Experimental and Theoretical Investigation of the Dynamics and Stability of Single Populations and Metapopulations of *Drosophila melanogaster* in the Laboratory

A Thesis Submitted for the Degree of

Doctor of Philosophy

by

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INDIA
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This thesis is dedicated to my family —

My parents, ***Shree Tapan Kanti Dey*** *and* ***Smt Sabita Dey****,*

and my brother, ***Punyatirtha Dey*** *—*

who always had faith in me even in those trying

moments of life when I had lost all of it.

Contents

Declaration

I declare that the matter presented in my thesis entitled "Experimental and Theoretical Investigation of the Dynamics and Stability of Single Populations and Metapopulations of *Drosophila melanogaster* in the Laboratory" is the result of studies carried out by me at the Evolutionary and Organismal Biology Unit of the Jawaharlal Nehru Centre for Advanced Scientific Research, Bangalore, India, under the mentorship of Prof. Amitabh Joshi, and that this work has not been submitted elsewhere for any other degree.

In keeping with the general practice of reporting scientific observations, due acknowledgement has been made wherever the work described has been based on the findings of other investigators. Any omission, which might have occurred by oversight or error of misjudgment, is regretted.

Place: Bangalore, India **Sutirth Dey**

Date: April 5, 2007

Evolutionary & Organismal Biology Unit
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5 April, 2007

CERTIFICATE

This is to certify that the work described in the thesis entitled "**Experimental and theoretical investigation of the dynamics and stability of single populations and metapopulations of *Drosophila melanogaster* in the laboratory**" is the result of investigations carried out by Mr. Sutirth Dey in the Evolutionary and Organismal Biology Unit of the Jawaharlal Nehru Centre for Advanced Scientific Research, Jakkur, Bangalore 560 064, under my supervision, and that the results presented in the thesis have not previously formed the basis for the award of any other diploma, degree or fellowship.

Amitabh Joshi, Ph.D.
Associate Professor

Acknowledgements

Working with Prof Amitabh Joshi has undoubtedly been the happiest and most fulfilling years of my academic life till date. Right on my first day in the lab, he had promised me to let me do whatever I choose with my time, and over the last five years, he has kept his promise. I doubt that there would be too many supervisors on this planet who would not object to their student devoting very large chunks of "research" time over non-scientific activities, let alone encourage him actively during the process. He did that, and much more, describing all of which will probably require a full chapter. However, to my mind, his biggest contribution in my case has been to demonstrate, through examples and not mere words, how science should be done and scientific problems should be tackled. He showed me that, correctly done, scientific pursuit can be as rich and rewarding as any spiritual journey, and for that alone, I would be grateful to him forever. To summarize, I acknowledge him as my *guru* in the true sense of the word.

I would like to take this opportunity to thank Prof P G Vaidya of National Institute of Advanced Studies and Prof Vijay Kumar Sharma of JNCASR, both of whom allowed me an unlimited access to their brains and time. Taking undue advantage of their kindness, I have barged into their rooms unannounced at all times of the day and night and have launched into animated descriptions of my latest findings, conjectures and frustrations. The fact that I was always encouraged to do so, and not kicked out even once, speaks volumes of their patience and tolerance, and for this I am really grateful to them.

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My seniors in the lab — Dr Mallikarjun Shakarad, Dr N.G. Prasad, and M. Rajamani — not only taught me how to handle flies, but also demonstrated that it was possible to have fun while doing serious work in the laboratory. All of them went far beyond what is normally expected of a professional relationship, and ended up as being cherished friends and well-wishers. Without them, much of the work presented in this thesis would not have been possible.

Experiments with flies are a tedious job, and always has the potential of turning into a living nightmare. I was able to escape that fate, thanks to some excellent colleagues in the laboratory — Raghavendra Narayan, J. Mohan, ShampaGhosh, K M Satish and Snigdhadip Dey — who shared the burden of routine fly maintenance, and also made life in the lab a lot more interesting than it would be otherwise. Special thanks are due to N. Rajanna and M. Manjesh whose help in the laboratory were essential for the smooth running of the experiments.

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Three people deserve an extra-large portion of thanks for their unconditional support. My senior Dr Vasu Sheeba, and friend Ruchira Sen, were instrumental in procuring hard to get references for me, the importance of which cannot be overstated. Nithin Nagaraj was the most patient listener and merciless critic of my work, and arguing with him over various aspects of nonlinear dynamics was instrumental in clearing several of my concepts.

Anand, Archana, Sajith, Pallavi, Sandeep, Sharmila, Dhanashree, Anitha, Shailesh, Shahnaz, Gitanjali, Ambika, Dhanya, Akarsh and Kaustubh were the people who made EOBU one of the most exciting places to be in. I would also like to mention my friends in various units — Rahul, Jaita, Ram, Ashish, Swami, Ashwin, Bhaswati, Jamal, Kirti, Shibu, Prasenjit and many more — without whom, the five years of my PhD would have been very boring indeed. Special words of gratitude for Chandrima and Rinki, who made several useful suggestions pertaining to the layout of this thesis.

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The five years of doctoral research were a journey that had its own ups and downs. However, the one thing that was constant during this entire period was the love, affection and support of my family. My parents, Shri Tapan Kanti Dey and Smt Sabita Dey, brother, Punyatirtha Dey, and grandma, Smt Kamakhya Biswas, were my constant source of strength. I cannot thank them any more than I can thank the air for the oxygen and the sun for the light.

List of publications

1. Prasad, N. G., **Dey, S**., Shakarad, M. and Joshi, A. 2003. The evolution of population stability as a by-product of life-history evolution. *Proceedings of the Royal Society of London: Biological Sciences* (*Supplement: Biology Letters*) **270**: S84-S86; DOI: 10.1098/rsbl.2003.0020.

2. **Dey, S**., Dabholkar, S., and Joshi, A. 2006. The effect of migration on metapopulation stability is qualitatively unaffected by spatial structuring of among patch variation. *Journal of Theoretical Biology* **238**, 78-84.

3. **Dey, S**., Dey, S., Mohan, J., and Joshi, A. 2006. Micro-environmental variations in pre-assay rearing conditions can lead to anomalies in the measurement of life-history traits. *Journal of Genet*ics **85**, 53-56.

4. **Dey, S.,** and Joshi, A. 2006. Stability via asynchrony in *Drosophila* metapopulations with low migration rates. *Science* **312**, 434-436.

5. **Dey, S.,** and Joshi, A. 2006. Response to comment on " Stability via asynchrony in *Drosophila* metapopulations with low migration rates." *Science* **314**, 420b.

6. **Dey, S.,** and Joshi, A. 2007. Local perturbations do not affect stability of laboratory fruitfly metapopulations. PLoS ONE **2**(2): e233.

SUMMARY

For my doctoral thesis, I have used a combination of experiments and simulations to investigate the various factors that affect the dynamics and stability of spatially-structured as well as spatially unstructured populations. A brief description of my work is as follows:

Metapopulation stability

Although classical population ecology theory treats individuals as being homogeneously distributed over space, most natural populations exhibit some degree of spatial structuring into metapopulations: ensembles of local populations (henceforth, subpopulations) that are connected by migration. Using Ricker-based coupled map lattice simulations, I show that the precise spatial arrangement of the subpopulations does not interact with migration in determining metapopulation stability. This indicates that the fine-scale details of the spatial arrangement of subpopulations can often be safely ignored while modeling metapopulation dynamics. In a continuation of this work, I show that, at least for systems in which the subpopulations follow Ricker dynamics, maximum metapopulation stability is attained at intermediate migration rates, regardless of whether the migration rate is density-dependent, density-independent or stochastic. However, migration rate can stabilize the dynamics of a metapopulation only when the migration events take place very frequently. These results were found to be robust to different spatial arrangements of patches.

The above studies indicated that a metapopulation would be most stable at intermediate rates of migration - a prediction that I tested using laboratory metapopulations of *Drosophila melanogaster*. I show that a low migration rate (10%) stabilizes *D. melanogaster* metapopulations by inducing asynchrony between neighboring subpopulations. On the other hand, higher migration rate (30%) synchronizes the neighboring subpopulations, thus leading to metapopulation instability. Simulations based on a simple non-species specific population growth model (Ricker map) captured most features of the data, suggesting that the results are generalizable. A subsequent simulation study indicated that, contrary to the concern raised by some other workers, asynchrony at intermediate migration rates is a very likely outcome in real metapopulations.

I have also empirically investigated the effects of constant localized perturbations on the stability of metapopulations. The experimental data suggests that constant addition of individuals to a particular subpopulation in every generation stabilizes that population locally, but does not have an effect on the dynamics of the metapopulation in any way. Simulations of the experimental system, based on the Ricker map, were able to recover the empirical findings, indicating the generality of the results. I also simulated the possible consequences of perturbing more subpopulations, increasing the strength of perturbations and different rates of migration, but found that none of these conditions were expected to alter the outcomes of our experiments. Finally, I show that the main results of this study are robust to the presence of local extinctions in the metapopulation.

Stability of spatially unstructured populations

Prior studies have indicated that the dynamics of *D. melanogaster* single populations are affected by three major density-dependent feedback loops: larval density acting on 1) larval survivorship and 2) adult fecundity, and 3) the effects of adult density on adult fecundity. In an experimental study on replicate *D. melanogaster* single populations, I altered the relative strengths of these loops by manipulating the quantity and quality of nutrition available to the larvae and the adults. This study led to several insights into how the three density-dependent loops interact to shape the dynamics of *D. melanogaster* populations in the laboratory.

In an experimental study, I examined the effects of four different rates of adult mortality (control, 20%, 40% and 60%) on the stability of replicate *D. melanogaster* single populations under two different nutritional regimes. When the intrinsic growth rate was low, there was no significant effect of different mortality rates on stability. However, under high rates of intrinsic growth, the effects of mortality rates on stability varied based on the index chosen to quantify stability. Specifically, under high growth rates, the variation in population size (as measured by coefficient of variation, CV) across generations, decreased monotonically with increasing rates of mortality. However, the average one-step fluctuation in population size (as measured by fluctuation index, FI) was significantly larger at lower mortality rate (20%). The extinction probabilities of the low mortality treatment were also found to be different from the controls.

I also investigated the issue of evolution of population stability as a result of selection acting on the life history of organisms. Although there were several hypotheses about the mechanism of evolution of population stability, none of them had any empirical support. A previous study had provided the first experimental demonstration that population stability can evolve as a correlated (and not direct) response to selection on life-history traits. In a subsequent study, which extends the above work, I show that the evolution of one type of stability property (constancy) does not necessarily guarantee that other stability properties would also evolve simultaneously. Moreover, manifestation of stability properties was found to depend critically on the fine details of the environment under which the populations are maintained.

Finally, in another experimental study, I demonstrate that minor variations in pre-assay rearing conditions can lead to systematic bias in life-history traits like fecundity. This underlines the importance of an often-neglected source of stochastic variations that can potentially affect the dynamics of populations, even under controlled laboratory conditions.

CHAPTER 1

INTRODUCTION

Herbert Spencer (Spencer 1864)) contended that a species or population could persist over long periods of time only if the forces governing population growth were in equilibrium with those affecting death. This notion of an interaction between various forces acting on a population resulting in a balance of numbers, was the precursor of the concept of stability in ecology (Mueller and Joshi 2000). In the approximately one-and-a-half century since Spencer, our understanding of the various factors that affect population stability has progressed a great deal, facilitated by a large number of theoretical studies on the subject. Despite a strong tradition of laboratory experiments in the early years of population ecology (Pearl and Parker 1922, Park 1948, Nicholson 1957, Huffaker 1958), many of the insights gained from the theoretical studies have never been empirically verified. One reason for this lacuna can be traced back to the 1960s, when the emphasis of experimental population ecology shifted to investigating natural populations, especially the role of competition and other species interactions in structuring biological communities (Kingsland 1995). Single population studies in this period tended to focus on whether field populations were density-regulated or not (Kingsland 1995). This shift of focus from laboratory to natural systems posed problems for the rigorous verification of theoretical predictions, as it is generally difficult, if not impossible, to satisfy the assumptions of most theoretical models under natural conditions, leading to difficulties in interpreting results where the data do not support the theoretical predictions (Mueller and Joshi 2000). The interest in laboratory population ecology was revived in the 1990s, with several pioneering studies on systems as diverse as *Tribolium* (Costantino et al. 1997, Henson et al. 2001), protozoans (McCauley et al. 1999), mites (Ellner et al. 2001), bacteria (Kerr et al. 2002), *Drosophila* (Rodriguez 1989, Mueller and Huynh 1994,

Mueller et al. 2000) etc. However, enormous ground still remains to be covered in terms of verifying the extant predictions in the theoretical population ecology literature.

