with field data on the nest cycle of the halictid *Lasioglossum malachurum*.

Conclusion: Activity breaks are a counter-intuitive outcome of varying mortality rates that maximise the reproductive output of primitively eusocial nests.

4.1 BACKGROUND

Some of the most important components of life history decisions refer to the optimal timing of accumulation of resources and their allocation to growth and reproduction. At any time during its life an organism has not only to spend resources on the conflicting requirements for maintenance, somatic growth, and reproduction, but has also to decide on how much and when resources like food or building material should be accumulated in order to maximise reproductive output. Up to now, theoretical studies on life history strategies of eusocial insects have mainly focused on the first aspect: optimal resource allocation (Macevicz & Oster, 1976; Mirmirani & Oster, 1978; Brian *et al.*, 1981; Beekman *et al.*, 1998a). However, the obvious and ample variability in seasonal activity patterns within and between species of eusocial insects requires investigating the optimal timing of resource accumulation, too.

Seasonal activity patterns vary widely among the species of bees and wasps that have been studied as model organisms for the evolution of sociality in insects (Ross & Mathews, 1991; Michener, 1990, 2000). Many annual Polistes, Vespa, Xylocopa and Allodape species show continuous colony activity during the whole season (Miyano, 1980; Archer, 1993; Steen & Schwarz, 2000; Cronin, 2001). This results in a more or less continuous production of offspring as is assumed in the classical model of colony development by Macevicz and Oster (1976). Model predictions have been tested and were met in field data from Polistes and Vespa species (Macevicz & Oster, 1976).

However, the nest cycle of most halictids (e.g. in the genera *Lasioglossum* and *Halictus*) is characterised by several discrete broods that are separated by distinct activity breaks (Sakagami, 1974; Michener, 1990; Yanega, 1997; Knerer & Plateaux-Quenu, 1967; Knerer, 1980), but see (Knerer & Plateaux-Quenu, 1967) and (Knerer, 1980). During the solitary founding phase, halictid queens construct nests and supply brood cells with pollen and nectar as provisions for their larvae. After a break of a few weeks, during which the nest is closed and no activity outside the nest can be observed, a first worker brood emerges and starts collecting pollen and nectar to provision the eggs that are usually laid by the queen. Subsequent broods are also separated by breaks during which nests are closed and no outside activity can be observed. Activity breaks can last up to three weeks (Sakagami, 1974; Knerer, 1992; Weissel *et al.*, submitted). Usually sexuals emerge in the last brood only, while all other broods consist mainly of workers.

There are also species with an intermediate position between continuous growth and discrete broods. In *Bombus* species, for example, the nest cycle is organised in more or less discrete broods but without activity breaks and nest closure (Duchateau & Velthuis, 1988).

Due to temperature-dependence of their activity and resource availability, ectothermic organisms, like insects, have to adjust their life history to the seasonal conditions in temperate latitudes. Reproduction and growth must be completed within a limited time span and the unfavourable period has to be bridged by diapause. Variability in biotic and abiotic conditions during the reproductive period has been assumed to cause changes in activity patterns on a smaller time scale (Willmer & Stone, 2004). Usually bees will forage during the day when visibility is good and temperature is high enough for flying and foraging (Willmer, 1983; Richards, 1994; Strohm & Linsenmair, 1998; Stone *et al.*, 1999; Vogt, 2000). However, the evolutionary transitions to dim-light foraging have occurred repeatedly in bees, and may be associated with the escape from enemies or competitors (Wcislo *et al.*, 2004; Warrant *et al.*, 2004). The daily activity patterns of the solitary bee *Anthophora plumipes* has been attributed to variation in the thermal environment as well as quality and quantity of floral resources (Stone, 1994). The pattern of activity breaks in halictids has accordingly been related to patterns of resource availability and photoperiod (Knerer & Plateaux-Quenu, 1967; Knerer, 1987, 1992). By contrast, Kaitala *et al.*'s (1990) modelling approach for *L. malachurum* assumes synchronised nest closure in halictid nest aggregation to be due to an increasing threat of nest usurpation by intraspecific parasites, so called floater queens.

Furthermore one could suppose that activity breaks after the emergence of the first workers just appear when worker mortality is rather high and all workers of a brood have died before emergence of the individuals of a second brood. However, it is clear from field observations that the breaks do not occur simply because all workers of a brood have died. Some workers even survive a complete activity break and continue foraging when the nest is reopened (Knerer, 1992; Weissel and Strohm, unpublished). On the contrary, breaks occur even though there are still some workers alive in a nest, showing that there has to be some advantage of interrupting foraging activity.

The well-known colony growth model of Macevicz & Oster (1976) for insect colonies identifies the sequential production of workers first and sexuals just before the end of the flight season (so called bang-bang reproduction) as the optimal investment strategy to maximise colony fitness. Whereas this model assumes instantaneous occurrence of adult progeny the model that we present accounts for a certain development time of the larvae. The results of our model challenge the assumption that only variation in environmental factors governs the emergence of activity breaks. The model explains the evolution of the observed activity patterns rather by an asymmetric interaction between endogenous and exogenous factors of colony development.

4.2 RESULTS

4.2.1 A simple model of delayed exponential growth with activity breaks

We use a simple difference equation model to analyse colony development during a season of length L. Two main dependent variables describe the state of a colony: the number of workers (W_i) at time step i and the number of sexuals (S_i) at that time. For simplicity we do not distinguish between male and female sexuals (Macevicz & Oster, 1976). The colony cycle typically starts in spring with nest founding by inseminated hibernated queens. During the founding phase the queen works alone and performs all the foraging tasks that will be taken over by workers after their emergence later in the season (Michener, 2000). Thus we start with initial condition $W_1 = 1$ assuming that the founding queen acts like a single worker until the first eggs have developed to adults (Knerer, 1992). The dynamics in the number of nestmates is governed by two mechanisms: mortality and reproduction. Each individual survives from time step i to $i+1$ with a probability q_i (that might vary with time step i during the season). Resource allocation in each time step (i) is directly proportional to the current worker force (W_i). Each worker can provision c_i (worker efficiency) eggs (= brood cells) per time step. We assume that the actual egg laying rate of the queen is only limited by the number of eggs that can be successfully provisioned by the workers of the colony (Knerer, 1992). Adults emerge after a development time T. Halictid colonies suffer from numerous threats during activity periods (see discussion), so nest and especially brood mortality are rather high (Weissel *et al.*, submitted). As this parameter is not in the main focus of our analysis and field data are not readily available, we use the same survival probability (q_i) for eggs and for adult workers to keep the model simple (Additional numerical calculations have shown that our results differ only quantitatively if we uncouple worker and brood mortality). Additionally we assume that development time (T) does not correlate with either season length (L), caste or onset of development.

The portion u_i of resources spent in time step i is allocated to new workers. Consequently, the portion $(1-u_i)$ is invested in sexuals S_i. Thus, the number of workers (W_{i+1}) at time step $i+1$ can be calculated as

$$W_{i+1} = q_i W_i + u_{i-T} c_{i-T} W_{i-T} \prod_{j=i-T}^{i} q_j \tag{4.1}$$

In most halictid bees, life span of adult females is much longer than life span of workers (Sakagami, 1974). Female sexuals have to hibernate before nest founding in the following year, while workers live only for several weeks. Thus we neglect mortality of sexuals as has been done by Oster and Macevicz (1976) in most of their analyses and thus we get for the number of sexuals (S_{i+1}) at time step $i+1$

$$S_{i+1} = S_i + (1-u_{i-T})c_{i-T}W_{i-T} \prod_{j=i-T}^{i} q_j \tag{4.2}$$

These two equations describe the delayed (by development time T) exponential growth of an annual, primitively eusocial bee colony. Fitness of colonies following such nest dynamics can be measured by the final number of sexuals S_L. Oster and Wilson (1978) have studied such systems (in time continuous form and without delay) as optimal control problems with control variable u_i (allocation in workers) (Oster & Wilson, 1978). They found that the (time-dependent) optimal control solution that maximises S_L is switching in u_i from 1 to 0 at an optimal point in time (dichotomous bang-bang strategy, SWT = switching time). So the optimal temporal pattern of reproduction consists of two distinct phases: exclusive worker production followed by exclusive sexual production. This result also holds for delay systems (Perleson *et al.*, 1976; Mirmirani & Oster, 1978). In our simple model the optimal switching point can be found by a simple argument: Switching should take place when an egg just laid can not mature, eclose and contribute to rearing other individuals anymore. From time $L-T$ to L no eggs should be produced at all, because they would not emerge before the season ends. The last contribution of a worker to sexual production can occur at time $L-T-1$ and thus the last worker egg should be laid at $L-2T-1$. So we choose

$$u_i = \begin{cases} 1 & : \quad i \leq L-2T-1 \\ 0 & : \quad i > L-2T-1 \end{cases}$$

for further analysis.

We assume constant survival ($q_i = q$) and constant worker efficiency ($c_i = c$) throughout the whole season. If we ignore the influence of activity breaks on these parameters, we get nest dynamics as shown in figure 4.1 a. To take activity breaks into account, we have to modify both parameters during breaks. Each break starts at time B_1 and ends at B_2. During a break food allocation is impossible ($c = 0$), but survival probability is increased from q to $Q > q$. Accordingly we formulate

$$c_i = \begin{cases} 0 & : \quad B_1 < i < B_2 \\ c & : \quad \text{otherwise} \end{cases}$$

and

$$q_i = \begin{cases} Q & : \quad B_1 < i < B_2 \\ q & : \quad \text{otherwise} \end{cases}$$

Analogously additional activity breaks can be inserted into the nest cycle. However, here we focus on a single break as our main results are not changed by the simultaneous consideration of several breaks. To answer the question of whether there are

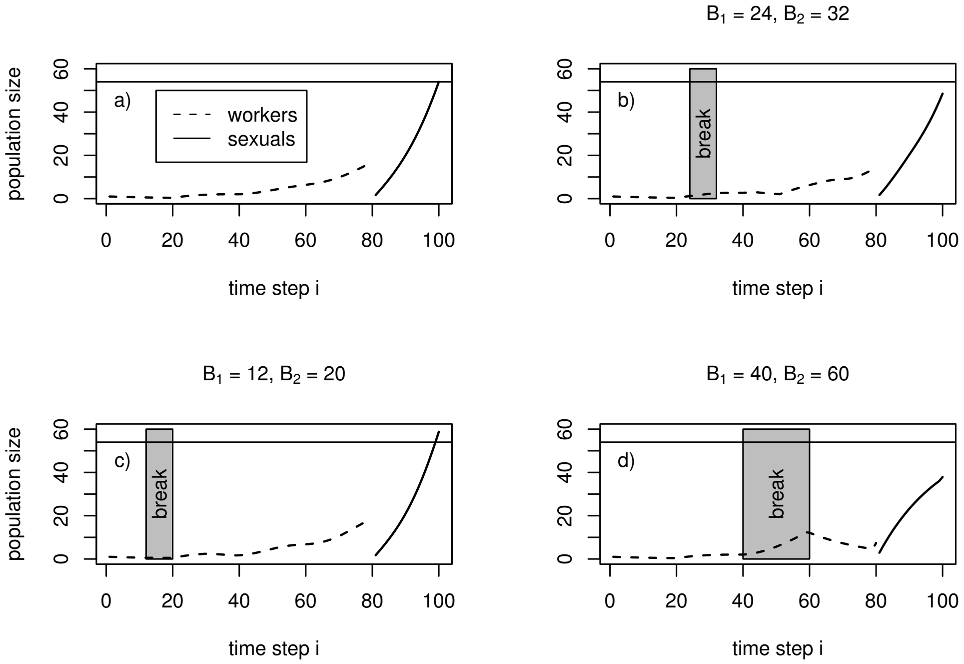


Figure 4.1: Development of worker and sexual numbers with and without a break. Different activity breaks can result in a decrease (b, d) or an increase in the overall production of sexuals (c). Model parameters: worker efficiency c = 0.7, off-break survival q = 0.95, development time T = 20, season length L = 100 and within-break survival Q = 0.985. The parameters B_1 and B_2 printed above each graph denote the onset and end of the break in question.

activity breaks that increase fitness when inserted into the nest cycle we analysed the complete B_1-B_2 parameter space by simple numerical calculations. We interpret B_1 and B_2 as life history parameters of the queen, who decides when to close and reopen her nest (Knerer, 1992). During a single B_1-B_2 space simulation all other parameters were kept constant. Computer simulations are conducted with the programming language R (Ihaka & Gentleman, 1996).

4.2.2 Estimating model parameters

We calibrated the model with data from the halictid species *L. malachurum*. In this species a typical season in central Europe lasts for about 100 to 140 days. Since the absolute length of the season did not change our results within this range we choose $L = 100$. The mean life-time of *L. malachurum* workers is about 24 days (Knerer, 1992). This results in a survival probability of $q = 0.95$ per time step. Development from egg to adult typically lasts $T = 20$ time steps (Knerer, 1992). There are no data available about the shelter effect of nest closure, so we studied the effect of within-break survival Q in the range from q (= 0.95) to 1. Worker efficiencies (c) from 0.5 to 1.0 (per time step) result in an output of about 20 to 80 sexuals, similar to typical

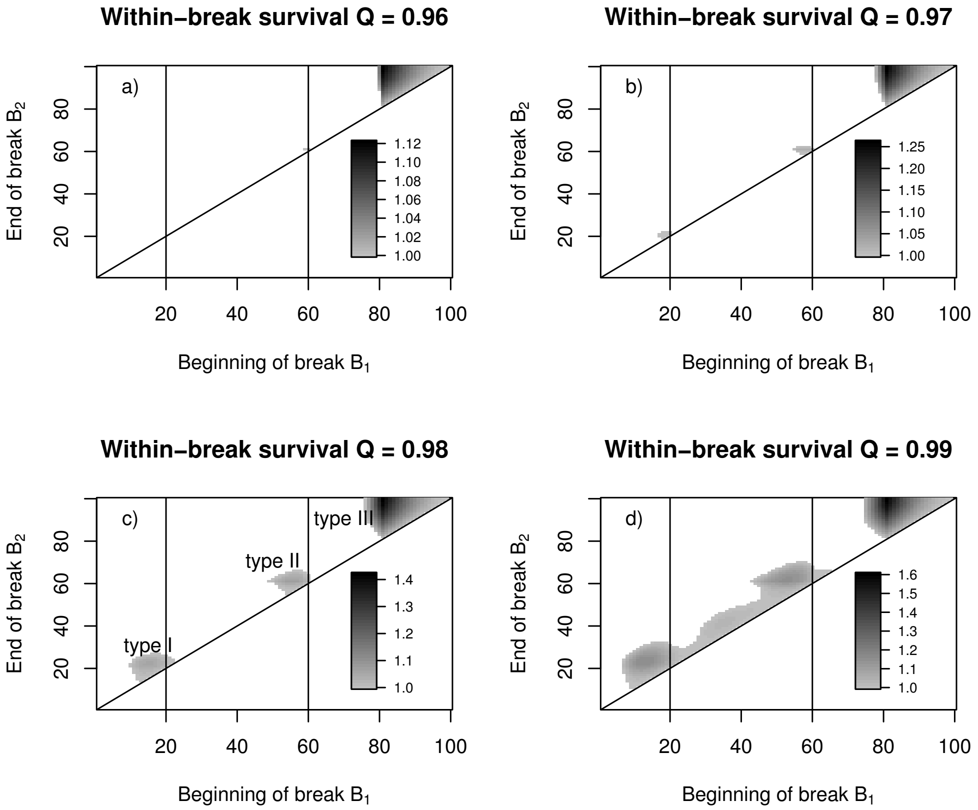


Figure 4.2: Relative fitness of single break strategies (compared to the case without a break) as a function of the time steps at the beginning (B_1) and the end of a break (B_2). Gray areas indicate beginning and end of fitness increasing breaks (shading of areas gives relative fitness of colonies following a respective break strategy). The different figures correspond to scenarios differing in within-break survival Q. Increasing within-break survival results in the emergence of two additional areas which represent fitness increasing breaks and which increase in size (b, c, d) with increasing protection during the breaks. For referring to the three prominent areas of fitness increasing breaks in the text we labelled them type I, II and III (c). Model parameters: worker efficiency $c = 0.5$, off-break survival $q = 0.95$, development time $T = 20$, season length $L = 100$.

colony sizes in field observations (Strohm & Bordon-Hauser, 2003).

4.2.3 Numerical results

The relative fitness gain due to activity breaks is shown in figure 4.2. Gray areas mark B_1-B_2 combinations that result in increased fitness compared to the case without breaks. This corresponds to nesting patterns which yield higher numbers of sexuals at the end of the season (see figure 4.1 c in comparison to 4.1 b and 4.1 d). To facilitate reference to the three prominent areas of fitness increasing breaks we labelled them type I, II and III (see figure 4.2 c). If activity breaks increase survival probability only slightly (figure 4.2 a) they will result in a net benefit for colony fitness only at a time where they do not cause any costs. This is the case for breaks which protect the devel-

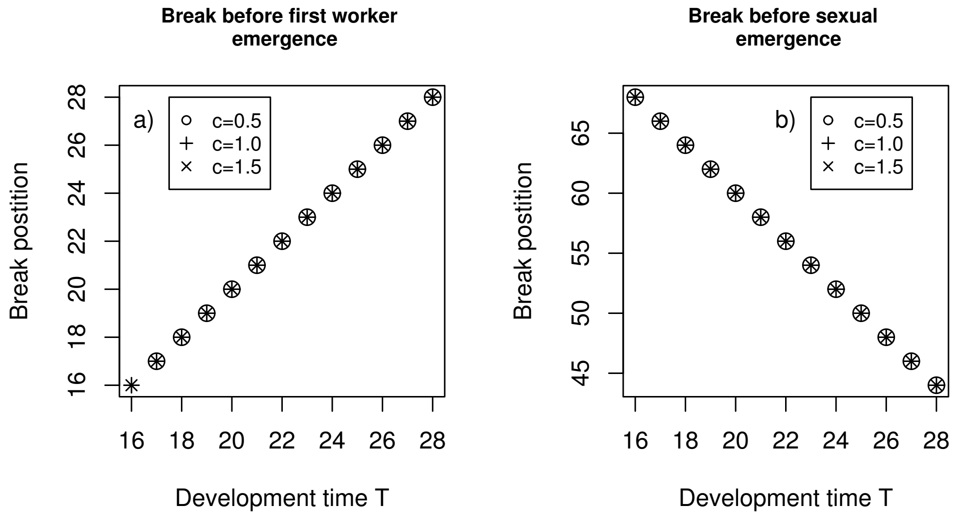


Figure 4.3: Temporal position of first (a) and second break (b) as a function of development time and worker efficiency. Since break duration differs when worker efficiency c and development time T are changed, optimal break timing was estimated for each parameter combination, when within-break Q was just high enough to ensure the emergence of a (very short) fitness increasing break. Model parameters: off-break survival q = 0.95, season length L = 100. Within-break survival (Q) was chosen sufficiently high to ensure the emergence of breaks of minimum duration.

opment of the sexuals at the end of the season (type III breaks). Such breaks do not cause any costs because only resources acquired (and allocated to the provisioning of workers or sexuals) before the last development period (of length T) will increase the colony's output of sexuals.

However, increased protection during breaks (figures 4.2 b – 4.2 d) causes a second and a third area of beneficial times for breaks (figure 4.2 b and 4.2 c) (type I and II). The position of these spots remains constant whereas their area increases with increasing break survival probability rate Q resulting in an extended area of beneficial break timings.

