An Empirical Study Linking Behaviour and Population Dynamics: Altering Spatial Food Availability in a Mite Model System

Gemma Jane Truelove

University of Stirling
School of Biological and Environmental Sciences

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ProQuest LLC.
789 East Eisenhower Parkway
P.O. Box 1346
Ann Arbor, MI 48106 – 1346

Author's Declaration

This thesis and the data presented in it are the results of my own original work, except where due acknowledgement has been made. No part of this work has been submitted in any previous application for a higher degree. The views expressed in this thesis are mine and not those of the University.

Gemma Jane Truelove

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Table of Contents

Chapter 1: General Introduction

An Empirical Study Linking Behaviour and Population Dynamics: Altering Spatial Food Availability in a Mite Model System.

Recent research in the field of population dynamics has focussed upon the importance of a thorough knowledge of the biology of an organism in order to obtain realistic quantitative predictions of how a population will respond to perturbation. In other words, how an organisms biology 'filters' external environmental noise through internal population processes, such as demographic stochasticity, into the allocation decisions that shape the life history (Benton and Beckerman in press). Since an individual's behavioural responses to internal and external stimuli will determine its life history and the sum of all the individuals' responses within a population will determine its dynamics, it is intuitively appealing to search for a role of individual behaviour and variation in behaviour in determining dynamics. Previously, there was considered little data to support this idea and manipulative studies into the role of behaviour in population dynamics were called for (e.g. Anholt 1990). Population models that successfully incorporate behaviour do exist (e.g. Goss-Custard et al 1983, 1995a, 1995b and 2002, Sutherland 1996, Stillman et al 2000). However further research into the link between processes at the individual, life historical and population level are valuable. This study will relate observed differences in population dynamics to differences in intraspecific competition due to the spatial availability of food.

1.1 Determinants of population dynamics

In real populations, dynamics will be a factor of the interaction between extrinsic environmental and intrinsic population factors. Single species population dynamics' theory can predict stable to highly unstable dynamics depending upon density and the type of competition (reviews: May et al 1974, May 1975, May and Oster 1976, Hassell Lawton and May 1976 and Bellows 1981). The type of competition refers to how resources are partitioned between animals and density dependence is the effect that resource partitioning has upon some measure of fitness according to density. The response of a population to increasing density, mediated through competition for resources, largely determines the population dynamics for a single species in a constant environment.

As well as population stability being affected by the form of density dependence, the stage structure of a population (Cameron and Benton 2004) and stage and age specific effects of density dependence have implications for population dynamics (McNair 1995). In addition to these numerical effects of density, a population's dynamics is often affected by time lags between an environmental stimulus and a population response. These lagged effects may be mediated through the life history by historical effects such as maternal effects (e.g. Benton et al 2001). The regulatory delays due to the time lag between the effect of density and the factor controlling density tend to destabilise dynamics (Benton et al. 2001). For example juvenile animals may be affected most strongly by density and yet the factor determining the density of juveniles may be the adult sector of the population (mediated via the fecundity of the juveniles parents). Hence a factor of life history such as fecundity can lead to a regulatory delay (McNair 1995).

1.2 Modes of competition

The mode of density dependence of a life history variable is generally used to define the type of competition present at a population level in terms of access to resources through (most simply) competition curves (Begon et al 1990). A competition curve plots initial density against either mortality or survivorship at that density. Hence a relationship is gained between increasing initial density and the affects upon the measure of fitness. Compensatory density dependence describes a decrease in population growth with increasing density up to some stable point. At this point intraspecific competition is regulating the population size around a level that can be sustained by the environment, the carrying capacity (figure 1.1). These species are said to be 'K' selected and to be displaying contest competition whereby there are winners and losers in terms of access to resources and therefore the effects of a shortage are not equal amongst individuals. Over-compensatory density dependence describes a 'humped' curve for mortality with increasing density where a population is overcompensating for an increase in density and is said to be displaying scramble competition whereby, in terms of resources, all individuals within a population suffer equally from a shortage (figure 1.1).

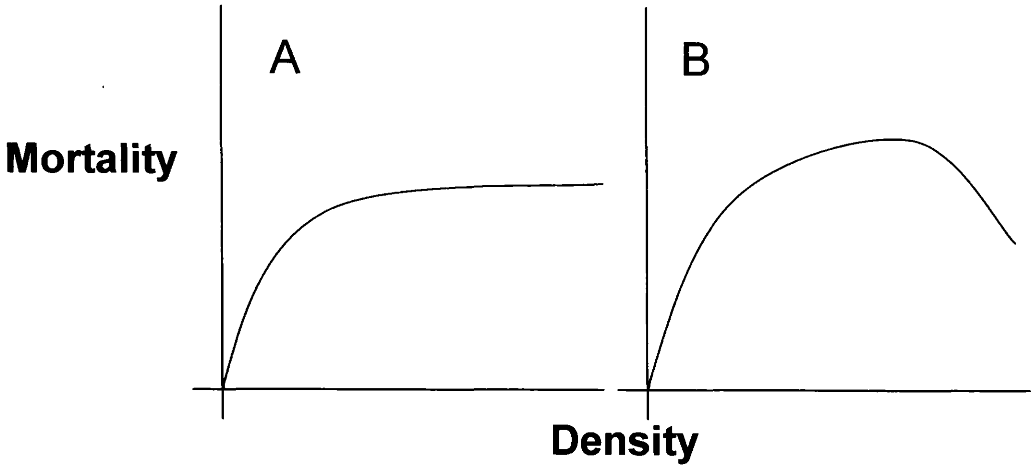

Figure 1.1 Competition curves for compensatory (A) and over-compensatory (B) density dependence.

Density-dependence may also be under-compensatory; there may be density-independence or indeed density-dependence may not be restricted to purely one type or be pure scramble or contest competition.

Through over-compensatory density-dependence scramble competition can lead to instability in population dynamics whereas contest competition (through compensatory density-dependence) tends to be stabilising (May 1975). Predictions of the advantageousness of contest and scramble competition generally support contest as being the most advantageous in terms of the stability of the equilibrium level (Lomnicki 1992). However Henson and Cushing (1996) investigated the advantageousness of each type of competition using a continuous hierarchically age structured model and found that the predictions of 'advantageousness' in terms of equilibrium level and resilience criteria depended upon the shape of the resource uptake curve of a population - in some conditions causing contest to be more advantageous and in others scramble.

Scramble and contest completion are translated at an individual level as exploitation (or depletion) and interference (Nicholson 1954, Toquenga 1993). Exploitation (scramble) competition describes individuals depleting resources, making them unavailable to others; interference (contest) competition describes where individuals control access to resources by e.g. competitive superiority. It can then be predicted that differences in life history stem from differences in behaviour at the individual level through choices that animals make on how to distribute the resources they gain. The resources they gain being determined in part by the availability of resources spatially. Therefore, there should be measurable differences in life history through allocation decisions such as size and age structure that lead to differences in dynamics.

1.3 Density dependence, competition and their effects upon life histories

There is evidence of the effects of density dependence and competition upon life history parameters. Sinclair (1989) gives a summary of this evidence for density-dependence in various groups of animals. Intra-specific competition acts to shape the life histories of many organisms from *Daphnia* (MacIsaac and Gilbert 1991) to birds (Lewis et al 2001). Various studies in this area relate differences in competition with changes in life history. Some discussed this in terms of the importance of intra-specific competition in population processes and distinguished between food limitation and density effects (Peckarsky 1991, Weeks 1990, Cross & Benke 2002), others were more specific and discussed results in terms of contest and scramble competition (MacIsaac and Gilbert 1991, Anholt 1990, Toquenga 1993, Hanes & Ciborowski 1992, Lord 1998, Shimada et al 2001) whereas others focused at the individual level specifically upon the life historical effects of interference competition. However diverse the species used and specific the life historical effects investigated there was a commonality in the mechanisms searched for: the evidence for the effects of competition through either increased density or decreased food availability.

Those studies detailed here which were intended to separate the effects of contest and scramble competition upon life history variables, found variously, for example, that density had a negative effect and increasing food a positive effect on immature survival, duration of development and female size at emergence of *Aedes albopictus* (Diptera) (Lord 1998) and that depending upon the age of *Hexagenia rigida* (Ephemeroptera) larvae, density and food influenced larval size and development (Hanes and Ciborowski 1992) those reared at the lowest density and highest food level having the greatest size. Interference competition investigated specifically was found in the western tree-hole mosquito, *Aedes sierrensis* (Broadie and Bradshaw 1991) through larval density to affect pupation success, development time and pupal weight. In another mosquito species

Aedes aegypti (Dye 1984) interference competition again through larval competition, was found to effect the developmental rate of younger smaller larvae more than older larger larvae where densities were kept constant, showing that physical interference can have a profound and stage specific effect based upon size of a group of individuals. Extreme contest competition was shown in populations of seed beetles – where two larvae developed in one seed both adults emerged but one tended to be 60% larger than the other (Shimada et al 2001). Studies concerning intraspecific competition found that in the lotic snail species *E. cahambensis* and *E. carinifera* both grew faster with enhanced food levels at lower density (Cross and Benke 2002). Weeks (1990) whilst only considering intra-specific competition as density increased found similarly that increasing tadpole shrimp (*Triops longicaudus*) density significantly reduced growth and subsequently egg production in this species.

1.4 Importance for individual behaviour at the population level

As mentioned, it is intuitively appealing to search for a link between individual behaviour (and variation within and between individuals) in determining population dynamics. Population ecology focuses the outcome of ecological and biological changes whereas behavioural ecology focuses upon the adaptive and evolutionary significance of behaviour (Hassell and May 1984). These two approaches can be complementary; the adaptive significance of behavioural change according to ecological circumstances will have implications for the response in terms of the population level. Smith and Sibly (1984) state that *"behavioural ecology reveals the mechanisms that that limit population increase or enforce population decrease and hence determine the carrying capacity of the environment...Behavioural ecology therefore has the potential to explain the differences in dynamics between populations".* Smith et al (2000) in investigating the population consequences of reproductive decisions in the bitterling found that basing the predicted population consequences upon the observed mechanism of spawning produced a 6% difference in population estimate versus that modelled on random spawning; and in this case the behavioural mechanism that maximised individual fitness reduced population size.

Behaviourally-based individual models aim to predict the response of a population in novel situations based upon knowledge of how animals react to each other. For example Goss-Custard et al (1994) estimated the number of oystercatchers dying over-winter according to population density from a game theoretic model. Other possible methods include Dynamic Energy Budget (DEB) modelling (Nisbet et al 2000) whereby describing how individuals acquire and utilize energy can give mechanistic explanations for behaviour and allocation decisions and be a possible method of linking molecular processes through to ecosystem dynamics. In terms of practical use for species that are a target for conservation, individual based models may be at present too time consuming to construct to an extent that they are not appropriate when urgent measures are needed. However, population level models may not be able to provide the quantitative details of the exact response of a population to management measures (Bradbury et al 2001). Studies have found that the effects of individual variation can be substantial (Smith et al 2000 and Bjornstad et al 1994) and yet there is no monotonic relationship between individual variation and population processes (Grimm and Uchmanski 2002) but that knowledge of lower level processes in population dynamics may be important and lead to “meaningful simplification, not greater complexity” (Schoener 1986).

1.5 Interference and exploitation

Competition at the individual level can therefore be important at the population level. Contest and scramble competition describe the extremes of competition at the life historical level but at an individual level in terms of how resources are divided between individuals the terms interference and exploitation are used. Exploitation (scramble) competition describes individuals depleting resources, making them unavailable to others; interference (contest) competition describes where individuals control access to resources by e.g. competitive superiority. If as Grimm and Uchmanski (2002) found, that there is no monotonic relationship between individual variability and population dynamics then subtleties in competition between individuals may have important consequences and that the assumption of stability in terms of competition may be sensitive to circumstances.

1.6 Foraging theory and experimental studies

Within behavioural ecology optimal foraging theory has been a major area of research predicting and testing for adaptive feeding behaviour in animals. These models predict that with a given morphology and in a given environment an animal can optimise its foraging behaviour in order to maximise its fitness. Other assumptions are implicit in these models in order that their predictions are reasonable, such as the relationship between foraging behaviour and fitness is known (see e.g. Pyke 1984). The optimality approach has also been used to predict optimal foraging group size, optimal foraging space and even movement (For a review of these see Schoener 1971 and Pyke 1984). Two main categories of optimal foraging are prey and patch models (Marginal Value Theorem, Charnov 1976) both of which are concerned with long term maximisation of the average rate of energy intake over an animal's lifetime. They predict optimal diet selection and optimal patch residence time respectively. In both prey and patch models animals optimise intake as some function of an encounter with food, handling time and search time. There are many expansions to optimal foraging models incorporating variation in food availability (Belovsky and Ritchie 1989) but in terms of the study presented here the importance is how the foraging behaviour of individuals is explicitly stated in terms of gain and loss. As such an animals foraging can be seen as periods of intake punctuated by periods of search behaviour (i.e. moving).

The balance or maximisation of these costs versus benefits can be affected by many variables including for example, variation in food availability (Belovsky & Ritchie 1989); variations in the environment (risk sensitive foraging e.g. Caraco 1980); variations in food quality (Belovsky 1978) and indeed intra-specific competition. The effects of interference and exploitative competition at the individual level may interact with all or none of these. Hassall et al (2002) showed that in *Porcellio scaber* individual foraging behaviour differed with the clumping of resources, quality of resources and animal density – less time was spent feeding and more time moving when density increased. Pitt and Ritchie 2002 similarly found that skinks foraging success depended upon the dispersal of resources – their intake being higher when foraging in large clumps of food rather than when it was distributed in many smaller clumps. Interference in blackbirds was also found to vary with patch conditions (Cresswell et al 2001). Blackbirds had a much lower feeding rate at the same density in patches where prey were visible rather than covered. Cresswell et al (2001) also found individual variation in feeding rate according to patch type i.e. an individuals foraging in one patch type was not necessarily a good indicator of its ability to feed in another type. Lowe and Butt (2002) found that in earthworm foraging food particle size was important in determining growth of individuals - animals grew faster when fed smaller food particles (this affect was more profound the smaller the animal was) and that the affect of conspecifics also had greater effect with smaller particles of food. Further to this, different life stages of animals have been found to feed differently. Merritt (1987) found that older and therefore larger larval instars of *Aedes* *triseratus* tended to eat coarser material than younger instars suggesting selective feeding and indeed a possible response to or a mechanism of avoiding intraspecific competition. Buskirk (1992) also found that younger larvae of the dragonfly *Aeshna juncea* significantly changed their behaviour whilst in the presence of larger older larvae by reducing and changing the time of their activity thereby incurring a decrease in feeding success.

These studies (Caraco 1980, Merritt 1987, Belovsky 1988, Belovsky & Ritchie 1989, Buskirk 1992, Cresswell et al 2001, Hassall et al 2002, Lowe and Butt 2002, Pitt and Ritchie 2002) do not however directly test the mechanisms of interference and exploitation they are merely intimated by the increase in food or in density. Tests manipulating behaviour in this way have been few. One example of an experimental study is Anholt (1990), who tried to separate the effects of interference and exploitation competition in a larval damselfly. This study was carried out by altering the habitat complexity through increasing the number of perches per environment (to alter the degree of behavioural interaction) and simultaneously altering density and food supply. Animals distributed themselves more evenly in an area when given more perches. This species display aggressive stances when encountering other individuals on perches however, the costs of perch availability were found to be insignificant (in terms of effects on survival, timing of and mass at emergence) compared to those of changing the food supply and density alone. The results refute the importance of feeding related interference competition in this species despite the response to density, leaving open the question of density dependence resource depression. Toquenga and Fujii (1990) discuss whether it is sufficient to assume behavioural mechanisms of competition from data at the life historical level through e.g. competition curves as is often done. They found that competition curves did accurately reflect the mechanisms of competition (i.e. scramble competition curves did result from interference at the individual level) in the two species of bruchid beetle they investigated. If demographic and behavioural models are to inform each other to create more accurate quantitative models of the population responses to perturbation, then to be specific and accurate about how resources are allocated between individuals must be a priority.

1.7 The mite model System

The experiments in this study are based upon laboratory populations of the soil mite *Sancassania berlesei* collected from agricultural manure in 1996 and 1998. This is an acarid mite species, a relative of the house dust mite and is commonly found in soil, poultry litter and as a pest in stored foods. There are five life stages in this species: egg, hexapod larva, protonmyph, tritonymph and adult. There is also a facultative deutonmpyh - the hypopus - which is a non-feeding stage, thought to have a dispersal function (figure 1.2). For brevity, here the larval and nymphal stages (not including the hypopus) are referred to as first (larval), second (proto) and third (trito) instar juveniles. Males and females are dimorphic in this species – distinguishable by various elements of shape, size and the presence of longer setae (abdominal hairs) in the male. Males can also be dimorphic, in low density colonies fighter males appear who are able to kill rival males with a pair of armoured legs (Radwan et al 2002). Females are oviparous and can lay several to a few hundred eggs which are produced during the whole life of the female (Chmielewski and Lipa 1967). There is considerable plasticity in the timing of development and longevity of these animals seen in the laboratory. Eggs can hatch from 2-5 days after laying, juveniles can mature into adults from 4 to more than 50 days after hatching, adults can live for approximately 10 – 50 days and thus total longevity varies from 3 to more than 7 weeks depending upon resource conditions (Beckerman et al 2003, Benton & Beckerman *in press*)

This model system has been used extensively to investigate the interplay between density dependence and environmental variation (e.g. Benton et al 2001a, b and c, Benton et al 2002, Cameron and Benton 2004, Benton & Beckerman *in press*).

1.8 Aims of study

Previous data found that empirically, in this system changing the spatial food availability changed the population dynamics. Colonies given food as a clumped ball of yeast, rather than as spread powdered yeast, displayed dynamics that changed from stability to decaying oscillations. Intra-specific competition between individuals and life stages is thought to be important in this system as previous research has found that harvesting different life stages caused differential responses at the population level (Cameron and Benton 2004) e.g. harvesting of eggs had a greater positive effect upon the number of adults whereas harvesting juveniles did not. This indicates that reducing eggs reduces the number of first instar juveniles which eases competition and increases maturation whereas removing juveniles of all stages does not change the competitive structure and doesn't have such a positive effect upon maturation. This indicates that competition between first instar juveniles may be particularly important process in the population dynamics and the nature of resource allocation at this stage will play a large part in determining this. Further, it is known that the relationship between age and size at maturity is important in many animals and Benton et al (*in review*) have found evidence for an L shaped developmental threshold in laboratory populations of *Sancassania berlesei* which is dependent upon juvenile growth rate – which again is a function of intraspecific resource allocation. Not only are current conditions found to be important but also previous conditions. Maternal condition affects total number of and allocation to each egg and therefore, previous resource conditions can affect future generations via maternal allocation decisions which again affect juvenile growth (Benton et al *in review*). Maternal effects are predicted to have a destabilising effect upon the dynamics of a population (Benton et al 2001).

It is predicted that the clumping of the resources when colonies are fed a ball of yeast is leading to greater interference competition as there is a limited surface area of food and so feeding animals prevent other animals having access to food. It allows for competitive ability through size to become important – larger animals being able to more easily monopolise food resources. This study aims to test for and link responses to competition for food within and between life stages at the individual and the life historical level through to differences in the dynamics at the population level. Chapter Two investigates whether changing the spatial availability of food changes population dynamics and distribution of sizes (life history) of individuals. Chapter Three investigates whether any differences in life history and dynamics are related to differences in time budgets between animals. Chapter Four tests the predictions of the behavioural mechanisms of interference and exploitative competition upon intake rates and Chapter Five investigates the life historical mechanisms of competition through the trade off between age and size at reproduction.

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Chapter 2: Population and Life Historical Responses to Changes in Spatial Food Availability

2.1 Abstract

Differences in the spatial availability of food can cause significant differences in the dynamics, age structure and size structure of a population. Replicated laboratory colonies of the soil mite *Sancassania berlesei* were fed the same absolute amount of food (yeast) daily, given either in a clumped form (or as a ball of yeast) or as a fine powder which was spread evenly. Animals were left to reproduce freely and population counts and measurements of animal length were taken every four days for 300 days.

Animals in colonies fed clumped yeast have a higher initial oscillation in egg, juvenile and adult numbers than those fed a dispersed resource. In addition male and female lengths are larger in colonies fed clumped food, although the variance in length is also greater. Later in the time series adult numbers become similar between the two treatments, but the colonies fed clumped food maintained a roughly two-fold higher egg and juvenile number than colonies fed powder. The results are consistent with the idea that spatial arrangement of food can influence the type of competition acting at the individual level.

2.2 Introduction

Aspects of foraging theory relate changes in food availability to changes in behavioural strategies and indeed the central tenet of optimal foraging is that these changes occur so as to maximise some measure of fitness (e.g. Schoener 1971, Charnov 1976 and Pyke 1984). Therefore, behaviour can be seen as a mechanism to maximise fitness in terms of life history parameters, e.g. fecundity or mortality.

In a theoretical population, stability to oscillating cycles are predicted depending upon the density of animals and the type of competition amongst them (May 1975, Bellows 1981). The response of a population to increasing density, through the nature of competition between animals, is one factor that determines the population dynamics. The mode of density dependence of a life history parameter is generally used to define the type of competition present at a population level in terms of access to resources through (most simply) competition curves (Begon et al 1990). A competition curve plots density against either mortality or survivorship at that density. Hence a relationship is gained between increasing density and the effects upon the measure of fitness.

Compensatory density dependence describes a decrease in population growth with increasing density up to some stable point whereby intraspecific competition is regulating the population size around a level that can be sustained by the environment, the carrying capacity. These species are said to be ‘K’ selected and to be displaying contest competition whereby there are winners and losers in terms of access to resources and therefore, the effects of a shortage are not equal among the individuals of a population (Lomnicki 1992).

Over-compensatory density dependence describes a 'humped' curve for mortality with increasing density. This curve describes a population that is overcompensating for an increase in density and is said to be displaying scramble competition whereby, in terms of resources, all individuals within a population suffer equally from a shortage (Lomnicki 1992). Density-dependence may also be under-compensatory or populations may be density-independent. In many biological systems there is often both contest and scramble competition acting (Lord 1998).

Scramble competition can lead to instability in population dynamics whereas contest competition tends to be stabilising (May 1975). This can be true in a single species context and can be further complicated by life history delays that can lead to regulatory delays (May 1975); for example by the density dependence acting upon one specific life stage (McNair 1995) or influencing maternal effects upon future generations (Benton et al 2001). Predictions of the 'advantageousness' (in terms of equilibrium size and resilience) of each type of competition can also be found to depend upon resource uptake relationships within a population (Henson and Cushing 1995) and so the degree and nature of density-dependence have profound, and often complicated effects upon populations. It is clear however that differences in population dynamics stem from differences in life history.

Scramble and contest completion are translated at an individual level as exploitation (or depletion) and interference (Nicholson 1954, Toquenaga 1993). Exploitation (scramble) competition describes individuals depleting resources, making them unavailable to others; interference (contest) competition describes where individuals control access to resources by e.g. competitive superiority. It could then be predicted that differences in life history stem from differences in behaviour at the individual level through choices that animals make on how they distribute the resources they gain (Benton et al, under review). The resources they gain being determined in part by the availability of resources spatially. Therefore, there should be measurable differences in life history through allocation decisions, such as size and age structure, that lead to differences in dynamics.

Other studies investigating the effects of intra-specific competition have shown that increases in density can have a negative effect on life history parameters such as duration of development and individual size, with increasing food levels having the opposite effect (Dye 1984, Weeks 1990, Broadie and Bradshaw 1991, Hanes & Ciborowski 1992, Lord 1998, Shimada et al 2001, Cross and Benke 2002). The effects of density and food level do not necessarily act upon all life stages equally (Dye 1984), for example larvae of the mosquito *Aedes aegypti* are more effected by density when they are younger and smaller, showing that physical interference can have a profound and stage specific effect.

In the mite model system previous data (Figure 1, Benton and Beckerman in press) showed empirically that changing the spatial food availability changed the population dynamics. Providing mite colonies with a clumped ball of food (granulated food in Figure 1) resulted in the population undergoing oscillating cycles whilst feeding the mites powdered yeast led to population stability.