The aim of the current study is to narrow down the gap between theoretical and empirical studies on population stability. The experiments consist of laboratory studies on small populations of a single species, the fruitfly *Drosophila melanogaster*. The benefits of choosing *D. melanogaster* as an experimental system are many, including relatively small generation time, ease of manipulation, and a vast body of extant knowledge about the laboratory ecology and life-history of the species (Prasad and Joshi 2003, Mueller et al. 2005). The theoretical part of the work reported in this thesis comprises of simulations based on simple models of population dynamics that are generalizable and have heuristic value. Here, unlike many previous studies (e.g. May and Oster 1976, Earn et al. 2000), the focus is not on deriving analytical solutions to mathematical models, but to set up models with some degree of realism and derive predictions that are relatively straightforward to verify against empirical data. The thesis is divided into two sections: section I (chapters 2-5) dealing with stability in spatially structured populations (metapopulations) and section II (chapters 6-9) describing the dynamics of spatially unstructured populations.

Chapter 2 reports a simulation study on the interaction of migration rate, intrinsic growth rate and spatial structuring in shaping the dynamics of metapopulations. This study predicted that intermediate rates of migration are likely to stabilize metapopulation dynamics, whereas high rates of migration would lead to destabilization of the

metapopulation dynamics. This prediction was empirically verified using laboratory metapopulations of *D. melanogaster* and the results were shown to be likely ubiquitous under natural conditions (Chapter 3). Another simulation study (Chapter 4) dealt with the effects of relaxing various simplifying assumptions that had been made in the simulations and experiments reported in chapters 2 and 3, respectively. Finally, the last chapter of section I investigates the possible role of restricted localized perturbations (pinning) in stabilizing the global dynamics of experimental metapopulations.

The four chapters making up section II look at various issues concerning stability of single populations. Chapter 6 deals with the evolution of population stability in laboratory populations of *D. melanogaster* and shows, *inter alia*, how seemingly minor features of the environment can have large effects on the manifestation of different stability properties. Chapter 7 reports an experiment on the effects of different rates of density-independent mortality on the stability of *D. melanogaster* populations. An empirical study on the effects of four different nutritional regimes on the stability of fruitfly populations is described in chapter 8. The final chapter of section II empirically demonstrates that, even under rigorously controlled laboratory conditions, minor variations in pre-assay rearing conditions can lead to systematic deviations in life-history traits related to population dynamics, like female fecundity. Since fecundity is intimately related to stability determining demographic parameters like intrinsic growth rate, this in turn can introduce a hitherto unappreciated component of stochasticity into the dynamics of laboratory populations.

In conclusion, the salient findings from the thesis are summarized and possible lines of future investigations are discussed in chapter 10. Some of the chapters (2,3,5,9) are slightly extended / modified versions of already published manuscripts, while others (4,6,7,8) are based on manuscripts in the process of being written up for submission.

CHAPTER 2

EFFECTS OF SPATIAL ARRANGEMENT

The effects of migration rate on metapopulation stability do not depend upon either the precise spatial arrangement of the subpopulations, or on the presence of a moderate proportion of vacant (uninhabitable) patches in the lattice.

Dey, S., Dabholkar, S., and Joshi, A. 2006. The effect of migration on metapopulation stability is qualitatively unaffected by spatial structuring of among patch variation. *Journal of Theoretical Biology* **238**, 78-84.

INTRODUCTION

The role of spatial structuring in shaping the dynamics of populations has received considerable attention from both theoreticians and experimentalists (for comprehensive reviews, see Hanski 1999, Hanski and Gaggiotti 2004). Coupled map lattices (CMLs), consisting of two or more simple discrete maps coupled by migration, have been widely used to model metapopulation dynamics, and such models predict a spectrum of spatiotemporal patterns. The simplest form of a CML consists of two one-dimensional maps, such as the logistic or the Ricker equation, connected by migration, and such CMLs have been studied extensively using both analytical and numerical methods (Gyllenberg et al. 1993, Hastings 1993, Kendall and Fox 1998). In symmetrical two map CMLs (i.e. both maps have the same value of the intrinsic growth rate parameter, r) using the logistic map, it was seen that when the rate of migration is low, the two patches behave as though their dynamics are independent, whereas for high levels of migration the system behaves as though it were a single patch (Hastings 1993). However, for moderate levels of migration, there are regions in the parameter space where simple dynamics (limit cycles) can be observed even in systems where the r-value is high enough to yield chaotic dynamics in a single patch (Gyllenberg et al. 1993, Hastings 1993). This pattern of effects of migration rate on CML dynamics remained qualitatively unchanged when the two maps were made asymmetric (i.e. differed in the values of the growth rate parameter, r). Kendall & Fox (1998), *inter alia*, made a detailed numerical investigation of the asymmetric case for different rates of migration. They found that high levels of migration (> 0.25), together with differing growth rates in the two maps, led to

only in-phase attractors. However, under low rates of migration (< 0.25) and different growth rates in the two maps, both in-phase and out-of-phase dynamics were possible. There was also a qualitative change in the pattern of the dynamics at intermediate levels of asymmetry between the maps (Gyllenberg et al. 1993, Kendall and Fox 1998).

In real metapopulations consisting of more than two subpopulations, considerable variation in demographic and environmental parameters is expected among subpopulations occupying different patches. Moreover, it is possible that differing patterns of environmental heterogeneity across patches can give rise to corresponding patterns in the spatial arrangement of demographic parameters among subpopulations. If such spatial patterns have major effects on metapopulation dynamics, it would constrain the applicability of models that do not explicitly consider variation in the spatial arrangement of demographic parameters among subpopulations occupying different patches. However, in such a case, given that most real metapopulations are expected to consist of multiple patches, the number of possible combinations to take into account would become unmanageably high. This important issue has not been addressed in the past: most previous studies on multi-patch metapopulations assume that all the patches have similar parameter values (e.g. Kaneko 1987, 1989, Hassell et al. 1991, Rohani and Miramontes 1995; but see also Singh et al. 2004). Given that the variation in the growth rate parameter r between subpopulations affects the nature of the dynamics in two-map CMLs, I decided to investigate the effect of different spatial arrangements of subpopulations varying in r (demographic heterogeneity) on the interplay between migration rate and metapopulation dynamics in multi-patch CML models. I also

examined whether introducing a moderate proportion of vacant (uninhabitable) patches in the lattice (spatial heterogeneity) affected the interaction between migration rate and metapopulation dynamics.

THE MODEL

I modeled subpopulation dynamics with the Ricker equation (Ricker 1954),

$$n_{t+1}' = n_t \exp\,(r\,(\,1 - n_t / K)), \qquad (1)$$

where n_t represents the population size at time t, and r and K refer to the intrinsic per capita growth rate of the subpopulation and carrying capacity of the patch, respectively. The behavior of this map has been extensively studied and it is known that the qualitative nature of its dynamics depends solely on the parameter r (May and Oster 1976). This map is a close relative of the logistic map and can show chaotic behavior for r-values higher than 2.692. I studied the behavior of metapopulations consisting of 64 coupled Ricker maps arranged in either a one- or a two-dimensional array, with each map having a different value of r. Every generation, after reproduction, a constant fraction (m) of each sub-population emigrates and gets distributed equally into the neighboring patches. In the one-dimensional case, the patches were assumed to be arranged linearly with periodic boundary condition (i.e. on the periphery of a circle), with migration possible only between immediate neighbors. Thus, the population size for any patch j in generation $t+1$ was given by

$$n_{t+1,j} = (\,1 - m\,)\, n_{t+1,\,j}' + 0.5\, m\, (n_{t+1,\,j-1}' + n_{t+1,\,j+1}'), \qquad (2)$$

where

$n_{t,j}$ = Population size in the j^{th} patch at the t^{th} time step,

r_j = Maximal intrinsic growth rate of the population in the j^{th} patch,

K = Carrying capacity of the patch (assumed to be same for all patches), and

m = Migration rate ($0 \leq m \leq 1$).

The size of the entire metapopulation at time t was given by

$$N_t = \sum_{j=1}^{J} n_{t,j} \quad , \tag{3}$$

where J was the total number of patches in the metapopulation. Similarly, in the two-dimensional case, the 64 patches were assumed to be arranged on a 8×8 square grid with migration possible between the four nearest neighbors under periodic boundary condition (i.e. on the surface of a torus).

In this study, I simulated three different kinds of metapopulations, differing in the way in which r varied across the subpopulations: (1) linear, wherein the r-values of the subpopulations increased linearly, (2) alternate, where alternate subpopulations had high and low r-values, and (3) random, in which the subpopulations with different r-values were distributed randomly on the array. Many simulations, with different ranges of possible r-values of the subpopulations, were carried out for each of the three types of metapopulation. The mean r of the metapopulations, averaged across subpopulations, ranged from 2.25 to 4.95 in different simulations, with the r-values assigned to the subpopulations in any one simulation having a range of 1 centered symmetrically around the mean (i.e. mean ± 0.5). The r-values of the subpopulations were increased in steps of $1/J$, where J was the total number of patches in the metapopulation. The values of K (=

600) and initial population size, $n_{0,j}$ (=100), were kept constant for all the subpopulations. In case of the random arrangement of *r*-values, I ran several simulations but failed to detect any qualitative differences among the results generated and, hence, present here a randomly chosen set of figures for the relevant migration rates.

In the case of the two-dimensional lattices, I also investigated the effect of spatial heterogeneity on the interplay between migration rate and metapopulation dynamics. Spatial heterogeneity was introduced by designating certain randomly chosen patches in the lattice as voids, which can be thought to represent uninhabitable patches. Immigrants were assumed to be capable of reaching such patches, but were not permitted to reproduce there. Consequently, in the subsequent generation, no emigration from these voids would occur. The presence of a void in the lattice, thus, considerably affects the pattern of migration in the patches surrounding it. While it is clear that introducing an arbitrarily large number of voids will alter the dynamics of a metapopulation in such models, my purpose was to examine the effects of small to moderate levels of spatial heterogeneity on the interplay of migration and metapopulation dynamics. Hence, I considered only the effect of introducing between two (~3% of patches) and ten (~16% of patches) voids in the 64-patch metapopulations.

All programs were written in QBASIC v 4.5 and run on a Pentium III PC. In each individual simulation, equation 2, or its equivalent in the two-dimensional cases, was iterated for 1000 time steps, the first 900 values were discarded as transients, and the values of N_t (equation 3) for the remaining 100 generations were recorded. Many such

simulations, differing in the mean r-value used, were run for each combination of migration rate × patch arrangement, and the metapopulation size data (N_t) from all simulations of a given migration rate × patch arrangement combination are plotted in figures 2.1-2.5 as a function of the mean r for that set of simulations. These figures, thus, represent bifurcation diagrams for metapopulation size for different migration rate × patch arrangement combinations. I stress that the primary interest in this study was to examine the effect, if any, of patterns of demographic and spatial heterogeneity on the interplay of migration rate and metapopulation dynamics. Consequently, my focus is on total metapopulation sizes and their dynamic behaviour under different migration rate × patch arrangement × r combinations. I am not, at this point, interested in examining the possibility of localized patterns of spatial synchrony in these systems, although I appreciate the importance of such patterns in understanding the population ecology of spatially structured systems (Mueller and Joshi 2000, Singh et al. 2004).

RESULTS AND DISCUSSION

The bifurcation diagrams of the metapopulations (Fig. 2.1-2.5), with the mean r as the bifurcation parameter, reveal that the precise spatial arrangement of the subpopulations with heterogeneous r does not lead to major qualitative differences in the dynamics of the system for any migration rate. Moreover, there is not much difference in the behavior of the system whether one considers a one-dimensional or a two-dimensional lattice.