For a more detailed analysis of the temporal position of the type I and II breaks we first calculated the optimal length and position of the trivial break (type III, see above and figure 4.2) and based all further analyses on a colony cycle including this optimal type III break. The temporal position of the type I and II breaks was then investigated in relation to development time (T). In each scenario with fixed model parameters c (efficiency), q (survival probability) and particular development time T we chose the minimal Q-value (within break survival) to ensure break emergence of type I and type II respectively. This results in a linear relationship between development time T and break position for break types I and II (figure 4.3 a and figure 4.3 b). So breaks of type I can be interpreted as breaks just before the emergence of the first workers. And breaks of type II are breaks shortly before the production switch (SWT) from workers

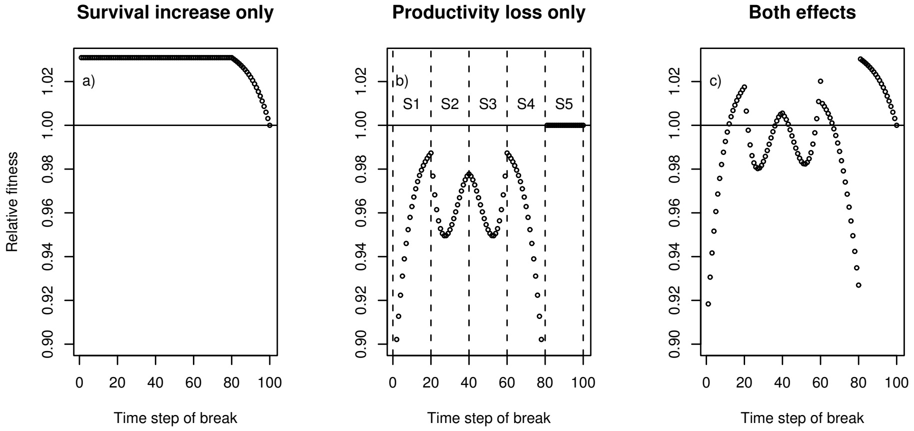


Figure 4.4: Influence of the temporal position of short (lasting only for a single time step) activity breaks on relative colony fitness in different scenarios: a) when productivity is not decreased during breaks ($c_i = c$), b) when survival is not increased during breaks ($Q = q$) and c) when both mechanisms are kept in the model. Model parameters: worker efficiency c = 0.5, off-break survival q = 0.97, development time T = 20, season length L = 100 and within-break survival Q = 1.0.

to sexuals. The results show broad stability over a wide range of the worker efficiency parameter c.

For a deeper analysis of the mechanisms responsible for the position of activity breaks we slightly modified our model and allowed only activity breaks lasting for exactly one time step. We first focused on the effect of mortality and ignored the reduction in worker efficiency during breaks (the loss part in fitness balance). Thus, activity breaks only increase survival but do not reduce resource allocation (figure 4.4 a). This increases relative fitness (compared to the standard scenario without modification) by a constant factor until the first sexuals emerge. As long as brood is produced the increase in survival (lasting for one time step) operates as a multiplier of the final nest output regardless of the actual time step it happens (see equation 4.1). Thus, an increase in survival of 1% translates directly into a fitness gain of 1% as all sexuals profit from the benefit. As soon as the first sexuals emerge (T time steps before the season ends) a break can only protect the development of the remaining brood and consequently the beneficial effect of increased survival declines with each emerging sexual.

Next we reduced efficiency during breaks but kept survival rate (the gain part in fitness balance) constant. This has a more complex effect (figure 4.4 b). In the last period of the colony cycle (figure 4.4 b, S5) brood production has ceased and thus, fitness is not affected by late reduction in efficiency. During the prior period (starting at switching time SWT, figure 4.4 b, S4) only eggs for sexuals are laid which contribute to fitness in an additive way. Consequently fitness loss (caused by reduced worker efficiency) is directly proportional to number of workers and as worker number increases during this period, fitness decreases. During the solitary phase of colony

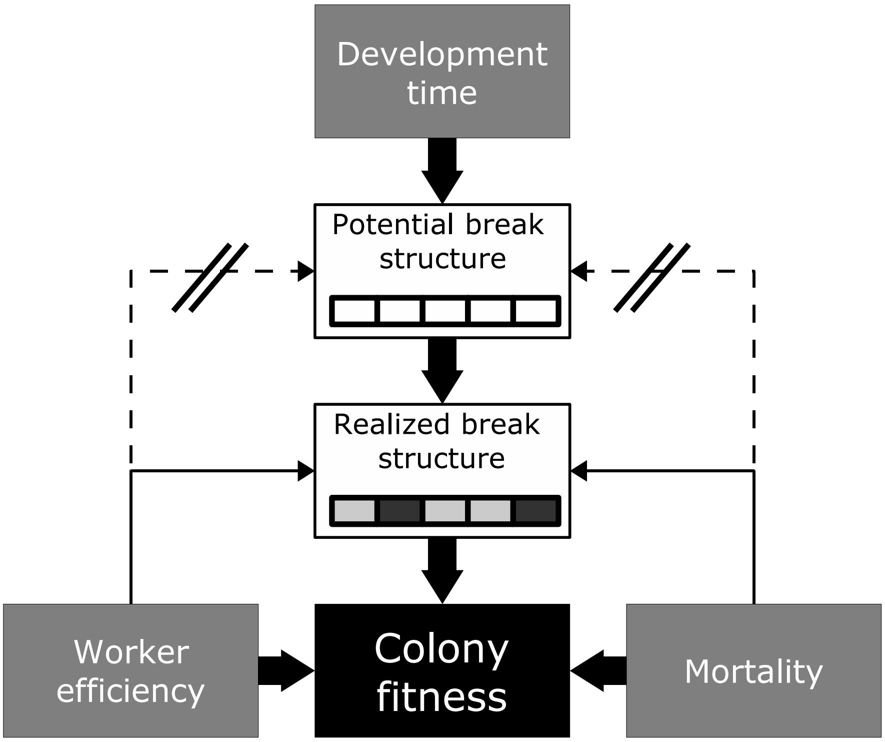


Figure 4.5: Schematic illustration of the factors influencing the emergence of fitness increasing breaks. Development time determines the potential temporal structure of breaks. Whether or not a potential break actually increases fitness, is determined by the increase in colony survival during breaks.

development (figure 4.4 b, S1) sensitivity to productivity loss decreases with time (and relative fitness increases). This effect is not changed at all by different mortality rates (not shown in figure 4.4 b). It is solely caused by the decreasing value of eggs developing into workers. The later a worker egg is produced in the season the less it contributes to overall fitness. At the beginning of the intermediate periods (S2 and S3) the first workers emerge and the oscillating pattern of the relative fitness function is governed by the interaction of both processes acting separately in periods S1 and S4.

The overall effect (without modifications of the mechanisms) of single time step breaks on the system performance is shown in figure 4.4 c. It results from a superposition of figure 4.4 a and 4.4 b and shows the position of suitable breaks as the position of fitness peaks that surpass the critical fitness = 1 level. In this way productivity loss (figure 4.4 b) can be identified as the crucial process responsible for the shape of the fitness function. The mentioned mechanisms do not alter the position of the peaks even if efficiency and mortality are varied. Temporal structure is stable under a wide range of values for efficiency and mortality. Only extreme values of efficiency and mortality can cancel the break benefit completely (see figure 4.5 for a schematic illustration).

To assess the validity of our model we compared the break pattern with data from

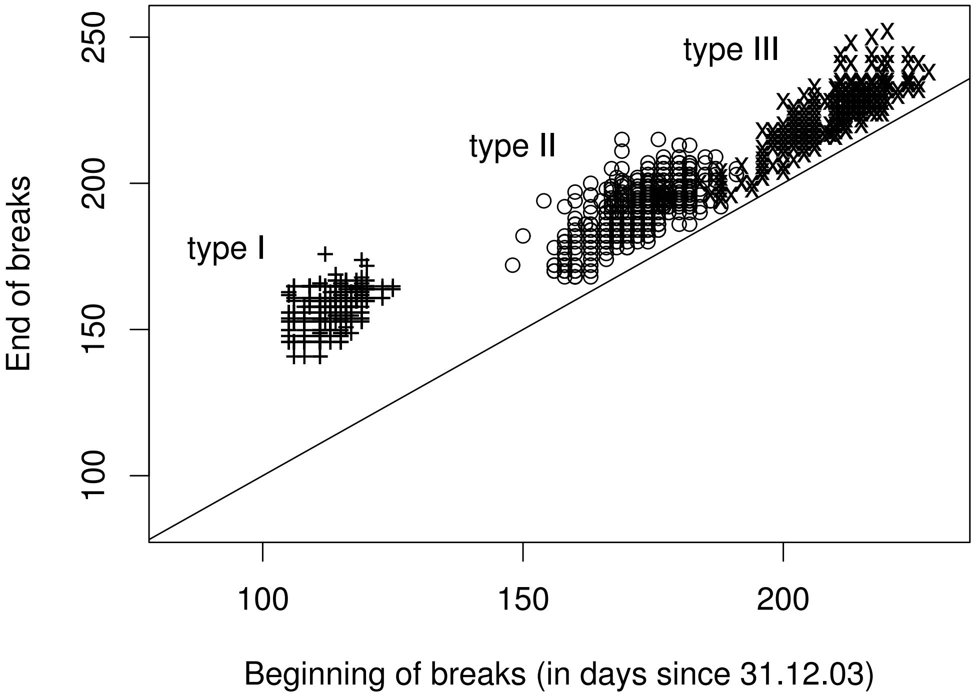


Figure 4.6: Observed activity breaks of *L. malachurum* colonies in Wuerzburg, Germany. Data is based on the nesting activities of 1138 nests within 13 observation patches (within an area of 4 km^2) near Wuerzburg in northern Bavaria in 2004. Nesting activity (defined as either open nest entrance, burrowing activity, and/or the presence of a guarding bee) of each colony was recorded every other day during the whole flight season of *L. malachurum* starting in the beginning of April and lasting until the end of September (Weissel & al., in press). Each point of the figure represents a specific combination of start and end date (Julian days) of an activity break (i.e. a sequence of days, when the nest of a single colony was closed with no signs of activity outside the nest). Both, nest closure and reopening was more or less synchronous among the nests. Symbols: + first break of a colony, o second break of a colony; x third break of a colony.

field observations. The activity pattern of about 1200 nests was recorded throughout the flight period in 2004. The observed pattern (figure 4.6) is surprisingly similar to the pattern that was generated by the model with a particular combination of q and Q. Only the position and duration of the first break differs somewhat from the model prediction: observed breaks begin later and last longer than predicted by the model.

4.3 DISCUSSION

In our modelling approach the emergence of activity breaks is caused by an increased protection of developing larvae and provisioned brood cells when colonies are closed during activity breaks. The main difference from Macevicz and Oster's (1976) model is the consideration of development time. The essential predictions of our model are (1) that there are activity breaks that increase colony fitness (and might consequently be favoured by selection), (2) a clustered temporal structure of fitness increasing activity breaks similar to that observed in the field and (3) a remarkable stability of the temporal pattern within a wide range of model parameters.

As long as development time is not included in a model of colony dynamics, temporal variation in the nesting cycle can only be explained by variability in external factors: When resource availability is low (e.g. low worker efficiency rate c) and predation risk is high (high mortality rate 1-q), nests should be closed to protect brood and adults of the colony, otherwise the colony should be active. Without such environmental variation the temporal course of worker numbers would always be monotonically increasing (until the optimal switching time is reached) and thus, the beneficial effect of nest closure (decreased mortality) can never outbalance the effect of productivity loss due to the wastage of time. Thus, nest closure could never increase fitness within the simple concept of temporally constant parameters (Macevicz & Oster, 1976).

However, as soon as a non negligible time for development of the larvae is taken into account (Perleson *et al.*, 1976; Beekman *et al.*, 1998a), growth is delayed and the temporal course of colony size exhibits increasing as well as decreasing phases (figure 4.1). With finite development time of larvae, fitness increasing activity breaks evolve as an emergent property and there is no need to assume external factors like environmental variation. Certainly environmental variation may trigger the appearance of activity breaks, too, but our model provides a more general explanation that is in excellent accordance with inter- and intraspecific stability of the observed phenomenon even on a geographical scale of a species' range (Richards, 2000; Wyman & Richards, 2003; Cronin & Hirata, 2003).

Weissel *et al.* (in revision, and unpublished) have shown that the temporal pattern of the colony cycle in the halictid bee *L. malachurum* depends on soil temperature, but not on resource availability or predation intensity. This result is consistent with our model prediction. We found that the potential temporal structure of active and inactive phases is only determined by development time (in relation to season length) as the main time constant of the system (figure 4.5). The close relationship between development time and temperature is well known in many insect species in general (Gilbert & Raworth, 1996; Trudgill *et al.*, 2005) and in bees (e.g. Whitfield & Richards, 1992). Constant mortality rates and worker efficiency just determine the occurrence of the potential breaks while the temporal position of breaks is affected by the effect of soil temperature on development time. Although the influence of frequency dependent selection (e.g. the threat of usurpation by floater females) will tend to synchronise the temporal pattern of all externally driven activity breaks (Kaitala *et al.*, 1990), the observed synchronisation of colony activity in aggregations of e.g. *L. malachurum* is readily explained by the shelter a closed nest provides for the developing brood.

Activity breaks will of course reduce any mortality that is experienced by bees during foraging, e.g. by spiders, birds and wasps. In particular some crabronid wasp species of the genus *Cerceris* are specialised on hunting halictid bees as provisions for their own progeny (Bohart & Menke, 1976). We have observed individuals of *C. rybyensis* nesting within aggregations of *L. malachurum* so that they could easily find and paralyse workers returning from foraging trips. There are also conopid flies that wait in the nesting area and parasitise adult bees (Knerer, 1973). Other predators that are excluded by closing the nest are the specialised parasite bee *Sphecodes monilicornis* that violently enters nests and oviposits into brood cells (Legewie, 1925a; Sick *et al.*, 1994) as well as predatory ants that could destroy the whole nest (Knerer, 1973). Notably, vespid wasps whose more or less open nests would not be much better protected by activity breaks do not show such breaks.

Although seasonal activity patterns of annual halictids with discrete broods have been described quite often (Knerer, 1980; Packer & Knerer, 1985; Coelho, 2002; Cronin & Hirata, 2003), exact data on the temporal course of active and inactive phases are scarce. Weissel *et al.* (in press) provide data on the seasonal activity state of about 1200 colonies of *L. malachurum* in northern Bavaria observed during a complete season in 2004 (figure 4.6). For an appropriate and reasonable choice of survival rates in our model (Weissel *et al.*, in press) the number and temporal position of the observed activity breaks in the field are in very good accordance with our model predictions (figure 4.2 c). Discrepancies between field data and model predictions mainly concern the position and length of the first break. This may be due to the fact that the exact time of colony founding or beginning of egg production is difficult to determine in the field. There is also a number of simplifying assumptions in our model which particularly influence the position and length of the first break. First, we have assumed that egg production starts immediately when the colony has been founded. Second, our model does not account for any differences between founding phase and ergonomic (growth) phase of colony development. During the solitary founding phase mortality will probably be higher than later in the season, when the nest is guarded by a worker (Knerer, 1992). Finally, larval development time might take longer when the temperature is lower early in season. As the model assumes temporally constant mortality and development time the predicted timing of the first break can only be an imprecise estimation and a more detailed model would result in a slightly longer first activity break later in the season.

So far we did not analyse the simultaneous optimisation of resource allocation and activity strategies. Although the temporal pattern of fitness increasing breaks turned out to be remarkably stable in our model there will be interactions between the optimal switching point (representing the resource allocation strategy (Macevicz & Oster, 1976)) and break emergence (representing the resource accumulation strategy). In addition there might be constraints like egg number or egg laying rate limitation of the queens as has been observed and analysed in bumble bees (Rosenheim, 1996; Beekman *et al.*, 1998a; Heimpel & Rosenheim, 1998; Casas *et al.*, 2000) that have only a minor influence on activity patterns, but result in completely different optimal switching points and may even cause a different number of broods within the annual colony cycle (Strohm & Bordon-Hauser, 2003).

Our model provides an explanation for the switch from continuous colony growth to reproduction with several discrete broods in social insects (Knerer & Plateaux-Quenu, 1967). In contrast to the continuous growth model of Oster and Wilson (1978) we provide a model for colonies which show a number of discrete broods per season, separated by distinct activity breaks. There is some evidence that the predicted transition between these two types of reproduction might occur in the field. Populations of *Halictus ligatus* have been observed exhibiting both strategies in different years (Richards & Packer, 1995). The presence of adult workers within closed colonies or even worker survival for more than one brood also gives empirical indication of transitions between continuous and discrete growth (Knerer, 1992).

Although continuous colony growth is usually taken as the standard type of colony dynamics in eusocial insects, there is no reason to assume that this is the primary state and reproduction with discrete brood periods during a season evolved from that primary state. Our model does not make any predictions about the evolutionary sequence of these two types of colony dynamics. When continuous colony growth is assumed to be the primary type of nest dynamics, then reproduction in discrete broods separated by activity breaks might be assumed to be a derived character. However, the contrary order seems more realistic. Hunt & Amdam (2005) analysed discrete broods as an advanced state of multivoltine reproduction of solitary species. According to their analysis social species evolved most probably from multivoltine solitary species with discrete brood events in the course of the season, as can be found in many solitary bees and wasps. Thus, the first social species most likely had discrete broods rather than continuous colony growth. On this account discrete brood reproduction can be interpreted as an evolutionary link between non-social and advanced eusocial insects like many Apidae (Michener, 2000). The analysis of multivoltinism within a social context (Packer & Knerer, 1985; Hunt & Amdam, 2005) illuminates particular aspects of the first potential transition between non-social reproduction to discrete broods while our modelling approach allows one to determine the necessary conditions for the evolution of continuous reproduction. A more detailed analysis of model parameters (season length, development time, efficiency and mortality) would be useful to determine the optimal reproductive pattern within the whole parameter space.

Part II

Growth versus reproduction

Photo by Andrey Gogala

Chapter 5

Depletion of fat reserves during hibernation and nest establishment in foundress queens of the halictid *Lasioglossum malachurum*

with Norbert Weissel (first author), Hans-Joachim Poethke and Erhard Strohm

IN PREP

Abstract. Insects mainly store excess nutrients as lipids because of their high energy value and low isocaloric weight. These fat reserves supply insects with energy for development, long-distance flight, hibernation, and reproduction. In annual eusocial insects with a solitary nest founding phase, large fat reserves might be of particular importance for the foundress queens, which have to perform all nesting activities including nest establishment without the help of workers. In the present study, we analysed how hibernation and especially the solitary nest founding phase influenced the abdominal fat content of female sexuals and foundress queens in the primitively eusocial ground nesting bee *Lasioglossum malachurum* (Hymenoptera, Halictidae). As expected, we observed a decrease in abdominal fat content (absolute and relative) from newly emerged female sexuals of the 3rd brood in 2003 to foundress queens at the end of the solitary founding phase in 2004. The females lost nearly 62% of their fat reserves form emerging to the end of nest founding in the following year. Fat loss during the four weeks long colony founding phase was twice as high as fat loss during the six months of hibernation. This shows that solitary nest founding entails very high energetic costs for foundress queens. Thus, the amount of energy reserves of foundress queens and their ability to obtain additional food might be crucial not only for survival and nest initiation, but also for the ability to produce workers and sexuals, thereby strongly influencing the success of the colony.

5.1 INTRODUCTION

The vast majority of animal species use fat as their main energy storage because it yields more than twice as much energy per unit of weight as e.g. carbohydrates (Schmidt-Nielsen, 1997). In insects, the fat body, which is largely located in the abdomen, is the main storage site for excess nutrients and a source for lipids, proteins, and glycogen (Dettner & Peters, 2003). Of these storage molecules, lipids in particular are a crucial source of energy for the development, long-distance flight, hibernation, and especially for the reproduction of insects (Beenakkers *et al.*, 1981, 1984, 1985; Dettner & Peters, 2003; Leather *et al.*, 1995).

For annual eusocial insect species fat reserves might be of particular importance during the solitary nest founding phase, during which the foundress queen has to perform all nesting activities without the help of workers and when environmental conditions might be particularly harsh. Consequently, the ability of the queen to build the nest, to forage for pollen and nectar, to protect the nest against parasites, and to produce a sufficiently large worker force determines the success of the colony. Any shortage of resources or a lack of suitable food during the solitary nesting period would be detrimental for the queen's fitness. As colony growth is at heart an exponential process (Macevicz & Oster, 1976) high selection pressures will shape especially the early investment in the founding phase.

Species establish various strategies to meet the demands of colony founding. Claustral nest founding in ants is assumed to be a main characteristic of high eusociality. The evolution of claustral and semi-claustral nest founding in ants has been widely interpreted as a response to the costs entailed by alternative founding behaviours (Wheeler & Buck, 1996; Johnson, 2002; Brown & Bonhoeffer, 2003). Nest founding in wasps (swarm-founding versus a single foundress) has often been studied in the context of relatedness within the colony (for review see Henshaw *et al.*, 2001). However, the relevance of the queen's quality has mostly been ignored (but see Leathwick, 1997). Up to now, the effect of colony initiation on the physiological condition of foundress queens and thereby on colony survival and success has not received much attention in primitively eusocial insects.