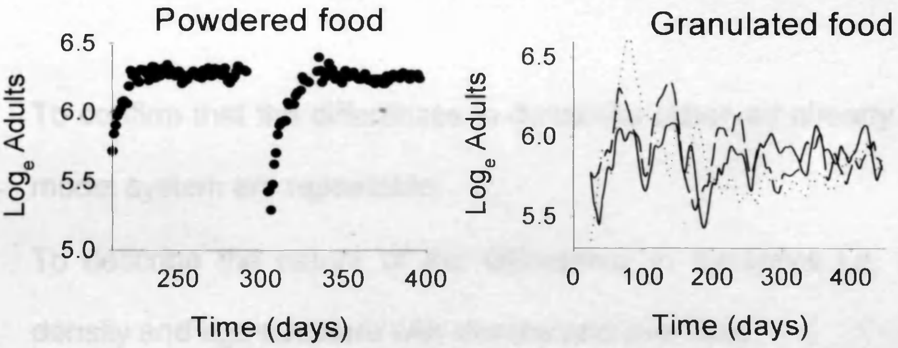

Figure 1 The Population dynamics of colonies given the same absolute food in different forms; balls of yeast and powdered yeast.

In this case it is predicted that the colonies fed balls of yeast are experiencing over-compensatory density dependence and those fed powder are experiencing compensatory density-dependence. Therefore, colonies fed balls of yeast display unstable dynamics whereas those fed powder will tend to stability. Contrary to theory it is predicted here that the clumping of resources creates a ‘winners and losers' situation with respect to resource gain i.e. interference/contest competition, leading to over-compensatory density dependence and unstable dynamics rather than the compensatory dynamics theory predicts (May 1975). In terms of animal size, it is predicted that clumping of resources, leading to inequality in the distribution of resources, results in a greater variance in size of animals fed balls than powder.

This paper investigates the hypothesis that differences in competition between individuals caused by differential spatial access to food lead to differences in life histories. The study aims are:

- To confirm that the differences in dynamics observed already in the mite model system are repeatable.
- To describe the nature of the differences in dynamics i.e. variation in density and age structure with density and over time.
- To investigate whether there are differences in life histories between food types in terms of animal size.
- To describe the nature of the differences in life histories i.e. variation in sizes with density and over time.

2.3 Materials and Methods

2.3.1 The Mite Model System

This study used a species of acarid soil mite *Sancassania berlese* collected from agricultural refuse (composted poultry manure) in 1996 and 1998. Populations were kept in stock cultures in unlit incubators, kept at a constant temperature of 24°C and fed dried yeast. The life cycle of *S. berlesei* consists of an egg and 3 larval stages before development into the adult mite. There is considerable plasticity in the timing of development and consequently in total life span, (from c10-50 days), dependent upon density and food availability (Benton and Beckerman *in press*).

2.3.2 Long-term Population level Experiment

The purpose of this experiment was to look at the effects of differing spatial arrays of food on animals in freely reproducing populations. For this purpose animals were removed from the stock culture (1998) and placed in flat bottomed test tubes with a diameter of 20mm and a height of 50mm. The tubes were ¾ filled with plaster of Paris, which when moistened maintains humidity, and sealed with filter paper and a plastic lid with ventilation holes. Each tube had a sampling grid, dividing the area into quarters, scored on the plaster. The plaster was also coloured with food dye to aid the counting of individuals.

Colonies were begun with 20 males and 20 females from the high density stock cultures (see above) and fed one of two diets which differed in yeast grain size but not in mean weight of yeast. These were balls of yeast (1.25-1.4mm diameter, 0.00172g ± 0.00003 weight (± se)), and fine powdered yeast (0.00185 ± 0.00010 weight (± se)). The powdered yeast was spread evenly over the tube surface to create differing spatial food availabilities. Each treatment consisted of 8 tubes each of which was fed once per day.

2.3.3 Counts

A Leica MZ8 binocular microscope and a hand-counter were used to census populations. All adults present were counted whilst counts of eggs and juveniles were taken from one of the quarter segments, initially chosen at random, and then counted throughout the experiment.

For the treatment groups balls and powder, data were collected for 306 days (11/6/2002 – 7/4/2003) with counts being taken every four days. Data were collected on alternate days for each treatment to give time for behavioural observations to be taken (presented in Chapter Two).

2.3.4 Perturbation

In order to see whether the transient effects or population dynamics differed between treatments the populations were perturbed after they reached equilibrium on day 137 and 138 respectively. Half the tubes in each treatment had half of their contents removed; the remaining tubes received the animals from the former. However, this data is not dealt with in this study rather the data is dealt with separately as pre- and post-perturbation analyses.

2.3.5 Measures

Measurements (length and width) were taken on the same days as the count data for all treatments. Length was taken from the tip of the hypostome to the tip of the opithosoma. Two individuals per tube per group (females, males, juveniles and eggs) were sampled, a total of 16 measures (each for length and width) per group per count day. A Leica MZ8 binocular microscope with a magnification 10*14 on maximum zoom (5) was used with a graticule; measurements were taken in graticule units.

Data for balls and powder run from day 5 until day 307 (pre- and post-perturbation).

2.3.6 Analysis

The data was divided into three sections for analysis; pre-perturbation, days 0 to 138; perturbation, days 140 to 200 (whereby the effects of perturbation within treatment were no longer distinguishable) and post-perturbation, days 200 to

307. Here only pre- and post- perturbation data are considered as the effects of treatment were the focus of this study and not the perturbation itself.

2.3.7 Animal Density

Treatment effects on time series

The time series data were separated according to group (total adults, juveniles and eggs) and the density data were bootstrapped to gain a mean per treatment per day. Where the bootstrapped mean and confidence intervals did not overlap the treatments were considered to be significantly different

To further support the bootstrap data, exact binomial tests were carried out testing the difference in density due to treatment as the number of times the mean density of balls was greater than the mean density of powder (for each group separately). In the case of the adult group the time series was divided into three sections; days 0 to 50 with a binomial test; days 50 to 138 with a binomial test and days 200 to 307 with a Quasi-likelihood GLM as the data were over-dispersed. The exact binomial tests were used in the first sections of the data as the variability was such that linear analysis was not appropriate. In the last section of data the time series had stabilised allowing the use of more powerful linear analysis.

Mean densities and sizes according to food treatment

A descriptive analysis is given of mean densities and sizes per group over the entire time series according to food type.

Variation in Density

The time series was divided into days 0 to 50 over which time the first 'bounce' in density occurs for adults, juveniles and eggs, i.e. the time when competition is low and intake is high allowing rapid population growth, and days 51 to 140 where the time series begin to become more stable and therefore differences in the coefficient of variation may be expected. Mean and standard deviations were calculated per tube per group (adults, juveniles and eggs) and from these a coefficient of variation of the mean was taken for each tube (standard deviation/mean) over the duration of the time series considered. These 16 tube means per group were analysed with Residual Maximum Likelihood Models (REML) with food type, group and the interaction between them as fixed factors and tube as a random factor. Stepwise deletion found the minimal adequate model; results are given as Wald statistics per term and associated P value.

Variation in Sizes

The time series was again divided into the sections outlined above for adults, juveniles and eggs. Mean and standard deviations were calculated per tube per group (adults, juveniles and eggs) and from these a coefficient of variation of the mean was taken for each tube (standard deviation/mean) over the duration of the time series. REML analyses to investigate the effects of food type and group on the variation in size; tube was specified as a random factor. Stepwise deletion found the minimal adequate model; results are given as Wald statistics per term and associated P value.

Time Series of Length and Density

Quasi-likelihood Generalised Additive Models (GAM; with an identity link function and constant variance as data were over-dispersed) were fitted for total adult density, adult females and adult males separately for balls and powder treatment from days 0 to 140 (pre-perturbation data); where the time series varied most obviously. Models were fitted with varying degrees of freedom and the best fitting chosen using the Cp statistic as the data were not independent over time.

Variation in Length over Time

An alternative way to investigate differences in variation in size is to look at variance in size rather than the coefficient of variation. Daily variances in mean male and female length were calculated and Quasi-likelihood GAM models fitted to this data. Models were fitted with varying degrees of freedom and the best fitting chosen using the Cp statistic as the data were not independent over time. Data are presented as predicted mean variances per day.

Length and Density: food type and density effects upon individual length

The effects of treatment and lags in density on the length of individuals were investigated with REML analysis. Analyses were carried out for each group separately i.e. females, males, juveniles and eggs. Current density was not included as it was assumed it would only affect future not current individual size. Three lags in density were incorporated in the model; lag 1 (4 days), lag 2 (8 days) and lag 3 (12 days), the lag period was determined by being multiples of the measurement cycle. The maximal model was;

Current length ~treatment*densalag1*densjlag1*densalag2*densjlag2*
densalag3*densjlag3
* indicates all two-way interactions between factors
Random model: Tube + Day

2.3.8 Age structure

For the pre-perturbation data quasi-likelihood GAM's were fitted for each group and treatment separately. The adult:juvenile ratio was calculated per tube per day. The post-perturbation data were analysed with a t-test with unequal variance.

2.4 Results

2.4.1 Time Series

The spatial distribution of the food supply leads to markedly different population dynamics (Figure 1).

With an initially equal density of adults and food levels, there is a higher bounce in density of eggs, juveniles and subsequently adults in colonies fed balls than in those fed powder. Further to this there is a different carrying capacity for eggs and juveniles between the two food types that is maintained throughout the time series – higher in colonies fed balls of yeast than in those fed powdered yeast. The juvenile time series also display a greater variance around the carrying capacity in colonies fed balls of yeast than in colonies fed powdered yeast. If the population carrying capacities were the same and populations fluctuated randomly we might expect an equal proportion of days when the mean density of colonies fed powder was greater than that of colonies fed balls of yeast and vice versa. However, using an exact binomial test the probability of the observed pattern occurring under these assumptions for eggs and juveniles is $p<0.001$.

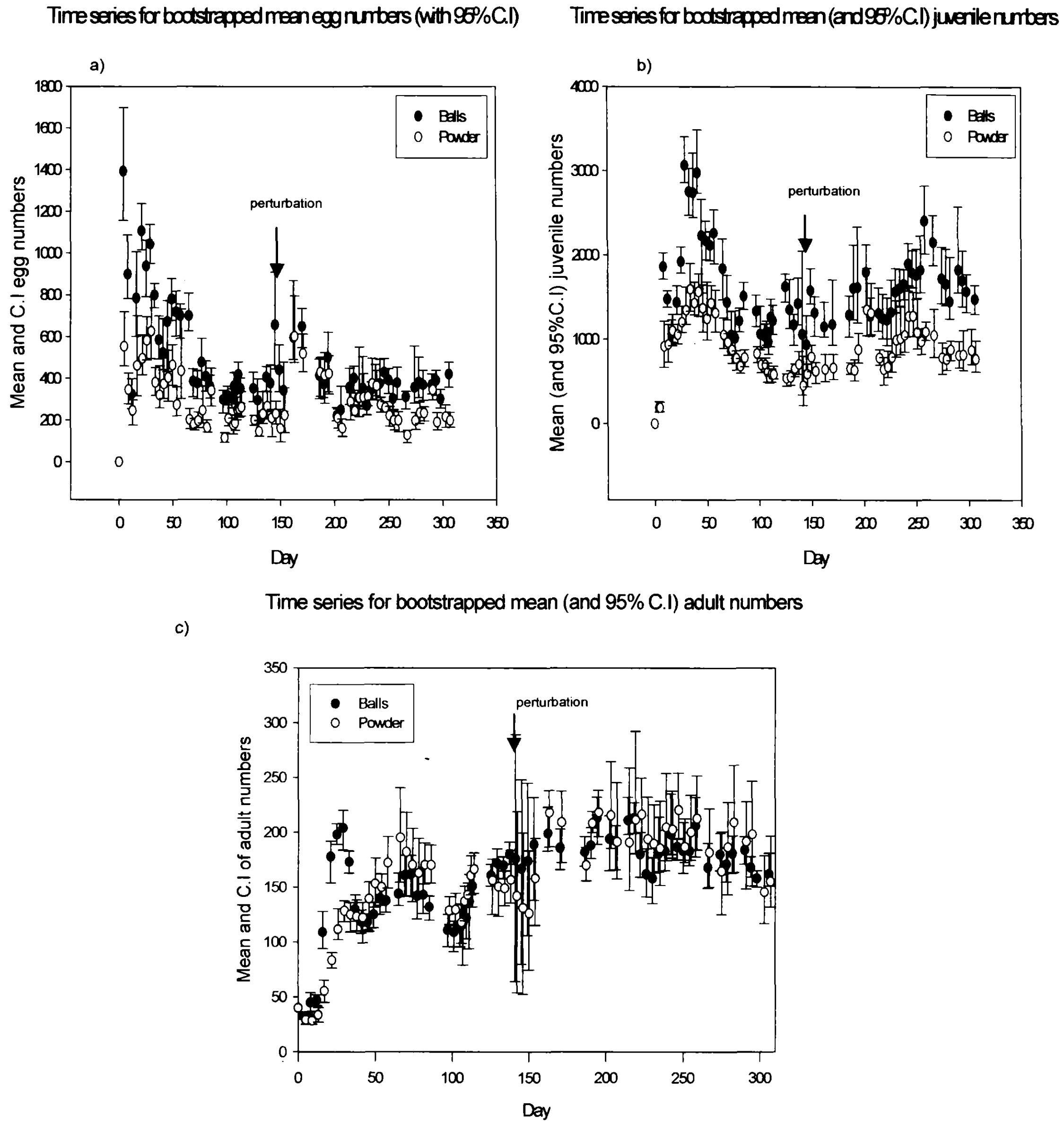

Figure 2 Time series for egg (a), juveniles (b) and adult (c) numbers for population fed either balls of or powdered yeast. Each point represents the mean density of 8 tubes and the 95% confidence interval for that mean estimate.

From approximately day 30 onwards the adult carrying capacity overlap in the balls and powdered yeast treatment. An exact binomial test for the initial bounce in adult numbers (days 0 to 50) supported the idea that the density is higher in balls than powder (as the powder colonies have a higher density than the balls colonies less than 50% of the time, p=0.1334; density higher in colonies fed balls 9 times out of 13). After this initial bounce there was an equal proportion of days when the mean density of colonies fed powder was greater than that of colonies fed balls of yeast and vice versa indicating that carrying capacity and density were the same (p=1).

2.4.1 Mean Densities and Sizes

Population dynamics, i.e. the nature of the variation in densities over time, differs between food types. We are interested in how the variation in density is related to the variation in life history through size. As a point of reference from which to discuss these relationships, the overall mean densities and sizes are considered.

Densities

Over the entire time series the mean densities of adults are equal between the two food treatments (table 1) The mean densities confirm the time series data in that there is an approximately two-fold higher number of juveniles and eggs in the colonies fed balls of yeast with respect to those fed powder.

Group	Treat	Mean density	95% confidence interval
Adults	Balls	158.04	153.22 - 162.86
	Powder	158.47	152.67 - 164.27
Juveniles	Balls	1556.96	1497.27 - 1616.66
	Powder	885.25	848.57 - 921.93
Eggs	Balls	470.89	446.79 - 494.99
	Powder	289.016	274.00 - 304.04

Table 1 Mean densities for each group and each food type for the entire time series

2.4.2 Mean Animal Sizes

Over the time series the mean sizes of females and males in balls is larger than that of powder however, the 95% confidence intervals for these values overlap indicating that they are not significantly different from each other. The mean size of juveniles and eggs is larger in powder but again the 95% confidence intervals overlap.

Group	**Treat**	**Mean length (graticule units)**	**95% confidence interval**
Females	Balls	40.52	40.21 - 40.83
	Powder	39.76	38.88 - 40.57
Males	Balls	32.91	32.64 - 33.18
	Powder	32.77	32.56 - 32.98
Juveniles	Balls	17.04	16.71 - 17.37
	Powder	17.42	17.09 - 17.74
Eggs	Balls	9.56	9.51 - 9.59
	Powder	9.53	9.48 - 9.58

Table 2 Mean animal sizes per group and each food type for the entire time series

2.4.3 Variation in Density and Sizes

The link between densities and sizes at a particular time are of interest due to the prediction that these are the indicators of differences in competition between the food types. Similarly if overall differences in competition can be uncovered then variation in density, linked with variation in size will be instructive as to the degree of competition between individuals.

Variation in Density

Due to the transient dynamics during the experiment, the time series was separated into early (days 1 – 50) and late (days 51 – 140) phases (Fig.2). The way that population density varied over these time frames was analysed using the coefficient of variation (CV: ratio of the standard deviation to the mean) for each tube.

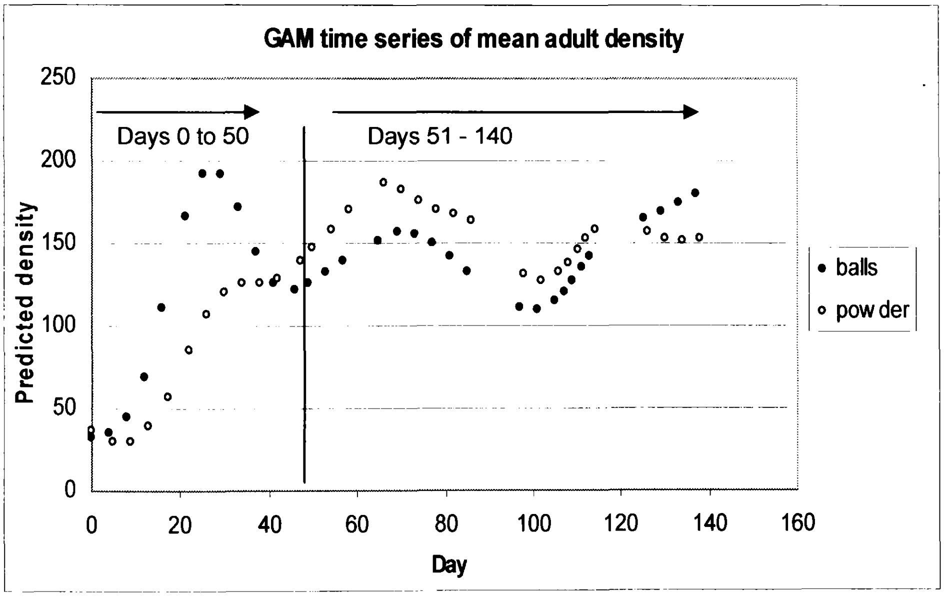

Figure 3 GAM time series for mean total adult density for the pre-perturbation time series

For the initial period, the treatment (food type) had a significant effect on tube CV (Wald statistic = 4.12, X^2_1 = 0.042, figure 3) but the life history stage (females, males, juveniles or eggs) had no effect, nor was there an interaction between life history stage and food type.

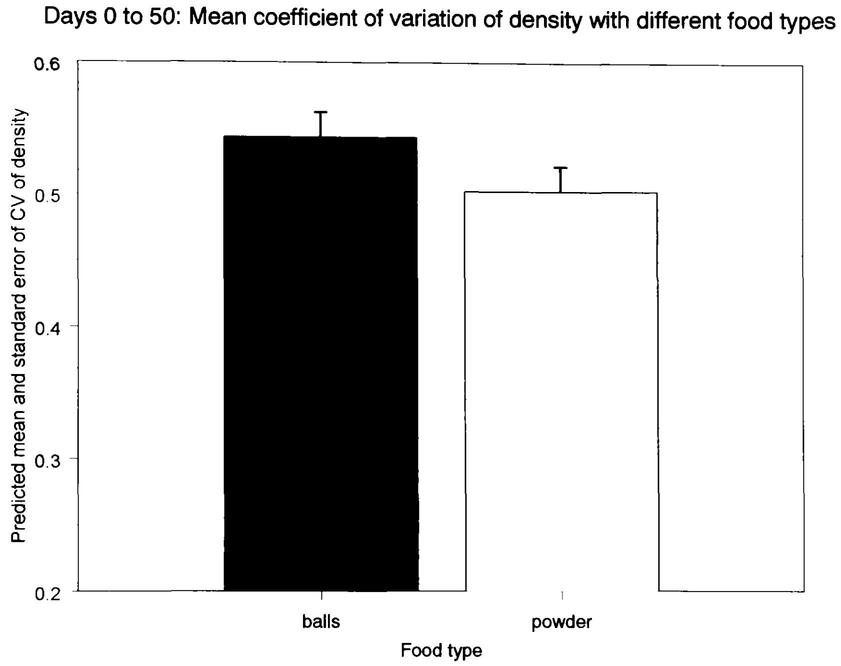

Figure 4 – Mean and standard error of the coefficient of variation of density according to food type.

For the later time period the life stages were found to have different CV's of density (Wald statistic = 30.06, $X^2_2<0.001$); eggs had the highest variation followed by juveniles and then adults (Figure 4). The food type did not affect the coefficient of variation in density and neither were there different amounts of variation within a life stage according to food type.

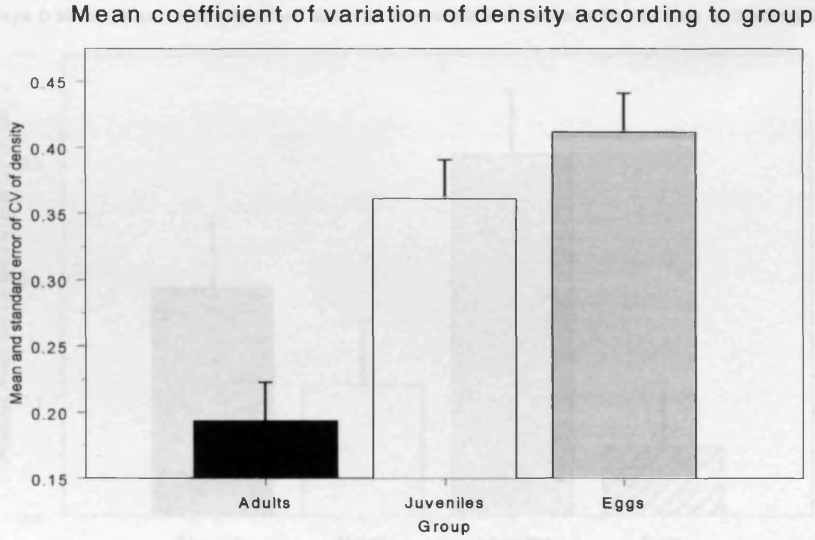

Figure 5 Mean and standard error of the coefficient of variation of density according to group.

Variation in Sizes

The coefficient of variation was calculated for the same sections of the time series for animal size as it was for population density. From days 0 to 50 per tube, food type did not significantly affect the coefficient of variation of animal size (Wald statistic = 0.34, X^2_3 = 0.561) neither did its interaction with group (Wald statistic = 0.87, X^2_3 = 0.453). The different groups did differ significantly in their coefficient of variation (Wald statistic = 8.06, X^2_3 =<0.001) with juveniles having the greatest variation followed by females, males and eggs having the least variation (figure 5).

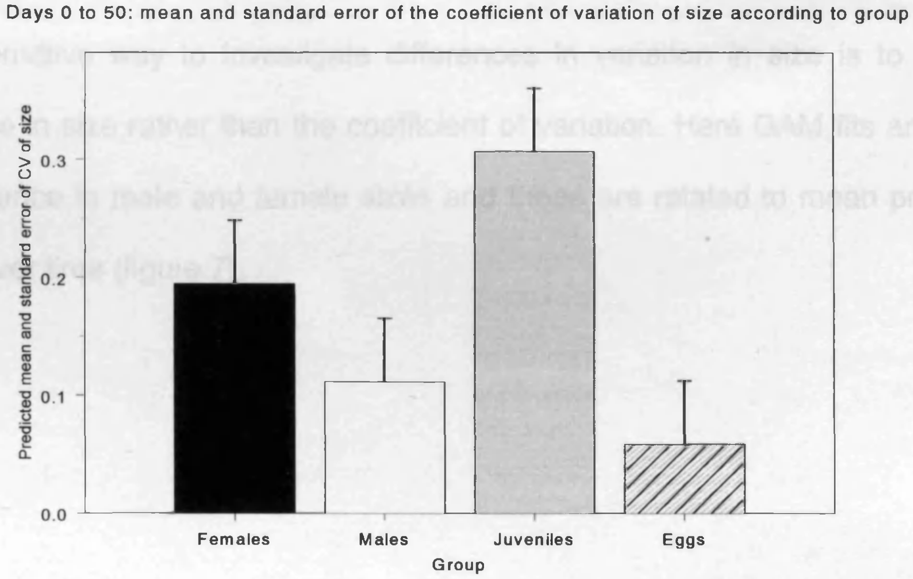

Figure 6 The coefficient of variation for size according to group for days 0 to 50 of the time series.