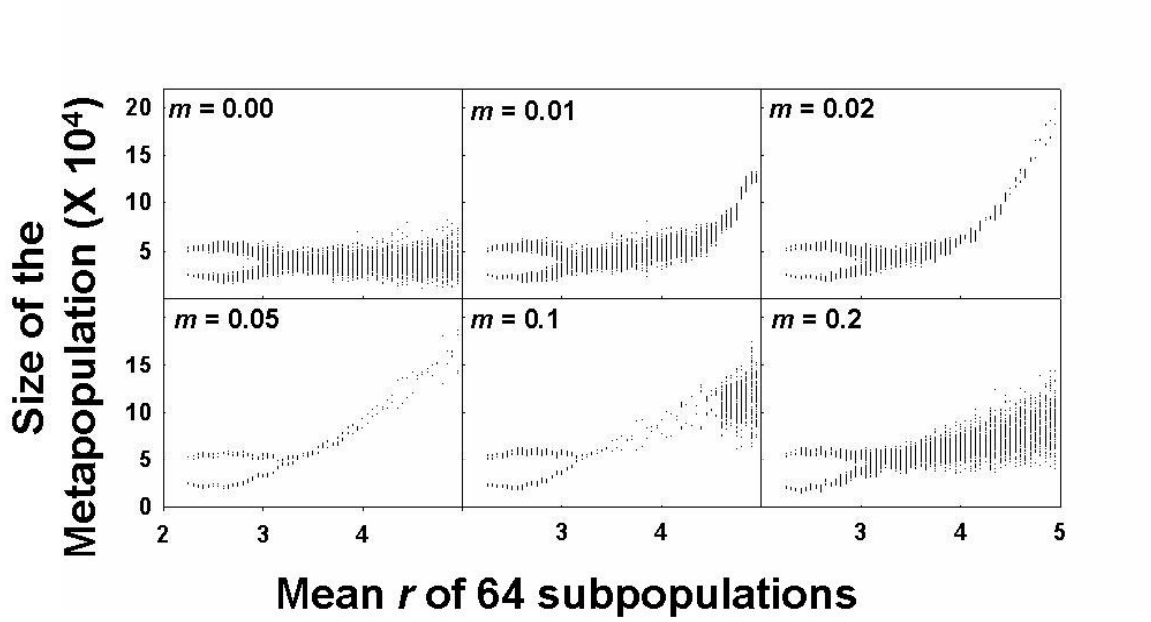

Figure 2.1. Behavior of the system when *r* increases linearly across patches, in a one-dimensional array. *m* refers to the fraction that migrates each generation to the two neighboring patches. See text for more details.

Although figures 2.1-2.5 were plotted for 64-patch metapopulations, the results also hold for metapopulations with a smaller number of patches (results not shown), as well as for cases when absorbing boundary conditions were applied (results not shown). It should also be noted that even different random arrangements of the 64 patches failed to produce any discernible difference in the pattern of the dynamics of the metapopulations. In other words, the interaction of migration rate with the average growth rate (*r*) of the metapopulation is independent of demographic heterogeneity, or the spatial arrangement of subpopulations with different *r*-values. Introduction of spatial heterogeneity in the form of voids (uninhabitable patches) also had no discernible qualitative effect on the dynamics of the model metapopulations (Fig. 2.5), suggesting that, at least for the functional form of the model and proportion of uninhabitable patches used here, spatial heterogeneity does not affect the gross dynamics of metapopulation size, and how it is

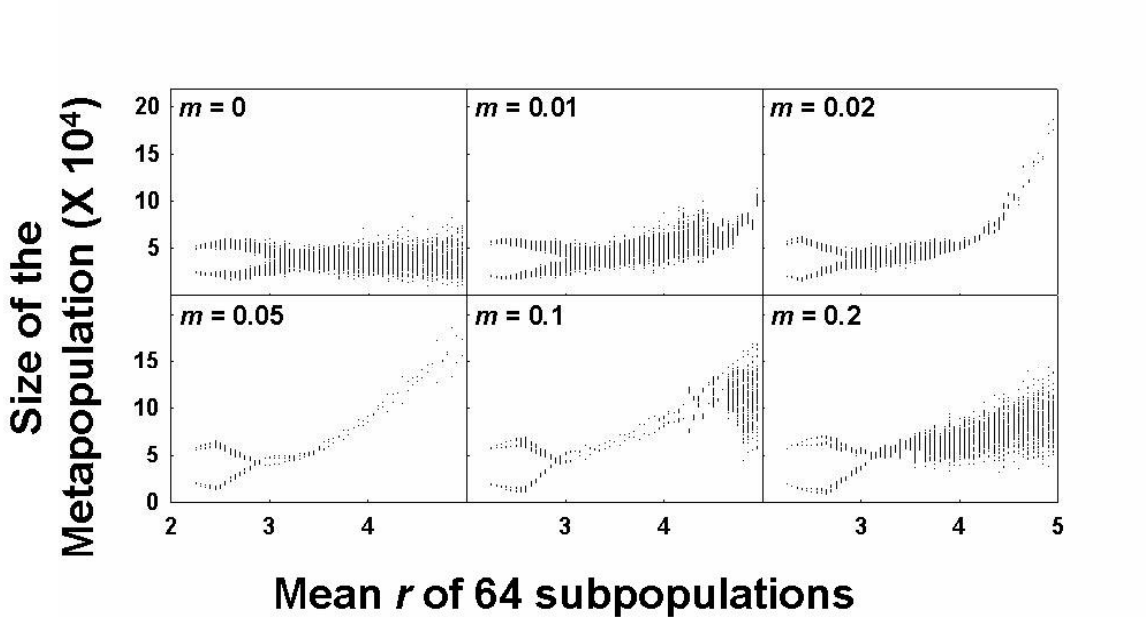

Figure 2.2. Behavior of the system when *r*-values alternate between high and low values across patches, in a one-dimensional array. See text for more details.

affected by migration rate. It has earlier been shown, albeit for a different class of model, that introducing even a small number of voids into a CML can promote asynchrony among subpopulations (Singh et al. 2004). Unfortunately, Singh et al. (2004) did not report the effect of introducing voids on the interplay between migration rate and metapopulation dynamics, making a detailed comparison of my results and those of Singh et al. (2004) difficult.

Overall, these results are reassuring because they suggest that the predictions of some typically used models of metapopulation dynamics are likely to be quite robust with regard to the different spatial arrangements of patches with varying demographic parameters, or vacant patches. Such robustness makes results from metapopulation models with arbitrary spatial distribution of demographic parameters generalizable to

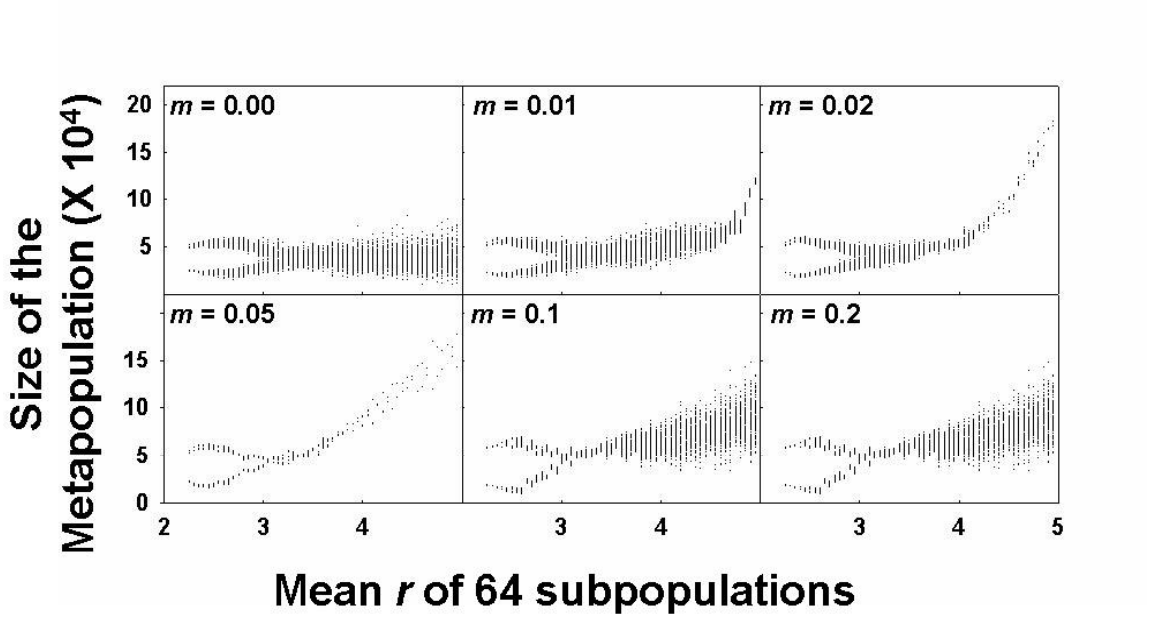

Figure 2.3. Behavior of the system when *r*-values are arranged randomly across patches, in a one-dimensional array. See text for more details.

real ecological scenarios. Whether the same robustness with regard to metapopulation size dynamics is observed for other types of metapopulation models, utilizing different functional forms to represent subpopulation dynamics, is a potential avenue of future work with important implications for application-oriented modeling.

The other observations from the present study are similar to those observed in case of two-patch CMLs (Gyllenberg et al. 1993, Hastings 1993, Kendall and Fox 1998, Singh et al. 2004). In case of zero migration (Fig. 2.1-2.5), all patches behave independently, the metapopulation as a whole shows complex dynamics, and the range of fluctuation of the population numbers is high. For low values of mean *r*, the metapopulation size N_t does not settle into limit cycles, and all values settle down to two distinct bands. Although in a mathematical sense, the system seems to be exhibiting a very high period cycle, or even

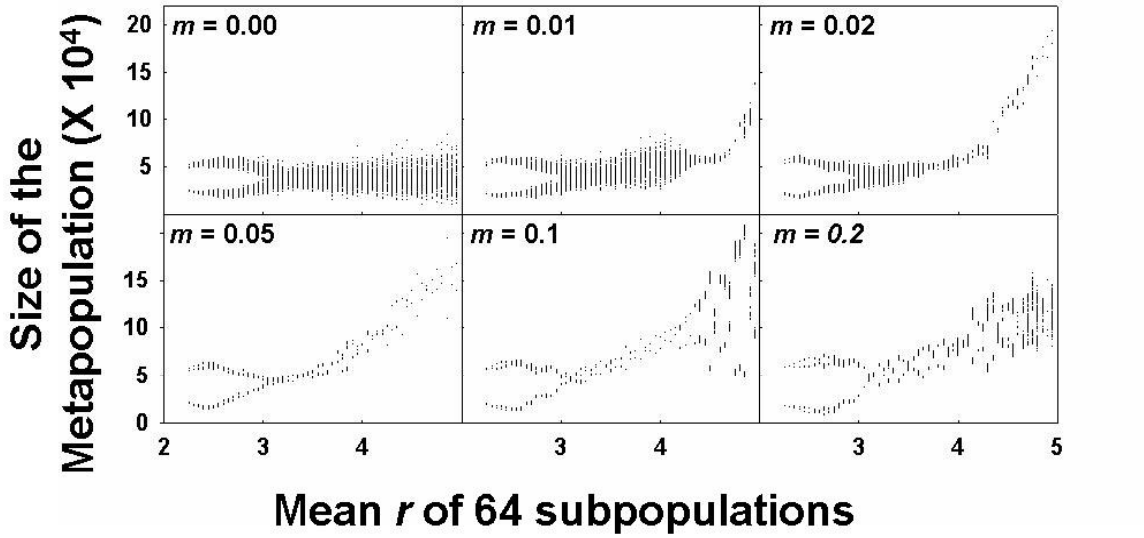

Figure 2.4. Behavior of the system when *r*-values are arranged randomly across patches, in a two-dimensional array. Note that we have presented only the random case here, as the nature of the dynamics were similar for the linear and alternate arrangements of *r*. See text for more details.

chaos, the statistical periodicity (*sensu* (Turchin 2003) of the system at this point is likely to be much lower. This is because the attractor, at such values of *r*, often consists of distinct regions that are visited by the trajectory in turn, rendering the system statistically indistinguishable from one exhibiting low period limit cycles with some amount of noise (Turchin 2003). As the mean *r* increases, the two bands come closer and finally merge. At this point, the statistical periodicity of the system is considerably higher and, hence, the stability of the system is reduced. With further increase in mean *r,* N_t fluctuates extensively, although remaining limited to a more or less defined range. As the migration rate is increased from 1% to 5%, the range of fluctuation of N_t gets reduced at low values of mean *r*, whereas for higher values of mean *r*, the system settles into simple limit cycles. However, in case of the one-dimensional array, as the rate of migration increases from 5% to 20%, the system reverts back to the behavior shown in the case when there is no migration (Fig. 2.1 – 2.3). This is probably because by then the system is coupled strongly enough to behave more or less like a single patch (Hastings 1993). While the

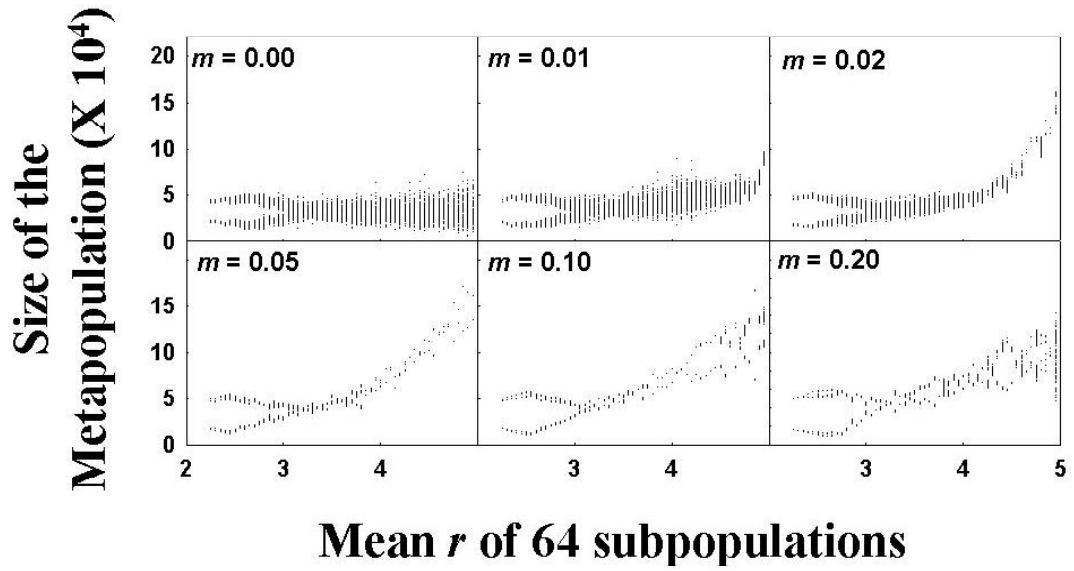

Figure 2.5. Behavior of the system when ten voids are introduced at random positions in a two-dimensional lattice with random arrangement of *r*-values. Note that voids were introduced at the same positions for simulations at different values of *m*. See text for more details.

same general pattern holds for the two-dimensional case (Fig. 2.4) too, the reversion to dynamics similar to the zero migration case happens at a higher rate of migration. Thus, the observation that intermediate rates of migration beget higher stability (Gyllenberg et al. 1993, Hastings 1993) seems to be borne out in the multi-patch case too.