In this study we focus on the quantification of fat reserves in the ground nesting, primitively eusocial halictid bee *Lasioglossum (Evylaeus) malachurum* (Kirby 1802). We investigate how the abdominal fat content of newly hatched female sexuals and foundress queens changes during hibernation and subsequent solitary nest founding. In *L. malachurum*, mated females hibernate and solitarily found a nest in early spring. The foundress queen has to find a suitable nesting site, excavate the nest and the brood cells, forage for pollen and nectar, lay about four to eight worker-destined eggs, and defend the nest against inter- and intraspecific parasites (Legewie, 1925b; Noll, 1931; Knerer, 1992; Michener, 2000). Founding queens are especially opposed to high intraspecific parasite pressure by so called floater females (Knerer, 1973; Smith & Weller, 1989). After provisioning of the first brood, the queen closes the nest for approximately four weeks until the first workers (Weissel *et al.*, in press) emerge. These workers take over foraging and provision a second brood of either sexuals or new workers, in which case the brood cycle continues. Former studies on *L. malachurum* have found a significant positive effect of worker number on the productivity of the colony and on the probability of producing sexuals at all (Strohm & Bordon-Hauser, 2003). These studies also suggest a minimum level of the worker number in the first brood as a precondition of colony success as was also shown in ants (Chang, 1985; Hee *et al.*, 2001). Additionally, failure rates of *L. malachurum* colonies are as far as twice as high during solitary nest founding as compared to failure rates during the subsequent broods (Weissel *et al.*, in press). After the emergence of the first workers the queen stays in the nest and lays the eggs. *L. malachurum*, like other social halictids, shows a clinal variation in social behaviour, with more worker broods produced in warmer climates (Knerer, 1992; Richards, 2000). In the population of *L. malachurum* at Wuerzburg colonies might show either one or two worker broods and may produce sexuals only in the 2nd, only in the 3rd brood or in both broods (Strohm & Bordon-Hauser, 2003; Weissel *et al.*, in press).

The activity break of four weeks seems puzzling since queens might be expected to produce as many workers as possible in order to maximise their reproductive success. However, several factors might make a maximisation of worker number counterproductive (e.g. Mitesser *et al.*, 2006). One main aspect that might select for a limited investment in the first brood is energy limitation (see also Strohm & Bordon-Hauser, 2003).

In this study we tested for possible effects of hibernation and solitary nest founding on the amount of fat stored in the abdomen of female sexuals and foundress queens of *L. malachurum*. We hypothesised that due to the well-known effect of hibernation on the energy reserves of insects (Alford, 1969; Chaplin & Wells, 1982; Krausse-Opatz *et al.*, 1995; Leather *et al.*, 1995; Stein & Fell, 1992; Zhou *et al.*, 1995; Strohm, 2000), overwintering female sexuals of *L. malachurum* should experience an ample loss in their abdominal fat content. Additionally, due to the high energy demands for solitary nesting queens (see above) and in accordance with studies on ant queens during claustral nest founding (Toom *et al.*, 1976; Martinez & Wheeler, 1994; Wheeler & Buck, 1996), we expected the foundress queens to loose the major part of their fat reserves during solitary nest founding. To test these hypotheses, we analysed female sexuals of the 3rd brood of 2003 foundress queens of 2004 at three distinct stages throughout the solitary nest founding phase. Depending on the quantity of remaining fat reserves, we tried to assess whether the fat reserves of queens might be limited.

5.2 MATERIALS AND METHODS

5.2.1 Study species and study site

Detailed information on the biology of the ground nesting halictid bee *Lasioglossum malachurum* is given in Knerer (1992) and Richards (2000). Further information on the remarkable nesting biology of *L. malachurum* at Wuerzburg can be found in Strohm and Bordon-Hauser (2003) and Weissel *et al.* (in press).

All samples of *L. malachurum* queens were taken from two natural nesting aggregations in the immediate vicinity of the campus of the University of Wuerzburg in 2003 and 2004. The distance between these two aggregations was about 800 m. Queens of the 3rd brood of 2003 were caught directly after emergence from their colonies by placing transparent polystyrene cups over the nest entrance. The foundress queens in 2004 were caught from the nesting aggregations at three distinct stages during the solitary nest founding phase using an insect net: (1) during the first flights of the queens after hibernation when they search for suitable nesting sites, (2) at the onset of provisioning activity after construction of the nests, and (3) at the end of the provisioning activity prior to the activity break. In the following, the four different samples of queens are abbreviated by PRE-HIB (female sexuals of the 3rd brood, before hibernation), FLIGHT (foundress queens - first flight), PROV (foundress queens - provisioning activity), and END (foundress queens - end of activity).

The queens of the 3rd brood (PRE-HIB) of 2003 emerged and were caught from July 22 to August 5. The hibernated queens started nest founding on March 16 2004. Provisioning of brood cells began on March 28, and the solitary nest founding phase ended on May 4 with the last colonies closing their nest entrance. Foundress queens were caught on March 18 (FLIGHT), on March 28 and 29 (PROV), and from April 21 to April 30 (END). The queens were freeze killed, dissected into three parts (head, thorax, and abdomen), and stored at -30 °C.

5.2.2 Body size and fat content

The body size of the queens was measured as head width with a modified caliper under the dissecting scope to the nearest 0.01 mm. For the analysis of the fat content of the queens, the abdomen of each queen was incised centrally from the first to the fifth sternum (the heads and thoraces were used for other investigations). The incised abdomens were placed in 1.5 ml Eppendorf cups, dried to constant weight at 60 °C for 3 days, and weighed on an analytical balance (Mettler MT 5) to the nearest 0.01 mg. The total amount of fat stored in the abdomen was determined by extraction of fat from the dried tissues (Richards & Packer, 1994). Each dried abdomen was soaked with 1.3 ml petroleum ether (Benzin 40-60, AppliChem, Darmstadt, Germany) for 5 days. The abdomens were removed and dried again at 60 °C for 3 days and weighed to the nearest 0.01 mg. The absolute fat content of the abdomen was calculated as the difference between the dry weight before and after fat extraction. Relative fat content was calculated dividing the absolute fat content by the dry weight of the abdomen before fat extraction.

5.2.3 Data analysis

We checked for normal distributions of our data by histogram plots and used Bartlett's test to control for unequal variances (Bartlett & Kendall, 1946). Appropriate transformations resulted in reasonable approximations of the data to the assumptions of parametric tests. The data on the relative fat content of the abdomen was arcsine square root transformed (Sokal & Rohlf, 1995). The head width as well as the absolute fat content of the abdomen was Box-Cox transformed (Box & Cox, 1964). Data are presented as means ± SD. A One-way ANOVA was calculated to test for differences between the four groups of female sexuals with regard to head width. We tested whether the four groups of *L. malachurum* queens differed in the absolute and relative fat content using a One-way ANOVA with Welch's correction for unequal group variances (Welch, 1951). To test whether the four groups of female sexuals showed a continuous decline in the absolute and relative fat content in the abdomen from the 3rd brood of 2003 to the end of the solitary nest founding phase, we compared means of fat content of PRE-HIB and FLIGHT, FLIGHT and PROV, and PROV and END using one-sided Welch tests. We used the Bonferroni correction for multiple tests to adjust the p-values of the

Table 5.1: Summary for the four different groups of female sexuals of *L. malachurum* in 2003 and 2004. Head width, absolute fat content, and relative fat content (mean ± SD) are given. Test statistics with p-values after Bonferroni correction for the comparison of the group means of the transformed data are given underneath the table.

	Female sexuals		Foundress queens				
	3rd brood		first flight		provisioning		end of activity
head width [mm]	2.32 ± 0.08		2.30 ± 0.09		2.32 ± 0.09		2.33 ± 0.07
absolute fat content [mg][a]	3.40 ± 1.06	–1–	2.00 ± 0.62	–2–	1.10 ± 0.48	–3–	0.68 ± 0.40
relative fat content [%][b]	63.8 ± 6.4	–4–	48.5 ± 9.0	–5–	34.2 ± 8.8	–6–	24.0 ± 8.9

[a] one-sided Welch tests: -1-: $t = 6.84$, $df = 41.5$, $p < 0.001$; -2-: $t = 6.82$, $df = 59.0$, $p < 0.001$;
-3-: $t = 5.53$, $df = 102$, $p < 0.001$

[b] one-sided Welch tests: -4-: $t = 7.71$, $df = 31.8$, $p < 0.001$; -5-: $t = 6.38$, $df = 48.5$, $p < 0.001$;
-6-: $t = 6.21$, $df = 104$, $p < 0.001$

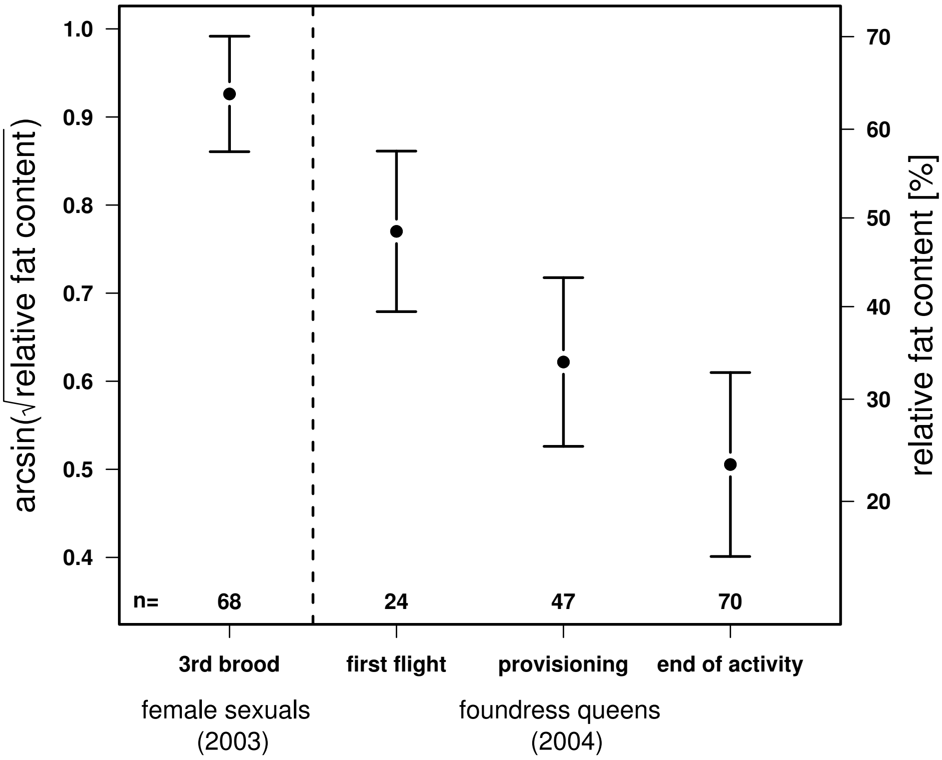


Figure 5.1: Relative fat content of the abdomen (arcsine square root transformed) of female sexuals at different stages throughout the flight season (± SD) in 2003 and 2004. Not transformed relative fat contents are given on the right axis. The values beneath the bars give the sample sizes of the four different groups.

three comparisons. Pearson correlation analyses were calculated to test for a correlation between head width and relative fat content of female sexuals of the four different groups. Non-parametric analyses on the untransformed data yielded qualitatively identical results. Tests were calculated using R 2.3.0 (Ihaka & Gentleman, 1996).

5.3 RESULTS

The head width of female sexuals of *L. malachurum* ranged from 2.07 to 2.47 mm ($n = 209$) and did not differ between the four groups of queens from different stages throughout the flight season (ANOVA: $F_{3,205} = 0.537$, $p = 0.657$). By contrast, the four groups of females differed significantly with respect to the absolute ($F_{3,85} = 209$, $p < 0.001$) and relative abdominal fat content ($F_{3,79} = 311$, $p < 0.001$). The mean values of head widths as well as absolute and relative fat contents for the different groups of queens are given in table 5.1.

The different groups of female sexuals showed a significant decline in the absolute

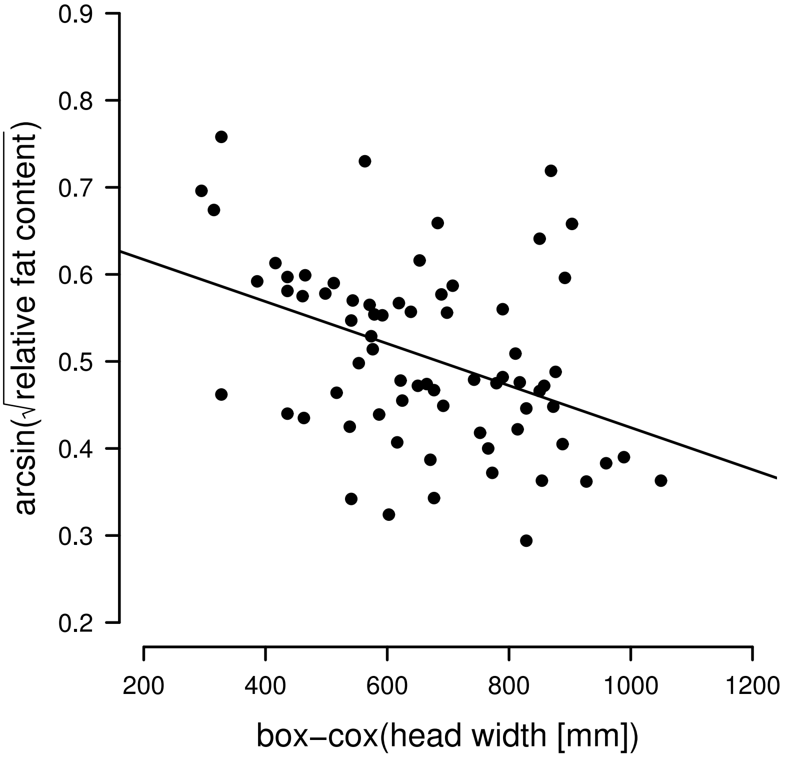


Figure 5.2: Relative fat content of the abdomen (arcsine square root transformed) as a function of head width (Box-Cox transformed) of foundress queens of FQ-EA. Linear regression line is given.

(Welch test: $p < 0.001$ for all comparisons, table 5.1) and relative amount ($p < 0.001$ for all comparisons, table 5.1, figure 5.1) from the time of their emergence to the end of the founding period. The queens lost on average 62% of their fat reserves from emergence to the end of provisioning of the first brood, starting with a fat content of 63.8 ± 6.4% (3.40 ± 1.06 mg, $n = 68$) and ending up with a value of 24.0 ± 8.9% (0.681 ± 0.402 mg, $n = 70$). By comparison, old foundress queens caught at the end of the 2nd brood showed an abdominal fat content of 7.76 ± 5.31% (0.136 ± 0.084 mg, $n = 13$, Weissel and Strohm, unpublished data). The vast majority of the abdominal fat storage was not spent during hibernation (fat loss from PRE-HIB to FLIGHT: 24.0%) but mainly during solitary nest founding (fat loss from FLIGHT to END: 50.5%).

Within the group END we found a significant negative correlation between head width and relative fat content (Pearson correlation: $r = -0.409$, $p < 0.001$, $n = 70$, figure 5.2). By contrast, the analysis of PRE-HIB, FLIGHT and PROV revealed no evidence for a correlation between head width and relative fat content (PRE-HIB: $r = 0.177$, $p = 0.149$, $n = 68$; FLIGHT: $r = -0.027$, $p = 0.900$, $n = 24$; PROV: $r = -0.164$, $p = 0.271$, $n = 47$).

5.4 DISCUSSION

The analysis of head widths of female sexuals and foundress queens of the four different groups revealed that the females did not differ in body size. This result might indicate that smaller females of *L. malachurum*, unlike bumble bee queens (Owen, 1988; Beekman *et al.*, 1998b), are not more likely to die during hibernation than larger females. Additionally, smaller foundress queens seem to have no higher mortality risk during solitary nest founding, although one would expect them to show a reduced ability to resist the attacks of inter- and intraspecific parasites (Smith & Weller, 1989), which often result in the death of the inferior female (Kaitala *et al.*, 1990; Knerer, 1973; Legewie, 1925a; Sick *et al.*, 1994).

We found a negative correlation between body size and relative fat content in the abdomen of queens at the end of nest founding (END). This observation clearly contradicts various studies on poikilotherm and homoiotherm species, which have found that energy consumption per gram decreases with increasing body size (Peters, 1983; Schmidt-Nielsen, 1997). Thus, our results might suggest that a small body size might be energetically advantageous for foundress queens, resulting in a greater amount of fat reserves at the end of the founding period. Alternatively, this could indicate that smaller queens were less active during the founding phase. The observed correlation might also suggest that smaller females are more likely to act as floater females with fewer opportunities to lay eggs, therefore ending up with fewer energy reserves consumed during colony initiation. However, there is no evidence for size differences between floater females and nest owners (Weissel and Strohm, unpublished data).

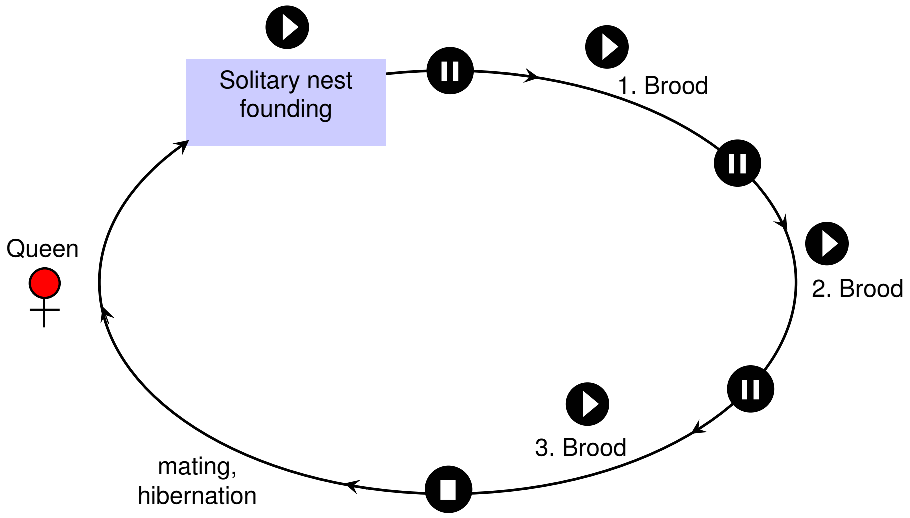
Newly hatched 3rd brood female sexuals of *L. malachurum* had an abdominal fat content of approx. 64%, which is in good accordance with former studies on *L. malachurum* at Wuerzburg (Bordon-Hauser and Strohm, unpublished data). Queens of the third brood hatch nearly at the end of the nesting period during August (Strohm & Bordon-Hauser, 2003; Weissel *et al.*, in press). Since they do not hibernate in their natal nest (Weissel and Strohm, unpublished data), they have to spend some time finding a suitable overwintering site. Thus, it is reasonable to assume that they have not much time and opportunities to actively forage for food to increase their fat reserves. However, not all foundress queens are female sexuals of the 3rd brood: Individuals of the 2nd brood emerge about three weeks earlier and have a significantly lower amount of abdominal fat reserves than 3rd brood females (Weissel and Strohm, unpublished data). We excluded the 2nd brood individuals from the original analysis, because these females might increase their fat reserves by foraging until the end of the season. Thus, their fat content after emergence is probably not a suitable predictor for pre-hibernation fat content. However, including them still yields a significant decrease in fat content, although the effect size is lower (Weissel, unpublished). In conclusion, the fat content of newly emerged 3rd brood females is likely to reflect the amount of fat reserves available for hibernating females at the beginning of diapause very closely.

Concerning the exhaustion of stored energy, the fat reserves of foundress queens were significantly reduced during hibernation, resulting in a total loss of 24% of the fat stored in the abdomen. This observation is consistent with various studies on insect species that hibernate as adults, like bumble bees (Alford, 1969), hornets (Stein & Fell, 1992), wasps (Harris & Beggs, 1995; see also Strohm 2000), and beetles (Krausse-Opatz *et al.*, 1995). The observed fat loss of 24%, however, seems to be a very moderate loss of stored energy, which might indicate that queens of *L. malachurum* are very well adapted to the extreme environmental conditions that they face during the winter. Furthermore, *L. malachurum* queens might also use other energy reserves in addition to fat such as glycogen or carbohydrate as winter 'fuel' (Leather *et al.*, 1995).

Compared to hibernation, solitary nest founding had a stronger impact on the depletion of the energy reserves of foundress queens of *L. malachurum*. Both absolute and relative abdominal fat content continuously declined during the solitary nest founding phase, resulting in an overall loss of 51% of the initial abdominal fat reserves after hibernation. A decline in fat reserves during solitary nest founding is in agreement with various studies on foundress queens of different ant species (Martinez & Wheeler, 1994; Toom *et al.*, 1976; Wheeler & Buck, 1996). However, compared to the fat loss of approx. 90% of ant queens during claustral colony founding reported by Wheeler and Buck (1996), the loss of fat of *L. malachurum* queens seems comparatively low. One explanation for this discrepancy could be the fact that halictid foundress queens, unlike the ant queens during claustral colony founding, have the opportunity to actively forage for food during nest founding to refill their energy storage. However, this exposes them to increased mortality and shows that the high demands of nest founding can be paid both in the currency of energy reserves and mortality risk.