The results per tube for coefficient of variation in size were similar in the later time series, treatment (Wald statistic = 0.63, X^2_1 = 0.427) and its interaction with group (Wald statistic = 1.10, X^2_3 = 0.348) were found not to have a significant affect upon the coefficient of variation of size. The different groups had significantly different coefficient of variations for size with juveniles having the highest CV followed by males, then eggs and then females.

The coefficients of variation for females, males and eggs reduced from the initial to the later time series. The differences in variation between densities in the food treatments for the initial time series, i.e. there being more variation in density in the balls than powder food type, is not reflected in the variation in sizes over the same period.

Patterns of variance in sizes

An alternative way to investigate differences in variation in size is to look at variance in size rather than the coefficient of variation. Here GAM fits are given for variance in male and female sizes and these are related to mean predicted sizes over time (figure 7).

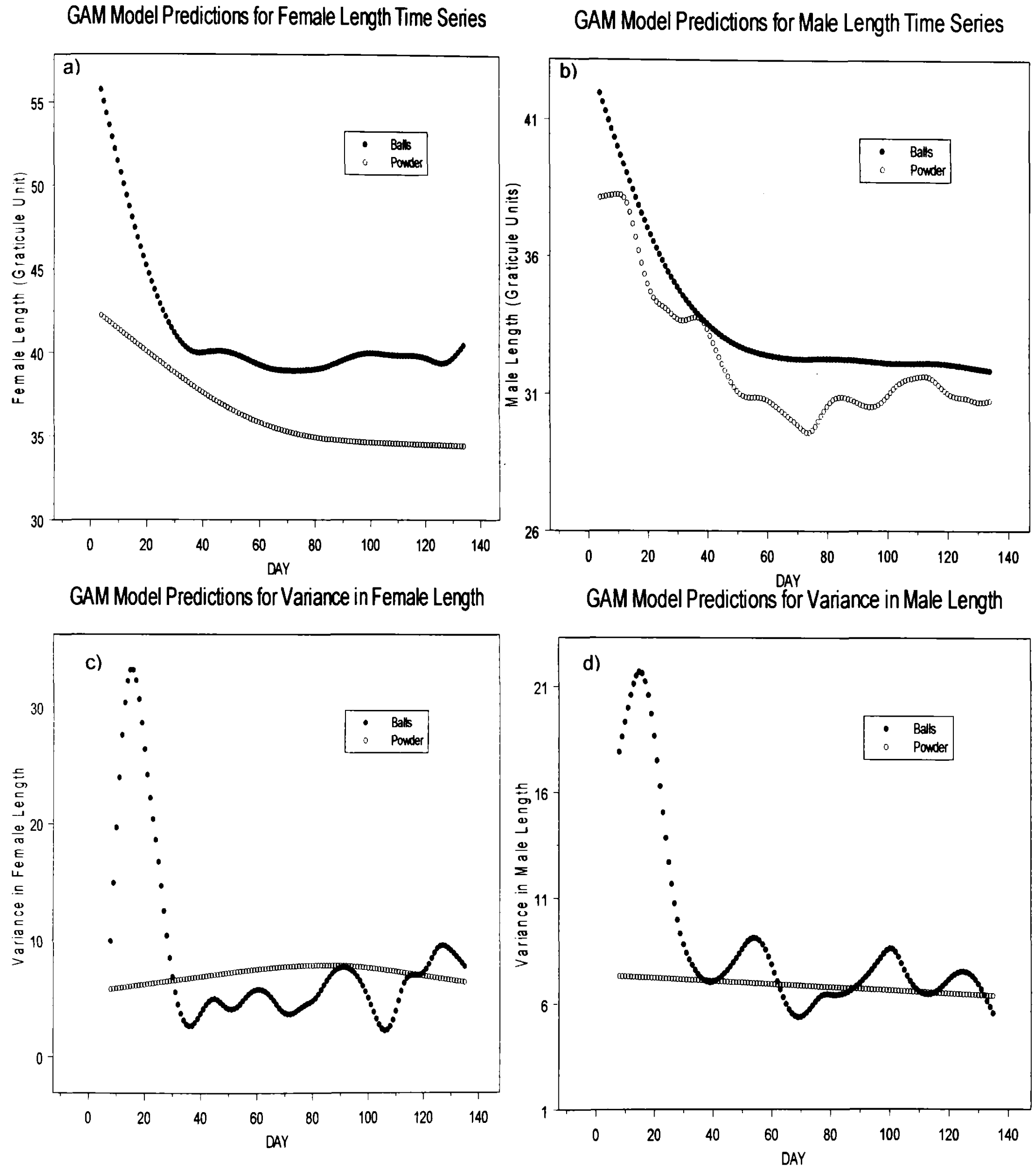

Figure 7 Mean GAM predictions of male and female length (a and b) and variation in length (c and d).

The initial bounce in density is related to a sharp decrease in male and female sizes in both treatments (Figures 7a and 7b, between days 1 – 50), as density increases steeply mean predicted size decreases. In this initial period variation in density is highest in colonies fed balls of yeast and for this period variation in male and female sizes are highest in the colonies fed balls – variation in density is related to variation in size. After the initial period of the time series, on average the variance in lengths of adults are equal and yet animals are on average larger in colonies fed balls of yeast than in colonies fed powdered yeast.

2.4.4 Animal Length and density

REML analyses were used to investigate the predictive affect of previous density (at lags of four, eight and twelve days – this was constrained by the four day frequency of population counts) upon current animal size (females, males, juveniles and eggs separately). Results from these analyses were complicated and here, for parsimony, are given only when they are significant as main factor effects (table 3).

Group	**Determinants of size**	**Significance**	**Predicted Effect and standard error**
Females	Adult density lag 12 days	Wald = 14.57, p<0.001	-0.0381, S.E 0.010036
Males	Juvenile density lag 12 days Adult density lag 8 days	Wald = 10.37, p<0.001 Wald = 10.05, p=0.044	-0.0005076, S.E=0.00015762 -0.008648, S.E=0.0042970
Juveniles	Adult density lag 4 days	Wald = 7.14, p=0.008	-0.00005416, S.E=.000262
Eggs	Juvenile density lag 4 days Juvenile density lag 12 days Adult density lag 12 days	Wald = 9.61, p=0.002 Wald = 7.75, p=0.005 Wald = 12.04, p<0.001	-0.00008713, S.E=0.0000313 -0.0001017, S.E = 0.0000328 -0.001856, S.E=0.000602

Table 3 Results for REML analysis for predicting size according to previous adult and juvenile density at lags of four, eight and twelve days.

Previous density effects animal size. These results are complex in that different groups (life stages) within the population are effected by the densities of different groups, to different degrees (different predicted effects) and at different times (i.e. at different lags). All the relationships are negative in that size decreases with increasing (previous) density and so increasing density increases competition leading to smaller animal sizes.

2.4.5 Adult: juvenile ratio

Given that there were different mean densities, sizes and variances in these associated with food type the stage structure of the population was investigated by analysing the ratio of adults: juveniles over time. The GAM fits for adult: juvenile ratio over time is shown in Figure 6.

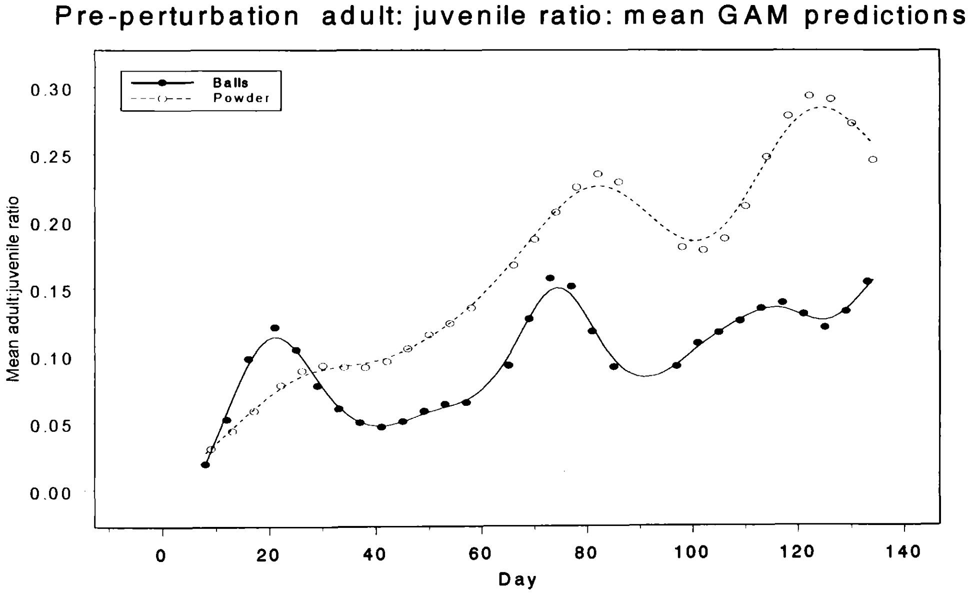

Figure 7 Mean Quasi-likelihood GAM predictions of adult: juvenile ratio from days 0 to 140. A model with 15 degrees of freedom was found to be the best fitting for balls Cp= 0.2711604. A model with 10 degrees of freedom was found to be the best fitting for the powder food treatment Cp= 0.5632775.

The shape of the time series of the ratio differs between treatments between days 0 and 40 where the balls colonies have a 'bounce' in the ratio which indicates that there was a strong negative correlation between adult and juvenile density i.e. juveniles did not mature until the previous cohort of adults had died. After day 30 there are consistently more juveniles per adult in balls than powder. In the later part of the time series (days 141 to 307), the adult; juvenile ratio stabilised and colonies fed balls supported double the number of juveniles than colonies fed powder – 1 to 4 versus 1 to 8 (t-test with unequal variance p<0.0001, Figure 7).

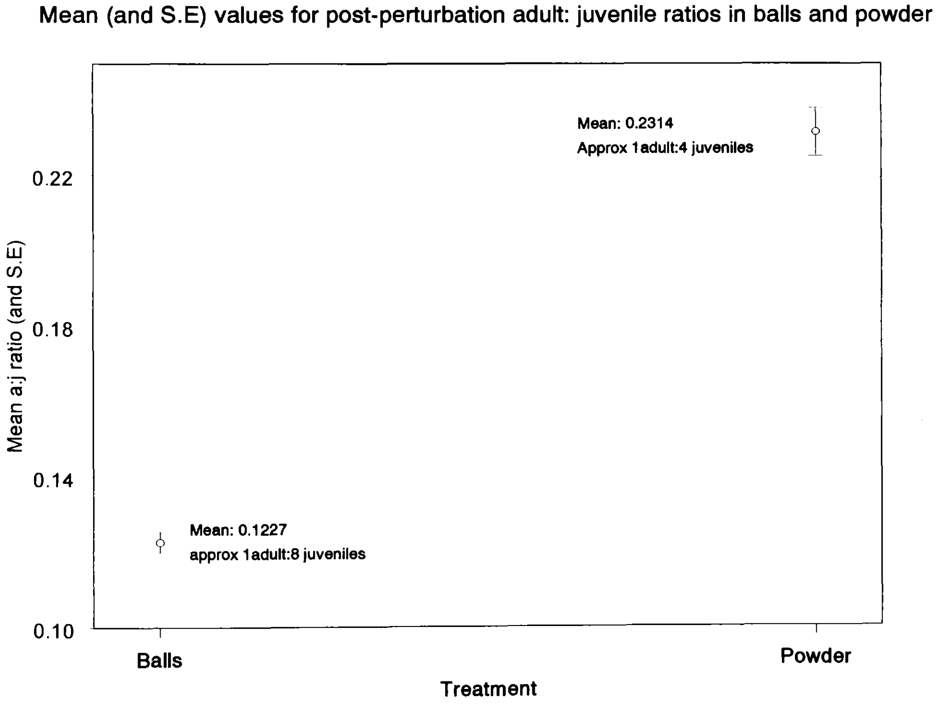

Figure 7 Mean adult: juvenile ratio per food type from days 140 to 307.

2.5 Discussion

It was predicted that colonies fed balls would display decaying oscillations and those fed powder stable dynamics, this is opposite to the theoretical conclusions of May (1975). The population dynamics of the colonies in this experiment differed between food types however, both treatments displayed dynamics intermediate between the stability and instability predicted. There are initially damped oscillations in the colonies fed balls with an equilibrium reached in adult numbers after day 200. In colonies fed powder, there is not a steady rise to equilibrium as predicted and oscillations in the numbers of all groups are seen. The oscillations in the colonies fed powder are generally smaller in magnitude than those in colonies fed balls.

With an equal initial density of adults and the equal amount of food provided it is seen that there is a higher initial 'bounce' in numbers of eggs, and subsequently juveniles and adults, in the colonies fed balls. This is consistent with the idea of a few individuals being able to monopolise resources and thus produce egg numbers beyond the carrying capacity of the environment (over-compensatory density dependence). The over-compensatory dynamics displayed in colonies fed balls is repeated, to a lesser extent, in colonies fed powder. This result deviates from the gradual increase to equilibrium that was predicted. An explanation of this result, other than that of unequal food levels, is that the dispersed distribution of the food led to variation in search and handling costs resulting in dynamics akin to those expected from monopolisation.

After the initial surge in density, the numbers of eggs and juveniles remain consistently higher in colonies fed balls, although adult numbers begin to overlap between treatments. This result suggests that in colonies fed balls juvenile survival is lower and accounts for the similar number of adults seen in each treatment. It can be concluded therefore, that the higher levels of competition in colonies fed balls is sufficient to prevent the maturation of a large proportion of the juveniles. Food type, although not having the predicted affect upon densities, has therefore, been shown to cause differences in the stage structure and density of the population.

Stability of a population can also be affected by its age structure. In *S. berlesei* the age structure has implications for how the population will react to perturbations (Cameron and Benton 2004). Adult to juvenile ratio, and how it changes over time with density, can also give an idea of the types of competition being exhibited by a population. In colonies fed balls of yeast it would be expected that monopolisation of the resource when adult density is high prevents juveniles from feeding; this is predicted to result in a see-saw effect between adult and juvenile density. GAM models of adult to juvenile ratio for the initial time series did show that those with access to a clumped resource had a high initial 'bounce' in this ratio indicating that there was a strong negative correlation between adult and juvenile density, i.e. the population maintained a cohort structure. After density had stabilised a two-fold higher number of juveniles than adults was maintained in colonies fed balls. The implication of this result is that despite each treatment displaying similar dynamics their reaction to perturbation would be different.

The variation in the size of individuals within treatments is also informative about the differences in competition between food types. The ability to monopolise the clumped food resource would be expected to give rise to a greater level of variation in size than in animals that compete through exploitation. However, there was no difference in the coefficient of variation between treatments for sizes of individuals. GAM models did show however, that males and females are larger in colonies fed balls than those fed powdered yeast (for the first half of the time series). The trend in both food types was for male and female size to be greatest in the early part of the time series, where density and presumably competition was lowest. It was also shown that the initial bounce in density in colonies fed balls of yeast was related to a high variance in male and female size, whereas in powder fed colonies there was a much lower variance in size and a more gradual decrease in variance over time.

The results of this experiment demonstrate that changing the spatial arrangement of food can produce differing population dynamics in terms of density and age structure, which are underlain by differences in size and variation in size indicating differences in resource gain between treatments. The results are consistent with the idea that if animals gain access to clumped food they are able to monopolise the resource. The competitive exclusion that results from this monopolisation results in a lower level of juvenile survival, which in turn leads to fewer larger animals laying more eggs. Results may also be consistent with the distribution of food in a spread manner incurring greater search and handling costs than for those who successfully feed from a clumped food source.

Populations displaying unstable dynamics are said to be experiencing scramble competition whereby all animals are affected equally by resource depletion; whereas those displaying stable dynamics are proposed to be experiencing contest competition whereby there are 'winners and losers' in terms of access to resources. It was predicted here that scramble competition would lead to stable dynamics and contest competition to unstable dynamics (opposite to theoretical predictions (May 1974)). Populations fed both food types initially displayed unstable dynamics, however this was much more marked in the colonies fed balls of yeast. The results suggests that both types of competition were acting in all colonies and yet feeding colonies balls of yeast allowed for a higher level of destabilising or scramble competition. Initially the colonies fed balls of yeast displayed a size structure of animals that indicated a 'winners and losers' situation as animal size was higher and yet more variable in those colonies i.e. that there was a greater variability in intake. This is consistent with contest competition leading to greater instability which is contrary to theory that predicts that clumped resources should lead to scramble competition (May 1975).

Previous studies into the life historical effects of competition have shown that increasing density and reducing food had a negative effect upon larval and adult weights in various species (Lord 1998, Hanes and Ciborowski 1992, Broadie and Bradshaw 1991). However this study does not separate these effects in a long-running colony and the results are not directly comparable. Further behavioural work may uncover the mechanism leading to the differences in resource allocation between these different food arrangements. However, it is clear that along with initial differences, feeding colonies of mites clumped or dispersed food creates and maintains a difference in population structure which could have implications for their responses to perturbation.

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Chapter 3: Behavioural Responses to changes in spatial food availability.

3.1 Abstract

Replicated laboratory populations of the soil mite *Sancassania berlesei* given food in different spatial arrangements display differences in their behavioural time budgets. Animals were left to reproduce freely and behavioural time budget information was gathered to investigate whether the spatial arrangement of food influenced the type of competition acting at the individual level.

All groups spend the majority (between 60 and 70%) of their time moving with males spending more time moving than females and juveniles. Animals fed a clumped resource (balls of yeast) feed longer than those in colonies fed on food that was dispersed (powdered yeast), who consequently spend more time moving than animals fed balls. Animals fed balls of yeast have a greater variation in the proportion of time spent feeding and moving between individuals than do those animals in colonies fed powder. Animals feed on average in more bouts in colonies fed powder than those fed balls. Animals also move in more bouts if fed powder, this is consistent with the idea of animals having to move in more bouts to feed in more bouts.

The results show that those colonies fed a dispersed food resource have a greater equivalence in time spent feeding between individuals and therefore, in food intake than those in colonies fed balls of yeast. In colonies fed a clumped resource there is inequality in time spent feeding (and intake) – some individuals

feed for longer than others. These results suggest that spatial arrangement of food determines the type of competition (inference or contest) acting at the level.

3.2 Introduction

It has been shown previously that in laboratory colonies of the soil mite *Sancassania berlesei* changing the spatial food availability from a clumped to a spread food resource causes differences in the initial population dynamics and age and size structure between populations (Chapter Two). At a life historical level, animal sizes and variances in size differed between food types in that those with a clumped food source (balls of yeast) were on average larger, although there was greater variation in size. This is consistent with exploitation competition in clumped food (balls of yeast) where there are 'winners and losers' and scramble competition in dispersed food (powdered yeast) where all individuals within a population suffer equally from a shortage.

Scramble and contest completion are translated at an individual level as exploitation (or depletion) and interference (Nicholson 1954, Toquenga 1993). Interference (contest) competition describes where individuals control access to resources by e.g. competitive superiority. Exploitation (scramble) competition describes individuals depleting resources, making them unavailable to others.

In foraging theory, the main behaviour considered other than feeding is moving in search of food(e.g. Schoener 1971, Pyke 1984 and Krebs & Davies 1993) and theory predicts how an animal will perform these behaviours to maximise fitness i.e. intake. In terms of changing spatial food availability it is predicted that animals fed a clumped resource can feed for longer and hence move less than animals in powder. Evidence from foraging studies using *Porcellio scaber* (Hassall et al 2002) supports this idea and showed that in individual foraging behaviour less time was spent feeding and more time moving as density increased.

In the case of *S. berlesei*, where the yeast food source is clumped animals feeding on the ball will be able to prevent others feeding by their physical presence, if surface area access to the food is limiting i.e. density is high. Where the food source is spread (powdered) animals are predicted to interact more through resource level than through physical interaction at the food source and e.g. by eating a granule of yeast, make it unavailable to others. Further to this, if an animal feeds on a ball of yeast its potential food intake, if it is able to maintain its place, is much greater than an animal fed powder as it does not have to search for small pieces of food. Pitt and Ritchie (2002) found that skinks foraging success depended upon the dispersal of resources – their intake being higher when foraging in large clumps of food rather than in areas where there were a larger number of small clumps of food. Clumping of the food source also increases the opportunity for dominance over the food source and it would be predicted that larger animals i.e. adult females, may be less easily displaced than smaller animals, i.e. juveniles, whereas a wide spread of food allows greater access for all. Therefore, in balls it could be predicted that larger animals will gain a greater proportion of food than other groups allowing them to perhaps gain an intake greater than the average intake per animal, allowing for the initial 'bounce' in fecundity seen (Chapter Two) in balls than in powder.

Lowe and Butt (2002) found that in earthworm foraging food particle size was important in determining growth of individuals - animals grew faster when fed smaller particles food (this affect was more profound the smaller the animal was) and that the affect of conspecifics also had greater effect with smaller particles of food. Further to this, different life stages of animals have been found to feed differently. Merritt (1987) found that older and therefore larger larval instars of *Aedes triseratus* tended to eat coarser material than younger instars suggesting selective feeding and indeed a possible response to or a mechanism of avoiding intraspecific competition. Buskirk (1992) also found that younger larvae of the dragonfly *Aeshna juncea* did significantly change their behaviour whilst in the presence of larger older larvae by reducing and changing the time of their activity and incurred a decrease in feeding success as a result.

Competition is defined at this level through the differential allocation of costs between individuals and it is important to consider whether changing the food availability could change these costs with increasing density. If surface area of food is limiting in a ball of yeast then beyond the threshold where all space on the clump is occupied, increasing density may simply increase variance in behaviour between individuals rather than altering the core number of animals who are able to feed and reproduce i.e. the number of winners will become proportionately smaller to the ‘losers’. This could alter according to the structure of the increase in density i.e. if larger animals are competitively superior then they will be more affected by an increase in the number of large animals. In the case of powdered food the ease of access to resources may confound competitive superiority and hence any increase in density would affect all groups more equally and more linearly with the increase in biomass and food depletion should occur more linearly with increasing density and time. It could then be predicted that differences in life history stem from differences in intake and allocation decisions determined by behavioural time budgets according, in part, to the availability of resources spatially and its interaction with population size and structure.

This study aims to test the predictions, that there will be differences in individual time budgets, consistent with the predictions of competition stated, in terms of:

- Proportion of time spent
- Variation in proportion of time spent
- Number of bouts a behaviour is performed in

Further to this that these time budgets will alter in terms of:

- Food type i.e. balls of yeast and powder
- Group i.e. females, males and juveniles
- Density i.e. differential affects due to mode of competition.

3.3 Materials and Methods

Behavioural observations were taken as part of the long-term experiment detailed in chapter one and hence for general methods refer to the information given previously.

3.3.1 Behavioural observations

The programme JWatcher was used (Macquirie University http://galliform.psy.mq.edu.au/jwatcher/) to take ten minute continuous recordings of a focal individuals' behaviour. Individuals of each group (females, males and juveniles) were selected at random and a pc running JWatcher, with the keyboard as an event logger, was used to record the incidence of behaviour. Observations were taken after the colony had been fed (time from feeding was recorded). 9-15 behavioural measures were taken per day, 3-5 per group (females, males and juveniles). For both the balls and powder treatments the data runs until days 153 and 154 with 38 days of observation per food type (every four days) within this. Within this time there were n average 17.6 observations per tube (N=8) for females and 16.9 observations per tube (N=8) for males and females. Preliminary observations were used to determine the behaviours that could be observed; these were recorded in this experiment (table 1).

Feeding	Chelicerae moving.
Jostling	Males only – competing for position on female.
Moving	Moving on tube substrate not in contact with others.
Milling	Moving in contact with other animals.
Mating	Male and female in copulatory position.
Flailing	Mite on its back.
Out of sight	Mite no longer visible.

Table 1 The behaviours recorded

3.3.2 Non-mutually exclusive behaviours

Not all behaviours were mutually exclusive with others. For example females have been observed moving and feeding whilst mating. JWatcher can accommodate non-mutually exclusive behaviours and as such for females the behaviours feeding, mating and moving also had the opposite cases of not feeding (not moving and not mating) in order that exclusive and non-exclusive bouts of behaviour could be distinguished if required.