One issue that also merits some discussion here is that of transients. The figures presented in this work were generated by discarding 900 time steps. It is known that sometimes CMLs can lead to very long transient behaviors or supertransients (Hanski 1999). However, it has been shown, albeit using a model other than the Ricker equation, that the range of conditions under which supertransients occur is fairly narrow (Labra et al. 2003). To be on the safe side, I iterated a randomly chosen subset of the simulations for 10,000 time steps, and plotted only the final 100 values. The resulting figures were more or less indistinguishable from the ones presented in this study. Moreover, it has often been argued that the timescales under which real populations exist are probably much shorter than the model-predicted time required to reach the equilibrium state. Thus,

at least sometimes, transients can be of greater value in ecology than the equilibrium behavior (for a detailed discussion of this issue, see Hastings 2004).

To summarize, I show that over a large range of mean intrinsic per capita growth rates (r), the precise spatial arrangement of patches with varying r, or of vacant uninhabitable patches, does not seem to have major qualitative effects on either metapopulation stability, or how the metapopulation dynamics is affected by migration rate. In this study, unlike many previous ones (Gyllenberg et al. 1993, Hastings 1993, Kendall and Fox 1998), I used the Ricker equation for modeling subpopulation dynamics. The Ricker equation is generally considered a better model for biological populations than the logistic, partly because it cannot take negative values. Moreover, it is known to give a better fit than the logistic to real life data of the dynamics of several populations (Cheke and Holt 1993, Sheeba and Joshi 1998, Ives et al. 2004). If the pattern of results reported here holds for other more complex and realistic models of population growth, then one might be able to rule out spatial configuration of patch quality as a major factor in the determination of the gross dynamic behavior of metapopulations.

CHAPTER 3

EFFECTS OF MIGRATION RATE

Low level of migration in a D. melanogaster experimental system enhances metapopulation stability via increased among-patch asynchrony, and simulations indicate that the phenomenon is likely to be ubiquitous among several species in nature.

Dey, S., and Joshi, A. 2006. Stability via asynchrony in *Drosophila* metapopulations with low migration rates. *Science* **312**, 434-436.

Dey, S., and Joshi, A. 2006. Response to comment on "Stability via asynchrony in *Drosophila* metapopulations with low migration rates." *Science* **314**, 420b.

INTRODUCTION

Although classical population ecology theory treats individuals as being homogeneously distributed over space, most natural populations exhibit some degree of spatial structuring. Consequently, ecologists are increasingly focussing on metapopulations: ensembles of local populations (henceforth, subpopulations) that are connected by migration (Hanski 1999). In particular, the effects of migration rate on dynamics and stability of metapopulations have been extensively investigated theoretically (Hanski 1999). Analytical (Gyllenberg et al. 1993, Kendall and Fox 1998) and simulation (Hastings 1993) studies have shown that even a simple system consisting of two subpopulations (modeled by a pair of logistic maps) with a constant rate of to and fro migration can exhibit rich dynamic behaviour. Subpopulations with high intrinsic growth rates (r) and low migration between them behave as though independent, and the ensuing dynamics of the metapopulation is complex. At intermediate migration rates, the two subpopulations oscillate out of phase (Kendall and Fox 1998), leading to reduced amplitude of oscillation and, hence, stability at the metapopulation level. When the migration rate is even higher, the dynamics of the subpopulations synchronize, resulting in high amplitude chaotic fluctuations in metapopulation size, giving rise to global instability. Similar results have been obtained by other workers using a variety of models more realistic than the logistic map. For example, a system of coupled Ricker maps can be stabilized by low levels of migration due to amplification of local noise under chaotic dynamics (Allen et al. 1993) or moderate levels of asynchrony (Ruxton 1994). The degree of subpopulation synchrony generally increases with migration rate (Ranta et al.

1998, Ripa 2000), although migration rate and environmental noise can interact in synchronizing the dynamics (Ranta et al. 1998, Kendall et al. 2000). Potential stabilizing effects of migration have also been demonstrated in studies on more complex systems (Nachman 1987, Lloyd and May 1996). Although it has been empirically shown that migration can stabilize dynamics (Mueller and Joshi 2000, Lecomte et al. 2004), most metapopulation experiments have been carried out within the classical extinction-recolonization framework (Levins 1969) that ignores the dynamics of population size. At the same time, laboratory tests of theoretical predictions regarding the effects of migration rate on metapopulation dynamics are rare (Mueller and Joshi 2000).

Similarly, despite a large corpus of theoretical studies, the effects of migration rates on mean population size have rarely been investigated experimentally. A simulation study of coupled Hassell maps on a two-dimensional lattice showed no major change in mean population size with increase in migration rate (Ruxton 1996). Using a model with different time scales for local and global dynamics, Hanski and Zhang (1993) showed that metapopulation size is maximal at an intermediate level of migration, whereas subpopulation size decreases monotonically with increase in migration rate. However, a model incorporating demographic stochasticity predicted maximum subpopulation size at intermediate levels of migration (Nachman 2000). To complicate matters further, a recent laboratory study on two-patch metapopulations of a fungus showed that mean subpopulation size increases monotonically with increase in rate of migration (Ives et al. 2004). This result was supported by Ricker map-based simulations that used parameter values from the experiments (Ives et al. 2004). However, the fungi used in this study are

asexual, have very high growth rate, and suffered no extinctions at the subpopulation level during the entire course of the experiment. Lack of replication at the metapopulation level, the somewhat restrictive experimental conditions, and the biology of the organism, taken together, make it difficult to generalize the findings of this study.

I studied the effects of low (10%) and high (30%) migration rates on the dynamics of replicated laboratory metapopulations of the fruitfly *D. melanogaster*, in a 21-generation long experiment. I also performed simulations using a simple non *D. melanogaster*-specific model to test whether the experimental results are generalizable, or were due to some specific aspect of the ecology or life-history of *D. melanogaster* cultures. I discuss results from the simulations and the experiments in the light of previous theoretical predictions and furnish probable reasons for some seemingly anomalous observations. Finally, I propose probable mechanisms for the principal finding that low migration rates lead to asynchrony among neighboring subpopulations and show that this is a very likely outcome under natural conditions.

MATERIALS AND METHODS

Experiments

One hundred and eight subpopulations, each represented by a single vial culture, were derived from a long-standing, outbreeding laboratory population (JB-1) of *D.*

melanogaster, maintained on a three-week discrete generation cycle. Details of the ancestry and regular maintenance regime of this population have been presented previously (Sheeba et al. 1998). Each subpopulation was initiated by placing exactly 20 eggs in a 30 ml glass vial containing ~1 ml of banana-jaggery medium. The flies resulting from these eggs were labeled as generation 0, and from that point onwards, no direct control was exercised on the density of eggs in a vial. Once the adults started eclosing around day 8-9 after egg-lay, they were collected daily in corresponding holding vials. The adults were transferred to fresh holding vials every alternate day, until day 18 after egg-lay. Extreme care was taken to ensure one-to-one correspondence between egg vials and adult collection vials. On day 18, the flies were supplied with excess live-yeast paste for three days, to enhance their fecundity. On day 21 after egg-lay, the adult flies were censused, subjected to migration, and allowed to lay eggs for 24 hours in vials containing ~1 ml banana-jaggery medium. After oviposition, the adults were discarded while the eggs formed the next generation. This maintenance regime (low larval and high adult food levels) has been extensively studied and is known to induce large amplitude periodic oscillations in population numbers (Mueller and Huynh 1994, Sheeba and Joshi 1998, Mueller and Joshi 2000, Prasad et al. 2003).

Twelve metapopulations, each consisting of nine subpopulations, were set up and sets of four metapopulations each were subjected to one of three different migration rates – control (no migration; CMs), low (10%; LMMs) and high (30%; HMMs). The nine subpopulations (single vial *D. melanogaster* cultures) were arranged on the periphery of a circle, with each vial exchanging migrants only with its two nearest neighbors i.e. a one-

dimensional array with periodic boundary conditions. In nature, such metapopulations might exist, for example, on the shorelines of lakes or along the edges of ecosystems. Migration was manually imposed by removing the required number of flies from a subpopulation and distributing them equally to the two neighboring vials, just prior to reproduction in every generation. Desired levels of migration were imposed by manually moving mated females, as the population dynamics of a sexual species is governed largely by the number of females. In order to calculate the number of females to be moved, the total count in a vial was halved (i.e. an equal sex ratio was assumed) and rounded upwards in case of fractions. This number was multiplied by the desired fraction (0.1 or 0.3) and rounded off in both directions to the nearest even integer, to give the total number of female migrants. All analyses were performed on total population size (i.e. number of males + females) after migration.

During the course of the experiment there were frequent subpopulation extinctions. A subpopulation was deemed extinct when it did not contain at least one male and one female fly. When a CM subpopulation became extinct, it was restarted using four males and four females from a backup vial. The backup vials were maintained in parallel to the three treatments, under high larval crowding and yeast supplement to the adults. There were no restarts in the LMMs or HMMs; extinct subpopulation vials remained empty until recolonized by migrants from a neighboring subpopulation.

Simulations

It has been analytically demonstrated that populations with uniform random spatial distribution and scramble competition exhibit Ricker dynamics (Brännström and Sumpter 2005). Since *D. melanogaster* cultures more or less satisfy both conditions, I modeled subpopulation dynamics with the one-dimensional, discrete version of the Ricker map , $[n_{t+1} = n_t \exp(r(1 - n_t / K))]$ (Ricker 1954), where n_t represents the subpopulation size at time t, and r and K refer to the intrinsic per capita growth rate of the subpopulation and carrying capacity of the patch, respectively. This model is known to give a good fit to data from many insect populations (Cheke and Holt 1993), including small laboratory populations of *D. melanogaster* (Sheeba and Joshi 1998). The qualitative behavior of the Ricker map is determined solely by one parameter, the intrinsic rate of growth, r, and the model exhibits a period-doubling route to chaos with increase in r (May and Oster 1976). This model is simple, not *D. melanogaster*-specific, and widely applicable to many species.

In the simulations, a metapopulation consisted of nine linearly arranged subpopulations, with nearest neighbor migration under periodic boundary condition. The migration rates were restricted to those used in the experiments: no migration (CMs), 10% (LMMs) and 30% (HMMs). All the subpopulations in a given run had the same value of r with a noise term ε ($0 < \varepsilon < 0.2$; uniform random distribution) added to r for each subpopulation at every generation, to simulate stochastic variation in population growth rates. I estimated the value of r in *D. melanogaster* cultures, by fitting the Ricker map to the experimental

time series derived from the subpopulations of the CMs. Based on these estimates, I simulated the experimental system for *r*-values of the subpopulations ranging from 2.7 to 3.0 in increments of 0.02. Since a Ricker map does not take zero values, I stipulated a 50% probability of extinction when the population size fell below four. Further, all extinctions in the controls were reset to a value of eight whereas there was no such resetting in the LMMs and HMMs. Each migration rate × *r* combination of metapopulation was simulated 10 times and all statistics were calculated on the first 100 time steps of the simulated populations. This means that I explicitly looked at the transient behaviour of the model, rather than the equilibrium conditions. I consider this more ecologically meaningful as often very large number of iterations (supertransients) are needed for a coupled map lattice to reach equilibrium (Hastings and Higgins 1994, Hastings 2004); numbers that are much larger than the lifetime of any natural population, let alone the duration of my experiment. I also performed a series of simulations, based on the above framework, to investigate the interaction of stochasticity and variations in initial population sizes on the synchrony among neighboring subpopulations.