Fat reserves are almost completely depleted at the end of the season. Thus, energy limitation might have a crucial influence on the specific reproductive strategy of *L. malachurum*. In the population of *L. malachurum* at Wuerzburg colonies might show either one or two worker broods and may produce sexuals only in the 2nd, only in the 3rd brood or in both broods (Strohm & Bordon-Hauser, 2003; Weissel *et al.*, in press). Macevicz and Oster have proposed a classical evolutionary model for the reproductive pattern in annual, eusocial insect colonies based on time limitation (1976). They found that the optimal investment strategy is exclusive production of workers followed by exclusive production of sexuals. The timing of the transition between worker and sexual production can be predicted by the demographic parameters of the colony. However, Macevicz and Oster (1976) did not allow for a strategic adjustment of the investment rate itself, only the fraction of the investment (of the currently allocated resources) into workers was assumed to be variable. Adding energy limitation of the queen as another constraint to the strategic model would change the optimal switching point according to the energy reserves of the queen. This might be an explanation for the plasticity in brood production observed in *L. malachurum*. Thus, variation of the switching point due to energy limitation could just be a result of mismanagement in the founding phase: Queens with low energy reserves would be forced to produce sexuals early as a result of energy depletion. However, shortage of resources could be avoided by reducing the investment rate during nest founding. This strategy would be more beneficial, because the multiplicative effect of workers could be utilised for a longer time. Behavioural plasticity as a result of variation in the queens' energy reserves might still be a valid argument since observations have shown that a minimum worker number is required after colony founding to ensure successful future development (Strohm & Bordon-Hauser, 2003). In this case the production rate of the queen must not fall below a specific level and promote the production of sexuals already in the second brood.

In conclusion, the results of our study on *L. malachurum* indicate that the solitary founding period entails substantial costs for foundress queens. Obviously, more research focusing on the solitary nest founding phase and its implications for foundress queens and their colonies is necessary to better understand the nesting ecology and its adaptive relevance in social bee species.


Solitary nest founding
1. Brood
2. Brood
3. Brood
mating, hibernation
Queen

Chapter 6

Optimal investment allocation in primitively eusocial bees: a balance model based on resource limitation of the queen

with Norbert Weissel, Erhard Strohm and Hans-Joachim Poethke

SUBMITTED TO INSECTES SOCIAUX

Abstract. The classical model of colony dynamics developed by Macevicz and Oster predicts that optimal colony fitness in annual eusocial insects is achieved by a bang-bang strategy of reproduction: exclusive production of workers (ergonomic phase) followed by exclusive production of sexuals (reproductive phase). We propose an alternative model that assumes limitation of the overall investment potential of the queen. Based on the costs for producing eggs, workers, and sexuals and the efficiency of individuals we predict the optimal number of workers and sexuals in the colony for each brood of the colony cycle that maximises overall colony fitness. To link our model assumptions to the real world we chose model parameters according to field data of the halictid bee *Lasioglossum malachurum*. However, our model represents the colony development of a large number of species with an annual life cycle and with discrete broods. Our model shows that the optimal partitioning of resources, i.e. the optimal workers/sexuals ratio depends on rearing cost for sexuals as well as productivity of workers but not on the queens' total investment, egg cost, or rearing cost for workers. In complete accordance to Macevicz and Oster we predict a bang-bang reproduction strategy despite the differences in the basic assumptions. Potential deviations from this strategy and transitions from social to solitary breeding are discussed in the framework of our model.

6.1 INTRODUCTION

The optimal allocation of acquired resources to growth, maintenance, and reproduction is the central topic of life history theory. At any time during its life an organism must decide between allocating resources to maintenance, somatic growth (that will give larger reproductive potential later), and reproduction. In particular the trade-off between growth and reproduction has been well-confirmed (Roff, 1992; Stearns, 1992) and much theoretical and field work has been conducted to analyse the time dependent investment of organisms into growth and reproduction and to predict which allocation strategies will maximise an organism's fitness (Cohen, 1971; Iwasa, 2000). The optimal allocation pattern crucially depends on the constraints that determine the trade-off between growth and reproduction. When the end of the season is approaching an individual should not grow any further but start reproduction. Such time limitation has successfully been used to explain optimal allocation patterns in plants (Cohen, 1971; Kozlowski & Teriokhin, 1999; Pugliese, 1988), as well as in insects (Sevenster *et al.*, 1998; Rosenheim, 1999b; Heimpel *et al.*, 1998) and vertebrates (Kozlowski & Teriokhin, 1999).

For social insects the allocation problem not only refers to growth and reproduction of individuals but also to the colony level: which portion of resources should be spent to increase worker force or to produce sexuals instead and how should the production of workers and sexuals be timed? According to the classical colony growth model of Macevicz & Oster (1976), time limitation determines the pattern of worker and sexual production in social insect colonies, too. In their model the number of sexuals is used as a simple measure of fitness that is maximised by the allocation strategy. Macevicz & Oster (1976) showed that the optimal reproductive strategy of a colony is to start the colony cycle with the exclusive production of workers. Approximately one mean worker lifespan before the end of the season the colony should switch to the production of sexuals.

Basically, such a life cycle is exhibited by many primitively eusocial species of vespid wasps, bumble bees, and sweat bees (Sakagami, 1974; Packer & Knerer, 1985; Michener, 1990; Ross & Mathews, 1991; Yanega, 1997; Wyman & Richards, 2003). However, the temporal position of the observed switching point is not always in accordance with the prediction of the model (Bowers, 1986; Duchateau & Velthuis, 1988; Müller *et al.*, 1992). Both in bumble bees and in vespid wasps deviations from model predictions and the observation of local plasticity in allocation strategies gave rise to more detailed modelling approaches. In these models time limitation has been combined with limitation in egg laying rate and additional behavioural mechanisms (Karsai *et al.*, 1996; Beekman *et al.*, 1998a; Martin, 1991).

The nest cycle of many halictid bees is characterised by discrete broods separated by distinct activity breaks (Sakagami, 1974; Yanega, 1997; Michener, 1990). During a founding phase, the queen constructs a simple nest, lays eggs, and provisions the eggs with pollen and nectar. After a short activity break, during which the nest is closed and all foraging ceases, a first worker brood emerges and starts collecting pollen and nectar to provision the eggs laid by the queen. The subsequent broods are also separated by activity breaks with nest closure. Usually sexuals emerge in the last brood while all other broods consist of workers only. Since Macevicz and Oster (1976) assume continuous reproduction, their approach cannot be used to model the discrete broods and periods of inactivity in halictids.

Moreover, there is evidence that time limitation might not be the dominant constraint responsible for the allocation pattern observed in this group. For example, field observations of the halictid bee *Lasioglossum malachurum* show that colonies within the same aggregation vary considerably in their nesting strategy and in particular with regard to the end of the colony cycle (Knerer, 1987; Strohm & Bordon-Hauser, 2003). Some colonies produce two broods of workers and a third brood of sexuals. Most colonies produce workers in the first brood, then a mixed brood consisting of workers and sexuals and a third brood of sexuals. Some nests, however, produce only one worker brood and a second brood of sexuals, thus ending their colony cycle well before the end of the flight season (Weissel *et al.*, in press). Both early and late ending colonies produce sexuals at the end of their nest cycle, thus ending early is not just due to colony failure but must be part of the life history strategy. The apparent wastage of time in colonies with only one worker brood can hardly be explained within the framework of time limitation and is in complete contrast to the clinal variaton in the social behaviour of *L. malachurum*, with more worker broods produced in warmer climates with a prolonged season length (Knerer, 1992; Richards, 2000).

Other life history constraints which have been investigated in particular in parasitic wasps are rate limitation (e.g. egg laying or cell building rate, (Rosenheim, 1996; Wheeler & Buck, 1996; Sevenster *et al.*, 1998; Heimpel *et al.*, 1998) or resource limitation (Driessen & Hemerik, 1992; Mangel & Heimpel, 1998; Rosenheim *et al.*, 2000)). Field observations and theoretical modelling have shown that parasitic wasps are on average at an intermediate position in an egg laying rate-time limitation continuum with a bias towards time limitation (Rosenheim, 1996; Heimpel *et al.*, 1998; Rosenheim, 1999a; West & Rivero, 2000). However, egg laying rate can hardly be the main limiting factor in halictid bees, since realised egg laying rate is clearly lower than the potential rate measured in the laboratory (Knerer, 1992). Moreover, rate limitation would select for a prolongation of the flight season, not for the shortening that is observed in *L. malachurum*.

Up to now, the cost of reproduction and the corresponding trade-offs between cur-

rent and future reproduction have rarely been studied in social insects (Wheeler, 1996; Strohm & Marliani, 2002) and mainly in the context of social conflicts (Oster & Wilson, 1978; Reuter & Keller, 2001) . At the same time colony success in social bees undoubtedly depends on queen quality (Archer, 1981a,b; Leathwick, 1997; Hatch *et al.*, 1999; Gilley *et al.*, 2003; Liebig *et al.*, 2005). Queens of highly evolved eusocial insects like ants, vespine wasps, and termites might have negligible costs of reproduction since they are continuously supplied with ample resources by their workers.
However, this is not necessarily true for primitively eusocial species like many halictids. In these species accelerated aging of ovaries can be detected during the season and the queen's oviposition capability might decline due to the depletion of certain resources (Knerer, 1992). This problem might be exaggerated by the fact that eggs of halictid bees are relatively large compared to highly eusocial species (Boomsma & Eickwort, 1993). During the solitary nest founding phase the founding females of primitively eusocial halictids incur very expensive processes like nest construction and solitary provisioning of the first eggs (Michener, 2000). These investments may reduce the expected life span of founding queens or reduce their physiological resources for egg production as has been shown for the worker caste of many social and for solitary insects (Neukirch, 1982; Schmid-Hempel, 1991; Cartar, 1992; Biesmeijer & Toth, 1998; Strohm & Marliani, 2002; Strohm *et al.*, 2002; Willmer & Stone, 2004). Similar to observations of ant queens with claustral nest founding (Wheeler, 1996; Wheeler & Buck, 1996), we have clear evidence for a considerable decrease in fat reserves of queens of *L. malachurum* during the nest founding phase (Strohm & Weissel, unpublished).

Taking these considerations into account we developed a simple colony model based on limitation of the queen's investment to analsse the optimal production pattern for workers and sexuals as a function of physiological parameters. This model is a rather simple realisation of the general life history problem stated by Gadgil & Bossert (1970) and Schaffer (1983). To base our model on realistic assumptions we used data on the halictid bee *L. malachurum* as a reference. Nevertheless, the model is basically applicable for primitively eusocial species with solitary nest founding and an annual life cycle.

6.2 A SIMPLE INVESTMENT BALANCE MODEL

We consider a bee colony characterised by the number of workers W_i and sexuals S_i in each brood i. For the sake of simplicity we assume that after the founding phase only two broods are produced, i.e. the colony cycle consists of a solitary founding phase and two activity periods (interrupted by phases of inactivity as it is realised in *L. malachurum* and many other halictids; Sakagami, 1974). We also examined an

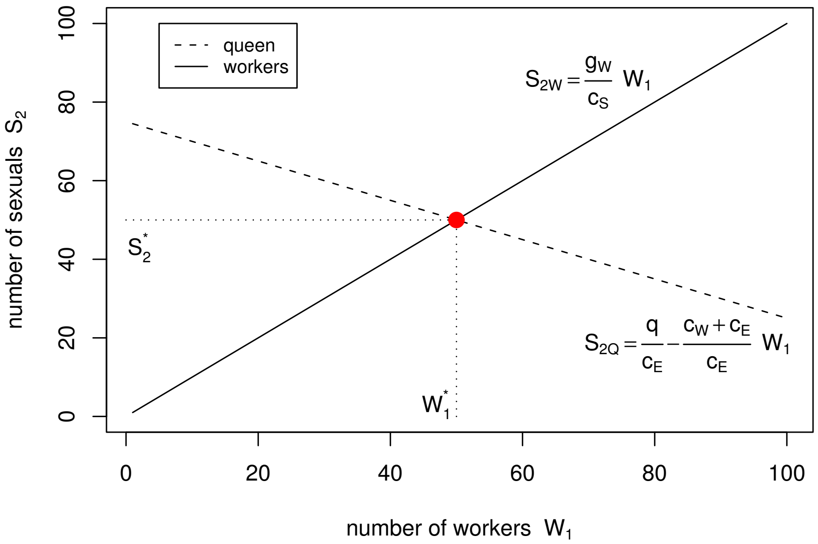


Figure 6.1: Schematic investment balance diagram for queen and worker capacities of reproduction. The descending line gives the number of eggs a queen can produce after she has already raised W_1 workers while the ascending line gives the number of sexuals S_2 that can be provisioned by W_1 workers. The intersection of both lines determines the optimal resource allocation pattern where exactly all available resources are consumed and production of sexuals is maximised.

extension of the model to three and more broods. Since these extended models do not produce qualitatively different results we will focus on the simple two-brood version here.

We assume that the queen is the sole reproductive individual in the colony and her life-time investment in reproduction (q) is limited. She has to invest a part of these resources in the production of eggs of $W_1 + W_2$ workers and $S_1 + S_2$ sexuals. However, the queen also has to forage to provision the brood cells of the individuals of the first brood. We assume that the cost of an egg (c_E) does not depend on whether it will develop into a worker or a sexual. However, since female sexuals are significantly larger than workers, the provisioning of workers (c_W) is less costly than provisioning of sexuals (c_S). For simplicity, we did not differentiate between male and female sexuals. Thus, the total investment during the nest founding phase is $(W_1 + S_1)c_E + W_1 c_W + S_1 c_S$ and the life-time investment of the queen (q) sums up to

$$q = (W_1 + S_1 + W_2 + S_2)c_E + W_1 c_W + S_1 c_S \tag{6.1}$$

After the founding phase the queen will stay in the nest and lay eggs. All other tasks like nest construction, foraging, and provisioning of larvae will then be adopted by workers. Thus W_1 workers will have to provision W_2 workers plus S_2 sexuals. Assuming that each of the W_1 workers can contribute g_W resources during its life-time (Knerer, 1992), the balance equation for worker investment reads as

$$g_W W_1 = W_2 c_W + S_2 c_S \tag{6.2}$$

Like Oster & Wilson (1978) we will take the total number of sexuals $F = S_1 + S_2$ in both broods as a simple measure of colony fitness. Workers in the second brood (W_2) cannot increase the production of sexuals, since no third brood is produced. Thus, it is obvious from equation 6.2 that W_2 must be 0 to maximise S_2, in order to maximise F in turn. This is in complete accordance with the findings of Macevicz & Oster (1976): the nest cycle should be finished with exclusive production of sexuals. Using equation 6.1 and equation 6.2 the number of workers W_1 can be eliminated and the number of sexuals S_2 can be expressed by S_1 only. For the total fitness we find

$$F = S_1 + S_2 = S_1 + \frac{q - S_1(c_E + c_S)}{c_S c_E / g_W + c_E + c_S c_W / g_W} \tag{6.3}$$

It follows from this equation that sociality is coupled to the condition

$$g_W > c_E + c_W \tag{6.4}$$

If the contribution (g_W) of a single worker to future reproduction is higher than the queen's investment in that worker ($c_E + c_W$), then it pays to produce workers, even if more than one worker is needed to produce one sexual ($g_W < c_E + c_S$). Evidently the queen should not produce any workers, if workers cost more than they will contribute during their life-time. If worker productivity would be less than their cost the model no longer would predict $S_1 = 0$ (see equation 6.3), but $S_1 = q/(c_E + c_S)$. In this case the queen should stay solitary and the queen's investment should be spent in a single brood of exclusively sexuals. In all other cases equation 6.3 shows, that fitness (F) decreases with increasing S_1. Consequently, the foundress should produce only workers in the first brood ($S_1 = 0$). This prediction, too, is in complete accordance with the bang-bang model (Macevicz & Oster, 1976).

No workers are produced in the second brood ($W_2 = 0$). Thus all workers (W_1) have to be provisioned by the queen. However, since total queen investment (q) is limited, the more workers the queen produces the fewer reserves remain for the production of sexuals (figure 6.1, dotted line). Based on equation 6.1, the number of eggs for sexuals (S_2) the queen can produce decreases with increasing worker number and is calculated as follows:

$$S_{2Q} = \frac{q}{c_E} - \left(\frac{c_E + c_W}{c_E}\right) W_1 \tag{6.5}$$

On the other hand workers are needed to provision the brood cells for the sexuals of the second brood. Equation 6.2 yields the number of sexuals which can be provisioned by W_1 workers of the first brood. The more workers are available for this task, the more sexuals can be produced (figure 6.1, ascending line):

$$S_{2W} = \frac{g_W}{c_S} W_1 \tag{6.6}$$

Worker number (W_1) should be adjusted by the queen in such a way that the number of eggs she is able to produce (S_{2Q}) equals the number of sexuals (S_{2W}) that can be provisioned by these workers ($S_{2W} = S_{2Q}$). This is the case, when both lines in figure 6.1 intersect and leads to the following expressions for the optimal number of workers (W_1^*) and sexuals (S_2^*):

$$W_1^* = \frac{c_S q}{(c_W + c_E)c_S + c_E g_W} \tag{6.7}$$

and

$$S_2^* = \frac{g_W q}{(c_W + c_E)c_S + c_E g_W} \tag{6.8}$$

It is obvious from figure 6.1 that colony efficiency (S_2/W_1) is affected by worker efficiency and cost of sexuals, but neither by the amount of resources available to the queen nor by worker and egg cost. If the cost of workers (c_W) increases (or decreases), both the optimal number of workers and the optimal number of sexuals decrease (or increase) by the same factor without changing their ratio (the ratio S_2/W_1 does not change along the line S_{2W} in figure 6.1, because it is a line through the origin). Total colony fitness (S_2) depends on all model parameters.

Further model results are given in table 6.1 and can be summarised as follows: (i) The optimal number of workers and sexuals results from the total queen investment (q) and worker efficiency (g_W) as well as from the cost of laying eggs (c_E), rearing workers (c_W), and rearing sexuals (c_S). (ii) Increasing costs for eggs, workers, and sexuals (c_E, c_W, c_S) reduce the number of sexuals (colony fitness) as well as the optimal number

Table 6.1: Relationship between model parameters and both the state variables of the colony (number of sexuals in the second brood (= fitness) and worker number in the first brood) and colony efficiency. "+" indicates a positive and "-" a negative correlation between variable and model parameter. "0" indicates that the corresponding variable does not vary with the model parameter.

	Fitness	Worker number	Colony efficiency
	S_2	W_1	S_2/W_1
Queen's quality q	+	+	0
Worker efficiency g_W	+	-	+
Egg cost c_E	-	-	0
Worker cost c_W	-	-	0
Sexual cost c_S	-	+	-

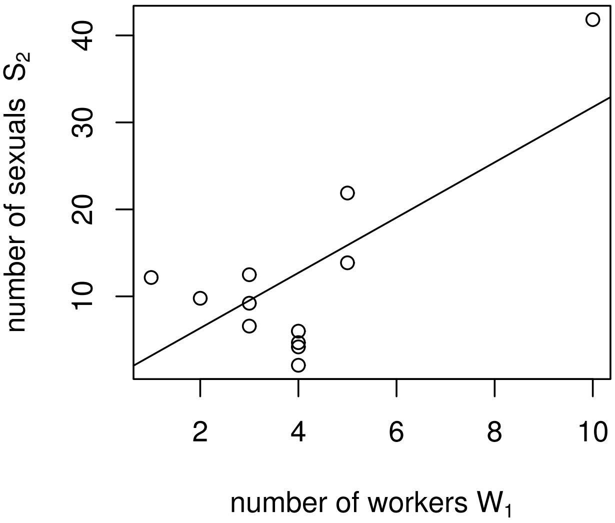


Figure 6.2: Number of sexuals as a function of the number of workers in colonies of *L. malachurum* with exactly one worker brood, slope = 3.2 ± 0.5, $R^2 = 0.82$, $p < 0.001$ ($n = 12$). Ignoring the point representing the highest number of sexuals would result in slope = 2.5 ± 0.5, $R^2 = 0.68$, $p < 0.001$ ($n = 11$).

of workers. Optimal worker number increases with cost of sexuals (c_S); (iii) Colony efficiency (S_2/W_1) decreases with increasing cost (whenever sexuals are more costly then workers).

6.2.1 Parameter estimation for Lasioglossum malachurum

Macevicz & Oster (1976) used demographic data from continuously reproducing colonies to determine parameters of their model. Evidently, these cannot be used for parameter estimation in our model. Unfortunately, demographic data of colony cycles with a distinct temporal structure of broods are hardly available in the literature. However, we had access to unpublished data of the life cycle of colonies of *L. malachurum* from different former studies (Strohm & Bordon-Hauser, 2003; Strohm & Heidinger, unpublished). Moreover, data on the typical colony size of this species is available (Legewie, 1925a; Knerer, 1992; Strohm & Bordon-Hauser, 2003).