3.3.3 JWatcher

Here JWatcher is used as a simple event recorder. During the ten minute focal observations the incidence of the above behaviours were recorded. The data displayed here are the proportions of time within the focal observations that the individuals spent performing certain behaviours and the frequency (number of bouts) of that behaviour within an observation. The proportion is calculated from the time the individual spent in sight rather than the total focal length. If an individual went out of sight it generally resulted in the end of an observation, unless it was certain that the individual recovered was the original focal animal.

3.3.4 Time budgets

Time budgets are displayed as the mean proportion of time spent performing each behaviour per group (females, males and juveniles) and per treatment (balls and powder). Each behaviour was separately analysed using Generalised Linear Models (GLM) with binomial errors or by the quasi-likelihood method if the data were under-dispersed (link function = logit, variance function = mu(1-mu)). The maximal model fitted to explain the incidence of behaviours was as follows:

Proportion of time spent (in sight) Adult density*Juvenile density*group*TFF*Treatment/Tube

- Indicates all two-way interactions.
- Tube is nested within treatment.
- TFF = time from feeding.

Stepwise deletion tests were used to reduce the maximal model. Each behaviour is represented as part of a time budget according to group and treatment and also separately to describe other factors affecting the incidence of the behaviour. For analysis, moving and milling behaviours were combined into a general measure of moving.

3.3.5 Variation in behaviour

Not only the proportion of time spent on a behaviour but also the variation between individuals is important in determining the difference in competitive environments. The method of data collection makes determining this variation more complicated as both group and treatment are of interest and yet only three individuals per group per day were available to calculate variance from. This number was considered too low for a robust mean and hence the proportional deviation from an overall mean was used to represent variation in time spent feeding and moving.

Overall mean: mean time spent for all values
Individual deviance = individual time spent – overall mean
Proportional deviance = individual deviance/overall mean

All data were converted to positive values as the magnitude and not the direction of the difference were of interest. The proportional mean - calculated above as a ratio of individual deviance to the overall mean time spent feeding or moving – was analysed with a quasi- likelihood GLM with an identity link and constant variance.

Proportional deviance~ Adult density * Juvenile density* Group* Treatment/Tube
* indicates all two-way interactions

Stepwise deletion tests were used to reduce the maximal model. This analysis was carried out for feeding and combined moving behaviours only – those that represented the majority of the time budget for all groups.

3.3.6 Number of bouts of behaviour

Also important in indicating the type of competition is the number of bouts of behaviour that occur within a focal observation. For both feeding and combined moving behaviours, analysis was carried out with a quasi-likelihood GLM (identity link and constant variance). The maximal model fitted was as follows:

No. bouts ~ Adult density*Juvenile density* Group*TFF*Treatment/Tube

- * Indicates all two-way interactions.
- Tube is nested within treatment.
- TFF = time from feeding.

The model was reduced by stepwise deletion.

3.4 Results

3.4.1 Differences in behaviour due to group – time budgets of females, males and juveniles

All groups spend the majority (between 60 and 70%) of their time moving with males spending more time moving than females and juveniles ($F_{2,409}$= 3.20, pr(F)=0.042, figure 1 to 3). Animals spend the greater proportion of the remaining time feeding; juveniles are found to spend most time feeding followed by females and then males ($pr(X^2)=<0.05$). Jostling, where more than one male competes for access to a female, is a behaviour only performed by males and when in conjunction with mating shows that males invest more time in reproductive behaviours than females (mating, $X^2_1=0.027$). Juveniles spend the greatest time being stationary (at an approximate mean 10% of focal time), followed by males and females ($F_{2, 406}$ = 5.12, pr (F) = 0.006). Time spent flailing did not differ significantly between groups and ($F_{1, 408}$ = 0.77, pr (F) = 0.46, X^2_2 = 0.44)

Time Budgets according to group

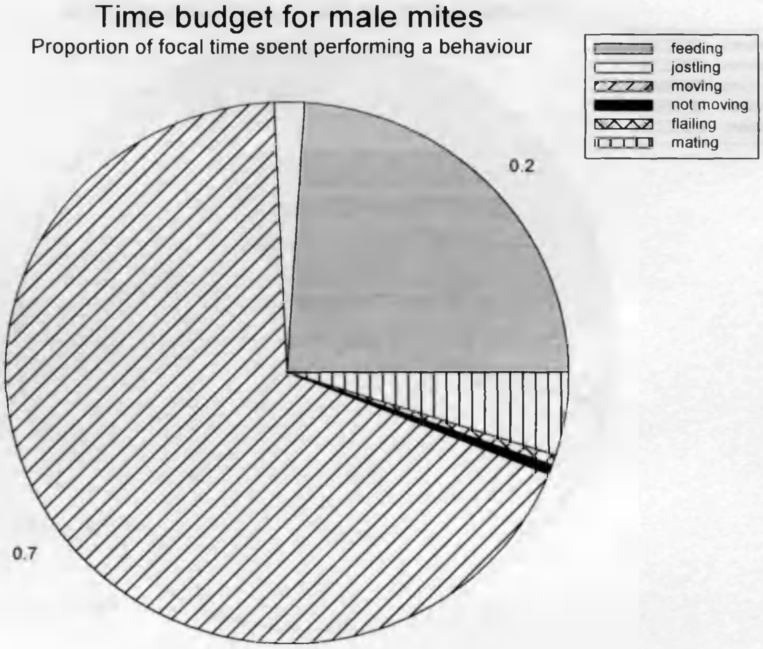

Figure 8 Time budget of male mites – data given are mean proportions of total focal time spent feeding for the whole time series. Feeding behaviour was recorded when chelicerae were moving; jostling behaviour indicates where more than one male was on a female's back; moving behaviour indicates an animal moving over the substrate or other animals; not moving indicates where animals were stationary; flailing indicated an animal on its back and mating behaviour was recorded where a male occupied a copulatory position on a females back.

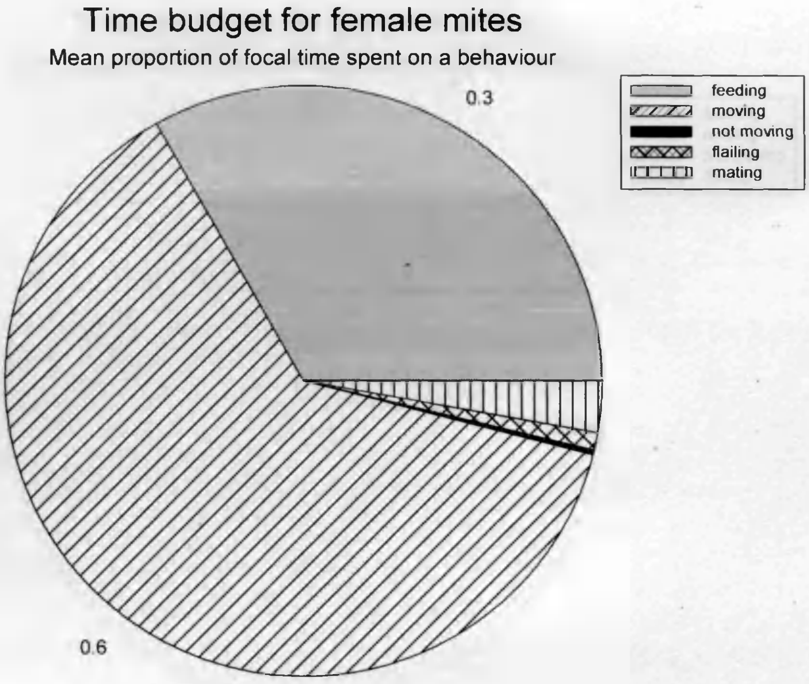

Figure 9 Time budget of female mites – data given are mean proportions of total focal time spent feeding for the whole time series. Feeding behaviour was recorded when chelicerae were moving; moving behaviour indicates an animal moving over the substrate or other animals; not moving indicates where animals were stationary; flailing indicated an animal on its back and mating behaviour was recorded where a male occupied a copulatory position on a females back.

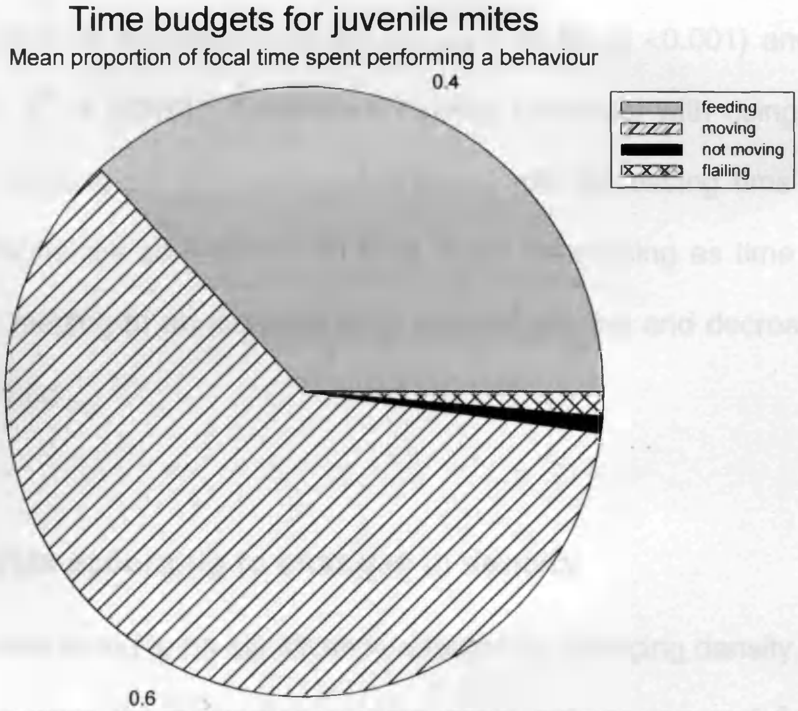

Figure 10 Time budget of juvenile mites – data given are mean proportions of total focal time spent feeding for the whole time series. Feeding behaviour was recorded when chelicerae were moving; moving behaviour indicates an animal moving over the substrate or other animals; not moving indicates where animals were stationary; flailing indicated an animal on its back and mating behaviour was recorded where a male occupied a copulatory position on a females back

3.4.2 Time budgets according to time from feeding

Time of feeding was recorded every day as was the time from feeding (in hours) when a behavioural observation was taken. It was assumed that as time from feeding increased then resource level would decrease. It was also predicted that depletion would happen more rapidly when animals were fed powdered rather than balls of yeast due to greater access by all animals to the food source; therefore differences between the food types in terms of feeding and searching behaviours were expected. The time since feeding was found to significantly change the proportion of time spent moving ($F_{1,\ 409} = 11.90$, $p < 0.001$) and not moving (dropterm, $X^2_1 = 0.040$). Time spent moving increased with rising time from feeding and time spent not moving decreased with increasing time from feeding. These results are consistent with food levels decreasing as time from feeding increases leading to an increase in time spent moving and decrease in time spent not moving

3.4.3 Time budgets according to changes in density

Few behaviours were found to be significantly affected by changing density, as a single term, these were the proportion of time spent not moving and flailing. Increasing adult density decreased the time spent moving in all groups ($p(F_{1,406}) > 0.001$, dropterm results, figure 4) and increased the time spent flailing ($F_{1,\ 408} = 3.08$, $p = 0.08$, approaching significance, figure 5).

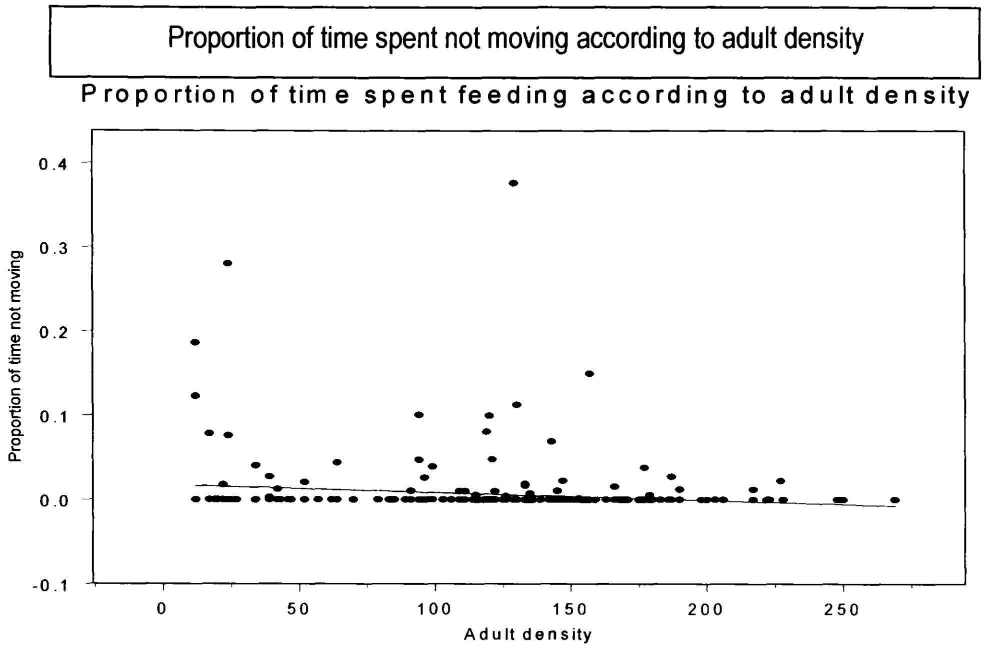

Figure 11 Linear fit of the raw values of adult density plotted against the proportion of time spent not moving per individual

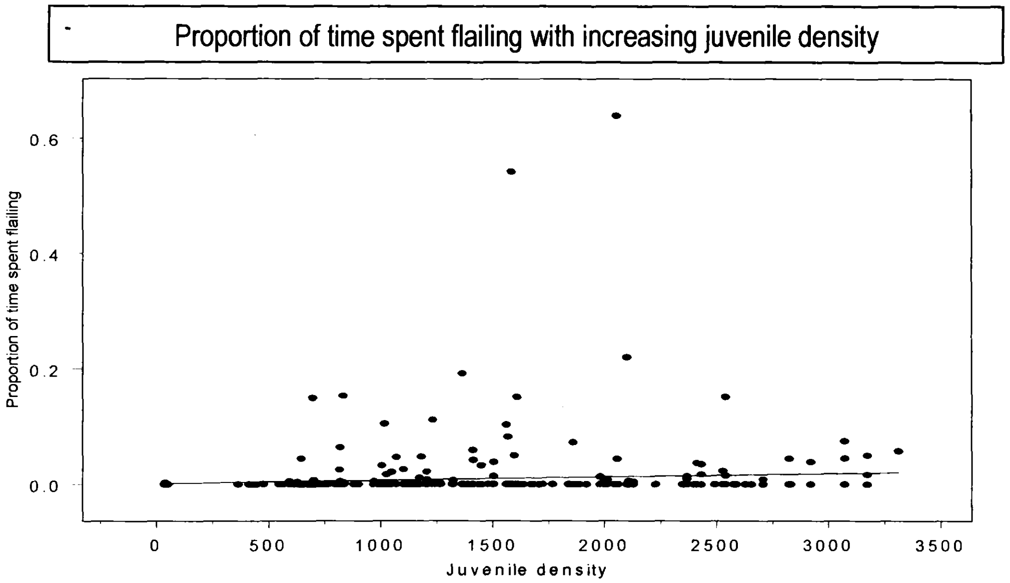

Figure 12 Linear fit of raw values of juvenile density plotted against the proportion of time spent flailing per individual

As adult density increased, time spent not moving decreased as competition levels rose between individuals for access to food. There is a shallow positive relationship between juvenile density and time spent flailing which approaches significance ($F_{1, 408}$= 3.08, p = 0.082) indicating that as juvenile density increases for all groups and both treatments, the amount of time spent flailing (on back) increases. This supports the idea that increasing density causes a rise in the levels of interference between animals and that juvenile density is the most important driver for this behaviour. However the levels of time spent in this behaviour suggest it is still an unusual and perhaps unimportant occurrence.

3.4.4 Time Budgets according to food type

On average the focal individuals fed on balls spent significantly longer feeding than those fed on powder (p = 0.015, figure 6). Animals fed on powder on average spent more time moving than those fed on balls of yeast ($F_{1, 409}$= 15.40, p >0.001). There was no difference in time spent in reproductive behaviours between treatments, neither in jostling between males in the different treatments (pr (X^2_1) = 0.99) nor in mating between males and females combined within each food type ($F_{1, 274}$ = 0.64, p = 0.42). The treatments did not differ overall in the time they spent flailing ($F_{1, 406}$ =0.23, p = 0.63), or not moving ($F_{1, 406}$ =0.11, p = 0.74). However the treatments did differ in the time they spent not moving according to group. Overall juveniles spent more time not moving than males, with females spending the least time not moving in colonies fed on balls ($F_{2,406} = 5.12$, p = 0.006).

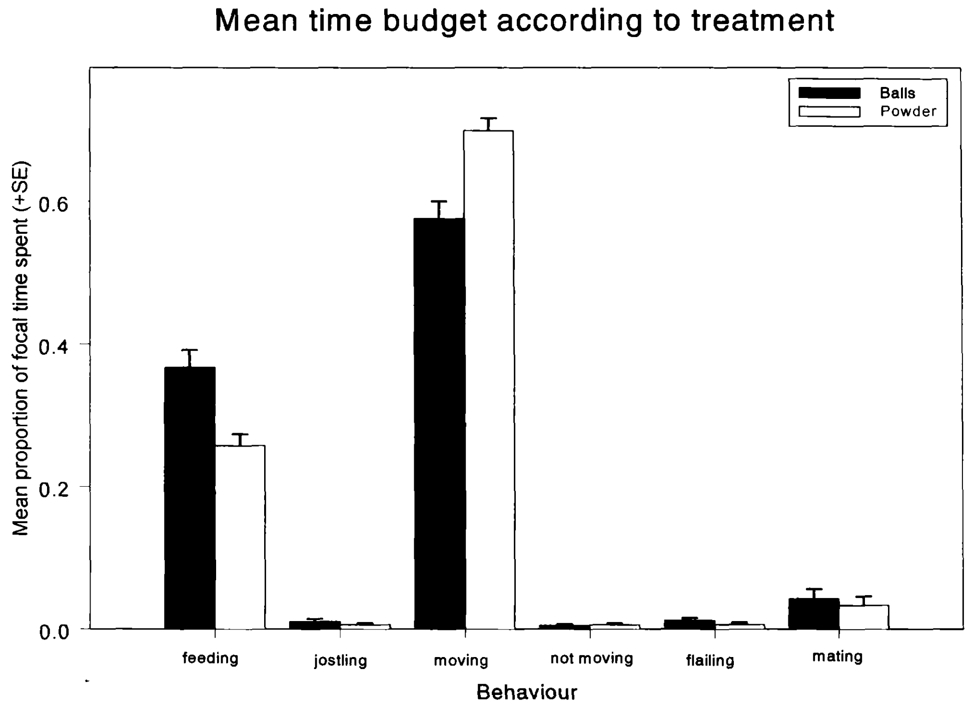

Figure 13 The mean time budget for all groups according to food type.

3.4.5 Variation in behaviour between food types

The main difference between animals in the two different food types is in the feeding and moving behaviours. Animals on average feed more and move less when fed on balls of yeast with respect to those fed on powdered yeast. Further to this difference in proportion of focal time spent in these two behaviours are differences in the variances in the proportion of time spent performing certain behaviours and in the mean number of bouts the behaviour is performed in.

To examine the between individual variation in feeding and moving behaviour, the mean proportional deviation (calculated from all focal observations) from an overall population mean for a particular behaviour was calculated and the predictive effects of density , life stage and food type upon this measure of deviation was tested with a quasi-likelihood GLM. Animals fed on balls had a greater variation in the proportion of time spent feeding between individuals than did those animals in colonies fed on powder (Quasi-likelihood GLM, $F_{1, 406}$ = 38.49, $p<0.001$, Figure 7). This shows that in powder there is a greater equivalence in time spent feeding between individuals and therefore, in food intake than in the balls treatment, where there is inequality in time spent feeding (and intake) – some individuals feed for longer than others.

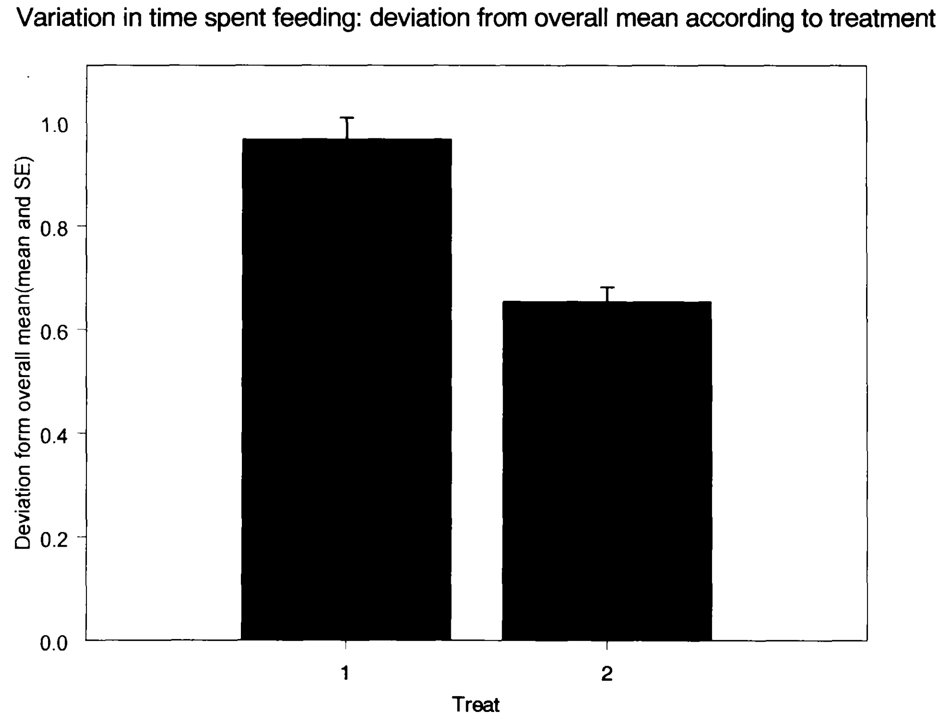

Figure 14 Variation in the proportion of focal time spent feeding between food types as measured by deviation of an individual from the food type mean.

Animals in balls also have a greater variation in the proportion of time spent moving than animals in powder (Quasi-likelihood GLM, $F_{1,409} = 25.33$, $p<0.001$). The variation in time spent moving is also affected by the juvenile density within a colony with increasing density increasing the variance in time spent moving in both treatments ($F_{1,409} = 15.46$, $p < 0.001$,Figure 8). This suggests that as density increases interference also increases, feeding becomes more difficult and thus individuals are forced to spend more time in search behaviours. This also suggests that juveniles interfere with all groups of animals more than adults.

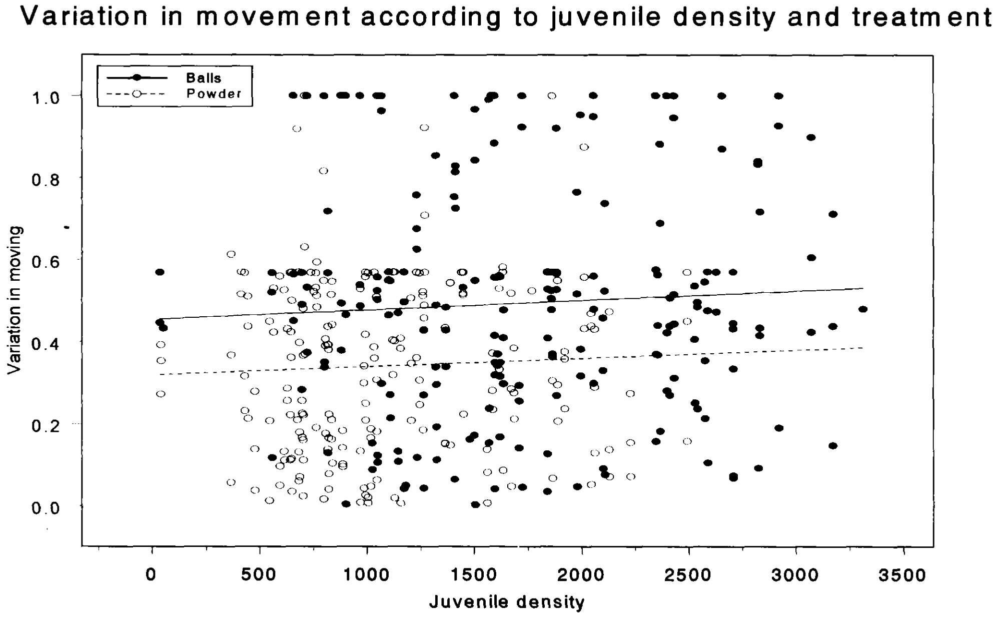

Figure 15 Linear fit of raw data of variation in time spent feeding (calculated as deviance from an overall population mean as detailed in the methods section) per focal individual plotted against juvenile density (in the focal individual's tube) and life stage of the focal individual

The effect of juvenile density upon variation in moving also varies according to the type of animals within a group i.e. a female, male or juvenile ($F_{2,409} = 4.81$, p

= 0.009). Females and juveniles are affected by increasing juvenile density in that their time spent moving increases however the male group are insensitive to density (Figure 9). This suggests that males are less susceptible to interference by juveniles than females or other juveniles.