Measures of stability

I define a population whose size fluctuates with higher amplitude across time to be less stable than one that has lower amplitude of fluctuation ("constancy" attribute of stability *sensu* Grimm and Wissel 1997). Although several measures of stability exist in the ecological literature (Grimm and Wissel 1997), the two most commonly used ones in experimental studies are the S-index (standard deviation of log/ln-transformed data) and

the coefficient of variation (CV) of population size over time. However, both these statistics had certain undesirable properties that make them unsuitable for measuring fluctuation in the present study. For example, in the case of S-index, since log transform is undefined at 0, a common feature of ecological data, it is general practice to replace zeroes by 1 or use log (N_{t+1}). This transformation leads to a severe underestimation of the true variability, and the more the zeroes, the worse the bias (McArdle et al. 1990). Since there were frequent extinctions in the populations in the current study, I decided to avoid this measure. Although CV is free from the problem of zero-values, it is a biased estimate when the distribution being sampled has a long tail (McArdle et al. 1990 and references therein). This is because a long-tailed original distribution leads to a heavily skewed distribution of sample variances. This is important in the context of my experiment, as exploratory analysis revealed that the distribution of the population sizes in the experiment does have a long tail. Moreover, both measures have the undesirable property that they are independent of the sequence of values in the time series. Consider two time series:

i) 100, 500, 100, 500, 100, 500.... and, ii) 100, 100, 100, 500, 500, 500.....

Both time series will have equal values of CV and S-index, yet series i) represents a two-point limit cycle while series ii) is a system with neutrally stable equilibrium. Thus, the differences in dynamics and stability properties of these two time series, leading to very different ecological implications, would not be captured by measures such as the CV or S-index.

To address these issues I introduce a measure of stability, the fluctuation index (FI) of a series, given as:

$$\mathrm{FI} = \frac{1}{T\overline{N}} \sum_{t=0}^{T-1} \mathrm{abs}\,(N_{t+1} - N_t)\ ,$$

where N_t is the population size at time t and $\overline{N}$ is the mean population size over T generations. FI thus reflects the mean one-step change in population size, scaled by average population size over the study duration, and is inversely related with stability: higher FI signifies lower stability and vice versa. FI has the several desirable properties that makes it suitable for the present ecological experiment. It is a dimensionless quantity and hence can be used to compare the stability of even populations with widely differing mean sizes. Since it is free from the problem of zero-values, no data transform is needed, thus avoiding potential bias. Moreover, by formulation, it takes into account the sequence of values in the series and hence is a better measure of fluctuation from generation to generation, a phenomenon directly related to the concept of constancy stability (Grimm and Wissel 1997). Finally, since FI is not a measure of variability, it should be unaffected by the biased distribution of sample variances owing to the long-tailed distribution.

Measures of synchrony and statistical analysis

Presence of long-term trends and temporal autocorrelations in the data complicate the quantification of synchrony across multiple time series (Liebhold et al. 2004). Correlations arising due to long-term trends in population size can potentially mask the synchrony on shorter time scales. On the other hand, presence of temporal autocorrelation within the series leads to the violation of the among-sample independence assumption for

any parametric test of significance (Buonaccorsi et al. 2001). Several statistics, each with its own strengths and weaknesses, have been proposed to measure synchrony across two or more time series (Buonaccorsi et al. 2001, Liebhold et al. 2004). In the present study, I measure synchrony using cross-correlation at lag zero of first differenced natural log-transformed data (Bjørnstad et al. 1999). Log-transformation of data makes the variance independent of the mean (Sokal and Rohlf 1995), while first differencing the series leads to the study of the rates of change, which obviates the need for any further detrending (Liebhold et al. 2004). The problem of temporal autocorrelation is taken care of as I have multiple time series and a single test for synchrony can be performed using the pairwise correlations between nearest neighbors (Liebhold et al. 2004). This leads to the new complication that the correlations between the various series (subpopulations) are not independent due to migration. However, I used four independent replicate metapopulations (random factors), nested within the migration treatments (fixed factor) for the analysis of variance (ANOVA). The conclusions drawn are based on the observed significance levels of the factor 'migration' which is tested over a denominator term reflecting the average variation among replicate metapopulations within migration regime. Since the metapopulations themselves are independent of each other, the between sample independence assumption of ANOVA is not violated in my analysis. I use the same analytical framework for all statistical analyses in this chapter.

In order to check the robustness of my conclusions, I also measured synchrony amongst nearest neighbors using two other statistics:

1. Cross-correlation of untransformed series values: the Pearson correlation coefficient is a very commonly used statistic that provides a direct measure of the synchrony in population sizes (Buonaccorsi et al. 2001).

2. Measure based on number of times two series change in the same direction: the number of times two series increase or decrease together, can be used as a measure of synchrony between them. In case of multiple series, the average of these values is also the proportion of times that pairs of series change in the same direction (Buonaccorsi et al. 2001).

RESULTS AND DISCUSSION

Experiment

The metapopulations experiencing low levels of migration among subpopulations (LMMs), had lower FI in metapopulation size than either the control metapopulations (no migration; henceforth, CMs) or those experiencing high levels of migration (henceforth, HMMs) (Fig. 3.1A). Nevertheless, the FI for subpopulation size in LMMs was significantly higher than in the HMMs or CMs (Fig. 3.1B). Thus, low levels of migration caused global metapopulation stability, despite increased local instability in the subpopulations. The underlying mechanism was revealed by examining the cross-correlations at lag zero of first differenced time series of log abundance ($\ln(N_{t+1}) - \ln(N_t)$) of all possible subpopulation pairs in a metapopulation, following Bjørnstad et al.

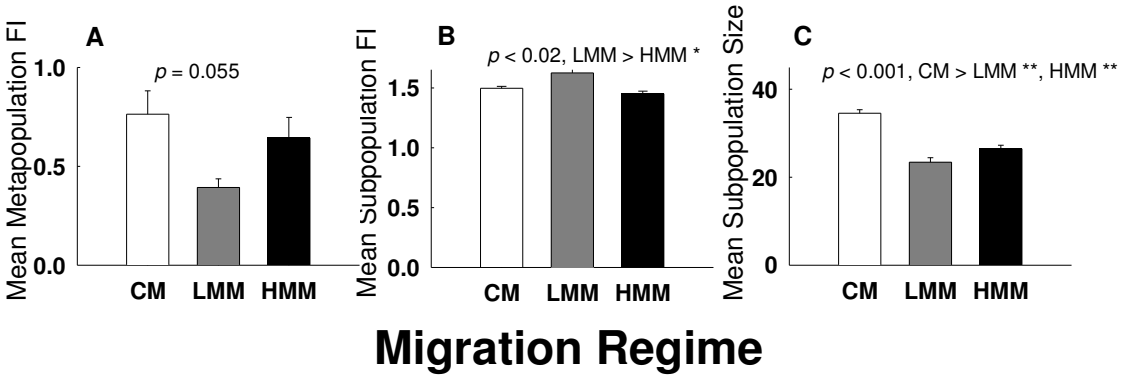

Figure 3.1. Experimental results. The *p*-values indicate the significance level from the corresponding mixed model ANOVA. The inequalities denote the means that were found different at the .05 (*) or .001 (**) level of significance using Tukey's HSD test. CM = no migration, LMM = low levels of migration (10%), HMM = high levels of migration (30%). Error bars are standard errors around the mean for four replicate metapopulations. (**A**) Mean Fluctuation Index (FI) of LMMs was lower than either CMs or HMMs, indicating higher constancy stability. (**B**) Mean FI of the subpopulations was highest in the LMMs, suggesting lower stability at that migration rate. (**C**) Mean subpopulation size of CMs was higher than both LMMs and HMMs, which is unexpected. See text for possible explanations.

(1999). The mean cross-correlation, averaged across all subpopulation pairs, was significantly positive in both CMs and HMMs, but close to zero in the LMMs (Fig. 3.2A). This indicates that in the CMs and HMMs, the subpopulations tended to reach peak and trough population sizes together, thus leading to high amplitude oscillations at the metapopulation level. However, there was no such synchrony in subpopulation sizes in the LMMs, rendering the metapopulation dynamics relatively more stable.

Since migration in the current experiment was confined to the nearest neighbors, I further investigated the spatial patterns of subpopulation synchrony, by examining the cross-correlations for all nearest neighbor pairs. The LMMs showed a significantly negative mean cross-correlation (Fig. 3.2B), indicating that the immediate neighboring subpopulations were often out of phase, thus confirming some theoretical predictions

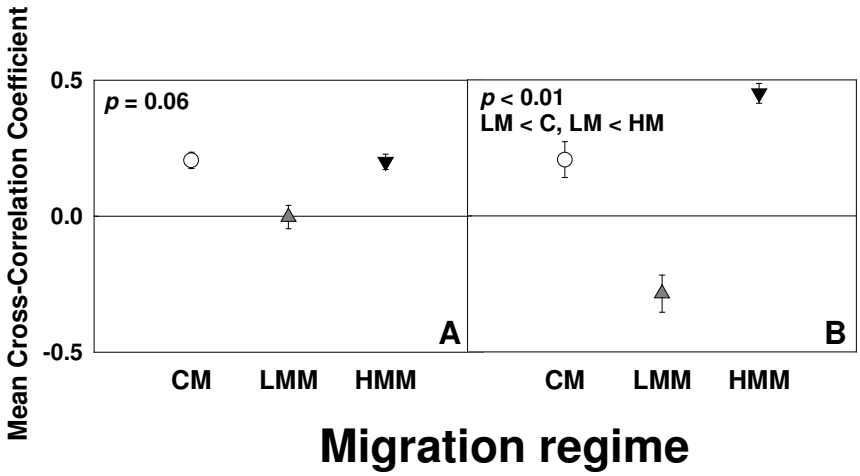

Figure 3.2. Mean (± SE) cross-correlation coefficients from the experimental data. (**A**) The means for all possible pairs of subpopulations are positive for CMs and HMMs, indicating synchrony between the subpopulations. (**B**) The mean nearest neighbor cross-correlation coefficient is significantly negative for the LMMs. This indicates that neighboring subpopulations are oscillating out of phase with each other, which leads to the observed patterns of stability. X-axis labels and interpretation of inequalities in the insets are as in figure 3.1.

(Gyllenberg et al. 1993, Kendall and Fox 1998). On the other hand, the CMs and HMMs showed significantly positive mean cross-correlations between nearest neighbors (Fig. 3.2B). Similar conclusions were reached when I considered the two other statistics for measuring synchrony between the nearest neighbors. The average cross-correlation coefficient of untransformed data, across the nearest neighbors was found to be significantly different amongst the three migration treatments ($F_{2,9} = 10.02$, $p < 0.005$). The average for the LMMs was found to be negative and significantly different (Tukey's HSD, $p < 0.01$) from CMs and HMMs, both of which were positive in sign. Similarly, ANOVA on the statistic measuring the number of times two time series change in the same direction suggested that there was a significant effect of migration ($F_{2,9} = 11.08$, $p < 0.004$) with the LMM subpopulations having the lowest average value for number of times the neighboring subpopulations increased or decreased together. Together, these

bolster the conclusion that in the LMMs, the nearest neighbors are out of phase with each other.

While high migration rate is predicted to induce synchrony (positive correlation) between the subpopulations (Nachman 1987, Ranta et al. 1998, Ripa 2000), zero migration (as in the CMs) is not expected to do the same, particularly under constant laboratory conditions. In the absence of migration, the subpopulations are independent of each other and their dynamics should not become synchronized except in the presence of external environmental forcing (Moran 1953), which is unlikely to occur in the strictly maintained constant environmental conditions of the laboratory. However, subpopulations in the CMs suffered frequent extinctions, averaging 3.35 out of 9 subpopulations per generation. Upon extinction, these subpopulations were restarted by the introduction of eight flies from a backup vial. Thus, about a third of the subpopulations in each CM were equalized for population size every generation, potentially leading to artifactual positive cross-correlations among them. Overall, my results on the effects of migration rate on subpopulation synchrony, and therefore metapopulation stability, seem to confirm the existing predictions in the theoretical ecology literature.