We may reduce the number of parameters to be estimated by standardisation. Thus, setting life-time investment of the queen to $q = 1$, we interpret all other parameter values in relation to the queen's total investment. The number of eggs in *L. malachurum* colonies with two broods almost never exceeds 50 (Legewie, 1925a). To ensure investment reserves for construction and breeding, egg cost must thus be $c_E < 0.02$. We estimate typical egg cost by $c_E = 0.01$. As there is only a small size dimorphism in *L. malachurum* (Strohm & Bordon-Hauser, 2003) and in most bees foraging success does not depend on body size (Strohm and Liebig, submitted), we assume worker foraging ability to be similar to that of queens ($g_W = 1.0$). Worker efficiency (the ratio g_W/c_S) can be estimated from field data of two-brood colonies of *L. malachurum* in southern Germany (figure 6.2). Simple regression yields $g_W/c_S = 3.2 \pm 1.4$. As equation 6.6 does not depend on total queen investment, regression can be calculated without knowledge of this parameter. In *L. malachurum* the mean worker number in the first brood is about 5. This determines the typical cost of workers (c_W) and sexuals (c_S) (here 0.16 and 0.31). Thus, the typical ratio between the cost of a worker and the cost of a sexual is about 1:2. Lower actual worker productivity would imply higher cost for workers and lower cost for sexuals. It is not surprising that costs of workers and sexuals differ by a factor of 2 while productivities of both castes are similar, because the queens' additional cost for hibernation and nest founding (Weissel *et al.*, in press) are not considered in the model. Field observations have shown that brood cells for sexuals are supplied with more nectar and pollen than cells for workers ($c_S > c_W$; Legewie, 1925a; Knerer, 1973; Bohrer, 1987).

Sociality is coupled to the condition that worker productivity must be higher than worker cost ($g_W > c_E + c_W$). For *L. malachurum* this condition is obviously fulfilled within the plausible parameter space compatible with our field data.

6.3 DISCUSSION

Investment allocation in the context of insect colonies is usually analysed in the framework outlined by Macevicz & Oster (1976). Their model is based on time limitation for colony development and uses the mathematical methods of control theory to predict optimal colony allocation patterns. We propose an alternative model based on colony development in discrete broods (instead of continuous colony growth) and limitation of the overall investment potential of the queen. We assume that: a) A queen's potential investment in laying eggs (for all individuals) and raising a first brood of offspring is limited (equation 6.1; figure 6.1); b) Individuals of a second brood are reared by workers from the first brood. We further assume that colony productivity is directly proportional to worker number (equation 6.2; figure 6.1). Combining both mechanisms is sufficient to fully determine an optimal resource allocation strategy. As long as worker production is profitable at all, the first brood should consist of workers only, and the second brood should consist exclusively of sexuals. While the optimal number of workers depends on a number of model parameters (total queen investment, q; worker efficiency, g_W; cost of eggs, c_E; cost of rearing workers, c_W and cost of rearing sexuals, c_S), colony efficiency (S^*/W^*) is only affected by worker efficiency g_W and cost of sexuals c_S.

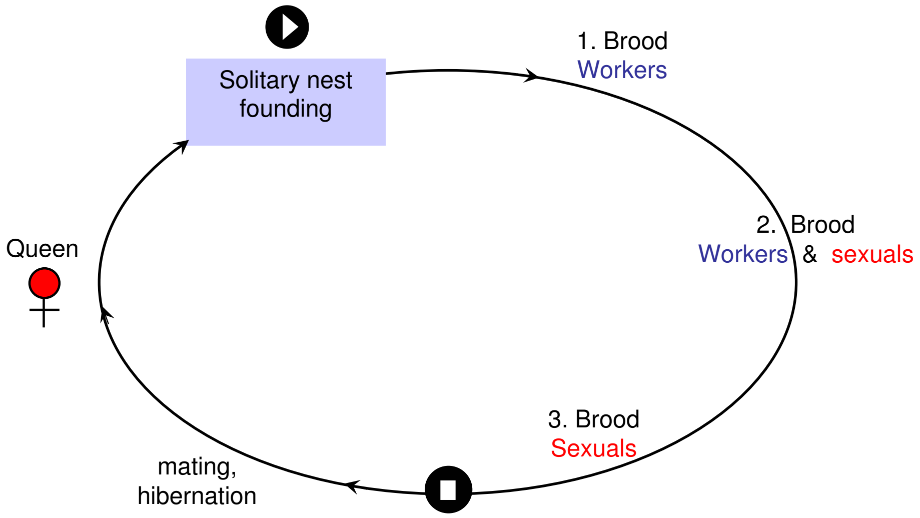
Although the investment balance approach differs essentially from the demographic model of Macevicz & Oster (1976), the results are in excellent agreement. Both approaches predict a bang-bang strategy of reproduction, i.e. colonies should start with the exclusive production of workers and later on switch to the exclusive production of sexuals. Macevicz & Oster (1976) assumed that offspring production is only a function of the total foraging effort of workers: the more resources the workers collect, the more eggs the queen lays. We attenuated this assumption: The more resources workers collect, the more eggs can be provisioned (assumption b). Additionally our model yields a simple characterisation of sociality: Only if the overall investment in workers (for eggs and provisioning) is exceeded by their productivity, optimal worker number is greater than 0. There are several mechanisms which might reduce worker efficiency (g_W) to a value below the critical cost ($c_E + c_W$): a) reduced resource availability, b) reduced foraging time available during a worker's life-time, and c) changes in the trade-off between worker productivity rate and worker cost (not considered here). All these effects may be responsible for the loss of sociality which has been observed in different species of halictids (Danforth, 2002; Danforth *et al.*, 2003), while reduced foraging time is most probably the reason for the loss of sociality in populations of *Halictus rubicundus* living in high altitudes (Yanega, 1997). Both effects a) and b) are likely to occur at the end of the season. As halictid reproduction is organised in discrete broods of fixed length (Mitesser *et al.*, 2006; Weissel *et al.*, in press) and the development time of the brood (not considered by Macevicz & Oster, 1976) determines a very stable temporal sequence of active and inactive periods, early termination of reproduction can only be achieved by skipping a complete brood when worker productivity falls below the critical value.

Our model is based on resource limitation of the queen. Such limitation can be observed in many insect species (Heimpel *et al.*, 1996; Mangel & Heimpel, 1998) and in contrast to pure time limitation it can explain the frequently observed wastage of time at the end of the season and the local variation in the number of broods among nests of a population (Strohm & Bordon-Hauser, 2003). A more advanced analysis could combine investment balance with the dynamic approach of Oster & Wilson (1978). There are certainly many further factors like social aggression (Kukuk & May, 1991; Knerer, 1992; Michener, 1990; Richards, 2000), worker reproduction (Kukuk & May, 1991; Wheeler, 1996; Wheeler & Buck, 1996), interactions with predators (Strassmann *et al.*, 1988; Shakarad & Gadagkar, 1995), intraspecific (Archer, 1985; Kaitala *et al.*, 1990) and interspecific parasites (Abrams & Eickwort, 1981; Wcislo, 1997b), that might influence the optimal number of workers and sexuals. A simple extension of the model could also differentiate between the costs for the production of an individual progeny (non depreciable costs, sensu Clutton-Brock 1991) and fixed costs (depreciable costs, sensu Clutton-Brock 1991) like part of the effort for nest construction and protection (Kukuk, 2002; Jeanne & Bouwma, 2004). However, this would considerably reduce the advantages of mathematical transparency and simplicity in our model. The analytical methods we use in the investment balance model (only basic algebraic manipulations) are much simpler compared to Functional Calculus and Optimal Control Theory in the approach by Macevicz & Oster (1976).

It has often been noticed that, in contrast to the clear bang-bang strategy predicted by the model of Macevicz and Oster (1976), graded control, i.e. a gradual increase in the fraction of resources invested in the production of sexuals, is observed not only in halictids (Strohm & Bordon-Hauser, 2003) but also in wasps (Greene *et al.*, 1976; Greene, 1984; Martin, 1991) and bumble bees (Müller & Schmid-Hempel, 1992). According to Oster & Wilson (1978) particularly two mechanisms may be responsible for the production of mixed broods consisting of sexuals and workers. On the one hand, unpredictable fluctuations in environmental factors like resource availability and the duration of the breeding seasons may result in graded control as a bet-hedging strategy to reduce the variance in colony success between seasons. On the other hand, decreasing returns to scale (sensu Oster & Wilson, 1978) in worker productivity (i.e. productivity g_W is a decreasing function of worker number ($g_W = g_W(W)$) or logistic growth of worker numbers will make a sigmoid increase in the production of sexuals evolutionarily superior to the bang-bang strategy. Particularly environmental fluctuations are assumed to trigger graded control (Oster & Wilson, 1978; Greene, 1984). However, theoretical considerations (Mitesser *et al.*, submitted) show that with the classical model of Macevicz and Oster (1976) enormous variation in the length of the breeding season is needed to produce graded control, whereas in the investment limitation model time is not the limiting factor and consequently temporal fluctuations cannot be responsible for deviations from the bang-bang strategy. Whenever productivity g_W is itself a decreasing function of worker number ($\frac{\partial g_W}{\partial W} < 0$; Michener (1964) has shown that this is in fact the case for several halictid species) there will be a threshold number of workers (W_{th}) with $g_W(W_{th}) = c_E + c_W$. Following equation 6.4 the colony will start with the production of sexuals as soon as this threshold is reached.

Our model does not predict any interaction of season length and optimal resource allocation as long as a season lasts long enough to have two broods (activity periods) (but see Beekman *et al.*, 1998a). Thus, the exact timing (duration of the activity periods and breaks) is influenced by other aspects, like the dynamics of resource availability, parasites and predators as well as the synchronisation of colony dynamics (Kaitala *et al.*, 1990). This could explain the observation, that in two-brood colonies of *L. malachurum*, the variance in worker and sexual number (figure 6.2) is not due to differences in timing, as all colonies show a very similar temporal activity pattern, in particular with regard to the switching time between worker and sexual production (Strohm & Bordon-Hauser, 2003).

Development time from egg to adult might play a key role in that context (Mitesser *et al.*, 2006). It triggers the evolution of activity breaks, which characterise the temporal activity pattern in many species of social bees (Sakagami, 1974; Michener, 2000). Though the model of Macevicz and Oster (1976) does not account for development time, a corresponding model extension would not change the bang-bang character of optimal timing (Perleson *et al.*, 1976; Mirmirani & Oster, 1978). Additionally, it might even provide a theoretical link between continuous colony dynamics (Macevicz & Oster, 1976) and reproduction in discrete broods (Beekman *et al.*, 1998a, and this study).


Solitary nest founding
1. Brood
Workers
2. Brood
Workers & sexuals
3. Brood
Sexuals
mating,
hibernation
Queen

Chapter 7

Adaptive dynamic resource allocation in annual eusocial insects: Environmental variation will not necessarily promote graded control

with Norbert Weissel, Erhard Strohm and Hans-Joachim Poethke

SUBMITTED TO BMC ECOLOGY

Abstract. Background: According to the classical model of Macevicz and Oster annual eusocial insects should show a clear dichotomous strategy of resource allocation: Colony fitness is maximised when a period of pure colony growth (exclusive production of workers) is followed by a single reproductive period characterised by the exclusive production of sexuals. However, in several species of vespid wasps, bumble bees, and halictid bees, graded investment strategies with a simultaneous production of workers and sexuals have been observed. Such deviations from a dichotomous "bang-bang" strategy are usually assumed to be an adaptive (bet-hedging) response to environmental fluctuations like variation in season length or food availability. For the prediction of optimal investment patterns of insect colonies in fluctuating environments we slightly modified Macevicz and Oster's classical model of annual colony dynamics and used a dynamic programming approach nested into a recurrence procedure for the solution of this stochastic optimal control problem.

Results: 1) The optimal switching time between pure colony growth and the exclusive production of sexuals decreases with increasing environmental variance. 2) However, at least for low to intermediate environmental fluctuations no deviation from the typical bang-bang strategy is observed and exemplary model calculations for the halictid bee *Lasioglossum malachurum* revealed that bet-hedging is not likely to be the reason for the gradual allocation behaviour observed in this species. 3) When environmental variance reaches a critical level our model predicts an abrupt change from dichotomous behaviour to gradual allocation strategies, but the transition between colony growth and production of sexuals is not necessarily monotonic. Both, the critical level of environmental variance as well as the characteristic pattern of resource allocation strongly depend on the type of function used to describe environmental fluctuations.

Conclusions: Up to now bet-hedging as an evolutionary response to variation in season length has been the main argument to explain field observations of gradual resource allocation in annual eusocial insect species. Our model clearly shows that the classical bang-bang strategy of resource allocation allows to buffer small to intermediate fluctuations of environmental conditions and extremely high fluctuations are needed to trigger the evolution of gradual allocation strategies. Detailed quantitative observations on resource allocation in eusocial insects are needed to analyse the relevance of alternative explanations, e.g. logistic colony growth, for the evolution of gradual allocation strategies.

7.1 BACKGROUND

The optimal allocation of accumulated resources to maintenance, growth, and reproduction is the central topic of life history theory. At any time during its life an organism must decide whether it will allocate available resources to maintenance, to somatic growth (that will allow for larger reproductive potential in the future), or to reproduction. In particular, the trade-off between growth and reproduction has been well-confirmed (Roff, 1992; Stearns, 1992). Much theoretical and field work has been conducted to analyse the pattern of investment in growth and reproduction and to predict which allocation strategies will maximise an organism's fitness (Cohen, 1971; Perrin & Sibly, 1993; Iwasa, 2000). Since the first paper by Cole (1954) theoretical analysis of life history strategies has been focused on solitary organisms (for review see Kozlowski & Teriokhin, 1999; Perrin & Sibly, 1993; Roff, 1992; Stearns, 1992), while the evolutionary analysis of eusocial nest cycle dynamics has not gained much attention (but see Beekman *et al.*, 1998a; Mitesser *et al.*, 2006) ever since the eminent work of Macevicz and Oster (1976). For social insects the problem of an optimised investment in growth and reproduction not only refers to growth and reproduction of individuals but also of the colony as a whole: how much resources should be spent to increase worker force or to produce sexuals instead? As the correct answer to this problem strongly depends on the time left until the end of the season and as this quantity continuously changes we refer to optimal investment patterns as dynamic strategies. Dynamic allocation strategies in eusocial insects have first been analysed in the seminal papers of Macevicz and Oster (1976) and Oster and Wilson (1978).

Macevicz and Oster (1976) analysed the prototype of an annual eusocial colony cycle as exhibited by many vespid wasps, bumble bees and halictid bees and calculated optimal resource allocation strategies for the case of predictable or constant season length (Macevicz & Oster, 1976; Michener, 2000). When season length is fixed and model parameters are constant during the season the optimal investment pattern is a simple "bang-bang" strategy: The annual productivity cycle is divided into two phases. Colonies start with a phase of colony growth when workers should be produced exclusively and end with a reproductive phase with exclusive production of male and female sexuals. The temporal position of the optimal switching point between the two phases is entirely determined by the season length, worker productivity rate, and worker mortality rate and can be expressed analytically (Macevicz & Oster, 1976).

However, as Greene (1976) has already pointed out colony development of many annual eusocial insects does not show the abrupt switch from colony growth to reproduction as predicted by the bang-bang strategy but a graded transition between these phases characterised by a gradual shift from the production of workers to the production of sexuals. Such graded control has been reported in wasps (Smith, 1956;

Blackith & Stevenson, 1958; Greene *et al.*, 1976; Haggard & Gamboa, 1980; Greene, 1984; Kolmes, 1986; Martin, 1991), bumble bees (Roseler, 1970; Müller & Schmid-Hempel, 1992) and halictids (Yanega, 1988, 1993; Strohm & Bordon-Hauser, 2003; Hirata *et al.*, 2005). Recent studies of the halictid bee *Lasioglossum malachurum* around Wuerzburg (northern Bavaria, Germany) provide detailed data on the timing of reproduction (Strohm & Bordon-Hauser, 2003; Weissel *et al.*, in press). These data, too, clearly demonstrate graded control and allow quantifying the length of the transition zone.

Graded resource allocation strategies are often interpreted as an evolutionary, risk spreading response (bet-hedging) to environmental stochasticity (Roff, 1992; Stearns, 1992). If the complete population under consideration suffers from identical but unpredictable year to year variations in productivity rate, mortality rate, or season length we expect bet-hedging strategies to be favoured by natural selection (e.g. Menu *et al.*, 2000; Menu & Desouhant, 2002). As a response to fluctuating season length plants should simultaneously produce offspring with different diapause strategies (Kozlowski & Ziolko, 1988; Menu *et al.*, 2000), crickets should produce micropterous and macropterous individuals simultaneously as a consequence of variation in the availability of annual thermal energy (Bradford & Roff, 1997) and young mice and voles should vary in age of maturity within populations in risky environments (Kaitala *et al.*, 1997). For solitary insects Hopper (1999) has reviewed numerous cases where mixed strategies have been linked to the spreading of risk.

Oster and Wilson (1978) were the first to apply the general argument of bet-hedging to colony dynamics and suggested that it could be the ultimate mechanism responsible for graded control in social insects: "It can be demonstrated that stochastic variation in the system parameters will always promote graded control." (Oster & Wilson, 1978). Following Oster (figure 2.16 Oster & Wilson, 1978) a risk spreading investment strategy in eusocial insects would be realised as a gradual sigmoid (instead of a dichotomous) transition between worker and sexual production. As a causal relationship between random variation in season length (as a specific and common realisation of environmental fluctuations) and graded strategies is supported by many studies on the evolution of mixed strategies (King & Roughgarden, 1982a; McNamara, 1994; Bradford & Roff, 1997), variation in season length is often consulted to explain graded control in annual eusocial insects (Oster & Wilson, 1978; Greene, 1984; Yanega, 1988, 1993; Beekman *et al.*, 1998a).

However, Hopper (1999) reviewed several types of risk spreading in solitary organisms: temporal, metapopulation, and within-generation spreading of risk. His review shows that empirical evidence for bet-hedging as the important driver for the evolution of facultative diapause, migration polyphenism, spatial distribution of oviposition, egg size, and other traits is weak or doubtful and inter-annual environmental variability often turns out to be too weak to favour much risk spreading. As the plausible verbal arguments of Oster and Wilson (1978) in favour of bet-hedging as the ultimate cause for graded control have never been worked out in detail, it remains an open question, if environmental fluctuations are a sufficient precondition for the evolution of graded investment strategies in eusocial insects.

Here we present a theoretical analysis of the influence of environmental stochasticity (realised as fluctuations in season length) on the investment strategy of social insects. Based on the colony model of Macevicz and Oster (1976) we analyse how the temporal pattern of optimal resource allocation is influenced by the distribution of environmental conditions (mean, variance and shape of the distribution of expected season length). For the special case of *Lasioglossum malachurum* we will derive estimates of the variability of seasons. Our calculations are based on data that are tightly correlated to season length of bee colonies like soil temperature (triggering brood development) and the availability of different nectar plants. This will allow to predict optimal temporal resource allocation for *L. malachurum* and to check whether environmental fluctuations are sufficient to explain the broad transition phase between colony growth and reproduction observed in this species.

7.2 RESULTS

7.2.1 Deterministic environments

Our analysis of the consequences of fluctuations in season length is organised in two steps: First, we present a deterministic model of the colony cycle with constant season length. As numerical optimisation methods are required later and the nocturnal inactivity of the colonies provides a natural time base, we use a time-discrete version of the classical model of Macevicz and Oster (1976) with a time step of one day; Secondly we calculate the optimal investment strategy when season length varies according to a given distribution.