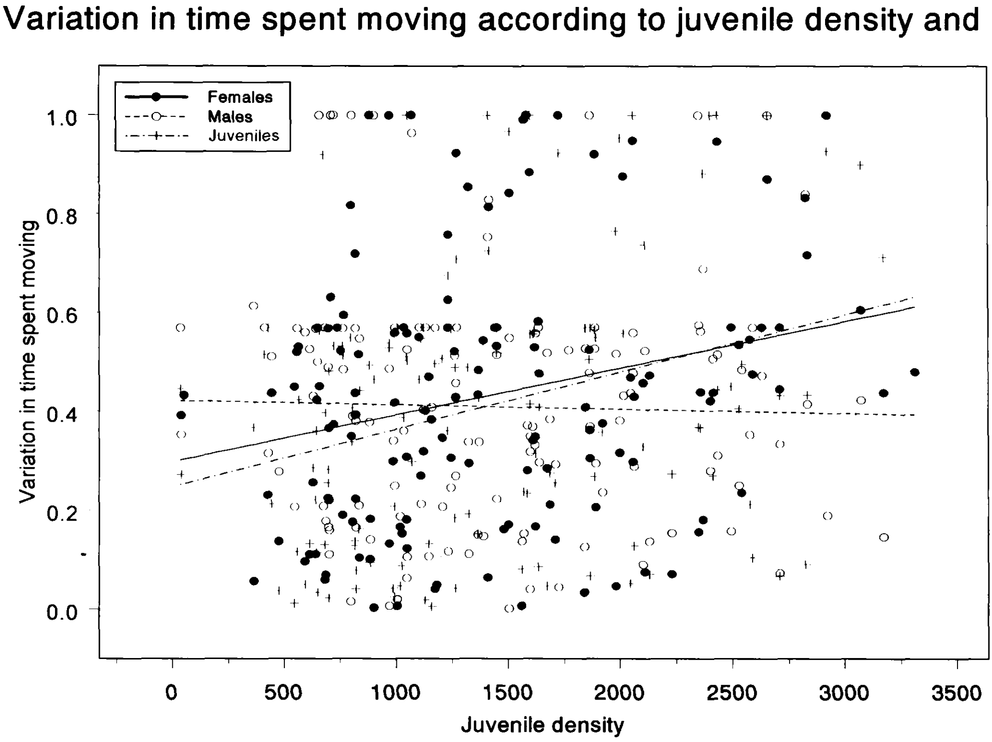

Figure 16 Linear fit of the raw data of variation in time spent moving (calculated as deviance from an overall population mean as detailed in the methods section) per focal individual plotted against juvenile density (in the focal individual's tube) and life stage of the focal individual.

As predicted, variation in moving behaviours is higher in balls than powder further supporting the idea of winners and losers as those animals that get to feed, feed for longer and move less and those that do not get access to food and spend the majority of their time moving. A further way to investigate the difference in feeding and moving behaviours between the food types is to consider the number of bouts in which the behaviour is performed.

3.4.6 Number of Bouts of Feeding and Moving

In considering variation in feeding and moving behaviours further, an individual's time budget can be viewed as bouts of feeding punctuated with periods of search behaviour. As such considering the patterns of number of bouts of feeding and moving behaviours in the different food types can give information about the pattern of an animals' behaviour i.e. feeding clumped or spread food should lead to different patterns of search and feeding to maximise fitness (intake) as should increasing competition through density and increasing time from feeding (resource depletion). Here the predictive effects of food type, time from feeding, density and life stage upon the number of bouts of feeding and moving were tested using quasi-likelihood GLM.

The food type was found to have a significant effect upon number of bouts of feeding and moving within a focal observation. Animals feed in more bouts in powder than in balls (Quasi-likelihood GLM, $F_{1, 408} = 38.09$, $p > 0.001$, Figure 10). This agrees with the prediction that in balls if you feed, you feed for longer, whereas powdered food is available in smaller amounts, spread widely making monopolisation difficult. As the food resource can not be monopolised in the powdered treatment it is necessary to find more than one source of food and hence have a greater number of bouts of feeding.

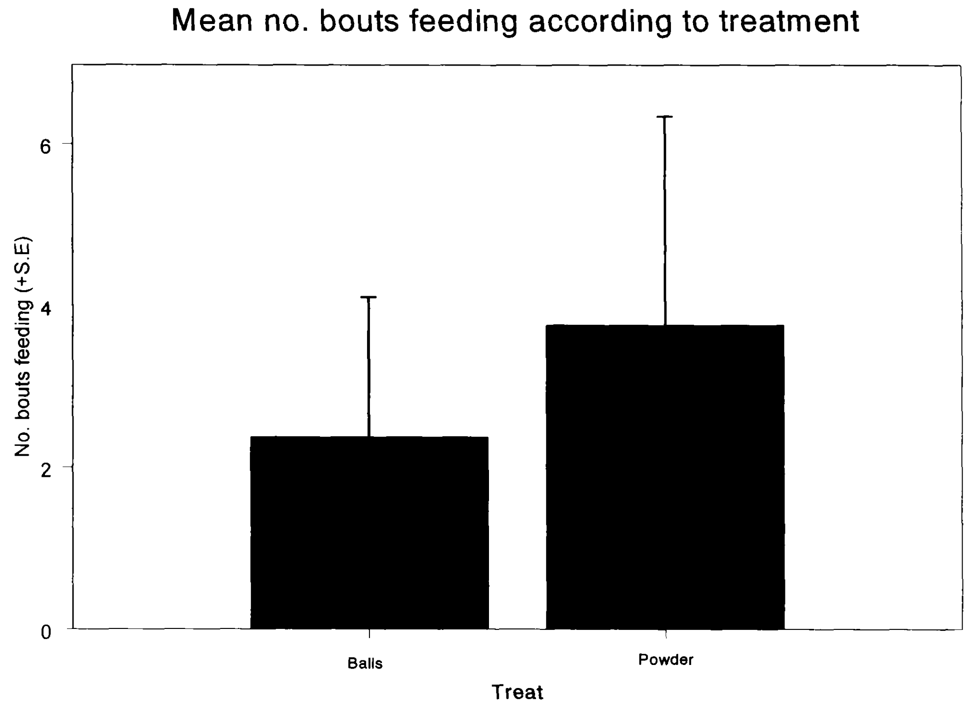

Figure 17 Mean number of bouts of feeding according to food type. The data are mean numbers for all individuals per treatment that displayed feeding behaviour.

Animals also move in more bouts in powder than balls (consistent with the idea of animals having to move in more bouts to feed in more bouts (Quasi-likelihood GLM, $F_{1,409} = 46.70$, $p < 0.001$).

The number of bouts of feeding decreases with increasing juvenile (Quasi-likelihood GLM, $F_{1, 409} = 4.17$, $p = 0.041$, figure 11) and adult density (Quasi-likelihood GLM, $F_{1, 409} = 20.61$, $p < 0.001$) presumably as density increases a greater time is spent moving and is broken by fewer bouts of other behaviours in favour of search behaviours. This density dependence did not differ with the different food types.

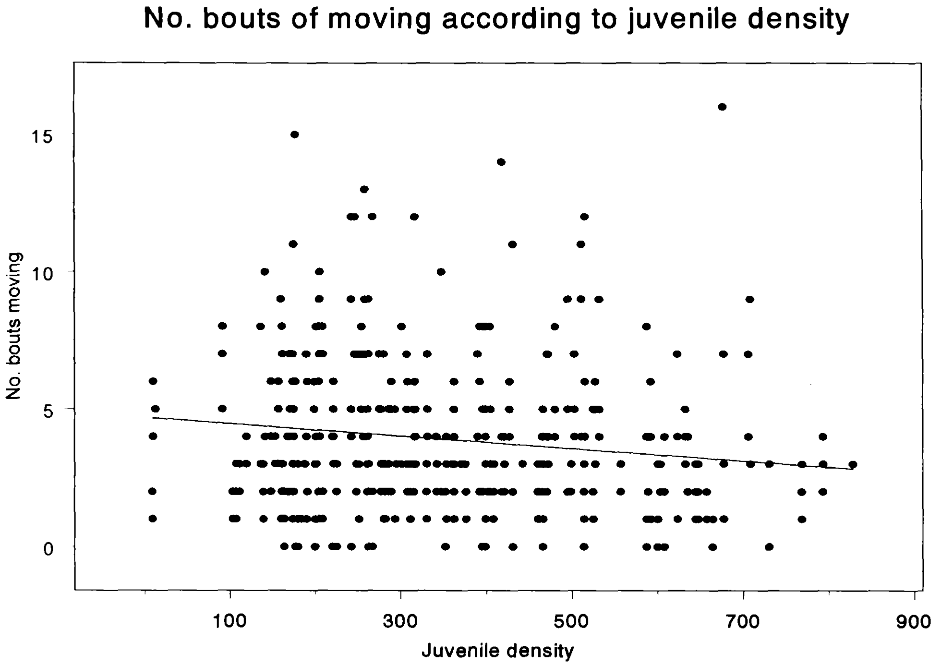

Figure 11 A linear fit of the raw data of the number of bouts of moving per focal individual within an observation plotted against the juvenile density in the tube the focal animal's tube on that day. This density dependence of number of bouts of moving within a focal time did not differ between food types.

3.5 Discussion

Changing the spatial availability of food caused measurable changes in the behavioural time budget of mites in freely reproducing colonies. Independent of other factors, there were differences between time budgets in males, female and juveniles. Males spent more time moving and in reproductive behaviours (mating and jostling) than females. Females spent more time feeding than males but less than juveniles. These results suggest that different life stages and sexes within a population can have different motivations to perform certain behaviours under the same conditions; these same results have been demonstrated by others (e.g. Buskirk 1992). The results of this experiment suggest that females have a greater need to feed than males due to the fact that after maturation, females need to fuel egg production. Males spend more time in reproductive behaviours in order to maximise their potential of contributing to the next generation whilst juveniles need to develop quickly results in a large proportion of their time being used for feeding.

There was little clear evidence for the roles of food depletion (increasing time from feeding) and increasing density on the behavioural time budgets of males, females or juveniles in colonies fed balls of, or powdered yeast. It was predicted that changing the spread of food and hence food particle size would lead to different effects of increasing density; as has been found in other studies (Lowe and Butt 2002). Decreasing food particle size (i.e. feeding colonies powdered yeast) was predicted to increase the effects of food depletion with increasing density by decreasing the time spent feeding. The results however, did not show this to be the case. It was also predicted that there would be between group differences in the effects of density and food depletion (Merritt 1987, Buskirk 2002) neither of these effects were detected.

The differences between the colonies fed different spatial arrangements of yeast were strong and consistent between life stages. In all colonies animals were found to spend the majority of their time either feeding or moving; the amount of time devoted to these behaviours was significantly different between food arrangements. Animals on average spent a greater proportion of their time feeding when fed balls than when fed powder, there was also greater variance in time spent feeding in colonies fed balls than those fed powder. Animals were also found to feed in fewer bouts in balls than powder. In colonies fed powder animals spend more time moving than those in balls and do so in a higher number of bouts. This suggests that when fed a dispersed resource animals spend more time searching for food, whereas those fed a clumped resource can feed for longer if able to monopolise the ball or if are competitively excluded spend more time moving. This is consistent with the idea that animals feeding on a clumped resource can prevent others from doing so i.e. interference competition. Interference competition is often associated with behaviours to actively prevent others feeding such as territoriality and/or aggression. However, no such active interference behaviours were seen in this study, animals were assumed to prevent others feeding simply by their presence on the food source. Other studies have also found that monopolisation can occur in non-aggressive species when the food source is defendable i.e. asynchronously dispersed (Weir and Grant 2004). In colonies fed powdered yeast the results are consistent with a situation whereby they feed less but there is greater equality in time spent feeding, i.e. each animal has equal access to food and are equally affected by a lack of resources – exploitative competition.

The spatial distribution of food is therefore found to effect the behavioural time budgets of animals including the proportion of time animals spend feeding. These differences happened concurrently with data in the previous chapter that linked differences in population level responses to differences in life histories through individual sizes. Higher mean sizes of animals in colonies fed balls of yeast were associated with animals spending a greater proportion of time feeding. Greater variation in time spent feeding was associated with a greater variation in size of animals in colonies fed balls of yeast versus those in colonies fed powdered yeast. These patterns indicate interference competition in colonies fed balls of yeast and exploitation competition in colonies fed powdered yeast.

Individual variation is predicted to be important at the population level (e.g. Smith et al 2000, Bjornstad et al 1994) and it has also shown that there is no monotonic relationship between the two (Grimm and Uchmanski 2002). This study suggests that specific knowledge of individual effects is important in determining the mechanisms of a populations dynamics. In this system individual time budget and life historical data indicated that interference competition, which is predicted to lead to stable dynamics (May 1974), is actually related to decaying oscillations in population dynamics in this species.

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Chapter 4:

The effects of density, food level and spatial food availability upon the behavioural mechanisms affecting intake in the soil mite *Sancassania berlesei.*

4.1 Introduction

The description of competition is often phenomenological and based upon evidence of density dependent reduction in survival, reproduction or growth of individuals. Scramble and contest were terms first used by Nicholson (1954) to describe two extremes of competitive mechanism, but have since become widely used to describe competition at the level of density dependence. These extremes of competition are predicted to have different effects upon population stability with contest asserting a stabilising effect whilst scramble has the potential to destabilise under certain conditions (May 1975, Varley Hassell and Gradwell 1973). It is often assumed but rarely proven that the outcome of competition, shown by the density dependence, stem from the same mechanism at an individual level, i.e. a 'scramble' outcome at the population level stems from 'scramble' mechanisms of competition between individuals (Toquenaga & Fuji 1990). For example Ives and May 1986 showed that where the underlying mechanism of competition was of a scramble type, the resulting competition curve was a contest type due to the aggregation behaviour of competitors. There is an intuitive appeal in searching for a role of individual behaviour in higher order interactions as a population's dynamics is the sum of each individual's response to its environment and conspecifics in terms of its growth, survival and reproduction. Behavioural ecology shows there is an adaptive, rule-based, basis to behaviour which suggests dynamics can be mechanistically as well as phenomenologically understood. More proximately, with greater pressure being put on ecological models to provide accurate quantitative as well as qualitative predictions for population management, (Bradbury et al 2001) there is a need to further investigate and review the importance of individual behaviour and mechanisms of competition and their importance in producing dynamics at the population level.

At an individual level, describing resource use, the terms scramble and contest equate in use in the literature to exploitation and interference competition respectively. Interference describes where animals compete through access to a resource where behavioural interactions between individuals cause a reduction in fitness, e.g. through resource monopolisation. Exploitation describes where individuals compete indirectly through depletion of a resource (Park 1962). Schoener (1983) identified some confusion in the use of these terms and used a more exact mechanistic six term taxonomy of competition, which for example included what would be considered a traditional exploitative mechanism in consumptive competition where animals consume a certain amount of resource making it unavailable to others; and traditional interference mechanisms in chemical competition (releasing toxins) and encounter competition (interactions between individuals which have a negative effect in terms of injury or energy loss). This taxonomy also included pre-emptive competition (where space is passively occupied) which was identified as including aspects of exploitation and interference. This raises the question as to whether the two classical individual based mechanisms can always be considered as distinct and indeed which is the most important in natural systems? Some studies have investigated and contrasted the importance of exploitative and interference competition, for example Anholt (1990) attempted an experimental separation of interference and exploitative competition in larval damselflies. It was found that although interference behaviour (through aggressive encounters over perches used for hunting) was obvious in the species studied, no evidence was found that through direct manipulation of the number of perches there were any density dependent changes in growth or development, i.e. the behaviour seemed costly but no cost was detected. This demonstrates that making assumptions relating mechanisms at the individual level to population dynamics is problematic; this argument is further strengthened by the apparent presence of both exploitation and interference simultaneously in other laboratory systems (MacIsaac & Gilbert 1991).

Optimal foraging theory predicts that foraging strategies will have evolved to maximise net energy gain whereby energy intake rate is a function of encounter rate, search time and cost, average handling time and energy gained (MacArthur and Pianka 1966). Broadly speaking optimal foraging models are separated into prey models, which predict the optimal diet and patch models (e.g. Charnov 1976), which predict the optimal patch residence time. In both cases energy gain is offset by search costs and both may be affected by food quality, spatial and temporal food availability and the presence of conspecifics. Increasing density and food aggregation have been fund to increase time spent searching for food (Hassall et al 2002), with more time spent in low quality food patches as aggregation increases (Tuck & Hassall 2004). Further to affecting the balance of energy gains whilst foraging, the clumping of a resource may also change the potential for that resource to be monopolised, as a smaller, more clumped area of resource may be less costly to defend. Grant and Guha (1993) showed that resource monopolisation by dominant individuals increases with increasing spatial clumping of food. Dominant animals also become more aggressive with increased clumping of food (Grant and Guha 1993) whilst also becoming more sedentary (Grand and Grant 1994). The probability of an individual gaining a food item may also dependent not only upon density but also relative competitive ability and animals may be switch between a contest between individuals at low density to a scramble for resources at higher densities (Tregenza et al 1996). Weir and Grant (2004) considered the importance of the interaction between the mode of competition and resource dispersion in causing resource monopolisation. Resource monopolisation is thought to depend upon whether the resources are economically defendable and whether animals are able to defend them. Hence it is assumed that monopolisation will be higher in groups that compete via interference than exploitation, their results confirmed this.

In laboratory populations of the soil mite *Sancassania berlesei*, there is empirical evidence that feeding the same amount of food in different spatial arrangements (clumped or spread) causes differences in population dynamics and individual behaviour between the different colonies (Truelove et al unpublished data). Animals fed clumped food display more stable dynamics whereas those fed spread food tend towards damped oscillations. Theory proposes that stable dynamics i.e. clumped food here, are underlain by contest/interference competition and vice versa for more unstable dynamics. Here it is proposed that changing the spatial arrangement of food is changing the individuals' access to food and therefore changing the mechanism of competition between individuals from a more interference-like environment when food is clumped (and feeding animals must interact more), to a more exploitation-like environment when food is spread (and behavioural interactions become less likely) and animals interact more through resource levels. There are no obviously aggressive interactions between individual mites in foraging behaviour (personal observation) it is rather proposed here that interference would act rather through pre-emptive and encounter competition (Schoener 1983). As far as we are aware there have been no previous studies which relate changing spatial availability of resources to changes in the competitive mechanism within a species. We intend to separate the effects of interference and exploitative competition by independently manipulating the density of individuals and food levels and to relate the mechanisms of competition at the behavioural level (through time budgets) to differences in the average intake rate of individuals. We consider that differences in intake related to differences in time budget would be evidence for the effects of competition linking behaviour to population dynamics as animals make different life historical decisions based upon their intake rate (Plaistow et al 2004, Benton and Beckerman 2005). Further to this, the spread of food will be increased to determine whether this changes the proportion of animals feeding, their behaviour and whether this has an impact on the average intake rate. The aims are to investigate whether:

- Increasing the density of animals (without decreasing per capita food) will decrease their average intake.
- Increasing per capita food (without changing density) increases average intake.
- Increasing the spread of food increases the proportion of animals feeding/average intake rate.

4.2 Experimental methods

Experimental animals were taken from a common environment fed 2 balls of yeast per day (average single ball weight 1.725×10^{3}g, S.E 3×10^{5}). These animals were kept under starvation for 24 hours previous to the beginning of the experiment, in single sex colonies, to allow them to feed maximally when the experiment began and to prevent, as far as possible, the laying of eggs by females during the experiment (which could have interfered with intake estimates).

Maximal Intake Rate

As a benchmark for comparison in later stages it was necessary to calculate the maximal intake rate of an individual. The methods for this experiment are given elsewhere (Truelove et al unpublished data). The results showed that females had a mean maximal intake rate of 2.96×10^{6} g/hr (2.87×10^{6}-3.04×10^{6} g/hr) and males 1.6×10^{6} g/hr (1.54×10^{6} – 1.65×10^{6} g/hr). This gives an equivalence of intake ratio of males to females of 1:1.8. This ratio was used to calculate the densities used in the main experiment (detailed below).

Interference and Exploitation

Here interference competition was increasing density whilst retaining the same per capita food (i.e. competition through access to food). Exploitation competition was modelled as a change in per capita food with no change in density (i.e.

competition through the level of resources). There were two different food arrangements. The experiment utilised 240 tubes across the treatments (Table 1).

Table 1. The number of tubes per treatment shown for 1 food disc, repeated for two food discs.

			Food level	
Group	No. food discs	Density of animals	Low	High
Females	1	Low	10	10
	1	Med.	10	10
	1	High	10	10
Males	1	Low	10	10
	1	Med.	10	10
	1	High	10	10

Food Spatial Arrangement

1 or 2 'hole-punched' discs (6mm diameter) were stuck to a filter paper base (moistened to retain humidity) with PVA glue to prevent animals feeding on the reverse of the disc and going out of sight (and which also prevented leaching of the yeast from the disc by making a waterproof layer).

Food levels and Density

Food levels were set at 25% and 150% of the maximal daily intake calculated. The densities were set at 10, 50 and 100 for females and were then set equivalently (so that their intake would be the same) for males i.e. 18, 80 and 180. Food levels to be given (dry weight of yeast) were calculated by using the maximal daily intake rate, adjusted for food treatment level, to create a daily intake per individual and multiplying that according to density. Solution concentrations for each food disc were calculated from a stock solution of 0.5g $10ml^{-1}$ (giving an average of 0.001g dry weight yeast per disc).

Experimental method

The food discs were weighed before and after the application of yeast solution so that the total weight of yeast given was known. The discs were then glued to a filter paper base and left to dry in an oven. These were left to cool and then were weighed again. The filter was then moistened the mites added and the lid then sealed with cling film.

1. Intake

The mites were left to feed for 24 hours, after this time the animals were removed (including any eggs left by females) the filter paper and food discs were left to dry in an oven for 24 hours and were then cooled and weighed. The intake rate is given as intake per individual per hour.

2. Proportion of animals feeding

For each of the 8 hours after the mites were added to an experimental tube the number of animals feeding was recorded. Data was collected using a Leica MZ8 binocular microscope and a hand-held tally counter. The data was converted into a proportion of the total number of animals in the tube feeding.

3. Individual Behaviour

Focal observations lasted for 5 minutes and were taken in between hourly counts of the number of animals feeding. As such, five focal observations were taken per hour from 5 experimental tubes per day; the tube number and time from feeding were recorded. Repeated measures were taken from tubes at varying times from feeding. The behaviours observed and recorded were feeding (chelicerae moving), Moving (in contact with substrate), milling (moving over other animals), flailing (mite on its back) and out of sight (mite not visible). Data are given as proportion of time in sight spent performing behaviours and also as the frequency of behaviour within any observation.

Statistical Analyses

1. Average intake

The data collected were not fully balanced so Residual Maximum Likelihood (REML) analysis was used to investigate the effects of treatment. No random model was fitted as tube is not a factor as there are no repeated measures.

Average yeast weight ingested ~

density+food+group+spatial+density.food+group.spatial

2. Proportion of animals feeding

The effects of treatment on the proportion of animals feeding were investigated with a Quasi-likelihood Generalised Linear Model (GLM) as the data were over-dispersed. Fully balanced data were available for this analysis; a model was fitted with all single terms and two-way interactions. A minimal adequate model was obtained by stepwise deletion from the maximal model. Analysis was carried out in S-Plus 6 professional.