I also examined the effects of different migration rates on metapopulation and subpopulation size. Mean subpopulation and metapopulation size of CMs were significantly higher than in the LMMs or HMMs (Fig. 3.1c), contradicting a previous study predicting a monotonic increase in population size with increase in migration rate (Ives et al. 2004). However, the controls (no migration) employed in that study (Ives et

al. 2004) underwent no subpopulation extinctions, whereas subpopulations in the CMs went extinct frequently and were restarted by introducing eight individuals. This influx of flies from outside is probably the reason behind the increased mean subpopulation size in the CMs. Since I examined only two migration rates, it is difficult to compare my results with simulations that predict highest metapopulation size at intermediate migration rates (Hanski and Zhang 1993, Nachman 2000). However, mean subpopulation size in the LMMs and HMMs did not differ significantly, thus contradicting predictions that local population size should decrease (Hanski and Zhang 1993) or increase (Ives et al. 2004) monotonically with increase in migration rate. This may be because of the specific model assumptions and restricted parameter range (Hanski and Zhang 1993), or very different experimental protocol than mine (Ives et al. 2004), in those studies. Thus, the effects of migration rate on metapopulation and subpopulation size seem to depend critically on model assumptions and the biology of the organisms, making it difficult to put forth general predictions.

The question now is whether my experimental results reflect a simple effect of migration rates on typical population dynamics, or an interaction of migration rate with some specific features of the life-history and ecology of *D. melanogaster* cultures. The generality of my empirical results depends largely on the answer to this question. One way to address this issue is to simulate the experimental system for a biologically relevant parameter range, but using a simple model of population dynamics that does not include any specific aspects of the life-history or ecology of *D. melanogaster* cultures. If such a simulation can capture at least the major trends seen in the experimental data, then

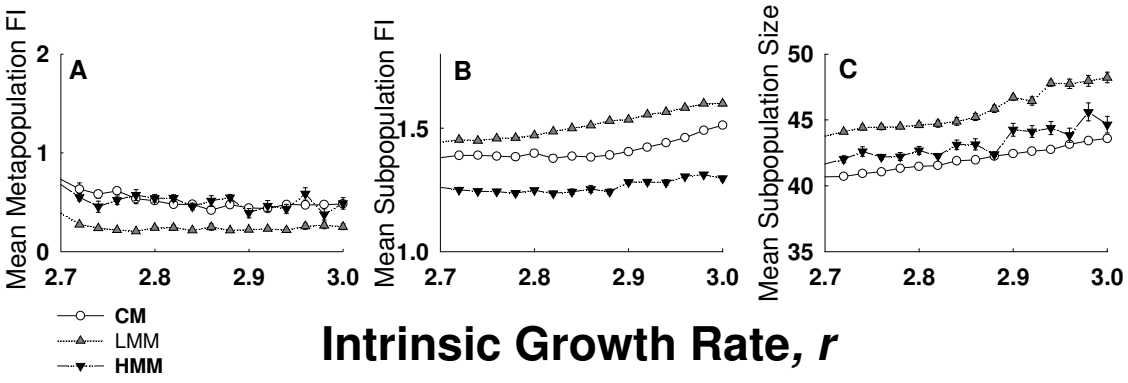

Figure 3.3. Simulation results averaged over 10 independent runs (Error bars represent SE around the mean). (**A**) Mean metapopulation FI were the lowest for LMMs and similar for CMs and HMMs (cf Fig 1A). (**B**) Mean subpopulation FI was the highest for LMMs (cf Fig 1B). (**C**) The average subpopulation size of CMs was found the lowest, contrary to the experimental findings (Fig 1C). See text for a possible explanation. X-axis labels and interpretation of inequalities in the insets are as in figure 3.1.

one can rule out the possibility that the experimental results are largely specific to *D. melanogaster*.

Simulations

The simulation of my experiment, with subpopulation dynamics following the Ricker map, yielded results very similar to the experimental data. The FI of the LMMs in the simulations was lower than both CMs and HMMs (*cf* Fig. 3.3A and 3.1A), whereas at the subpopulation level, FI for LMMs were the highest (*cf* Fig. 3.3B and 3.1B). The mean all pair and nearest neighbor cross-correlations were also found to be similar to the

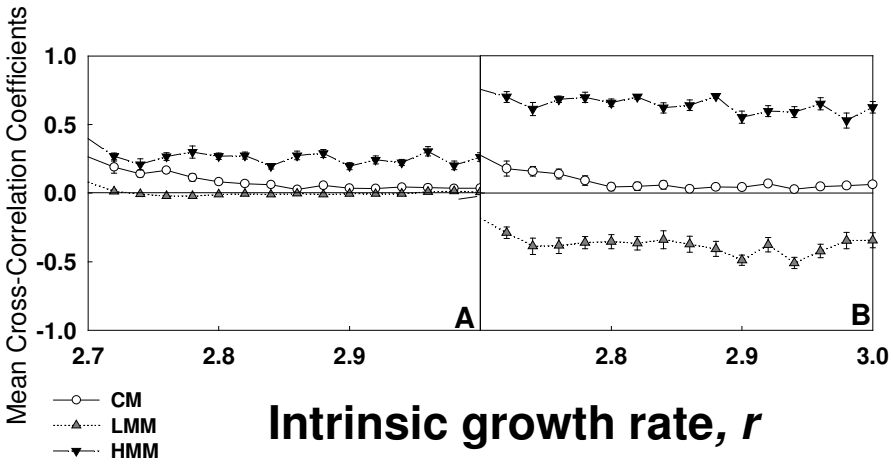

Figure 3.4. Mean (± SE) cross-correlation coefficients from the simulations. (**A**) The average cross-correlation coefficient between all possible subpopulation pairs was found to be close to zero for both CMs and LMMs. This indicates an overall lack of synchrony, and contradicts the corresponding empirical observation for the CMs (cf Fig 2A). See text for a possible explanation. (**B**) The average cross-correlation coefficients between the nearest neighbors was negative for the LMMs but close to zero for the CMs. This shows that while the LMM subpopulations were out of phase with each other, there was little synchrony among the CM subpopulations. X-axis labels and interpretation of inequalities in the insets are as in figure 3.1.

experimental data (*cf* Fig. 3.2 and 3.4), with nearest neighbors in the LMMs showing significantly negative correlations. However, in the simulations, subpopulation size exhibited the trend CMs < HMMs < LMMs (Fig. 3.3C), which does not agree with the observed trend in the experiment (CMs > LMMs ~ HMMs). Examining the subpopulation time series revealed that the number of extinctions in the simulations was much less than in the experiment. For example, in simulations with $r = 2.8$, comparable to the estimated r in my CM subpopulations, the mean extinction rate was 0.75 out of 9 subpopulations per generation, as compared to 3.35 out of 9 for experimental CMs. The criterion for subpopulation extinction in the experiment was the absence of at least one male-female pair. On the other hand, a subpopulation in the simulations was deemed extinct when there were zero individuals, as the Ricker map does not distinguish between the sexes. Consequently, there were fewer resets to $N_t = 8$ in the CM subpopulations of the simulations, ultimately leading to lower mean subpopulation size, as compared to the

experiments. Overall, I was able to recover almost all the major features of the experimental data from Ricker-based simulations in a biologically meaningful parameter range. Scramble competition for resources is experienced by animals across a wide range of taxonomic groups including most microbes, invertebrates, fishes and amphibians, and the Ricker model is known to be a good descriptor of dynamics under this type of competition (Brännström and Sumpter 2005). Moreover, similar results have been obtained using a suite of other commonly used models of population dynamics including the logistic (Gyllenberg et al. 1993, Kendall and Fox 1998), Hassell (Ranta and Kaitala 2006) and Maynard Smith-Slatkin model (Ranta and Kaitala 2006). My experimental results, therefore, are likely to hold true for a variety of species other than *D. melanogaster*.

Why does asynchrony arise?

Ranta and Kaitala have pointed out that the observed asynchrony among neighboring subpopulations in my experiment could have arisen due to an interaction between stochasticity and variation in initial population sizes (Ranta and Kaitala 2006). Using simulations based on a two-patch system of coupled logistic maps, they show that variations in initial conditions can interact with stochasticity to produce asynchrony. Their argument is based on the fact that under low rates of migration, in phase and out of phase dynamics form fractal basin boundaries on the initial population size (IPS) space and hence, stochasticity can tip a system into a zone of asynchrony. However, if the two types of basins of attraction are evenly distributed, as in some of the panels of (Ranta and

Kaitala 2006), then contra Ranta and Kaitala (2006), noise is equally likely to lead the subpopulations to either synchrony or asynchrony. This implies that, on an average, one would expect neighboring subpopulation sizes to be uncorrelated. Strictly speaking, the mechanism proposed by Ranta and Kaitala does not, therefore, explain the statistically significant subpopulation asynchrony seen in the experiments. However, this contention was based on the results of two-patch metapopulation simulations (Hanski and Zhang 1993, Ranta and Kaitala 2006). Since the actual outcome of the mechanism suggested by Ranta and Kaitala depends on the fine structure of the basin boundaries, one would need to refer to a corresponding 9-dimensional IPS space for making similar observations on my experimental system. As it is not possible to visualize such a space, I instead looked directly at the effects of variation in IPS and stochasticity on the synchrony of subpopulations in a 9-patch metapopulation, as used in the experiment. As high migration (30%) invariably led to synchrony (positive cross-correlation coefficient of first-differenced ln-transformed population sizes) under all conditions studied, here I restrict myself to reporting the effects of low migration (10%).

When IPS varied among subpopulations, both synchrony and asynchrony were observed, even without stochasticity (Fig. 3.5A). On introducing noise by adding ε ($0 < \varepsilon < .2$) to r in each patch every generation, as in the earlier simulations, the fraction of IPS combinations leading to asynchrony increased (Fig. 3.5B). Increments in either r or the level of noise in r further increased the proportion of IPS combinations leading to asynchrony. Upon adding a 50% probability of extinction when subpopulation size fell

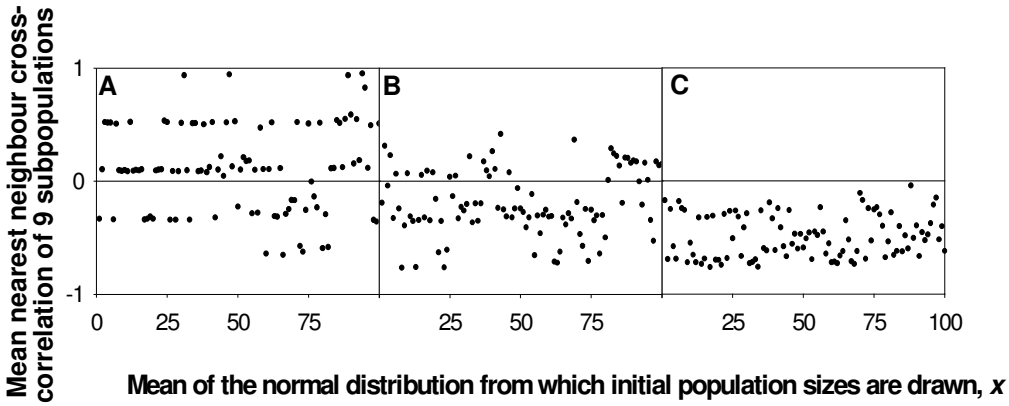

Figure 3.5. Average nearest neighbor cross-correlation coefficients in 9-patch Ricker-based metapopulations, with 10% nearest neighbor migration and periodic boundary conditions. The r and K in each subpopulation were fixed at 2.8 and 40 respectively, and only the first 100 iterations were considered, without discarding any transients. The abscissa represents the mean (x) of the normal distribution (standard deviation $10x$) from which the starting population sizes were drawn. The starting values were rounded off to the nearest integer and negative values were replaced by zeroes. (**A**) When the starting population sizes were randomly chosen, both synchrony and asynchrony were observed, even in the absence of any other kind of noise. (**B**) When stochasticity was introduced in the form of noise in the parameter r, the fraction of cases leading to asynchrony increased. (**C**) On adding further stochasticity in the form of probabilistic extinctions, asynchrony was observed in almost all cases, indicating that stochasticity interacts with starting population sizes in producing asynchrony. See text for more details of the simulations.

below 4, in conjunction with noise in r, asynchrony was observed in almost all the cases (Fig. 3.5C). Thus, while differences in IPS can give rise to either synchrony or asynchrony (Ranta and Kaitala, 2006, Fig. 3.5A), incorporating stochasticity and probabilistic extinction greatly increases the proportion of IPS conditions leading to asynchrony. Even if all the IPS are the same, stochasticity in r alone can induce asynchrony (Fig. 3.6A), at least for some of the IPS sets, and this proportion increases on increasing r, or the noise in r. If probabilistic extinction is added to noise in r, almost all IPS sets lead to asynchrony even when all IPS are the same (Fig. 3.6B). These observations indicate that in a multi-patch system, stochasticity alone can induce asynchrony under low migration rates, and differences in IPS can enhance this effect (*cf*