Our model represents colony development during a single season of length L (this condition will be relaxed later). Two main dependent variables describe the state of a colony: the number of workers (W_i) and the number of sexuals (S_i) at time step i. Like Macevicz and Oster (1976) we do not distinguish between male and female sexuals. The colony cycle typically starts in spring with nest founding by inseminated and hibernated females. During the founding phase the females work alone and perform all those foraging tasks that will be taken over by workers after their emergence later in the season (Michener, 2000). Thus, we start with initial condition $W_1 = 1$ assuming that the founding queen acts like a single worker until the first eggs have developed to adults (Knerer, 1992). The change in the number of nestmates is governed by two mechanisms: mortality and reproduction. Each individual survives from time step i to $i+1$ with probability q. Resource allocation in each time step (i) is directly proportional to the current worker force (W_i). Each worker can provision c (worker efficiency) eggs (= brood cells) per time step. For the sake of simplicity survival and efficiency of individuals are assumed to be constant during the whole season. We further assume that the actual egg laying rate of the queen is not limited, but the number of eggs that can be successfully provisioned depends (linearly) on the number of workers in the colony (Knerer, 1992). Only a time dependent fraction (u_i) of resources is allocated to the production of sexuals while the fraction $(1-u_i)$ is invested in the production of workers. Thus, the number of workers (W_{i+1}) at time step $i+1$ can be calculated as

$$W_{i+1} = qW_i + (1-u_i)cW_i \tag{7.1}$$

In most eusocial halictid bees, annual vespid wasps, and bumble bees life span of adult females is much longer than life span of workers (Sakagami, 1974). Female sexuals have to hibernate before nest founding in the following year, while workers live only for several weeks. Thus, we neglect mortality of sexuals as has been done by Macevicz and Oster (1976) in most of their analyses. Consequently the number of sexuals (S_{i+1}) at time step $i+1$ can be calculated as

$$S_{i+1} = S_i + u_i cW_i \tag{7.2}$$

These two equations fully determine the development of an annual primitively eusocial bee colony from nest founding at time step $i=0$ until the end of the season ($i=L$). Fitness of colonies following such nest dynamics can be measured by the final number of sexuals successfully raised (S_L). Macevicz and Oster (1976) as well as Oster and Wilson (1978) have studied such systems (in time continuous form) as optimal control problems with control variable u_i (fraction of resources allocated to the production of sexuals). In the deterministic case (when season length L does not change between years) they found that the (time-dependent) optimal control solution (u_i) that maximises S_L is a dichotomous bang-bang strategy and u_i should switch from 0 to 1 at an optimal switching time (SWT). Thus, the optimal temporal pattern of reproduction consists of two distinct phases, a growth phase with exclusive worker production ($u_i = 0$ for $1 \leq i < SWT$) followed by a reproductive phase characterised by the exclusive production of sexuals ($u_i = 1$ for $SWT \leq i \leq L$). Accordingly, the optimal strategy can be characterised by a single parameter, the optimal switching time $SWT \in 1,2,...,L$, when reproduction begins and u_i ($i \in 1,2,...,L$) changes from 0 to 1.

The switching time SWT can easily be calculated numerically: just generate L

different sequences $u = \{u_1 = 0, u_2 = 0, ..., u_{SWT} = 0, u_{SWT+1} = 1, ..., u_L = 1\}$ (corresponding to different SWTs), iterate equation 7.1 and equation 7.2 for each u, and choose that u sequence (and corresponding SWT) that maximises colony fitness S_L (The optimal SWT can also be found analytically in the case of time discrete dynamics, but can not be computed by the formula provided by Macevicz and Oster (1976) for the case of time-continuous dynamics, Mitesser (unpublished).). The optimal SWT is increasing with increasing survival q and increasing worker efficiency c (see also equation 6 and figure 8 in Macevicz & Oster, 1976). The growth phase of the resulting colony dynamics is characterised by an exponential increase in worker number while the number of sexuals stays at 0 until the optimal SWT is reached. After that, worker number exponentially decreases and the number of sexuals exponentially increases.

7.2.2 Environmental stochasticity

Coarse grained environmental stochasticity (sensu Yodiz, 1989) could affect the model system in several different ways: worker survival rate, worker productivity rate as well as season length can change from year to year. Here we restrict our analysis to the presumably most common effect in the context of bet-hedging: variation in season length (e.g. see Bradford & Roff, 1993, 1997; Hopper, 1999; Wong & Ackerly, 2005). Variation in season length might be caused by differences in both the beginning and the end of the season. However, to model variation in season length it is sufficient to change the number of time steps (L) available within a single year, as allocation strategies always refer to the time passed since colony foundation.

To analyse the optimal investment strategy in variable environments a few essential modifications of the model system have to be made. When all individuals of a population simultaneously suffer from identical (and unpredictable) environmental fluctuations, then the appropriate measure of fitness (F) is the geometric mean of single year reproductive output (Yodiz, 1989; Stearns, 1992; Roff, 1992). As season length L_j varies between years j, reproductive output S_{L_j} will also vary and different years will contribute differently to overall fitness. We use the frequency distribution $f(L)$ to describe the distribution of season lengths (L). Thus, each single year reproductive output S_{L_j} must be weighted according to the frequency $x_j = f(L_j)$ of the corresponding season length L_j and we get for the expected long term fitness of a strategy

$$F = (\prod_{j=1}^{n} S_{L_j}^{x_j})^{1/n} \tag{7.3}$$

Bet-hedging analyses have been based on various assumptions about the shape of the frequency distribution of environmental quality. However, season length $L = 0$ must always be excluded from the distribution of possible seasons ($f(0) = 0$) (e.g. Bradford & Roff, 1997), otherwise vanishing fitness in a single year with length $L = 0$

would imply that mean fitness F equals 0, whatever the rest of the distribution is like. Thus, every time discrete model must assume a minimum season length of at least one time step. Apart from this, distributions representing environmental fluctuations in modelling approaches may vary from uniform distributions (e.g. King & Roughgarden, 1982a; Taylor & Gabriel, 1993; typically characterised by their lower und upper boundary) to normal distributions (e.g. Bradford & Roff, 1997; characterised by mean and variance). Thus, we investigated optimal allocation strategies for uniform and normal distributions as representatives of two extreme frequency distributions, assuming that natural conditions can be found somewhere in between. As we analyse a time-discrete model system season length L_j in year j can only take integer values. If season length is normally distributed (as assumed by Bradford & Roff, 1997) with mean season length m and variance σ^2, then the exponent x_j can be calculated as follows:

$$x_j = \int_{L_j-1/2}^{L_j+1/2} \frac{1}{\sqrt{2\pi\sigma}} e^{\frac{(L-m)^2}{2\sigma^2}} dL \tag{7.4}$$

If season length is distributed uniformly between $B-m$ and $B+m$ (King & Roughgarden, 1982a) with mean season length m and width B, then x_j does not depend on j (for $B-m < j < B+m$) and can be calculated as follows:

$$x_j = \begin{cases} 1/2B & : \quad B-m < j < B+m \\ 0 & : \quad \text{otherwise} \end{cases} \tag{7.5}$$

To compare the effect of normally and uniformly distributed season length on the optimal strategy we characterised both distributions by their variance (for the uniform distribution with width B we get $\sigma^2 = B^2/3$).

In the following graded strategies will be characterised by the width w of the transition zone. This we define as the number of time steps between the time when u_i surpasses a value of 0.05 for the first time and the time when u_i has finally reached at least 0.95 (and does stay above this value for all remaining time steps).

For stochastic environments with variable season length (L) the control function u_i ($i = 0,...,L$) maximising fitness (F) cannot be calculated in a straight forward way as in the deterministic case. In general, a recurrence method is required (see section Methods). Numerical results were calculated with the computer algebra system Mathematica 4.0 (Wolfram Research, 1999) and figures were plotted with the programming language R 2.1 (Ihaka & Gentleman, 1996).

Variation in season length can be calculated on a rather coarse level, only. Data of the duration of the yearly number of foraging days in halictids are only available for a few years (Weissel, unpublished). Thus, we based our calculations on data that are correlated to season length of the halictid colonies. The length of the activity period is influenced by several factors like the soil temperature (triggering brood develop-

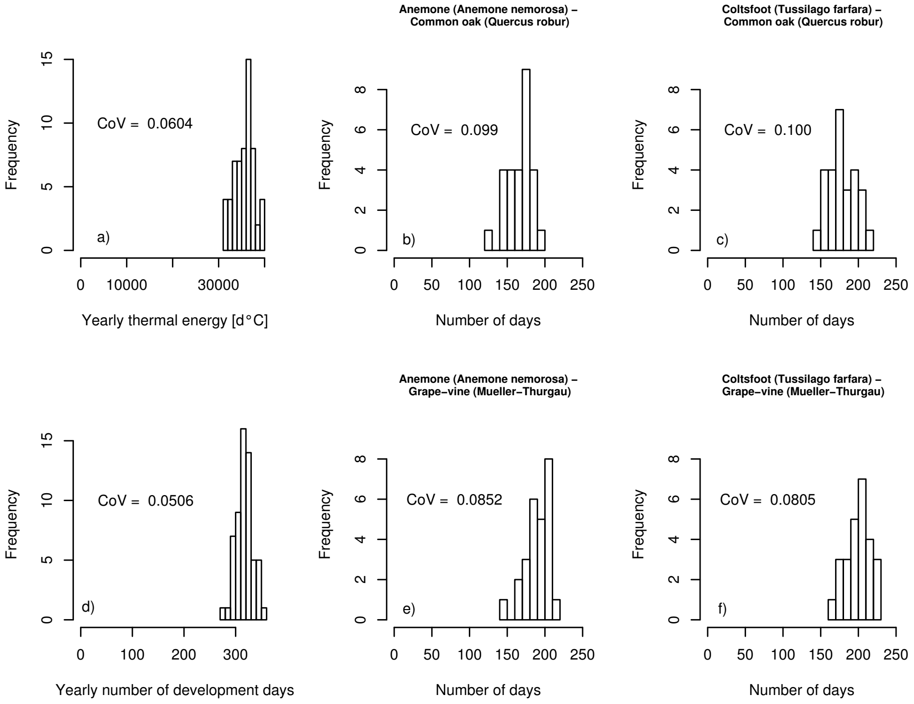


Figure 7.1: Frequency distribution of different indicators of season length: the yearly temperature sum [d°C] above the zero development temperature of 10.5 °C of *L. malachurum* (Weissel, unpublished), $n = 59$ (1a); the number of days with mean temperature above 10.5 °C, $n = 59$ (1d); the time span between first flowering of Anemona (*Anemona nemorosa*) and first fruits of Common oaks (*Quercus robur*), $n = 27$ (1b); the time span between first flowering of Anemona and grape gathering (Mueller-Thurgau), $n = 26$ (1d); the time span between first flowering of Coltsfoot (*Tussilago farfara*) and first fruits of Common oaks, $n = 27$ (1c); and the time span between first flowering of Coltsfoot and grape gathering, $n = 26$ (1f).

ment) and availability of flowers for delivering nectar and pollen. We calculated the coefficient of variation for six possible indicators of season length based on daily temperatures and phenological data on the annual vegetation cycle (provided by the German weather service, Deutscher Wetterdienst) since 1947 until now: available yearly temperature sum [d°C] above the zero development temperature of 10.5 °C of *L. malachurum* (Weissel, unpublished), the number of days with mean temperature above 10.5 °C, the time span between first flowering of Anemona (*Anemona nemorosa*) and first fruits of Common oaks (*Quercus robur*), the time span between first flowering of Anemona and grape gathering (Mueller-Thurgau), the time span between first flowering of Coltsfoot (*Tussilago farfara*) and first fruits of Common oaks, and the time span between first flowering of Coltsfoot and grape gathering. Anemona and Coltsfoot flower around the time of the emergence of *L. malachurum* queens and oak fruiting as well as grape gathering occur around the end of the emergence period of this halictid species.

7.2.3 Estimating model parameters

To quantify optimal allocation strategies we have to estimate the relevant parameters for both colony dynamics and environmental conditions. Field observations of the halictid bee *Lasioglossum malachurum* around Wuerzburg provide the most comprehensive data. In *L. malachurum* a typical (foraging) season length in central Europe lasts about 80 to 120 days (Weissel *et al.*, in press). However, the halictid nest cycle is organised as a sequence of active and inactive periods (Mitesser *et al.*, 2006), and only during approximately half of this time foraging and provisioning is observed. Thus, we assume a mean season length of $L = 50$ foraging days. Mean worker life-time during foraging is about three weeks and survival rate per day can be approximated by $q = 0.95$ (Knerer, 1992). Worker life-time efficiency in *L. malachurum* is about 3.2 offspring per worker (Strohm & Bordon-Hauser, 2003; Mitesser *et al.*, submitted). In combination with the survival rate this results in a worker productivity rate of $3.2/21 \approx 0.15$. These values yield overall sexual numbers of about 40 individuals, a typical number for *L. malachurum* colonies (Legewie, 1925a; Knerer, 1992; Strohm & Bordon-Hauser, 2003).

All estimates of the variability of season length for *L. malachurum* yielded similar values (figure 7.1). Thermal energy available for brood development typically varies by about 5% from year to year (figure 7.1 a and d). Variation due to flower availability is less than 10% for all data sets (figure 7.1 b, c, e, and f). If we use the maximum coefficient of variation (10% for the time span between first flowering of Coltsfoot (*Tussilago farfara*) and first fruits of Common oaks) observed in these data sets we would expect a typical standard deviation in the length of the foraging season of about 5 days. This is consistent with quantitative observations of the colony activity of *L. malachurum* within 2002, 2003 and 2004 (Weissel, unpublished).

7.2.4 Numerical results

To analyse the general behaviour of the model system we will first focus on a uniform distribution of season lengths (King & Roughgarden, 1982a). From this simple case we will then proceed to the normal distribution (Bradford & Roff, 1997) and point out the common pattern.

The optimal response of the model system to (uniformly distributed) fluctuating season length consists of two subsequent phases: 1) For low to moderate fluctuations of season length (figure 7.2 a and b) the typical bang-bang strategy with an abrupt transition between worker and sexual production is optimal. With increasing environmental variance the temporal position of the switching point between growth and reproduction

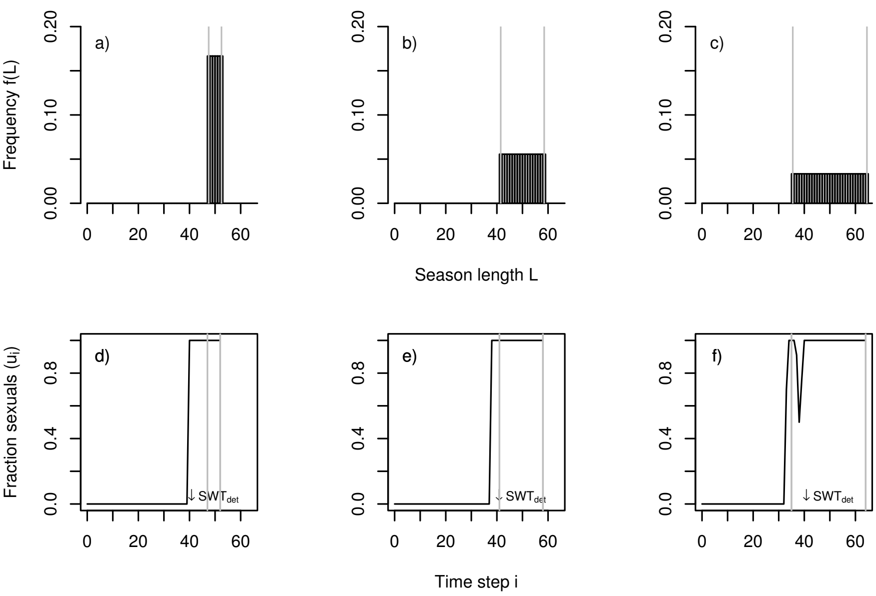


Figure 7.2: Uniformly distributed season length and corresponding strategy response. The upper row shows the frequency distribution of season length for three cases with increasing variance (a: width $B = 5$, b: $B = 10$, and c: $B = 15$, mean always = 50). The lower row shows the corresponding optimal strategy transitions: the fraction of sexuals produced by the colony as a function of time (d, e, and f, worker productivity rate $c = 0.15$, survival rate $q = 0.95$). A small arrow (SWT_{det}) indicates the temporal position of the optimal switching point in the case of a deterministic environment with season length $L = 50$. Vertical grey lines indicate the boundaries of the distribution of season length. Figures d and e demonstrate that the optimal response of the system to increasing variation in season length is initially realised by an earlier switching from worker to sexual production. Graded strategies only emerge if environmental variation reaches a critical level and earlier switching alone is not sufficient to buffer environmental fluctuations (c and f).

decreases (figure 7.2 d and e) but – in contrast to Oster & Wilson's prediction (1978) – the typical bang-bang strategy is not replaced by a gradual change from worker to sexual production. 2) However, when variance in season length exceeds a critical level (figure 7.2 c) the bang-bang strategy is no longer adequate and a graded resource allocation strategy with a continuous transition between pure colony growth and reproduction becomes optimal (figure 7.2 f). Graded resource allocation is characterised by a distinct phase of simultaneous production of workers and sexuals. It is a bet-hedging strategy to avoid complete colony failure (figure 7.2 f). With increasing variance of season length colonies start to reproduce earlier in their life cycle. However, while this temporal shift of the onset of reproduction is rather continuous (figure 7.3 a), the transition between a pure bang-bang strategy and graded resource allocation is rather abrupt (figure 7.3 b).

The transition between the phase of pure colony growth and exclusive reproduction is not characterised by a monotonous increase in the amount of resources allocated to

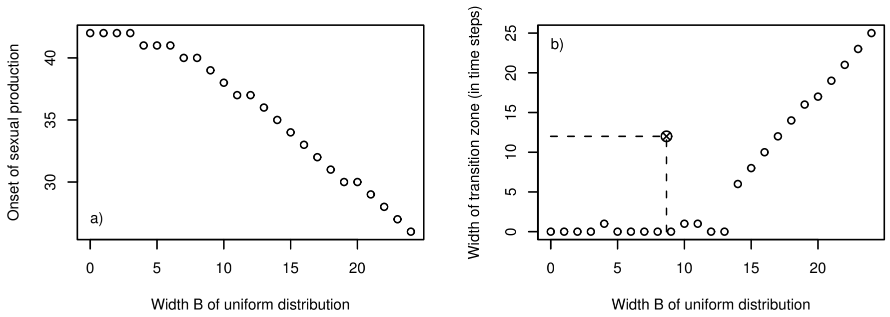


Figure 7.3: Onset of sexual production (a) and width w of the transition zone (b) between complete worker and complete sexual production as a function of the width of a uniform distribution of season length (B). As long as the width of the transition zone equals 0, the reproduction strategy is bang-bang (as in the deterministic case), but the optimal switching time moves to earlier points in time when variance increases (a). The single emphasised point in the right figure denotes the combination of strategy transition and estimation of environmental variance observed in *L. malachurum* (Model parameters: worker productivity rate $c = 0.15$, survival rate $q = 0.95$, mean season length = 50).

reproduction as suggested by Oster & Wilson (1978, see their Figure 2.16). In optimal resource allocation strategies the onset of the transition phase is characterised by a short pulse of nearly exclusive sexual production followed by a phase of simultaneous production of workers and sexuals before the colony cycle finally ends with the exclusive production of sexuals. With increasing variance of season length the transition zone between pure colony growth and pure reproduction gets broader and the hump of worker production inside this zone becomes more pronounced. Tests with more restricted strategy sets (not shown here, see discussion) showed that this humped transition zone in fact yields significantly higher fitness than a monotonous sigmoid transition.

The pattern described above clearly depends on the specific form of the distribution of season length. When the uniform distribution is replaced by a normal distribution, both phases of system response (shift of SWT and onset of graded control) emerge again, but the graded control strategy is achieved already for lower environmental variance than in the case of equally distributed season length (figure 7.4 and figure 7.5). This is not surprising, as the normal distribution is not bounded and even a very short season of one day cannot completely be ruled out. The normal distribution is characterised by very smooth slopes on both flanks of the distribution. The rather smooth increase of the probability density on the left flank is reflected in a smooth increase in sexual production. In contrast to the case of the rectangular distribution the strategy transition is thus nearly monotonic for normally distributed seasons (figure 7.4 f, in contrast to figure 7.2 f).