Proportion feeding ~ density*food*group*spatial*Time from feeding (hours)

3. Individual Behaviour

The effects of treatment on individual behaviours, i.e. feeding, combined moving (moving and milling), not moving and flailing, were investigated with Binomial Generalised Linear Mixed Models (GLMM) in GenStat v6.1. Fully balanced data were available for analysis and a model was fitted with all single terms and two-way interactions as shown below. Stepwise deletion tests were used to reduce the maximal model.

Behaviour ~ density*food*sex*spatial* Time from feeding (hours)
Random model: Tube

The number of bouts of feeding and moving were analysed with REML analysis and the same model with stepwise deletion.

4.3 Results

Interference – increasing density maintaining per capita food

Intake rate decreases with increasing density at both food levels, except in the case of the high density, high food treatment (Wald statistic = 70.58, X^2_2<0.001, Figure 1). This is associated with a change in behaviour as density increases – males and females responding differently (Wald statistic = 3.0, X^2_2 <0.050, Figure 2). Males spend a greater proportion of the focal time moving, with an increase in density whereas females spend less time moving as density increases. Both males and females fed in a greater number of bouts with increasing density. Animals did not change the proportion of time they spent feeding with increasing density although it did alter the number of bouts in which feeding was performed – males fed in a greater numbers of bouts per focal time at higher density whereas females fed in a smaller number of bouts per focal time (Wald statistic = 5.13, X^2_2=0.001). In terms of the proportion of animals feeding it was found that density and food level interact in their effect – at high food the proportion of animals feeding decreases with increasing density whereas at low food the proportion of animals feeding tends to increase with increasing density ($F_{2.215}$ = 45.39, P<0.001, Figure 3).

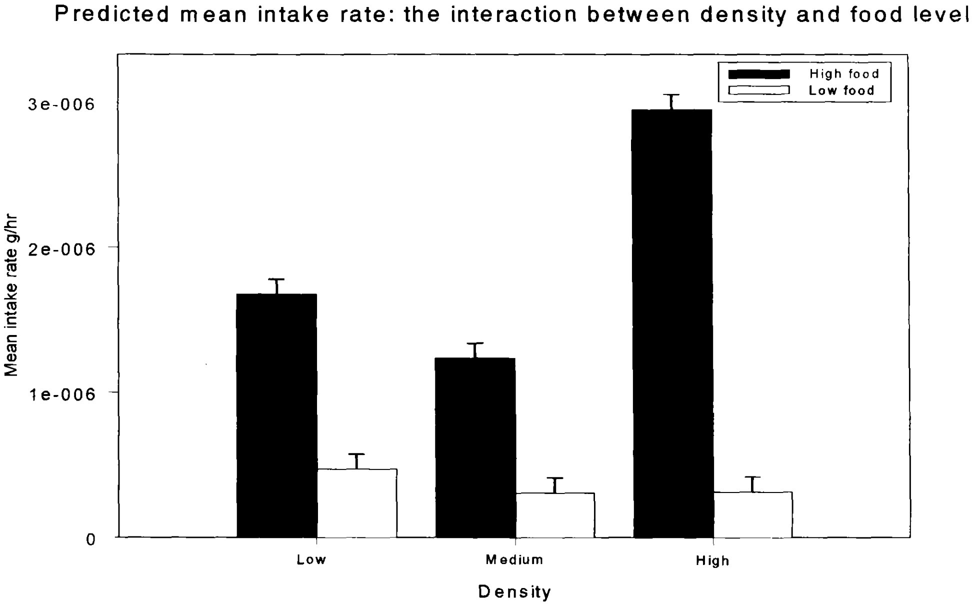

Figure 18 Predicted mean intake rates (and S.E) from REML analysis considering the interaction between animal density and food level (Wald statistic = 70.58, $X^2_2<0.001$).

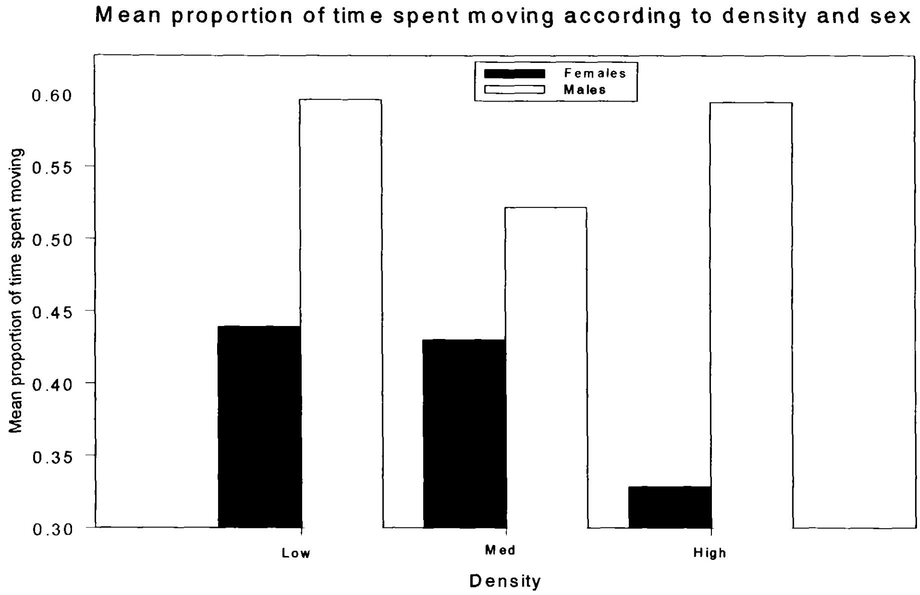

Figure 2 The predicted mean proportion of focal time animals spent moving according to the interaction between density and sex (Binomial GLMM analysis, Wald statistic = 3.0, $X^2_2 < 0.050$)

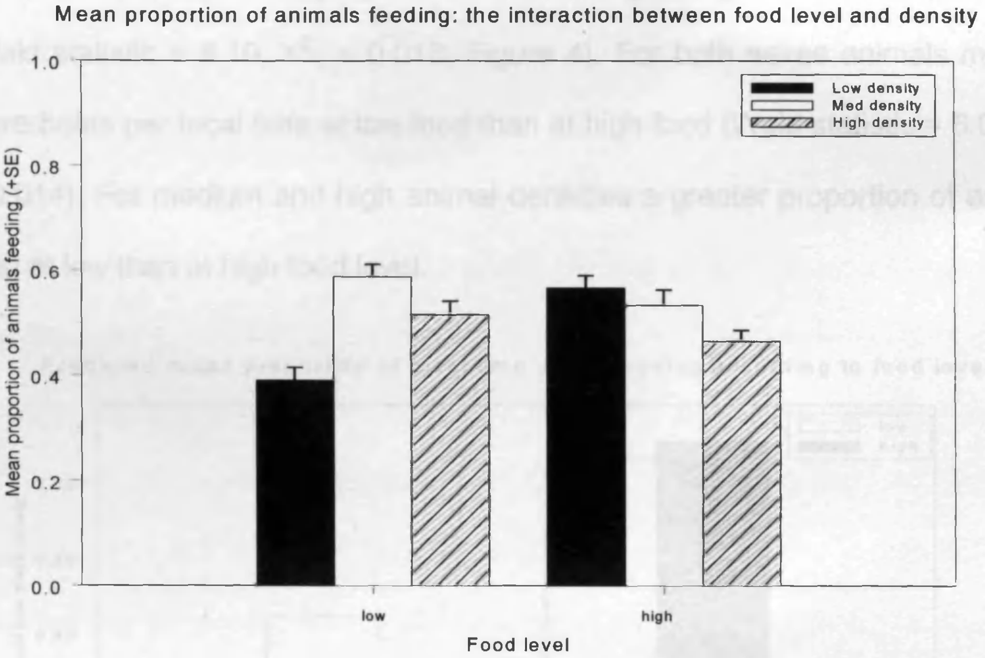

Figure 3 The mean and standard error of the predicted proportion of animals feeding (from quasi-likelihood GLM analysis) according to food level and animal density ($F_{2.215} = 45.39$, $P<0.001$).

Exploitation – changing per capita food, maintaining density.

For both spatial arrangements of food (Wald statistic = 690.99, $X^2_1 <0.001$) and all densities (Wald statistic = 70.58, $X^2_2 <0.001$) intake rate is higher in the high food treatment (Figure 1). Changing the per capita food level had no effect upon the proportion of focal time animals spent feeding (Wald statistic = 0.79, $X^2_1 = 0.375$) or upon the number of bouts of feeding per focal time (Wald statistic =1.90, $X^2_1 = 0.168$). Females spent more time moving at low than high food whereas males spend slightly more time moving at high food than at low food (Wald statistic = 6.10, $X^2_1 = 0.013$, Figure 4). For both sexes animals move in more bouts per focal time at low food than at high food (Wald statistic = 6.09, $X^2_1 = 0.014$). For medium and high animal densities a greater proportion of animals feed at low than at high food level.

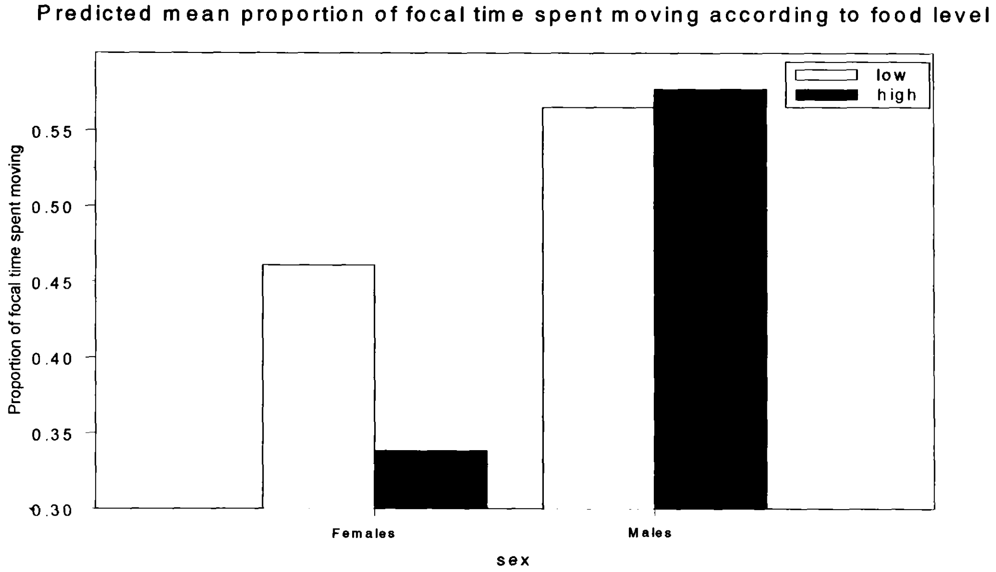

Figure 4 The predicted mean proportion of focal time animals spent moving according to food level (Binomial GLMM analysis, Wald statistic = 6.10, $X^2_1 < 0.013$)

Spatial arrangement

Males and females were found to respond differently to different spatial arrangements of food in this experiment (Wald statistic = 70.58, $X^2_1 < 0.001$, Figure 5). Females have an increased intake rate with spread food whilst males have an increased intake rate with clumped food. This effect upon intake rate was not to alter with density or food level. This difference in intake is associated with differences in behaviour: females spend more time feeding when food is spread than when food is clumped (X^2_1 = 0.010, Wald statistic = 6.62, Figure 6) whereas males spend more time feeding in clumped food (X^2_1 = 0.010, Wald statistic = 6.62, Figure 6). For both sexes, at low food increasing the spread of food decreases the time spent moving, however at high food time spent moving increases (X^2_1 = 0.006, Wald statistic = 7.36). As predicted, overall, increasing the spread of food increases the proportion of animals feeding ($F_{1, 215}$ = 17.57140, P = 0.0000416, Figure 7). With clumped food there is little difference between the proportion of animals feeding at high and low food, however with spread food, a greater proportion of animals feed at high than low food ($F_{1,215}$ = 8.9470, p = 0.0031).

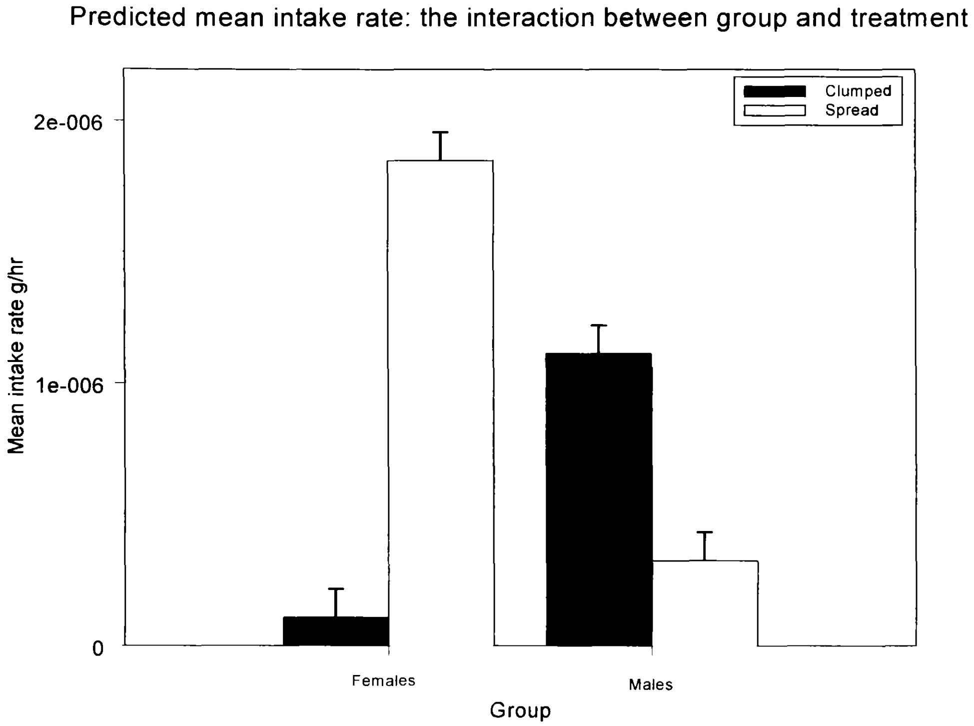

Figure 5 Predicted mean intake rates (and S.E) from REML analysis considering the interaction between group (sex) and treatment (clumped or spread food), Wald statistic = 70.58, X^2_1 <0.001.

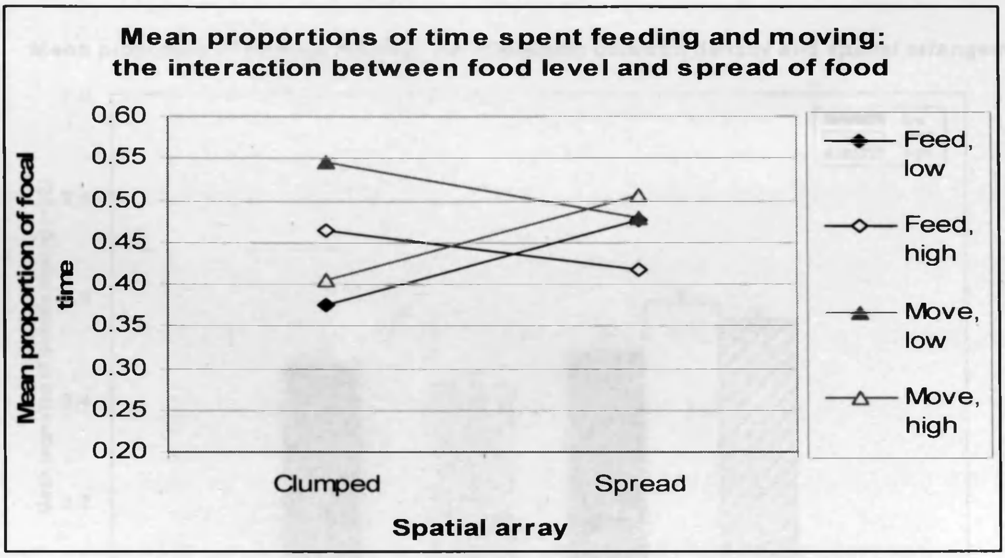

Figure 6 The predicted mean proportion of focal time animals spent moving (Wald statistic = 7.36, $X^2_1 = 0.006$) and feeding (Wald statistic = 6.62, $X^2_1 = 0.010$) according to the interaction between food level (low or high) and spread of food (clumped or spread).

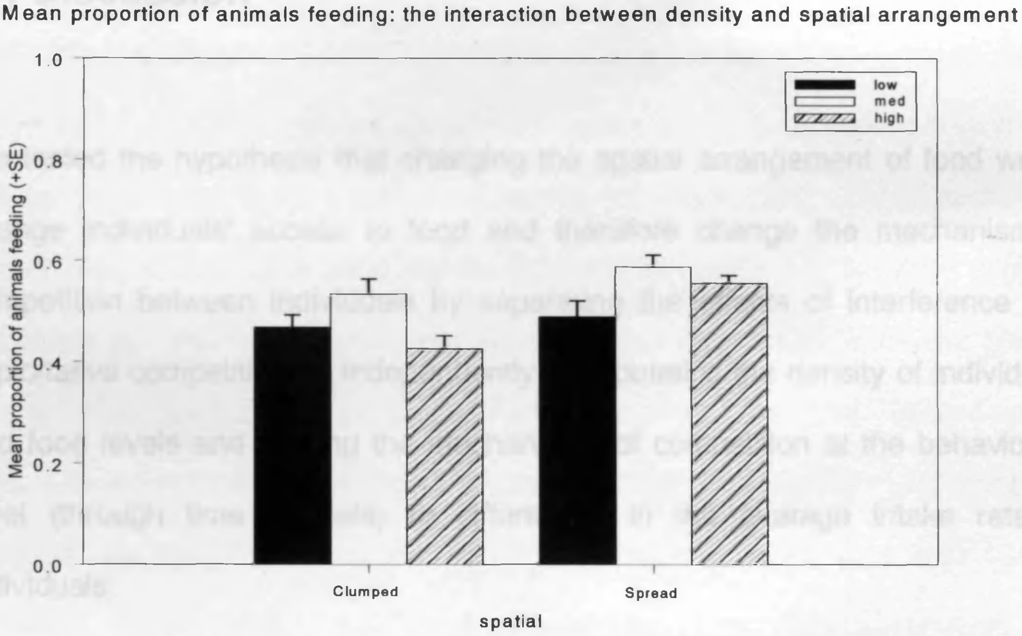

Figure 7 The mean and standard error of the predicted proportion of animals feeding (from quasi-likelihood GLM analysis) according to food level and animal density ($F_{1,215}$ = 17.57140, P = 0.0000416).

4.4 Discussion

We tested the hypothesis that changing the spatial arrangement of food would change individuals' access to food and therefore change the mechanism of competition between individuals by separating the effects of interference and exploitative competition by independently manipulating the density of individuals and food levels and relating the mechanisms of competition at the behavioural level (through time budgets) to differences in the average intake rate of individuals.

Effects of increasing density whilst maintaining per capita food levels (interference)

The evidence for interference competition in this experiment is that average intake was reduced for males and females as the density of individuals increased. There are behavioural time budget differences caused by an increase in animal density, however the behavioural mechanism of interference is unclear. Neither males nor females reduce their focal time spent feeding with increasing density. Males do feed in more bouts with increasing density which could incur higher metabolic costs; however females feed in fewer bouts i.e. their feeding is relatively less interrupted and yet they still experience a reduction in intake compared to lower densities. In calculating the profitability of foraging in a patch versus the cost of searching further, with increasing density a greater density of animals may indicate greater patch depletion and/or incur greater encounters with other individuals which cause them to move more often. Hassall et al (2002) found that the effect of increasing density upon searching behaviour in *Porcellio scaber* depended upon spatial clumping of resources; when food was homogeneous there was no difference in searching behaviour between different densities but when food became more clumped animals spent a greater proportion of their time searching at high than at low densities. There was no such interaction between density and spread of food found in this experiment and other studies have found negative effects of increasing density upon life historical variables independent of food arrangement (e.g. Dye 1984, Lord 1998 and Broadie and Bradshaw 1991). Studies have also shown that interference may appear to be a costly behaviour and bring about changes in the distribution of animals and yet incur little cost (Anholt 1990). As before manipulation of individual behaviour is important for determining the importance of behaviour in individual cases.

Effects of increasing food levels (exploitation)

Increasing food levels in all circumstances in this experiment increased average intake rate, however animals did not increase their time spent feeding, perhaps due to a reduced handling time. Therefore, animals must be able to physically, as well as behaviourally, alter their intake rate. At low food both males and females move in more bouts (indicating higher search costs) than at high food and also at high densities a smaller proportion of animals fed at any one time. Therefore perhaps higher food levels lead to a higher intake leads allowing less movement, with fewer animals feeding at any one time and hence less potential for interference. This shows that it is difficult to separate the effects of food limitation and interactions between conspecifics in this case; changing food levels may act through changing the degree of behavioural actions between individuals as well as food gains and we cannot determine from this data which is more important. In general, the mechanisms of food limitation are less well understood than those of interference (Sutherland and Anderson 1993) although there is much data showing the positive effects of food enhancement upon animal size and survivorship (e.g. MacIsaac and Gilbert 1991, Lord 1998 and Anholt 1990)

Effects of changing the spatial arrangement of food

Exploitation competition may therefore not be as simple as limiting food and more indicative of animals competing through resource levels rather than directly between individuals. The spread of food was increased and it was predicted that this would increase the access to food for animals allowing a greater proportion of animals to feed simultaneously (reducing the likelihood of monopolisation e.g. Grant and Guha 1993), thus increasing the average intake rate. For both sexes, a greater proportion of animals fed at any one time when food was spread rather than clumped. Females spent more time feeding on spread food and had a higher intake rate than on clumped food. However the reverse was true in the case of males who had a lower intake when fed spread food. It therefore seems that males and females have different responses to changes in the spatial arrangement of food.

In summary, this experiment found that both increasing density whilst maintaining per capita food and reducing food levels whilst maintaining density are found to decrease intake rate. Increasing the spread of food irrespective of density and food level increased intake for females and decreased intake for males. There are differences in behavioural time budgets associated with these differences in intake and hence there is evidence for the importance of individual behaviour at the population level – it has implications for the intake of individuals which will impact upon the animal's reproductive decisions and offspring condition as shown in other studies (e.g. MacIsaac and Gilbert 1991, Lord 1998, Anholt 1990, Dye 1984, Lord 1998 and Kendal et al 1991). However, in this study the behavioural mechanisms changing intake rate are not clear, for example, an increase in intake is not necessarily associated with an increase in feeding or decrease in energy expenditure through moving.

It is clear that factors other than density and food level played a role in determining the behavioural time budgets of mites in this experiment. The costs and benefits associated with the behaviours seen need to be further identified in order to determine fully the significance of the differences. The experiment was to separate the effects of food limitation, density and the spread of food and significant effects of each were identified (although it is difficult to compare these due to a lack of knowledge of how each factor scales to the other). However the experiment still used a correlational link between behaviour and intake rather than a direct manipulation of particular behaviours i.e. the number of interactions between animals. Differences in time budgets were seen between males and females and there are also likely to be differences between individuals within the sexes, which may also change with patch quality (Cresswell et al 2001) density (Tregenza et al 1996) or prior experience of competition and physiological state (Goubalt et al 2005).The results have dealt with average intakes whereas theory suggests that, the differences in predictions of population stability are due somewhat to differences in the predicted equality in distribution of resources between scramble and contest (Nicholson, 1954). It was not possible to measure inequality in intake rates here although it would be a valuable area of further research to determine whether differences in the proportion of animals feeding did equate to differences in the allocation of food.

Changing the spatial arrangement of food has been discussed as altering the mechanism of competition between and within life stages within populations of a single species. In general, the mode of competition is discussed as being set in the biology of a species (e.g. Weir and Grant 2004) in that the response of life-historical variable to increasing density is often used to describe a species and its predicted response in novel situations. However, differences in foraging strategies between individuals according to varying conditions of a species are often investigated (e.g. Huey and Pianka 1981, Pitt and Ritchie 2002 and Goubalt et al 2005) and yet the implications of this at the life-historical level are rarely considered. Certain aspects of the biology of *Sancassania berlesei* mark it out as an 'r' selected species in that it is a short-lived high fecundity species that tends to produce a large number of offspring as opposed to investing in a few high quality offspring. Changing the spatial availability of food for laboratory populations of *Sancassania berlesei* was shown to change the proportion of animals accessing that food, which could have implications for the stability of a population to resource depression. This is not generally considered in the prediction of population responses to novel environments but could be the case in other species. The importance of habitat complexity and fragmentation to persistence and population dynamics is much discussed (e.g. Kareiva 1987, 1990 and Kareiva and Wennergren 1995) and perhaps the importance of individual behavioural mechanisms in determining this should also receive more attention.