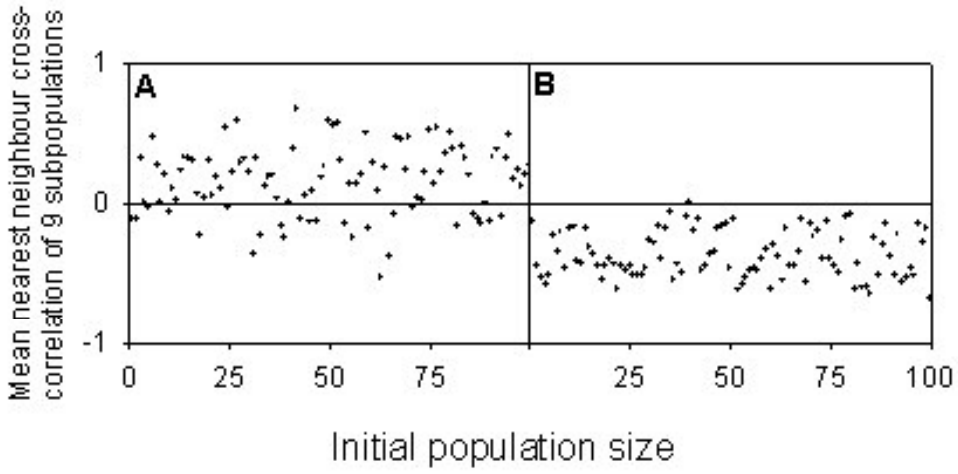

Figure 3.6. These simulations were similar to those represented in figure 1, except that the initial population size was kept same for all subpopulations. (**A**) shows that even when all populations are started from the same initial point, stochasticity in *r* is sufficient to lead to asynchrony in several cases. (**B**) shows that adding a probability of extinction results in asynchrony in almost all cases. Comparison of figures 3.5 and 3.6 indicate that stochasticity alone can induce asynchrony at least in some cases, but its effect is enhanced when there are differences in the starting size of the subpopulations.

Fig. 3.6A and 3.5B). Thus, my simulations show that intrinsic growth rate and different conditions of stochasticity and IPS can interact in a complex manner to produce out of phase behavior in subpopulations.

In natural metapopulations, stochasticity in demographic parameters, probabilistic extinction and variation in IPS are all likely ubiquitous. The current simulations suggest that under such circumstances, asynchrony among subpopulations is almost inevitable (Fig. 3.5C). One possible reason for this might be that under such conditions the multi-dimensional IPS space may lose the fractal structure and consist primarily of basins of attraction for asynchrony. Thus, the combination of low migration and high subpopulation growth rates is very likely to lead to stability via among-patch asynchrony in metapopulations in the laboratory or in nature.

This study, to the best of my knowledge, is the first rigorous empirical test of the effects of different migration rates on fluctuations in metapopulation size. Besides verifying several existing theoretical predictions, the results have potential practical implications. A major concern in conservation biology is the designing of migration corridors for stabilizing the dynamics of populations in isolated, patchy habitats. My results show that too much migration can actually increase the amplitude of fluctuations in metapopulation size, thus potentially endangering the metapopulation in the long run. However, migration in the experiment was confined to the two nearest neighbors, and it is known that the dynamics of a metapopulation can vary depending upon the scheme of migration (Earn et al. 2000). Moreover, the growth rate of *D. melanogaster* (and most insects, microbes and fishes) is higher than other animals such as mammals and birds, which are generally of more concern in terms of conservation. The intrinsic growth rates of subpopulations are known to interact strongly with migration rate (Dey et al. 2006a) and exact form of density dependence (Ims and Andreassen 2005) in producing observed metapopulation dynamics. Therefore, due caution should be exercised while extrapolating the results of the present study to natural populations.

CHAPTER 4

EFFECTS OF MIGRATION SCHEMES

The effects of migration rate on the dynamics of metapopulations depend on whether migration happens in every generation or not, but are otherwise unaffected by migration being density- independent, density dependent, or stochastic.

Dey, S., Biswas, S., Shakarad, M. and Joshi, A. An investigation of metapopulation stability under various schemes of migration and spatial arrangement of subpopulations. Manuscript under preparation

INTRODUCTION

Although classical population ecology theory treats individuals as being homogeneously distributed over space, many natural populations exhibit some degree of spatial structuring (Hanski 1999). Consequently, over the last two decades, a large number of studies have concentrated on metapopulations: ensembles of local populations (henceforth, subpopulations) that are connected by migration (see for a review Hanski and Gaggiotti 2004). In particular, many theoretical investigations have focused on the effects of migration on metapopulation dynamics (Gyllenberg et al. 1993, Hastings 1993, Kendall and Fox 1998, Earn et al. 2000). It has been shown that even a simple system consisting of two subpopulations with a constant, density-independent rate of to and fro migration can exhibit rich dynamic behavior (Gyllenberg et al. 1993, Hastings 1993, Kendall and Fox 1998). Subpopulations with high intrinsic growth rates (r), and low migration between them, behave as though independent, and the ensuing dynamics of the metapopulation is complex. At intermediate migration rates, the two subpopulations oscillate out of phase (Kendall and Fox 1998), thus resulting in stability at the metapopulation level. When the migration rate is even higher, the dynamics of the subpopulations synchronize, resulting in large fluctuations in metapopulation size. However, these results are based on the simplest case of two-subpopulation metapopulations and a number of other interesting considerations arise when the number of subpopulations is greater than two.

Increasing the number of subpopulations beyond two can sometimes lead to changes in the subpopulation dynamics (Ylikarjula et al. 2000), although the effects of density-independent migration rate on the global dynamics (von Bremen and Udwadia 2002, Dey and Joshi 2006b) remain unchanged. Even though each subpopulation might be chaotic individually, the metapopulation can exhibit periodic global behavior (von Bremen and Udwadia 2002). Moreover, although the dynamics can be altered by the scheme of migration (nearest neighbor versus global coupling) (Earn et al. 2000), or by the presence of correlated environmental noise (Kendall et al. 2000), there is no consistent differential effect of density-dependent or density-independent migration on metapopulation dynamics (Ylikarjula et al. 2000). There is also no gross qualitative effect of different kinds of spatial arrangements of subpopulations (Dey et al. 2006a).

In the current study, I build on the work of Dey et al. (2006) and investigate whether different kinds of migration schemes have any major effects on metapopulation stability. I consider metapopulations exhibiting stable point equilibria or low periodicity limit cycles to be more stable than metapopulations undergoing more complex limit cycles. I show that the effects of migration rate on metapopulation stability are not qualitatively altered if the migration rate is density-dependent, or varying stochastically. However, there is a marked destabilization of the global dynamics if the migration does not take place in every generation. These effects of migration were found to be robust across different spatial arrangements (linear, alternate and random; see Methods) of heterogeneous subpopulations, differing in their *r*-values.

METHODS

Following Dey et al. (2006), I modeled subpopulation dynamics with the Ricker equation (Ricker 1954),

$$n_{t+1}' = n_t \exp\,(r\,(\,1 - n_t / K)), \qquad (1)$$

where n_t represents the population size at generation t, and r and K refer to the intrinsic per capita growth rate of the subpopulation and the carrying capacity of the patch, respectively. The qualitative behavior of the Ricker map depends solely on the intrinsic growth rate, r, and the map exhibits stable point, limit cycles and chaotic behavior for $r < 2$, $2 < r < 2.692$ and $r > 2.692$ respectively (May and Oster 1976). Apart from being theoretically well understood, the Ricker map is known to be a good descriptor of the dynamics of several natural and laboratory populations (Cheke and Holt 1993, Mueller and Joshi 2000, Dey and Joshi 2006b). I studied the behavior of metapopulations consisting of coupled Ricker maps arranged in a one-dimensional array, with each map having a different value of r. Thus, I explicitly consider environmental heterogeneity, by stipulating different parameter values for the local subpopulations. I limit myself to the investigation of one-dimensional arrays as it has been shown by an earlier that there is no qualitative difference in the dynamics whether the subpopulations are arranged in 1-D or two-dimensional arrays (Dey et al., 2006; chapter2). When migration occurs, a fraction ($m_{t,j}$) of the j^{th} subpopulation emigrates and gets distributed equally into the immediate neighboring patches. The patches were assumed to be arranged linearly with periodic boundary condition (i.e. on the periphery of a circle), with migration possible only

between immediate neighbors. In nature, one might expect to find this kind of a system on the shores of lakes, or in the case of species living at the margins of ecosystems. The population size for any patch j in generation $t+1$ was given by

$$n_{t+1,j} = (1 - m_{t,j}) n_{t+1,j}' + 0.5 (m_{t+1,j-1} n_{t+1,j-1}' + m_{t+1,j+1} n_{t+1,j+1}') \qquad (2)$$

where $n_{t,j}$ is the subpopulation size in the j^{th} patch at the t^{th} generation, r_j denotes the maximal intrinsic growth rate of the subpopulation in the j^{th} patch, K is the carrying capacity of the patch (assumed to be same for all patches), and $m_{t,j}$ is the migration rate of the j^{th} patch at the t^{th} generation ($0 \le m_{t,j} \le 1$).

The size of the entire metapopulation at generation t was given by

$$N_t = \sum_{j=1}^{J} n_{t,j} \quad , \qquad (3)$$

where J is the total number of patches in the metapopulation.

In this study, I looked at three different kinds of spatial arrangements of subpopulations within the metapopulations. These were called (1) linear, when the r-values of the subpopulations increased linearly, (2) alternate, in which alternate subpopulations had high and low r-values, and (3) random, where the subpopulations with different r-values were distributed randomly on the array. Many simulations, with different ranges of possible r-values of the subpopulations, were carried out for each of the three types of metapopulation. The mean r of the metapopulations, averaged across subpopulations, ranged from 2.25 to 4.95 in different simulations, with the r-values assigned to the

subpopulations in any one simulation having a range of 1, centered symmetrically around the mean (i.e. mean ± 0.5). The *r*-values of the subpopulations were increased in steps of 1/*J*, where *J* was the total number of patches in the metapopulation. The values of *K* (= 600) and initial population size, $n_{0,j}$ (= 100), were kept constant for all the subpopulations in all simulations. In case of the random arrangement of *r*-values, I ran several simulations but failed to detect any qualitative differences among the results generated and, hence, present here a randomly chosen set of figures for the relevant cases. In all the figures, the mean *r* for a simulation is plotted on the x-axis while the corresponding metapopulation size at successive generation in that simulation (after discarding the transients) is plotted on the y-axis. Thus, these diagrams are analogous to the familiar bifurcation diagrams and can be interpreted similarly.

The effects of the following scenarios on metapopulation dynamics were studied:

Density-dependent migration rate: To model the density-dependent rate of migration, a quantity $\alpha_{t,j}$ was defined as:

$$\alpha_{t,j} = n_{t,j}/K$$

Then, the migration rate $m_{t,j}$ for the j^{th} patch at the t^{th} generation was given as

$$m_{t,j} \begin{cases} = \alpha_{t,j} \times \xi & ; \alpha_{t,j} \leq 1 \\ = \xi & ; \alpha_{t,j} > 1 \end{cases} \qquad (4)$$

where ξ is a constant. I examined six different values of ξ, namely .01, .02, .05, .1, .25 and .5, for each type of patch arrangement (linear, alternate, and random).

Stochastic migration rate: Here I looked at the effects of stochastically varying the migration rate on the dynamics of the population. For this, the migration rates for each patch in each generation were sampled from a normal distribution with a mean of m and standard deviation of either $m/10$, $m/5$ or $m/2$.

Periodic migration events: In this case, migration was periodic i.e. did not take place every generation. Nine different periodicities (ω = 2, 3, 4, 10, 15, 20, 40, 50 and 60 generations) were studied for each migration rate ($m_{t,j} = m$ = .01, .02, .05, .1, .2) × patch arrangement (linear, alternate and random) combination.

Stochastic migration events: To simulate a scenario where migration at a patch in a given generation is a stochastic event (i.e. there is a certain probability that a migration event shall take place), I defined a constant ψ such that

$$m_{t,j} \left\{ \begin{array}{ll} = m & ; rand \leq \psi \\ = 0 & ; rand > \psi \end{array} \right. \qquad (5)$$

where *rand* is a random number between 0 and 1, sampled separately for each $m_{t,j}$, from a uniform distribution. I used the in-built random number generator of QBASIC v 4.5,

for generating the values of *rand*. Three values of ψ namely, 0.99, 0.9 and 0.8, for each combination of patch arrangement $\times$ m, were investigated in this section.