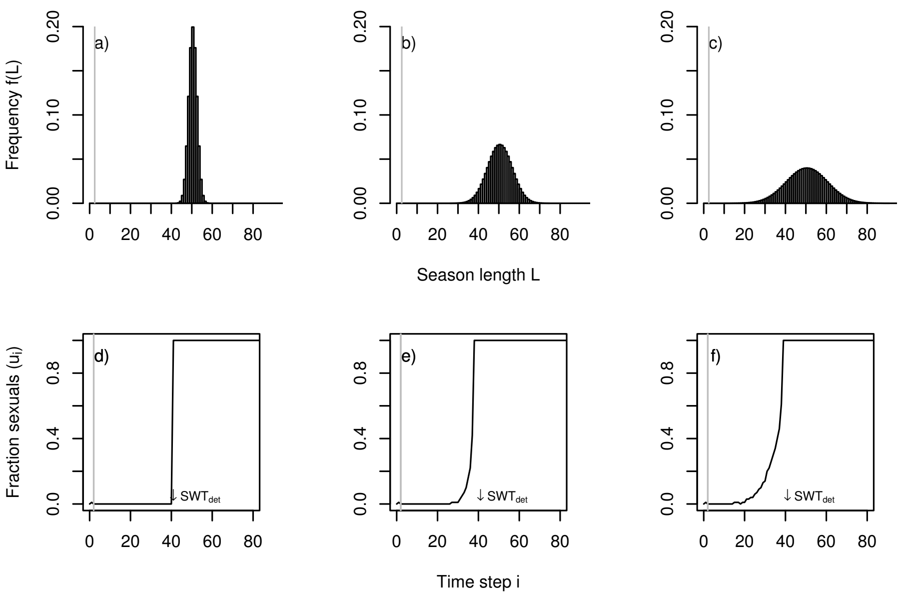


Figure 7.4: Normally distributed variation in season length and corresponding strategy response. The upper row shows the frequency distribution of season length for three cases with increasing variance (a: width standard deviation $\sigma = 2.9$, b: $\sigma = 5.8$, and c: $\sigma = 8.7$, mean always = 50). The lower row shows the corresponding optimal strategy transitions: the fraction of sexuals produced by the colony as a function of time (d, e, and f, worker productivity rate $c = 0.15$, survival rate $q = 0.95$). A small arrow (SWT_{det}) indicates the temporal position of the optimal switching point in the case of a deterministic environment with season length $L = 50$. The vertical grey lines indicate the lower boundary of the distribution of season length at $L = 1$. The optimal response of the system to increasing variation in season length is initially realised solely by switching earlier from worker to sexual production, and graded strategies are realised when environmental variation increases (e, f).

The field observations of colony dynamics of *L. malachurum* yielded a rather broad transition zone with a period of approximately 11 days with simultaneous production of workers and sexuals (Strohm & Bordon-Hauser, 2003; and unpublished). For realistic standard deviations of season length of about 5 days this transition zone is far too broad to be explained as a bet-hedging strategy. While bet-hedging would clearly predict a pure bang-bang strategy for such a standard deviation under a uniform distribution of season length (figure 7.3), even the assumption of a normal distribution would predict a transition zone of less than 5 (figure 7.5).

7.3 DISCUSSION

Our analysis of optimal resource allocation patterns in eusocial insect colonies clearly demonstrates that moderate fluctuations of environmental conditions (length of foraging season) will not necessarily foster the evolution of bet-hedging allocation strategies. This deviation from the rather intuitive predictions of Oster and Wilson is readily

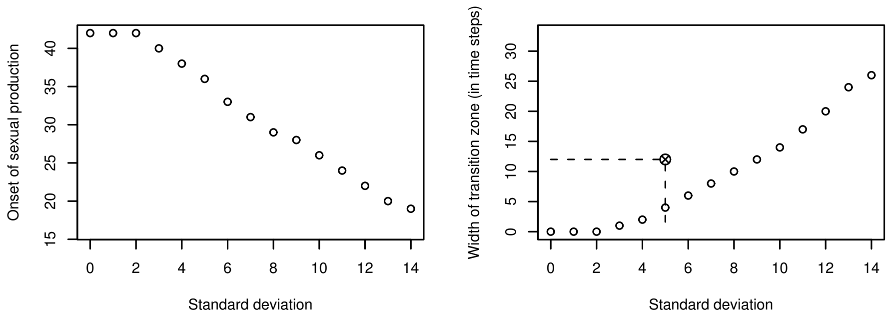


Figure 7.5: Onset of sexual production (a) and width *w* of the transition zone between complete worker and complete sexual production (b) as a function of the width of a normal distribution of season length (given as the standard deviation). As long as the width of the transition zone equals 0 (see b), the reproduction strategy is bang-bang (as in the deterministic case), but the optimal switching time moves to earlier points in time when variance increases (a). The single emphasised point in the right figure denotes the combination of strategy transition and estimation of environmental variance observed for *L. malachurum* (Model parameters: worker productivity rate $c = 0.15$, survival rate $q = 0.95$, mean season length = 50).

explained by the inherent buffering capacity of the bang-bang allocation strategy: Finite worker productivity and mortality rates determine an extended reproductive phase at the end of the season, when sexuals are produced exclusively. Thus, even for rather short seasons colony reproduction will not cease completely as long as the season ends after the onset of the reproductive phase. Consequently, rather high fluctuations of environmental conditions are needed to promote the evolution of graded allocation strategies with the simultaneous production of workers and sexuals.

The results of our model are rather robust against the variation of all model parameters (worker mortality, worker survival and mean season length). Parameter modifications within a plausible range did not generate any additional phenomena. It seems plausible to assume that increasing mean season might reduce the effect of environmental variance, as identical environmental variance decreases relatively when mean season length increases. This is not the case. Increasing mean season length will just prolong the period of complete worker production, but not influence the strategy transition. Even more, very short mean season length can result in strategies which start with the production of sexuals right from the beginning (see also King & Roughgarden, 1982a). As long as a season ends after the onset of the reproductive phase the pure bang-bang strategy is buffered against complete reproductive failure. The switch from the bang-bang strategy to a graded strategy thus strongly depends on the length of the reproductive phase. Worker efficiency and survival are the main determinants of the duration of sexual production in the deterministic case without environmental fluctuations. The optimal duration of sexual production is decreasing with increasing worker survival (q)

and increasing worker efficiency (c) (Macevicz & Oster, 1976). Populations in ideal conditions with high worker survival and high worker efficiency will thus switch to graded allocation strategies for much smaller variability of environmental conditions than populations that live under harsh environmental conditions.

Yet, at least for *Lasioglossum malachurum* the broad transition zone between pure colony growth and reproduction cannot be explained as an adaptive response to fluctuating environmental conditions. Even for normally distributed season length the observed transition zone is more than twice as long as predicted based on realistic estimates for the coefficients of variation for environmental fluctuations. Model results for evenly distributed season length indicate that with more realistic distribution functions and observed variability of season length graded control is rather improbable.

When environmental fluctuations are strong enough, they promote the evolution of graded allocation strategies with a pronounced transition zone. This zone is defined by the simultaneous production of workers and sexuals. However, it is not necessarily characterised by a smooth continuous (sigmoid) increase in the production of sexuals as has been predicted by Oster and Wilson (1978). The specific form of this transition strongly depends on the frequency distribution of season length. For evenly distributed season length with a very steep left flank the transition zone is characterised by a humped structure starting with a very abrupt increase in the amount of resources invested into reproduction and an intermediate zone of substantial colony growth with decreasing investment in reproduction. For the normal distribution on the other hand, with its very smooth left flank the transition zone is characterised by a monotonic transition from pure colony growth to pure investment in reproduction.

We have chosen the rectangular and the normal distribution because they are both commonly used types of frequency distribution representing the opposite sites of a continuum of distributions with increasingly steep flanks (King & Roughgarden, 1982a; Bradford & Roff, 1997). However, the normal distribution is an unbounded distribution and as the minimum as well as the maximum length of seasons is obviously limited this type of distribution with its extremely smooth flanks may easily produce artefacts in the context of bet-hedging. This can be seen, when the variance of season length is strongly increased. As we have to limit season length to a minimum of one day an increase in the variance of the normal distribution necessarily leads to steeper left flanks of this distribution. When we did this, the humped course of the strategy transition observed in the case of the uniform distribution occurred again. An increase of the lower boundary of the season length (in figure 7.3 and figure 7.5 we assumed that seasons cover at least one day , $L_{min} = 1$) will also re-establish the humped structure of the transition zone. A lower boundary of $L_{min} = 27$ (about half of the mean season length) which cuts only 1% of the normal distribution in figure 7.4 c will result in a

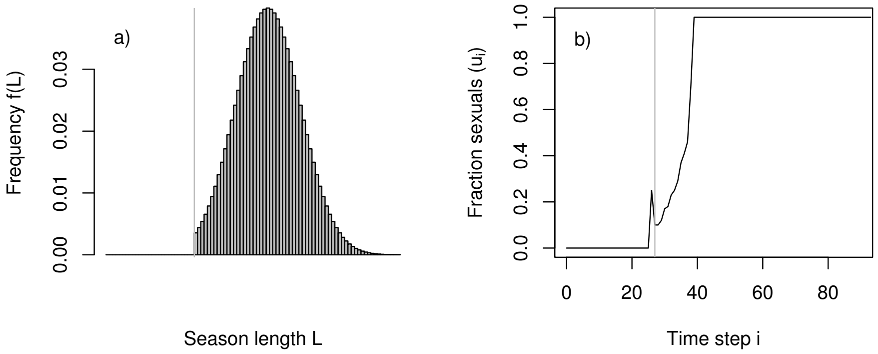


Figure 7.6: Optimal investment strategy (b), when 1% of the frequency distribution of season length is cut at the left side of the distribution (a). There is a prominent peak in sexual production just before minimum season length. Model parameters: worker productivity rate $c = 0.15$, survival rate $q = 0.95$, mean season length = 50, standard deviation $\sigma = 8.7$.

prominent peak in the strategy curve. Immediately after the onset of the reproductive phase nearly 30% of the resources are invested into the production of sexuals. This rather high investment decreases subsequently to values around 15% before it rises again to end with a pure sexual phase (figure 7.6). In general this hump becomes more pronounced when either the length of the season becomes more variable or when the left flank of the density distribution of season length becomes steeper (figure 7.2).

We have shown that variation in season length is not likely to be the reason for graded control in halictids. An alternative explanation could be the decline in worker (per capita) productivity, when colony size increases. That the latter in fact occurs has been shown by Michener for several halictid species (Michener, 1964). Although several theoretical approaches tried to analyse the effect of decreasing worker productivity within the framework of optimal dynamic resource allocation, the straightest analysis has never been performed: replacing the linear dependence of resource allocation on worker number (see equation 7.1 and equation 7.2) by a logistic relationship. Surprisingly, Macevicz and Oster (1976) used such a relationship only for the worker equation (see equation 7.1 here) to estimate model parameters from field data, but not for the dynamics of the sexuals, thus inevitably favouring the early production of sexuals. Their remark, that saturation of productivity can promote graded control only for very restrictive parameter combinations seems premature, and further theoretical effort on this topic could be worthwhile. Beekman & al. (1998) investigated the effect of limited egg laying rate in bumble bees. This is equivalent to saturation of colony productivity, but they allowed only for dichotomous strategy switches with variable switching time, so that the evolution of early switching is always accompanied by the waste of time and can never result in graded control.

7.4 METHODS

The numerical solution of optimal control problems with objective functions averaging over different realisations (here: different season length) of the dynamic system (here equation 7.1 and equation 7.2) in a nonlinear way (here: geometric mean) cannot be achieved with standard dynamic programming (Mangel & Clark, 1989). However, nesting the dynamic programming approach within a recurrence procedure is a suitable way to find the optimal control function, if the iteration converges.

We first focus on the longest season length L_{max} possible with respect to the distribution of season length. The optimal value $u_{L_{max}}$ can be chosen independently from state and control function at earlier time steps, just based on maximising $S_{L_{max}}$. Working backwards (dynamic programming) in time requires to redefine the objective function. To find $u_{L_{max}-1}$ we have to maximise $S_{L_{max}} \cdot S_{L_{max}-1}$. This expression can be expanded in terms of state and control function values in time step $L_{max}-1$. However, in general (for this and earlier time steps) it is not possible to find the value of u_i that maximises this expression without knowing the numbers of queens and workers in the current time step. Further more these values cannot be determined without knowing the values of u_i in previous time steps. This circularity can be broken by an iterative procedure. We first assume a trial solution $\tilde{u}_i$ for the control function and calculate the numbers of queens and workers in different time steps. Then an approximate value for u_i (not optimal yet) can be determined assuming the numbers of queens and workers just calculated. The approximate value can be calculated by derivating the objective function with respect to u_i symbolically and find the root numerically. This procedure is repeated for all time steps back to $i = 0$. This yields an approximate solution for u_i $(i = 0, \ldots, L_{max})$.

Now the numbers of queens and workers can be recalculated using the approximate values of u_i from above. Finally the optimal values of u_i can be recalculated, too. This process is repeated until the values of u_i have converged to the required accuracy (changes in the Euclidian norm of $(u_1, .., u_{L_{max}})$ less than 0.001).

There might also be an analytical solution of the optimal control problem based on the application of Pontryagin's Maximum Principle, but we did not follow this line of approach (for detailed instructions see King & Roughgarden, 1982a).

Summary

Plants and animals show a wide variety of individual life cycles. Evolutionary life history analysis tries to explain the different life history strategies in the light of adaptation and selection. Every life history reflects a temporal sequence of decisions between behavioural alternatives and is thus dynamic at heart. Initially, the classical analysis of life history strategies has concentrated on outstanding, singular events in the life of an individual: its birth, maturity, mating, reproduction, and death. As analytical methods have been improved over the course of time, modelling approaches covered more and more parts of the entire life cycles. Consequently, the prominent life history events themselves could be explained evolutionarily and their dynamic character became apparent: Reproduction is not necessarily a singular event, but can take place repeatedly; after maturity, growth is not essentially replaced completely by reproduction, but growth and reproduction can occur alternately or simultaneously.

The central problem of investigating life history strategies is the question of the optimal pattern of investment in growth and reproduction. In social insects the original question of dynamic life history strategies gains in complexity, as it is relevant not only at the level of single individuals, but also at the level of the whole colony: How should the investment be distributed between workers and sexuals to maximise the success of the colony? Stimulated by the seminal work of Macevicz, Oster and Wilson (1976, 1978) the investigation of dynamic life history strategies in social insects has attracted broad attention. However, the original theoretical concept for the investigation of colony development was barely extended or continued, but replaced by alternative modelling approaches, e.g. for the analysis of biased sex ratios in social insects and the evolution of matrifilial eusociality.

The present thesis tries to bridge the gap between the different approaches. In addition to the investigation of the optimal investment pattern under generalised environmental conditions we also analyse the optimal temporal structure of resource aggregation.

The first part of the thesis (chapters 2, 3, and 4) comprises two theoretical (chapters 2 and 4) and one empirical investigation (chapter 3) and deals with the choice between the extreme behavioural alternatives of activity versus inactivity. Chapter 2 takes an exceptional position as it is the only one not investigating behavioural strategies of so-

cial insects, but the life history decisions of a solitary social parasite. Thus, this chapter constitutes the bridge to the classical literature of theoretical life history analysis that is mainly focused on solitary organisms. In this section we analysed the optimal timing of larval development, a widespread question of dynamic life history strategies. The larvae of the butterfly *Maculinea rebeli* develop as parasites within ant colonies. Thus, the optimal development strategy of the butterfly must be investigated in the context of the dynamics of its social host. Extensive field studies in France show that approximately 25% of the larvae develop in the first year while the remaining larvae delay development until the subsequent year. We developed an analytical model to predict the evolutionarily stable fraction of fast-developing individuals. The model accounts for the additional mortality risk of slow-developing larvae, the effect of competition among larvae, and for an existing competitive advantage of slow-developing larvae over newly entering fast-developers. Kin-competition and the avoidance of renewed infection of the ant colonies stabilise the ratio of fast- and slow-developing larvae near 0.5. The competitive advantage of the slow-developers is the only mechanism potentially selecting for a fraction of fast-developing larvae smaller than 0.5. However, given the empirical data the evolutionarily stable fraction is predicted to be closer to 0.5 than to 0.25 as observed in the field. Presumably, hitherto unknown fitness benefits for slow-developing larvae also contribute to the evolution of delayed development and should be elucidated with future field and laboratory studies. The model developed in chapter 2 may be of general applicability for systems in which maturing relatives compete in small subgroups.

Chapters 3 (empirical investigation) and 4 (theoretical investigation) analyse delayed development at the level of colony dynamics in annual, primitively eusocial bees and wasps. An annual eusocial colony cycle is typical for nearly all bumble bees, yellow jackets and paper wasps. Halictid bees (Halictidae) show ample variations in the level of sociality, but about thousand species establish annual eusocial colonies. Unlike in wasps the annual nest cycle of halictids is interrupted by several activity breaks which each delay colony development for a couple of weeks. During the breaks the nests are protected against enemies, however, at the same time further resource allocation is impossible. In contrast to the majority of eusocial halictids some halictid species reproduce continuously like eusocial wasps or bumble bees.

Our field observations have provided comprehensive quantitative data on the activity pattern of more than thousend colonies of the halictid bee *Lasioglossum malachurum* in several locations around Wuerzburg (chapter 3). The colonies exhibited one or two worker broods and a terminal brood of sexuals, however, mixed broods with both worker and sexual production have been observed, too. Solitary nest founding as well as the different phases of colony development were separated by distinct activity

breaks. Soil temperature had a strong influence on the duration of the different periods of the nest cycle. In warmer locations the sequence of active and inactive phases proceeded much faster than in colder ones.
To investigate the fitness consequences of activity breaks (chapter 4) we had to expand the classical model of Oster and Wilson. The field observations on *Lasioglossum malachurum* yielded sufficiently detailed data to parameterise the extended model and to investigate the evolution of activity breaks. For certain critical ranges of individual mortality and productivity rates activity breaks are evolutionarily advantageous. For *L. malachurum* in Wuerzburg our model predicts a nest cycle with three activity breaks. This result is in excellent accordance with the empirical data. However, very high worker productivity or survival would favour continuous reproduction without breaks as observed in wasps and bumble bees. We could show that the typical sequence of active and inactive periods is not triggered by external factors such as variation in resource availability or predation, but is an emergent property of colony dynamics. The specific temporal pattern of breaks and activity is mainly governed by the development time of the brood – a quantity neglected completely in the original model of Macevicz and Oster (1976).

The second part of the thesis (chapters 5, 6, and 7) is focused on the investigation of the choice between growth and reproduction at the level of the eusocial colony. During the entire colony development individuals must continuously determine which fraction of the resources currently available should be invested into workers and which fraction into sexuals. This dynamic allocation problem was first solved by Macevicz and Oster (1976) under the assumption of a constant and limited season length. They predicted that exclusive production of workers at the beginning of the season followed by exclusive production of sexuals until the end of the season is the optimal strategy that yields maximum colony fitness. Their approach is rather general and can easily be modified and extended for the analysis of other dynamic questions of life history strategies in social insects (see above). However, this was never realised. This might be due to the mathematical difficulties of the analytical techniques required for the analysis of Macevicz and Oster's model. We show that the major part of their results could also be achieved with a much simpler modelling approach and we hope that our approach stimulates further research on dynamic life history strategies in social insects.

Chapters 5 and 6 demonstrate the way to one simplified model class based on investment limitation of the queen. This aspect has been neglected by Macevicz and Oster's model which is solely based on time limitation. However, an empirical study of the model species *L. malachurum* shows that the limited physiological resources of the queen also restrict the potential investment strategies of the colony, especially

during solitary nest foundation (chapter 5). During the founding phase the queen has to perform all nesting activities like nest construction and brood provisioning without the help of workers. Our field observations showed that the females lost more than 60% of their fat reserves between their emergence and the end of nest founding in the following year. Fat loss during the four weeks long colony founding phase was twice as high as fat loss during the six months of hibernation.

The evolutionary analysis of the activity pattern revealed that the activity phases are triggered by the rhythm of brood development (see above, chapter 4). Thus our alternative modelling approach of the nest cycle was based on the stable temporal pattern of reproduction – the successive broods were used as the coarse-grained time base – and on energy limitation of the queen (chapter 6). The resulting model is formally much simpler and its analysis does not require the advanced methods of Optimal Control Theory (Macevicz & Oster, 1976), but can be carried out purely algebraically. The analysis of the model shows in particular that in the simpler approach the typical bang-bang strategy also results as the optimal investment pattern.

Models based on discrete brood reproduction have also been used for theoretical analyses of variable sex ratios in primitively eusocial insects. Thus, our approach – together with the analysis of the activity pattern – closes the gap between the classical model of the colony cycle by Macevicz and Oster and the studies on sex ratios in eusocial insects. It provides a perspective for a common modelling hierarchy for the analysis of dynamic strategies in annual eusocial insects.

Numerous field observations indicate that the eusocial reproductive pattern often deviates from the pure bang-bang strategy predicted by Macevicz and Oster (1976) as the conceivably simplest realisation of the colony cycle. With so-called graded strategies workers and sexuals are produced simultaneously during a middle phase of colony development. Graded strategies are mostly associated with spreading of risk as an evolutionary answer to environmental variability. This has already been suggested by Oster and Wilson (1978), although they did not carry out a detailed analysis.

In the last chapter of this thesis (chapter 7) we present a detailed analysis of the potential causal relationship between variable seasonal length and gradual investment during the eusocial colony development. It turns out that gradual strategies emerge only with a highly variable season length. With moderate variability the behavioural optimum is – like in the deterministic case – a pure bang-bang strategy. Increasing variability just results in earlier (but still dichotomous) switches to sexual production. As the optimal time for the change from worker to sexual production is long before the end of the season, bang-bang reproduction itself can buffer fitness variation due to fluctuations in the season length. Reduction of season length does not result in zero sexual production as long as the shortened season still ends after the onset of sexual

production. Chapter 7 provides the closest relationship to the former analysis of Oster and Wilson (1978), because their model of colony dynamics could be used nearly unchanged and had only to be subjected to stochastic optimisation.