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Chapter Five:

The life historical and population level effects of changing spatial food availability in laboratory populations of the soil mite *Sancassania berlesei*

5.1 Introduction

There is theory and data to suggest that animals change their behaviour in response to changes in spatial food availability (e.g. MacArthur and Pianka 1966, Charnov 1976, Hassall et al 2002) and the importance of individual behaviour to population dynamics has gained increasing attention (Anholt 1990, Smith et al 2000, Bjornstad et al 1994), as pressure increases upon ecological models to produce more accurate quantitative as well as qualitative predictions of population responses to changing environments (Bradbury et al 2001). A foraging animal offsets the energy gained from gaining food with the loss of energy through searching and changing the spatial aggregation of food will affect the balance of these energy gains; increasing density and food aggregation have been found to increase the time animals spent searching for food (e.g. Hassall et al 2002). The clumping of a resource may also change the potential for that resource to be monopolised, as a smaller, more clumped area of resource may be less costly to defend. In this way changing the clumping of a resource may change the allocation of resources between individuals i.e. changing the manner of competitive interactions between animals. Where food is dispersed, food gains per individual may be more even but where food is more clumped food and monopolisation may be possible, gains may be less equal between individuals. Different forms of competition are predicted to lead to different dynamics for this reason (Nicholson 1954, Rees and Crawley 1989). How do these differences in individual behaviour link to population dynamics?

Foraging and food availability effort directly determine intake rate. Subsequent resource allocation decisions e.g. growth, maturation and fecundity will be made on the basis of intake, determining how an individual's current conditions will affect its life history and that of its offspring. With given resource conditions an animal must decide how to maximise its resource gains and how to allocate those gains to the various aspects of its life history e.g. current growth versus reproduction. Evolution (analysed in terms of optimisation, quantitative genetics or evolutionary stability according to the frequency dependence of fitness) will act upon the fitness consequences therein and it is the power of evolution to create these behavioural responses and not a conscious decision by the animal which is considered. Phenotypes may therefore change with environmental conditions and reaction norms are used to show how a phenotype will change over a range of conditions e.g. resource level versus age at reproduction. Animal size is often positively correlated with fecundity, growth and mortality/survivorship (Rivero and West 2002, Roff 1992) and life-history transitions tend to occur at younger ages and larger sizes as growth conditions improve. Day and Rowe (2002) found that theory did not predict this outcome without the inclusion of a development threshold whereby some condition must be reached before a life-history transition (e.g. maturation) can occur. With a developmental threshold, under poor conditions individuals grow slowly and are small when they reach the threshold. There is little advantage to be gained by delaying maturity at a small size. Consequently, in low food conditions there is predicted to be little variation in size at maturity but greater variation in age at maturity and vice versa for high food environments (Plaistow et al 2004). Similarly if the degree of food clumping affects the degree of equality in food distribution then it could also affect the distribution of sizes and ages at maturity of individuals within a colony. Differences in age and stage structures will have implications for the stability of populations to perturbation (Cameron and Benton 2004), and are important even in the absence of obvious differences in population numbers.

Historical as well as current conditions (Ergon et al 2001) are being found to be of increasing importance in the life history and population dynamics of species through delayed life history effects (Beckerman et al 2002). Examples include maternal effects, whereby the mother allocates resources to her offspring relative to her own conditions (and therefore current environmental effects are passed to future generations), (e.g. in mammals; Festa-Bianchet et al 2000 and in insects; e.g. Rossiter 1991); and compensatory growth (delayed growth costs) whereby current conditions for juveniles affect life history decisions later on in life (Metcalfe and Monaghan 2001, Yearsley et al 2004); both of which may create cohort effects, which occur when environmental effects are synchronised across an age or stage class (Beckerman et al 2002). These delayed effects are predicted to have a potential destabilising effect, dependent upon the underlying dynamics of a population (Lindstrom and Kokko 2002, Benton et al 2001, Plaistow et al 2004).

Effects of differential food availabilities in *S.berlesei*

Plaistow et al (2004) have shown that there is an L shaped reaction norm in *S. berlesei* between age and size at maturity and therefore differential food gains between individuals and in different environments, will give different distributions of ages and sizes of individuals. Maternal effects also are seen in this system as differential maternal allocation of resources to eggs as a function of current conditions and a female's age. The response of the offspring to maternal allocation is not simple and is found to vary in persistence and significance and in trait's affected according to their current food level and were measurable over three generations (Plaistow, Lapsley and Benton, in press). It is predicted that colonies fed different spatial distributions of food (and at different densities, if the effects of spatial food availability are density dependent) will have different behavioural time budgets and hence different distributions of intake rates (Truelove et al unpublished data). These intake rates are predicted to lead to different distributions of animal sizes, age and stage distributions and differences in dynamics. In this experiment colonies will be started with equal numbers of eggs and the effects of competition through resource availability will be determined by measuring the growth, size and age at maturity of the first generation. The effects upon the size and number of adult, juveniles and eggs in subsequent generations are also investigated. Here evidence of differences between the populations in terms of size, age and stage distributions correlated with differences in spatial food availability will be taken as evidence of the population level effects of individual behaviour.

5.2 Methods

Source of Experimental Eggs

Experimental eggs were derived from a half teaspoon of standard laboratory stock mites distributed amongst 10 holding tubes. After the mites were removed from the stock they were fed an excess of food (yeast) for 14 days. On the fifteenth day 400 adult females were removed and placed in eight laying tubes (density 50). Whilst in the laying tubes no food was given to avoid inter-tube variation in food amount and prevent eggs being laid directly on yeast. Three thousand eggs were removed the next morning and placed in 20 experimental tubes (4 treatments, 5 populations per treatment). Half of the experimental tubes were started with 250 eggs (high density treatment) and the other half with 50 eggs (low density treatment). In addition to the density treatments, two food treatments were prescribed across the density treatment with half the tubes receiving balls of yeast (1.25 – 1.4mm diameter) and the other half the equivalent weight (0.00172g ± 0.00003) of powdered yeast. The resultant four treatments were equally divided with five tubes in each treatment.

The Initial Cohort

For the initial cohort, a full daily count of the juveniles (initially the number hatched) at each instar (i.e. stage structure) was taken, including the number of senescent individuals. Each day 8 photographs of the cultures in each tube were taken at x40 zoom from which 10 measures of length per instar stage per tube were taken.

Later Cohorts

After the first generation it was no longer possible to accurately determine the 1st from subsequent generations. From this point there was a change in the methodology. Counts continued daily but were taken over a quarter of each tube as numbers of juveniles and eggs rose above 1000. Juvenile age structure was estimated by randomly sampling 50 juveniles per tube. Ten size measurements were taken for each group (1st, 2nd, and 3rd instar juveniles, males, females and eggs) in each tube. Photographs were taken at different magnifications for each group with eggs and juveniles being photographed at x40 and adults at x15 magnification. All photographs were taken using a Canon Powershot S40 digital camera attached to a Vision Engineering, 'Lynx' head-up stereo microscope. Length was measured as the distance from the tip of the hypostome to the tip of the opisothoma using the free software package Image J (1.28U); an image analysis package downloadable at http://rsb.info.nih.gov/ij.

The Proportion of Animals Feeding

An estimate of the proportion of animals (adults vs. juveniles) feeding was taken twice daily. Estimates were made at 1 and 5 hours after the addition of the daily food ration in two of the five tubes per treatment (8 tubes in total). The measurements were taken by counting all the individuals on a ball of yeast and counting the number of animals feeding in a ¼ of the powder tubes (multiplying up).

Statistical Analyses

Time series

The time series data were separated according to group (males, females, juveniles and eggs) and the density data were bootstrapped to gain a mean and 95% confidence interval per treatment per day. Where the bootstrapped mean and confidence intervals did not overlap the treatments were considered to be significantly different.

Size structure

Growth of the initial generation

For the first nine days of the time series (until animals began to mature), the mean and standard error of the daily juvenile size was calculated for each treatment. Each day's size is estimated from 30 individuals per tube = 250 individuals in total per treatment

Time series of animal lengths

Quasi –likelihood GAM models were fitted to the time series data for female, male, juvenile and egg sizes. Predicted fits are displayed on a response variable scale and a standard error of the predictions is given. To gain the best fitting model, differing degrees of freedom were fitted and compared using the Cp statistic as data were not independent according to time.

The overall effects of density and food type upon size

REML analyses were carried out into the predictive effects of start density and treatment (food type) and the interaction between them on female, male, egg and juvenile length. Day and Tube effects were included as a random model. Instar was added, as a factor, to the analysis of juvenile length.

Stage Structure

The Initial generation of juveniles

Binomial GAM models were fitted to the time series data for the proportion of first, second and third instars within the juvenile part of the population for the first 20 days of the time series. Predicted fits are displayed on a response variable scale (proportion of total juveniles) and a standard error of the predictions is given. To gain the best fitting model, differing degrees of freedom were fitted and compared using the Cp statistic as data were not independent according to time.

GAM models of stage structure in subsequent generations of juveniles

Binomial GAM models were fitted to the time series data for the proportion of first, second and third instars within the juvenile part of the population for the later part of the time series, days 20 to 37. Predicted fits are displayed on the response variable scale (proportion of total juveniles) and a standard error of the predictions is given. To gain the best fitting model, differing degrees of freedom were fitted and compared using the Cp statistic as data were not independent according to time.

Age Structure

The age structure is presented as Quasi-likelihood GAM model fits of the daily adult: juvenile ratio per treatment. Adult: juvenile ratio was the response variable with (a spline fit of) day and tube as factors. Data are represented as daily predicted ratios with a standard error. To gain the best fitting model, those with differing degrees of freedom were fitted and compared using the Cp statistic as the data were not independent according to time.

Proportion feeding

The proportion of juveniles, adults and total animals (those feeding i.e. the sum of adults and juveniles) feeding per time step (i.e. 1 or 5 hours from feeding) were calculated for each day and tube. For each proportion separately (total animals, adults and juveniles), a binomial GLMM was fitted considering the time from feeding (one or five hours), food type (balls or powder), starting density, adult density (per tube per day), juvenile density (per tube per day), and all the two way interactions between them with tube as a random factor. Stepwise deletion was carried out to gain the minimal model.

5.3 Results

Population Dynamical consequences of treatment effects

The time series data show clear differences in dynamics between the colonies fed on powdered yeast and those fed on balls of yeast and due to starting conditions (density). The mites in the powder treatment are lagged in respect to those fed balls of yeast for males, females, eggs and juveniles (Figures 1 and 2). Increasing density also has the effect of delaying the development of the populations within food type; both densities hatch at the same time and yet the development is slower in the colonies with a higher starting density. The low density colonies fed balls have on average the fastest development, with those at high density fed balls and those at low density fed powder apparently equal; those high density colonies fed powder had the slowest developmental rate. Whilst the two food treatments seem to produce roughly equal adult densities (powder treatments have slightly lower survival initially) both in the initial and F_1 generations, juvenile and egg densities are lower in colonies fed powder. Regardless of treatment the data suggests that males are longer lived than females with the initial and F_1 generations overlapping. This overlap in the male population avoids the marked decrease seen in the female data prior to the F_1 generation maturing.

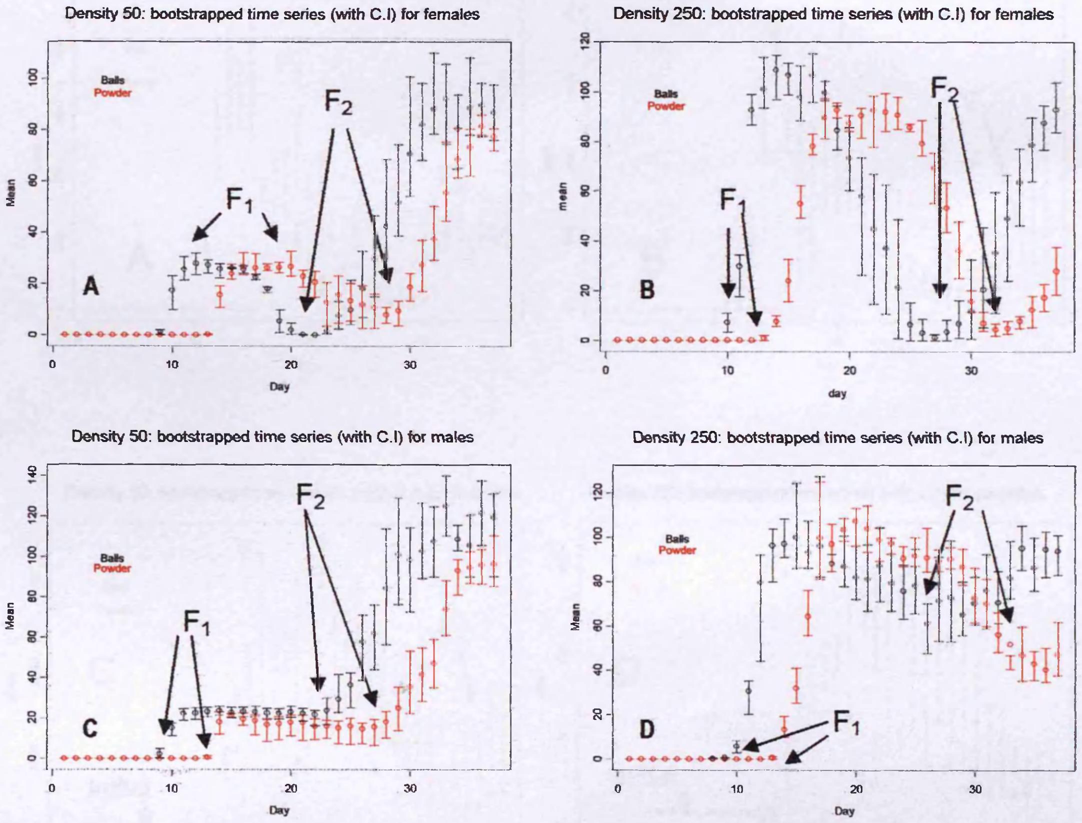


Figure 19 Figures 1A and 1B show the bootstrapped time series and 95% confidence interval (N=5), for females at density 50 and 250 respectively. Figures 1C and 1D show the bootstrapped time series and 95% confidence interval (N=5) for males at density 50 and 250 respectively. F_1 and F_2 arrows indicate the beginning of the generation in each case.

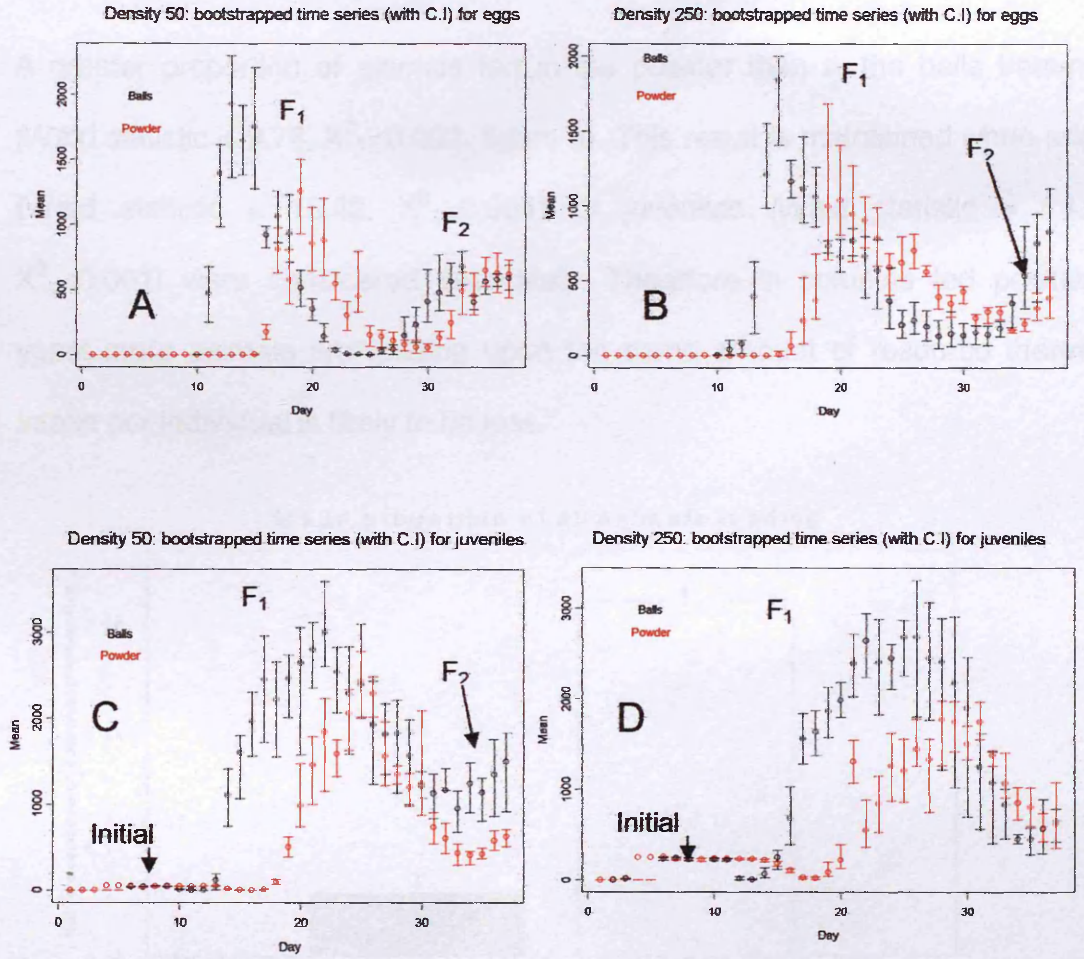


Figure 20 Figures 2A and 2B show the bootstrapped mean and 95% confidence interval (n=5) of egg numbers from a starting density of juveniles of 50 and 250 respectively. Figures 2C and 2D show the bootstrapped mean and 95% confidence interval (n=5) of juvenile numbers from a starting density of 50 and 250 respectively. Initial, F_1 and F_2 label the generations occur in the time series.

Mechanisms of Population level effects

1. Treatment effects upon the proportion of animals feeding

A greater proportion of animals fed in the powder than in the balls treatment (Wald statistic = 9.76, X^2_1=0.002, figure 3). This result is maintained when adults (Wald statistic = 15.42, X^2_1<0.001) or juveniles (Wald statistic = 14.97, X^2_1<0.001) were considered separately. Therefore in colonies fed powdered yeast more animals are feeding upon the same amount of resource therefore intake per individual is likely to be less.

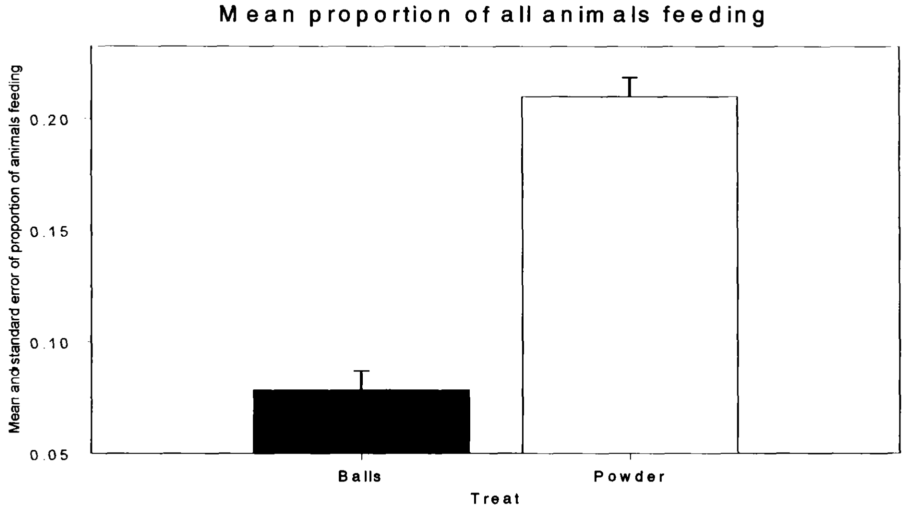


Figure 3 Predicted proportion feeding and standard errors from a binomial GLMM analysis according to food type i.e. balls of yeast or powdered yeast.

2. Treatment effects upon the growth of the initial cohort of juveniles

Animals fed balls of yeast are predicted to have a higher intake than those fed powdered yeast and in the initial generation, juvenile animals fed balls of yeast were found grow faster and were larger than those reared in colonies fed powdered yeast, irrespective of density Figure 4). The GAM fits for the proportion of juveniles of each instar in the initial generation show that there is no maintenance in the first generation of a mixed instar population for any length of time for either food type (figure 5). The individuals mature and pass to the next life stage as a single cohort (the proportion of any instar is either 0 or 1) although as previously mentioned colonies fed powdered yeast experience a lag in development with respect to those fed balls of yeast.

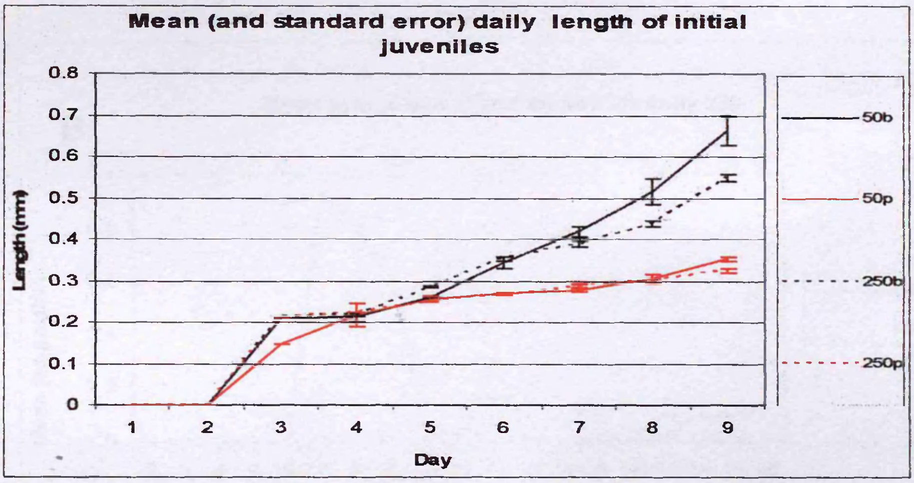
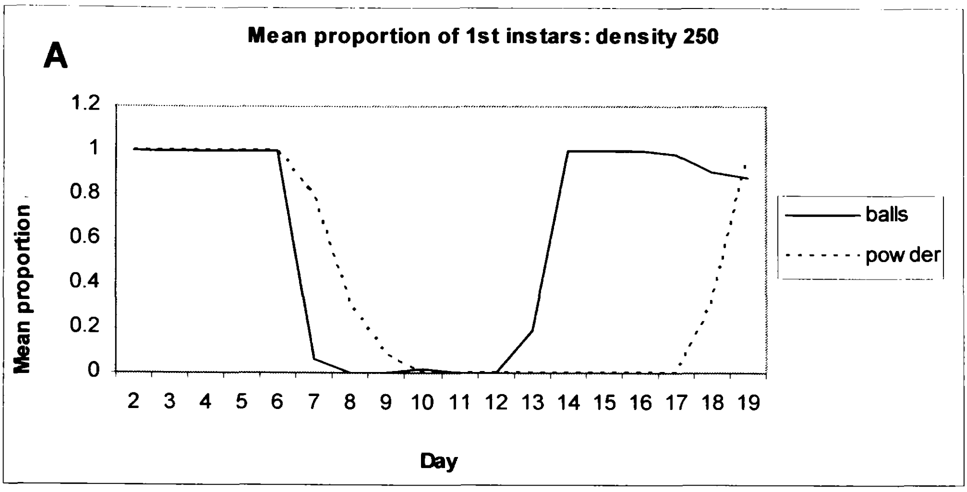
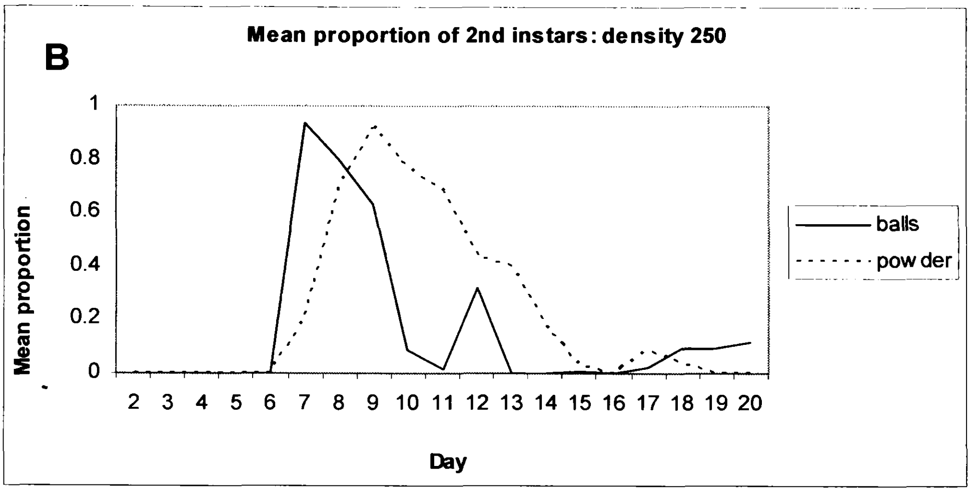


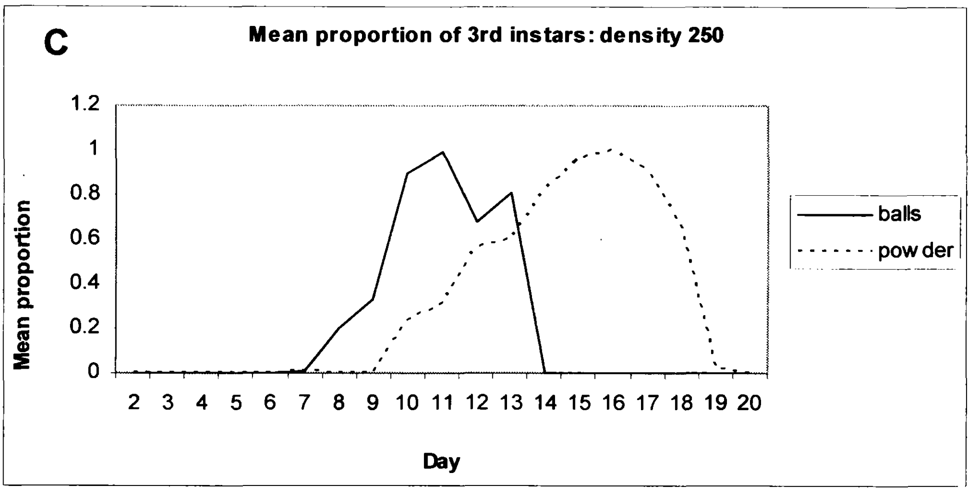
Figure 4 Mean and standard error of the daily juvenile size per treatment. Each day's size is estimated from 30 individuals per tube (tube mean) and the value given is the average of the tube means.