The single chapters of this work provide a wide spectrum of different examples of the dynamic character of life history strategies: Starting with a dichotomous strategy transition as a single event during the life span (chapters 5 and 6), over repeated strategy jumps (chapter 3 and 4) and gradual transitions (chapter 7), up to a nearly equal choice between the alternatives (chapter 2). A simple classification of the evolutionary reasons also yields a clear picture of the resultant optimal behaviour: in deterministic environments and with linear trade-offs optimisation models can yield only dichotomous strategy transitions. However, the number of strategy switches is not necessarily limited to a single event. External variability can favour several strategy switches, if the relative impact of the different investment alternatives changes in the course of time (King & Roughgarden, 1982b; not in this work). This is also the case if a strategy change entails a revaluation of the alternatives in combination with the internal dynamics of the system itself. This might lead to oscillations in the optimal decision (chapter 4). Gradual strategies can evolve in deterministic environments only if the dynamics of the system contain non-linear elements, such as the competitive influence on larval development (chapter 2).
Stochastic environmental variations, too, can lead to gradual changes of strategies. However, current investigations of solitary organisms have shown that the evolutionary relevance of such risk spreading strategies has often been overestimated. The analysis of the optimal investment pattern during eusocial colony development (chapter 7) confirms this result.

Zusammenfassung

Die Untersuchung von Lebenslaufstrategien vor dem Hintergrund von Adaption und Selektion liefert evolutionäre Erklärungen für die Entstehung der Vielfalt individueller Lebenszyklen. Jeder Lebenslauf spiegelt die zeitliche Abfolge von Entscheidungen zwischen Verhaltensalternativen wider und ist damit im Kern dynamisch. Die klassische Analyse von Lebenslaufstrategien hat sich zunächst auf gegebene, markante Einzelereignisse im Leben eines Individuums konzentriert, seine Geburt, die Geschlechtsreife, die Paarung, die Reproduktion und den Tod. Mit wachsenden analytischen Möglichkeiten hat jedoch die Beschreibung von Lebenszyklen an Vollständigkeit gewonnen, so dass auch die prominenten Ereignisse selbst erklärt und deren dynamischer Charakter aufgedeckt werden konnte. Reproduktion ist nicht zwangsläufig ein einmaliges Ereignis, sondern kann sich über lange Zeiträume erstrecken. Wachstum wird nicht zwangsläufig mit der Geschlechtsreife durch die Reproduktion abgelöst, sondern kann abwechselnd oder auch gleichzeitig mit ihr stattfinden.

Im Bereich der sozialen Insekten erreicht die Untersuchung dynamischer Lebenslaufstrategien eine neue Komplexitätsebene. Ein zentrales Problem der Untersuchung von Lebenslaufstrategien ist die Frage nach dem optimalen Investitionsmuster in Wachstum und Reproduktion. Bei sozialen Insekten ist dies nicht nur auf individueller Ebene relevant, sondern auch auf der Ebene der Kolonie: Wie sollte in Arbeiterinnen und Geschlechtstiere investiert werden, um den Kolonieerfolg zu maximieren? Nach den wegweisenden Arbeiten von Macevicz, Oster und Wilson (1976, 1978) hat die Analyse dynamischer Lebenslaufstrategien sozialer Insekten weitreichende Aufmerksamkeit gewonnen. Allerdings wurden die ursprünglichen Ideen zur Analyse des Kolonieverlaufs kaum erweitert und fortgeführt, sondern durch alternative Modellierungsansätze, z.B. zur Untersuchung des Geschlechterverhältnisses oder der Evolution von matrifilialer Eusozialität ersetzt.

Die vorliegende Arbeit versucht diese Lücke zu schließen und untersucht neben dem optimalen zeitlichen Muster der Investition auch die Dynamik der Ansammlung von Ressourcen. Der erste Teil (Kapitel 2, 3 und 4) befasst sich an Hand zweier theoretischer (Kapitel 2 und 4) und einer empirischen Untersuchung (Kapitel 3) mit Verhaltensentscheidung zwischen den extremen Alternativen von Aktivität und Inakti-

vität. Kapitel 2 nimmt in der Folge der einzelnen Kapitel insofern eine Sonderstellung ein, als dort nicht Strategien sozialer Insekten untersucht werden, sondern das Verhalten eines solitären Sozialparasiten. Der Abschnitt stellt damit die Brücke zur klassischen, vorwiegend auf solitäre Organismen konzentrierten Literatur der theoretischen Analyse von Lebenslaufstrategien dar. Er greift mit der Untersuchung des optimalen Verlaufs der Larvalentwicklung eine weit verbreitete Fragestellung dynamischer Lebenslaufstrategien auf. Die Larven des Schmetterlings *M. rebeli* entwickeln sich als Parasiten innerhalb von Ameisenkolonien. Dementsprechend muss die optimale Entwicklungsstrategie im Kontext der Dynamik des sozialen Wirts untersucht werden. Umfangreiche Freilanduntersuchungen in Frankreich zeigen, dass sich ca. 25% der Larven im ersten Jahr entwickeln, die übrigen aber erst verzögert im Folgejahr. Nach der Entwicklung eines analytischen Modells ließ sich der evolutionsstabile Anteil an Schnell-Entwicklern vorhersagen. Im Modell werden insbesondere das zusätzliche Mortalitätsrisiko der langsameren Larven, die Konkurrenz zwischen den Larven und der nachgewiesene Konkurrenzvorteil der langsameren Larven gegenüber neu hinzu kommenden Schnell-Entwicklern berücksichtigt. Es konnte gezeigt werden, dass alle Mechanismen die Evolution von verzögerter Entwicklung begünstigen. Insbesondere die Konkurrenz zwischen Geschwistern sowie die Vermeidung von wiederholter Infektion der Ameisenkolonien stabilisieren die optimale Strategie bei einem Wert von 0.5. Nur durch den Konkurrenzvorteil der Langsam-Entwickler ist es möglich, dass sich im ersten Jahr weniger als die Hälfte der Individuen entwickeln. Der Effekt ist allerdings nicht groß genug, um mit den an *M. rebeli* angepassten Modellparametern den beobachteten Wert von 0.25 vorherzusagen. Das Ergebnis lässt vermuten, dass es weitere, bisher unentdeckte Mechanismen gibt, die das verzögerte Wachstum begünstigen. Das Modell lässt sich auf andere Systeme übertragen, in denen verwandte Individuen während der Entwicklung in kleinen Gruppen konkurrieren.

In den Kapiteln 3 (empirische Untersuchung) und 4 (theoretische Untersuchung) wird verzögerte Entwicklung auf der Ebene des Kolonieverlaufs einjährigerer, primitiv eusozialer Bienen und Wespen untersucht. Knapp tausend Arten der Furchenbienen (Halictidae) bilden einjährige, eusoziale Kolonien. Charakteristisch für den jährlichen Nestzyklus sind einige mehrwöchige Aktivitätspausen, die die Kolonieentwicklung verzögern. Während der Pausen sind die Nester zwar vor Feinden geschützt, gleichzeitig ist aber auch weiterer Ressourceneintrag unmöglich. Im Gegensatz zur Mehrzahl der Halictiden sind auch einige Furchenbienenarten bekannt, die wie einjährige eusoziale Wespen oder Hummeln kontinuierlich aktiv sind.

Zunächst haben es umfassende Beobachtungsdaten ermöglicht das Aktivitätsmuster von über eintausend Kolonien der Furchenbiene *Lasioglossum malachurum* an mehreren Standorten im Raum Würzburg zu erfassen (Kapitel 3). Der Koloniezyklus bestand aus einer oder zwei Arbeiterinnenbruten und einer abschließenden Brut mit Geschlechtstieren, allerdings wurden auch gemischte Bruten, die sowohl aus Arbeiterinnen als auch Geschlechtstieren bestanden, beobachtet. Sowohl die solitäre Nestgründung als auch die einzelnen Phasen der Kolonieentwicklung waren durch Aktivitätspausen getrennt. Die Bodentemperatur hatte einen starken Einfluss auf den Verlauf des Aktivitätszyklus. An wärmeren Standorten lief die Folge von aktiven und inaktiven Phasen deutlich schneller ab.

Eine Erweiterung des klassischen Modells von Oster und Wilson konnte mit Hilfe der Freilanddaten parametrisiert werden und erlaubte es dann, die Fitnesskonsequenzen von Aktivitätspausen zu untersuchen (Kapitel 4). In sehr guter Übereinstimmung mit den Freilandbeobachtungen von *L. malachurum* sagt das Modell für diese Art im Raum Würzburg drei Aktivitätspausen voraus. Bei höheren Werten von individueller Mortalitäts- oder Produktivitätsrate besteht allerdings ein evolutionärer Nachteil der Strategie mit Aktivitätspausen gegenüber einer kontinuierlichen Reproduktion, wie sie bei Hummeln oder Wespen beobachtet wird.

Es konnte gezeigt werden, dass der charakteristische Aktivitätszyklus nicht durch äußere Faktoren wie beispielsweise Schwankungen im Nahrungsangebot oder der Nestgefährdung hervorgerufen wird, sondern eine emergente Eigenschaft der Koloniedynamik darstellt. Als kritische Bestimmungsgröße des Zeitverlaufs optimaler Aktivität hat sich die Entwicklungszeit der Brut erwiesen, die im ursprünglichen Modell von Macevicz und Oster (1976) vollständig vernachlässigt wurde.

Im zweiten Teil der Arbeit (Kapitel 5, 6, und 7) steht die Entscheidung zwischen Wachstum und Reproduktion auf der Ebene der eusozialen Kolonie im Vordergrund. Während der gesamten Kolonieentwicklung müssen die Individuen einer Kolonie kontinuierlich bestimmen, welcher Anteil der gegenwärtig verfügbaren Ressourcen in Arbeiterinnen und welcher Anteil in Geschlechtstiere investiert werden soll. Dieses dynamische Allokationsproblem wurde von Macevicz und Oster (1976) unter der Annahme konstanter und begrenzter Saisonlänge gelöst. Sie konnten zeigen, dass nur die ausschließliche Produktion von Arbeiterinnen zu Beginn der Saison und anschließend die ausschließliche Produktion von Geschlechtstieren maximale Fitness liefert. Die Vorgehensweise von Macevicz und Oster (1976) stellt einen sehr allgemeinen Ansatz dar und lässt sich für andere Fragestellungen aus dem Bereich dynamischer Lebenslaufstrategien sozialer Insekten einfach modifizieren und erweitern (siehe oben). Dies wurde bisher allerdings nicht versucht. Eine mögliche Ursache dafür könnte in den mathematischen Schwierigkeiten liegen, die mit dem Ansatz verbunden sind. Wir konnten zeigen, dass sich der größte Teil der Ergebnisse auch mit strukturell deutlich einfacheren Modellen erzielen lässt und hoffen, damit den Ausgangspunkt für weitere Arbeiten auf diesem Gebiet geschaffen zu haben.

Kapitel 5 und 6 zeigen den Weg zu einer solchen vereinfachten Modellklasse, die auf dem begrenzten Investitionspotenzial der Königin basiert. Dieser Aspekt wurde von Macevicz und Oster (1976), deren Modell ausschließlich auf Zeitlimitierung durch die begrenzte Saisonlänge beruht, nicht berücksichtigt. Wir konnten allerdings in einer empirischen Untersuchung der Modellart *L. malachurum* (Kapitel 5) nachweisen, dass der Kolonie nicht nur durch die Zeitlimitierung sondern auch durch die Verfügbarkeit von physiologischen Reserven ihrer Königin enge Grenzen für die Investitionsstrategie gesetzt werden – insbesondere während der Phase der solitären Nestgründung. Während der Nestgründung erledigt die Königin alle anstehenden Aufgaben des Nestbaus und der Verproviantierung der ersten Arbeiterinnenbrut alleine. Die Freilanduntersuchungen haben gezeigt, dass die Königinnen von ihrem Schlupf im Vorjahr bis zum Ende der Gründungsphase durch die energetischen Anforderungen der Überwinterung und der Nestgründung insgesamt mehr als die Hälfte ihrer Fettreserven verlieren. Dabei ist der Fettverlust in der vierwöchigen Gründungsphase doppelt so hoch wie während der Überwinterung.

Die evolutionäre Untersuchung des Aktivitätsmusters (siehe oben, Kapitel 4) hat ergeben, dass sich die Aktivitätsphasen am Schlupfrhythmus der Brut orientieren. Vor diesem Hintergrund bietet es sich an, die alternative Modellierung des Nestzyklus (Kapitel 6) sowohl auf Zeit- als auch auf Ressourcenlimitierung zu stützen und als grobes zeitliches Raster die aufeinander folgenden Bruten zu verwenden. Das resultierende Modell ist formal deutlich einfacher, da dessen Analyse nicht auf den anspruchsvollen Methoden der optimalen Kontrolltheorie beruht (Macevicz & Oster, 1976), sondern rein algebraisch durchgeführt werden kann. Die Modellanalyse zeigt insbesondere, dass auch der einfachere Ansatz die typische bang-bang Strategie als optimales Investitionsmuster liefert.

Modelle mit diskreten Bruten sind auch die Grundlage für theoretische Analysen der Dynamik des Geschlechterverhältnisses bei eusozialen Insekten. Damit schließt unser Ansatz – zusammen mit der Aktivitätsanalyse – die Lücke zwischen klassischer Modellierung des Koloniezyklus und den Arbeiten zu variablen Geschlechterverhältnissen bei eusozialen Insekten und eröffnet die Perspektive auf einen gemeinsamen Modellierungsansatz für dynamische Strategien bei allen einjährigen eusozialen Insekten.

Freilandbeobachtungen liefern zahlreiche Hinweise darauf, dass das eusoziale Reproduktionsmuster häufig von der bang-bang Strategie als denkbar einfachster Realisierung des Koloniezyklus abweicht. Bei so genannten graduellen Strategien werden während einer mittleren Phase der Kolonieentwicklung gleichzeitig Arbeiterinnen und Geschlechtstiere produziert. Graduelle Strategien werden meist mit Risikostreuung als evolutionärer Antwort auf Umweltvariabilität in Verbindung gebracht. Dies schlagen bereits Oster und Wilson (1978) vor, ohne eine detaillierte Analyse durchzuführen. Im letzten Kapitel dieser Arbeit (Kapitel 7) wird der mögliche Kausalzusammenhang zwischen variabler Saisondauer und gradueller Investition während der eusozialen Kolonieentwicklung näher untersucht. Es zeigt sich, dass graduelle Strategien erst bei sehr hoher Varianz in der Saisondauer zu erwarten sind. Bei mittlerer Variabilität ist – wie im deterministischen System – die reine bang-bang Strategie optimal, auch wenn sich der Strategiewechsel hin zu früheren Zeitpunkten verschiebt. Weil der optimale Wechsel zwischen Arbeiterinnen- und Geschlechtstierproduktion deutlich vor dem Saisonende liegt, beinhaltet bang-bang Reproduktion selbst bereits einen Fitnesspuffer gegenüber Fluktuationen in der Saisondauer. Bei moderat verkürzter Saisondauer sinkt die Geschlechtproduktion nicht zwangsläufig auf 0. Kapitel 7 dieser Arbeit besitzt die engste Verbindung zur früheren Analyse von Oster und Wilson, weil deren Modell der Koloniedynamik unverändert verwendet werden konnte und lediglich einer stochastischen Optimierung unterworfen werden musste.

Die Zusammenstellung der einzelnen Abschnitte liefert ein breites Spektrum an Beispielen zum dynamischen Charakter von Lebenslaufstrategien: Angefangen von einem während der Lebensspanne einmaligem Strategiewechsel (Kapitel 5 und 6), über mehrfache Strategiesprünge (Kapitel 3 und 4) und graduelle Übergänge (Kapitel 7), bis hin zu einer nahezu gleichmäßigen Auswahl der Alternativen (Kapitel 2). Eine einfache Klassifizierung der evolutionären Ursachen liefert auch ein übersichtliches Bild über das resultierende optimale Verhalten: In deterministischen Umwelten und bei linearen Trade-offs können Optimierungsmodelle nur dichotome Strategiewechsel liefern. Die Anzahl an derartigen Strategiewechseln muss allerdings nicht auf einen einzelnen beschränkt sein. Äußere Variabilität kann mehrere dichotome Strategiewechsel begünstigen, wenn sie die relative Bedeutung der verschiedenen Investitionsalternativen im Laufe der Zeit ändert (King & Roughgarden, 1982b; nicht in dieser Arbeit). Dasselbe ist der Fall, wenn ein Strategiewechsel im Zusammenspiel mit der internen Dynamik des Systems selbst eine Umbewertung der Alternativen zur Folge hat und dann zu Oszillationen in der optimalen Entscheidung führt (Kapitel 4). Graduelle Strategien können in deterministischen Umwelten nur entstehen, wenn die Dynamik des Systems nichtlineare Elemente enthält, wie beispielsweise die Regelung der Larvalentwicklung durch Konkurrenz (Kapitel 2). Stochastische Umweltschwankungen können ebenfalls zu graduellen Strategiewechseln führen. Aktuelle Untersuchungen an solitären Organismen haben jedoch inzwischen gezeigt, dass die evolutionäre Bedeutung der Risikostreuung als Ursache gradueller Strategiewechsel häufig überschätzt wurde. Auch die Analyse im Kapitel 7 kommt für das Reproduktionsmuster im Rahmen eusozialer Kolonieentwicklung zu diesem Ergebnis.

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Conferences & Talks

Conference contributions

Weissel, N., Mitesser, O., Liebig, J., Poethke, H.J. & Strohm, E. (2004). Life history plasticity and social conflict in a primitively eusocial bee (poster), Conference of the *Deutsche Zoologische Gesellschaft (DZG)*, Rostock, Germany

Mitesser, O. & Poethke, H.J. (2005). The evolution of activity breaks during the nest cycle of primitively eusocial bees (talk), Conference of the *International Union for the Study of Social Insects (IUSSI, German Section)*, Halle/Saale, Germany

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Hovestadt, T., Mitesser, O., Elmes, G., Thomas, J. & Hochberg, M. (2006). The evolution of dimorphic growth strategies in *Maculinea rebeli*, a social parasite of *Myrmica* ant colonies (talk), *British Ecological Society* Annual Meeting, Oxford, Great Britain

Heisswolf, A., Ulmann, S., Obermaier, E., Mitesser, O. & Poethke, H.J. (2006). Host plant finding in the specialized leaf beetle *Cassida canaliculata* – an analysis of small-scale movement behavior (poster), Annual Conference of the *Ecological Society of Germany, Switzerland and Austria (GFÖ)*, Bremen, Germany

Hovestadt, T., Mitesser, O., Elmes, G., Thomas, J. & Hochberg, M. (2006). The evolution of dimorphic growth strategies in *Maculinea rebeli*, a social parasite of *Myrmica* ant colonies (poster), Conference of the *Deutsche Zoologische Gesellschaft (DZG)*, Münster, Germany

External talks

Mitesser, O. & Poethke, H.J. (2006). Zeitabhängige Strategien zur optimalen Verteilung und Ansammlung von Resourcen, *Interdiszipliäres Oberseminar Kontrolltheorie und dynamische Systeme*, Lehrstuhl für Mathematik II (Prof. Dr. U. Helmke), Universität Würzburg

Mitesser, O., Weissel, N., Strohm, E. & Poethke, H.J. (2006). The evolution of activity breaks in the nest cycle of annual eusocial bees, *Zoologisches Kolloquium*, Universität Regensburg

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Organisation

Müller, C., Liebig, J., Kaltenpoth, M., Weissel, N., Mitesser, O. & E. Strohm (2005) Evolutionary chemical ecology. Graduate Meeting of the *Deutsche Zoologische Gesellschaft (DZG)* Section Evolutionary Biology

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Würzburg, 22. Dezember 2006

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Erklärung

gemäß § 4 Abs. 3 Ziff. 3, 5 und 8
der Promotionsordnung der Fakultät für Biologie der
Bayerischen Julius-Maximilians-Universität Würzburg

Hiermit erkläre ich ehrenwörtlich, die vorliegende Arbeit in allen Teilen selbständig und nur mit den angegebenen Quellen und Hilfsmitteln angefertigt zu haben.

Diese Dissertation hat weder in gleicher noch in ähnlicher Form in einem anderen Prüfungsverfahren vorgelegen.

Des Weiteren erkläre ich, daß ich früher weder akademische Grade erworben habe, noch zu erwerben versucht habe.

Würzburg, den 22. Dezember 2006

(Oliver Mitesser)