A Mean proportion of 1st instars: density 250



B Mean proportion of 2nd instars: density 250



C Mean proportion of 3rd instars: density 250

Figure 5 Binomial GAM model predictions of the proportion of each instar according to food type for colonies started at a density of 250 eggs.

3. Treatment effects upon size

The treatment effects (spatial arrangement of food) had a remarkable consistent effect upon female, male and egg sizes. Female length was significantly related to the interaction of initial density and food type (Wald statistic= 367.25, X^2_1 <0.001, figure 6), with smaller females produced in high density colonies and larger females found in tubes fed balls of yeast. The results for males mirror those of the adult females with the interaction between initial density and food type being significant (Wald statistic = 184.68, X^2_1 <0.001). As seen in females, the predicted length of males at low density in colonies fed powdered yeast overlaps with that predicted for high density males in balls. It appears that the feeding of yeast in powdered form is akin to that of increasing density five fold when animals are fed balls of yeast. When investigating the effects of treatment on the length of eggs from the F_1 generation onwards the interaction between initial density and food type is also significant (Wald statistic = 12.21, X^2_1 <0.001). Although adult sizes overlap between low density powder fed treatments and high density ball fed colonies, on average, the animals in the high density balls lay significantly smaller eggs than those in the low density powder treatment.

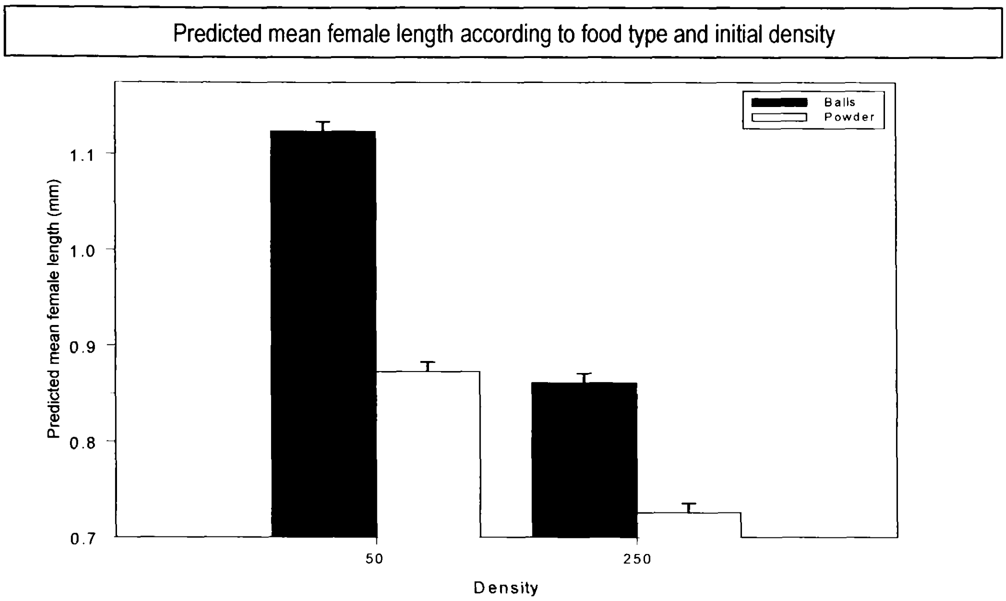


Figure 6 Predicted mean female length according to food type and density from REML analysis.

The treatment effects upon juvenile sizes are more complicated owing to the stage being separated into 3 instars before maturation. The interaction between initial density and food type with respect to juvenile length was not significant (Wald statistic = 1.25, X^2_1 = 0.264) contrary to the other life stages. However treatment (balls or powder) and initial density separately have a significant effect upon juvenile size in their interaction with instar. First and third instars are larger in colonies fed balls than powder whereas the reverse is true for second instars (Treat.Instar: Wald statistic = 73.43, $X^2_1<0.001$, table 1) and all instars are larger in colonies with a starting density of 50 than 250 (Start density. Instar: Wald statistic = 49.28, $X^2_1<0.001$, table 1). It is thought likely that 1st instar juveniles are larger than those in powder as they come from on average larger eggs, second instars may be smaller as competition is more intense as colonies fed balls tend to have higher juvenile numbers (Figure 2).

Food Treatment

	Juvenile Instar: mean predicted length		
Treatment	**First**	**Second**	**Third**
Balls	0.2338	0.3431	0.5114
Powder	0.2279	0.3563	0.5089
Initial density	**First**	**Second**	**Third**
50	0.2360	0.3548	0.5074
250	0.2256	0.3446	0.5130

Table 1 Predicted length per instar according to initial density from a REML analysis.

Treatment effects upon the time series of size

In terms of how animal length varies over time, simultaneously with the larger initial oscillation in adult number in colonies fed balls of yeast, adult female sizes are larger in colonies fed balls of yeast than in those fed powdered yeast (Figure 7 - males are smaller than females but the relationship between food treatments is the same). The GAM models for the female length time series also show that for all treatments (except high starting densities fed powdered yeast) animals are larger in the initial generation than in subsequent generations. The high density colonies fed powder maintain a relatively constant animal length. Towards the end of the time series adult lengths in these colonies overlap with those of the other treatments. Overall the trend is for adult sizes to decrease over the time series as overall colony size and therefore competition, increases.

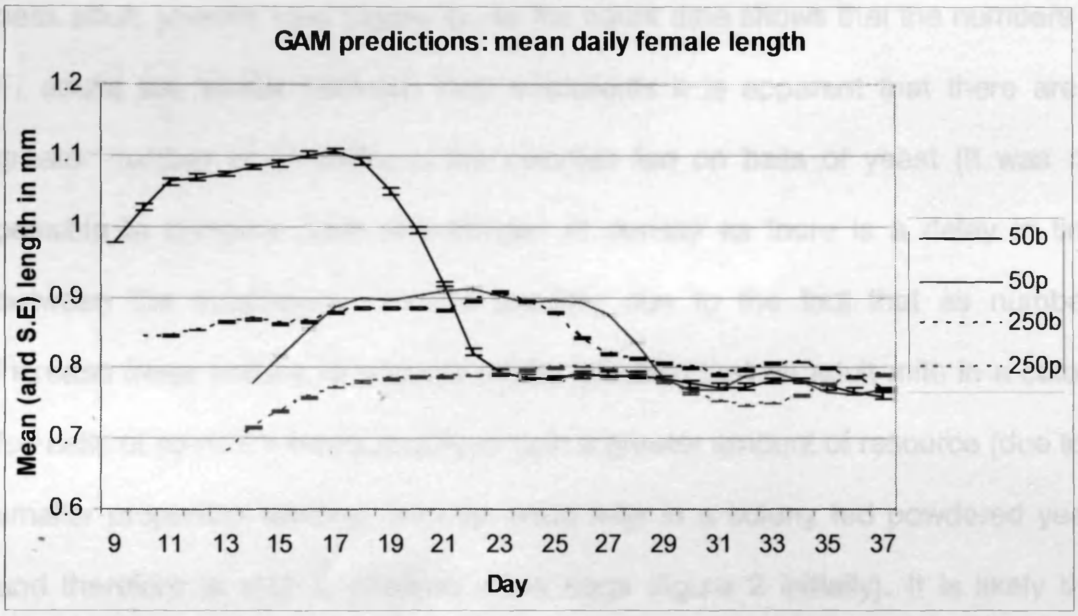


Figure 7 GAM predictions for the time series of mean daily female length according to food arrangement (balls or powder) and initial egg density (50 or 250).

Treatment effects upon the time series of the adult: juvenile ratio

Although adult sizes may become more similar as the time series progresses, the age structure data shows differences that are maintained between populations. At low densities, from day 20 to 37, those colonies fed balls of yeast have a lower peak adult: juvenile ratio (figure 8). As the count data shows that the numbers of F_1 adults are similar between food treatments it is apparent that there are a greater number of juveniles in the colonies fed on balls of yeast (It was not possible to compare balls and powder at density as there is a delay in time between the treatments). This is possibly due to the fact that as numbers increase fewer mature to become adults and also that an adult mite in a colony fed balls of yeast if it feeds, is able to gain a greater amount of resource (due to a smaller proportion feeding) than an adult mite in a colony fed powdered yeast and therefore is able to produce more eggs (figure 2 initially). It is likely that differential intakes between adults in the different food types are creating and perhaps would maintain these differences in adult: juvenile ratio (this has been seen in previous studies, Truelove et al unpublished data).

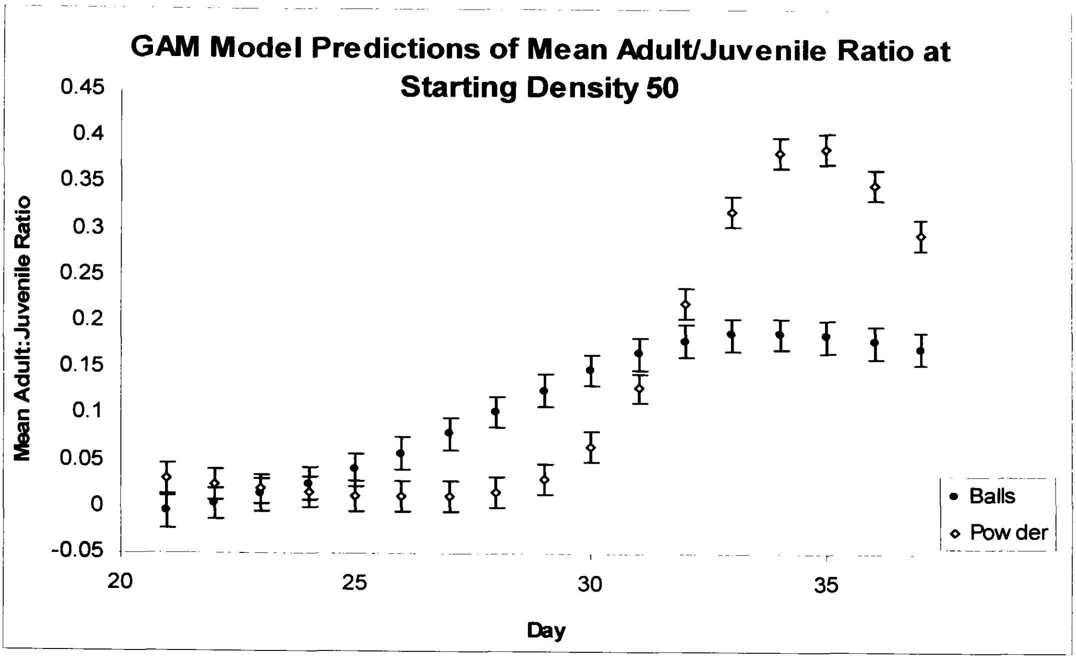


Figure 8 Mean and standard error of GAM predictions of the adult: juvenile ratio for days 20 to 37 at initial density 50.

5.4 Discussion

This experiment provides evidence that changing the spatial availability of food has an affect that links the individual's access to resources through life history to population structure and dynamics. In summary, a greater proportion of animals were found to feed in colonies fed powdered yeast than in colonies fed balls of yeast. This agrees with other studies which also show that food which is clumped is more easily monopolised (Grant and Guha 1993). Previous data from this system (Truelove et al, unpublished data), linked similar differences in the proportion of animals feeding to a decrease in average intake rate and differences in individual time budget. Animals in colonies fed balls of yeast were also found to be larger (over the whole time series) than in colonies fed powdered yeast and the initial generation of juveniles also grew faster than those animals. Over the time series as density increases adult sizes are found to decrease in all colonies and densities. In both density treatments, colonies fed powdered yeast displayed different dynamics and magnitude of numbers to colonies fed balls of yeast and these dynamics are delayed with respect to the other treatment. The effect of increasing density five-fold, whilst having the added effect of delaying dynamics by a couple of days in the case of powder and balls seems to be diminished compared to that of changing the spatial availability of food. This is demonstrated by the differences in growth rates between the treatments for the first group of juveniles – those fed balls of yeast grew faster and matured larger than those fed powdered yeast, irrespective of density.

Therefore a greater proportion of animals feeding in colonies fed powdered yeast (indicating a lower average intake) are linked to an overall smaller size of these animals, a lower magnitude of (damped) oscillations in population numbers and a different age structure.

Mechanisms predicted to be creating this link between behaviour and population dynamics were delayed life history effects (Beckerman et al 2001) through maternal effects in an egg size and number trade off (Benton et al, in press) and cohort cycles through an 'L' shaped reaction norm observed in this system between age and size at reproduction (Plaistow et al 2004). The reaction norm (with a maturation threshold) predicts that animals which are better provisioned and grow faster will mature younger and be more variable in size whereas those which grow more slowly will mature at the threshold (i.e. not be variable in size) and be more variable in age at maturity (Day and Rowe 2002). It was predicted that as a greater proportion of animals have access to food when fed powdered yeast, that each animal would have relatively a lower gain and would grow slower and hence maturation would be more variable between animals of the same cohort with respect to age. In the colonies fed balls of yeast it was predicted that although fewer animals would gain access to resources, those animals would gain a larger amount and thus grow and mature faster and earlier and be more variable with respect to size which may have created cohorts of juveniles maturing at a similar age and dying together creating the damped oscillations seen. No differences in juvenile stage structure were seen but there was a lag in development in animals fed powdered yeast with respect to those fed balls of yeast. The same trend of development through the cohorts was seen but this was delayed in the colonies fed powder with respect to those fed balls of yeast as development was initially slower. However the differences in initial dynamics can be linked to differences in initial sizes as predicted - initially animals in colonies fed balls of yeast were much larger than those in colonies fed powdered yeast and hence laid more eggs leading to the initial difference in magnitude of oscillations in numbers (and led to a greater degree of competition in the F1 generation).

The difference in the magnitude of the initial oscillations in dynamics between colonies fed balls of and powdered yeast is transient (i.e. decaying oscillations). Theory shows that in high fecundity populations, small differences in starting conditions (i.e. numbers) can create very different population dynamics (May 1974) as such these differences may simply be a result of differences in experiment set-up and not related to the different food types. However, source eggs were randomly assigned to tubes and tubes were randomly assigned to treatments and there were no significant differences in eggs among the treatment groups, thus we have confidence that the results reflect robust differences due to treatment effects. The dynamical differences are not unimportant because they are transient - more attention is being given to the analysis of transient dynamics (near-term sensitivity analysis e.g. Koons et al 2005, Yearsley 2004), indeed in terms of threatened populations transient dynamics may be more common than those which are asymptotic and in a variable world will continuously reoccur. Unstable age distributions lead to very different predictions for the growth rate and sensitivities of a population to those which are asymptotic (Koons et al 2005) and therefore an accurate knowledge of the populations initial structure is important for the accuracy of near-term sensitivity analysis (Yearsley 2004). The populations here displayed different age structures for colonies in the two food types over 37 days, hence during that time they would respond differently to perturbations such as harvesting (Cameron and Benton 2004). Previous data for this system suggest that this difference in age structure is maintained for over 300 days (Truelove et al unpublished data) and suggest that these populations will always respond differently.

Ultimately there is the question of the adaptive value and evolutionary potential of the changes described herein, as consistent differences in environment may lead to evolved responses; as discussed in the case of harvesting (Ernande et al 2003). In using optimality theory for animal behavioural and life history decisions and in considering the potential destabilising effect of these size-fecundity (Rees and Crawley 1989) and delayed life history effects (Beckerman et al 2002, Benton et al 2001) the question is posed as to the possible evolutionary pressure for population regulatory behaviour. We do not make any statements concerning the evolutionary consequences in this case as in order to do so a greater knowledge of the predicted optimal responses and genetic basis for the change of phenotype would be needed. Further to this, the importance of habitat complexity and fragmentation to persistence and population dynamics is much discussed (e.g. Kareiva 1987, 1990 and Kareiva and Wennergren 1995) we have shown that changing the spatial availability of food for laboratory populations of *Sancassania berlesei* changes the proportion of animals accessing that food, the initial size structure of adults, the initial magnitude of (decaying) oscillations in population numbers and the age structure. This is not generally considered in the prediction of population responses to novel environments but important on other species as a by-product of habitat fragmentation or degradation or for those who are a possible target species for supplementary feeding.

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Chapter 6: General Discussion

An Empirical Study Linking An Empirical Study Linking Behaviour and Population Dynamics: Altering Spatial Food Availability in a Mite Model System

Differing spatial availabilities of food were found to cause different behavioural time budgets, life histories and dynamics in laboratory populations of *Sancassania berlesei.* Differences in competition at the individual level have been shown to have implications at higher levels of population response. It has been discussed how theoretical studies have suggested that individual level processes could have profound implications for the predictions at the population level (e.g. Smith et al 2000) and yet that these influences of individual variation upon population variation may not be monotonic (Grimm and Uchmanski 2002). Indeed studies of the mechanisms of competition at the individual level have also called for greater research into the specifics of competition at different levels of response (Toquenga and Fujii 1990) and this study adds to the weight of research in support of this.

At an individual level many foraging studies have related changes in food availability to changes in behaviour and the effects of differences in competition on intake and life historical outcomes (e.g. Hassell et al 2002, Cresswell et al 2001, Peckarsky 1991, Weeks 1990 and Cross & Benke 2002). This study was in agreement with previous research, finding a strong effect of search time upon resource gain, its importance shown by optimal foraging theory. It was found that individual behaviour changed with food arrangement and was consistent with different types of competition described at the individual level in terms of resource allocation between individuals i.e. interference and exploitation. However further to this, these behavioural differences were linked to behavioural mechanisms of competition through average intake and the proportion of animals feeding. It was found that changing the spatial food availability from clumped to spread food changed the proportion of animals feeding i.e. the number of animals that could access a resource and subsequently the average intake of a group of animals. Hence a mechanism has been shown which could explain the life historical differences between food types and the population level differences therein.

Theory predicts that for a single species in a constant environment that over-compensatory density dependence will tend to be destabilising and compensatory density dependence will be stabilising (May et al 1974, May 1975, May and Oster 1976, Hassell Lawton and May 1976 and Bellows 1981). Over-compensatory density dependence is termed scramble competition, where all animals are said to suffer from a lack of resources equally; compensatory density-dependence is termed contest competition where there are winners and losers in access to resources and when experiencing resource depression some animals will always do better than others e.g. due to competitive superiority or territoriality. At an individual level scramble and contest competition have been assumed to equate to interference and exploitation competition respectively. At this level competition is described in terms of resource allocation between individuals whereby interference competition describes where animals control access to resources e.g. through territoriality, and exploitation competition describes where animals interact through the level of resource and by exploiting the resource to make it unavailable to others. In this case populations of soil mites fed balls of yeast i.e. clumped food displayed more instability in their dynamics i.e. a greater degree of over-compensatory dynamics than colonies of animals fed powdered yeast. Theory into the forms of competition leading to different population dynamics in a single-species context and a constant environment (e.g. May 1974) used to predict forms of competition at the individual level (Begon et al 1990) would have incorrectly predicted the mode of competition between individuals in this case. It is found here that interference-like competition, when food is given in a clumped manner, leads to fewer animals accessing the resource but a higher intake rate i.e. fewer animals accessing more resources which is similar to what is described for exploitation competition. In this study interference competition has been linked to contest competition - which would be predicted from theory - and yet that these competitive conditions can lead to a degree of over-compensatory density dependence and not compensatory density dependence as would be predicted. This shows the need to be specific about individual level processes in order to identify the correct mechanisms of competition.

In terms of the stability of the populations, here in colonies fed balls of yeast different resource allocation led to a different size distribution of animals compared to those fed powered yeast which allowed certain animals to gain more resources leading to an elevated egg number beyond the carrying capacity of the environment and the initial over-compensatory dynamics. Thus the dynamics in colonies fed balls of yeast are initially less stable than those fed powdered yeast and yet perhaps this high fecundity will lead to populations recovering more quickly from a perturbation and so the implications for the advantageousness of scramble and contest competition (Lomnicki 1992) are unclear here. Other, theoretical studies, have predicted that the 'advantageousness' of each form of competition depends upon resource uptake conditions, sometimes favouring scramble, sometimes contest (Henson and Cushing 1996).

These intra-specific individual processes are important for determining the evolutionary significance of plastic responses to environmental variability. Ernande and Dieckman (2004) suggested that within population processes are part of the organism's environment and create their own selection pressures. In this way an animal's performance and the fitness of that performance may depend in a frequency dependent way upon the performance of others. This can affect the evolution of plasticity through changing the efficiency at which resources are utilised and so subsequently the realised carrying capacity of the environment. This is found in the plasticity of the size and age at reproduction of soil mites, which is a function of their current and maternal resource conditions (Plaistow et al 2004). Plasticity in animal sizes were also found in this study and were related to differences in resource allocation and behavioural time budgets as a response to the differing spatial availability of food. These empirical results are assumed to be related to fitness benefits in behavioural and life historical plasticity. However direct fitness benefits were not measured in this study and whilst the implication that the form of competition between individuals is important, it has not been shown that these differences are adaptive. This is an area for further study.

The importance of individual level processes in population responses is receiving more attention particularly in the area where they are used for the management of populations at risk (Bradbury et al 2001). Knowledge of the mechanisms of competition at the individual level used as a basis for population models will reduce the likelihood of erroneous qualitative predictions of population responses to changes in environment (e.g. Sutherland 1996, on incorporating individual mechanisms) and has the potential to allow for more accurate quantitative predictions of population responses.

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