All programs were written in QBASIC v 4.5. In each individual simulation, the appropriate equations were iterated for 500 generations, the first 400 values discarded as transients, and the values of N_t (equation 3) for the remaining 100 generations were recorded. It has been earlier shown that systems consisting of coupled one-dimensional maps can give rise to very long transients, sometimes stretching to millions of iterations (Hastings and Higgins 1994, Kaneko 1998, Hanski 1999). This means that here I have explicitly looked at the transient behavior of the metapopulations, for which there were two reasons. First, an earlier study based on the same modeling framework (Dey et al. 2006a) did not find any difference in the patterns of figure 4.1, even on rejecting 9900 iterations as transients. Second, the time-scale of the existence of natural populations is far less than the time predicted by the models to reach the steady state. Thus, it has often been argued that the behavior of transients is more ecologically meaningful than the equilibrium behavior (Hastings and Higgins 1994, Hastings 2004), a view with which I concur.

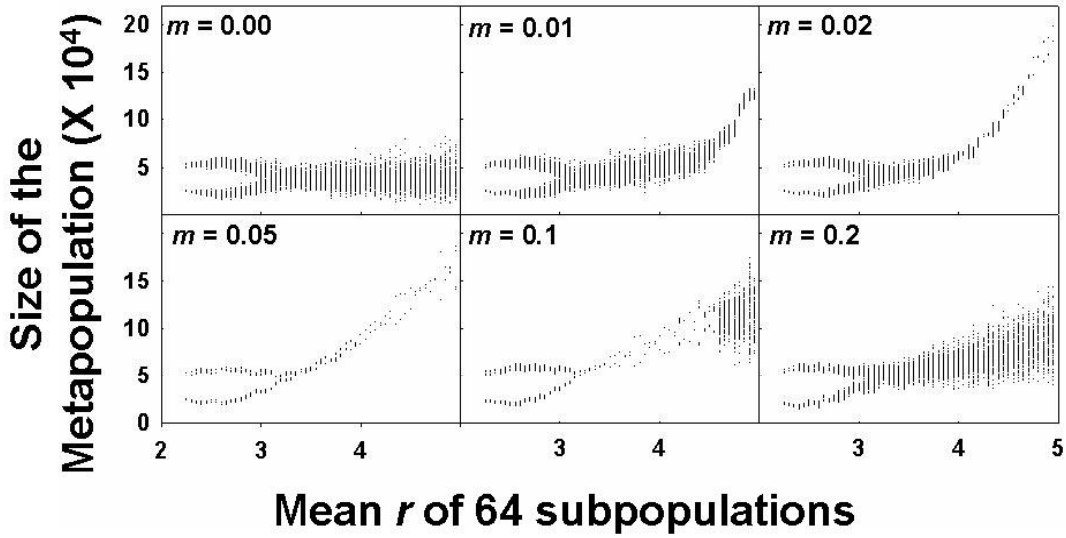

Figure 4.1. Bifurcation diagram of a system consisting of 64-subpopulations arranged on the periphery of a circle, with intrinsic growth rate, *r*, increasing linearly across patches. Nearest neighbor migration takes place every generation at a constant rate of *m*. Maximum metapopulation stability is seen at the intermediate value of $m = .05$. See text for more details.

RESULTS AND DISCUSSION

For the sake of comparison with previous work (Dey et al. 2006; chapter 2), I begin with a brief description of the behavior of the metapopulations when migration happens every generation at a constant, density-independent rate of m ($0 \leq m \leq 1$) for the linear arrangement of subpopulations (equation 2; Fig. 4.1). In all the figures, I have plotted the average of the intrinsic growth rate (r) of 64 subpopulations on the x-axis and the metapopulation size over hundred generations on the y-axis. These figures can therefore be considered as bifurcation diagrams and can be interpreted as such. In other words, for a given value of r, the number of points plotted represents the periodicity of the time series: a single point indicating a stable equilibrium, two points indicating a two-point limit cycle, and so on. Clearly, by the definition of stability used (Dey et al. 2006a), a

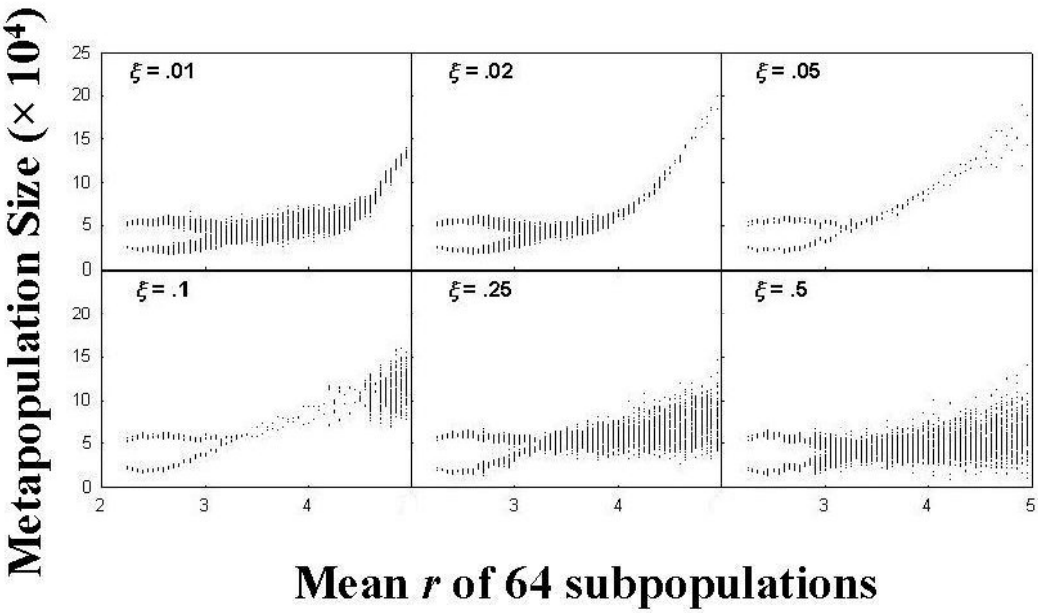

Figure 4.2. Bifurcation diagram of a system consisting of 64-subpopulations arranged on the periphery of a circle, with intrinsic growth rate, *r*, increasing linearly across patches. Nearest neighbor migration occurs every generation at a density-dependent rate as given in eq. 4 (see text). Higher values of ξ indicate a higher rate of migration. There is no appreciable difference in the dynamics with the case when migration rate is density-independent (fig 4.1).

larger number of points for a given value of *r* indicate greater instability. The description in the following paragraph is based on the results of Dey et al. (2006) and Fig. 4.1 of this study is essentially similar to Fig. 1 of Dey et al. (2006).

When there is no migration, all subpopulations are independent of each other, the metapopulation shows complex dynamics, and the range of fluctuations is high. For low values of mean *r*, all values of the population sizes settle into two distinct bands (Fig. 4.1). Although the system might be exhibiting chaos or high periodicity limit cycles, such a system is statistically indistinguishable from one undergoing a noisy two-point limit cycle (Turchin 2003). This is because at such values of *r*, the attractor consists of

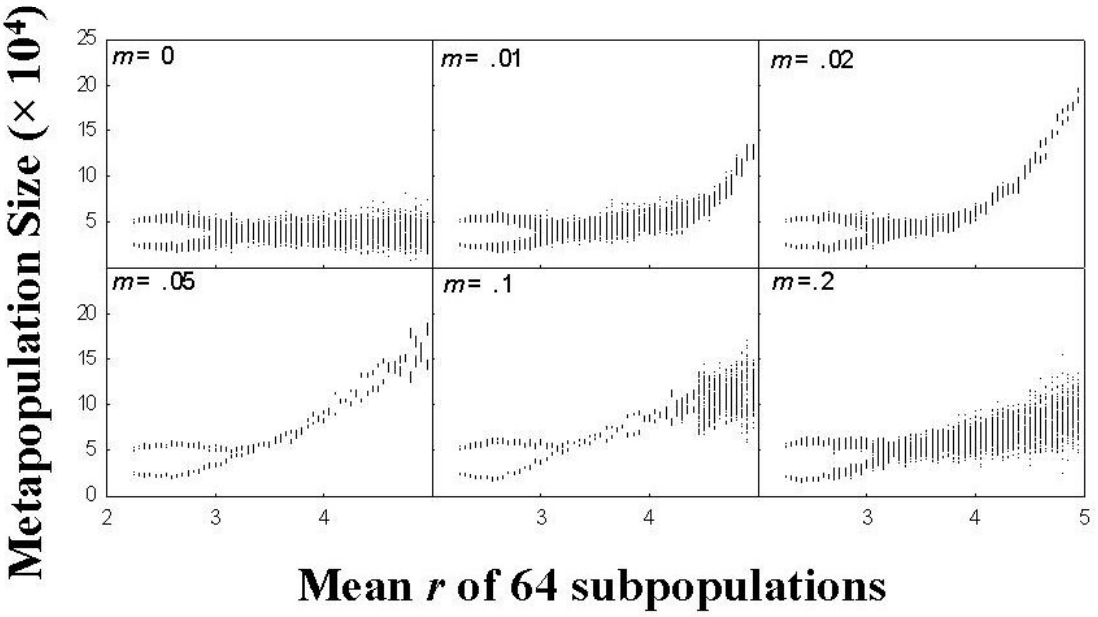

Figure 4.3a. Dynamics of 64-patch metapopulations when migration rate is density-independent, but drawn from a normal distribution of mean m and standard deviation of $m/10$. Comparison with fig 4.1 indicates that introducing stochasticity in migration destabilizes the metapopulations, without altering the pattern of maximum stability being attained at intermediate migration rates. See text for further discussion.

two distinct regions that are alternately visited by the trajectory (Dey et al. 2006a). On increasing mean r, the two bands come closer and finally merge, thus increasing the statistical periodicity and instability. As r increases even further, the population size fluctuates extensively within a more or less defined range. Increasing m from 1% to 5% reduces the range of fluctuation of population size at low values of mean r, whereas the system settles into limit cycles or stable points for higher values of mean r. However, as m increases further (5% to 20%), the system reverts back to the zero migration case. It has been shown earlier that this pattern is (a) independent of the spatial arrangement of the patches, (b) observed even in 2-dimensional lattices, and (c) robust to the presence of moderate numbers of empty patches in the lattice (Dey et al. 2006a).

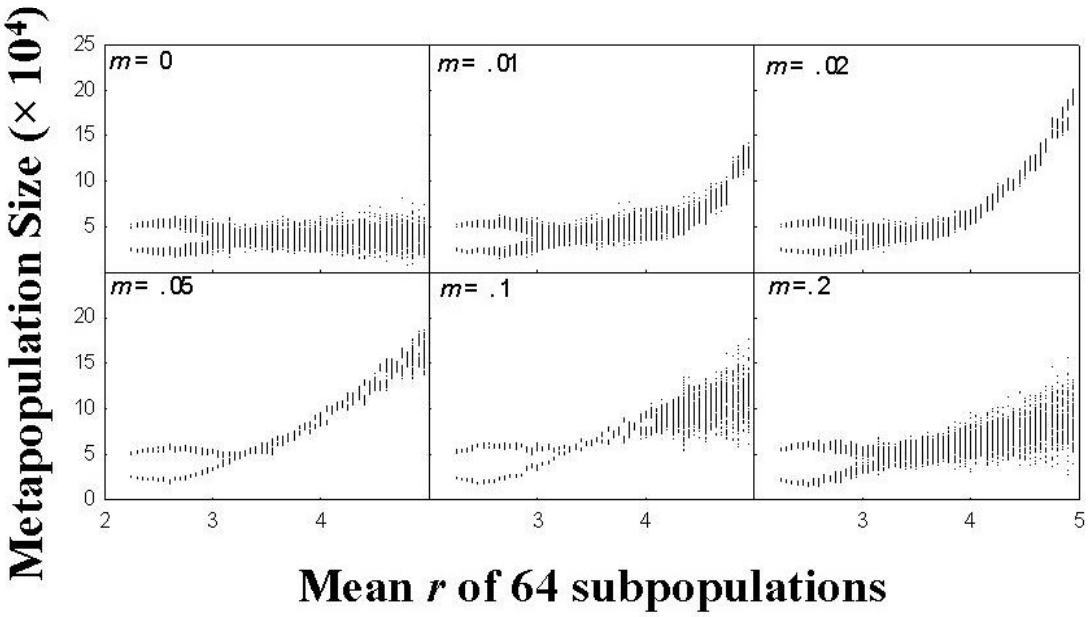

Figure 4.3b. Dynamics of 64-patch metapopulations when migration rate is density-independent, but drawn from a normal distribution of mean *m* and standard deviation of *m*/5. Comparison with fig 4.1 indicates that introducing stochasticity in migration destabilizes the metapopulations, without altering the pattern of maximum stability being attained at intermediate migration rates. See text for further discussion.

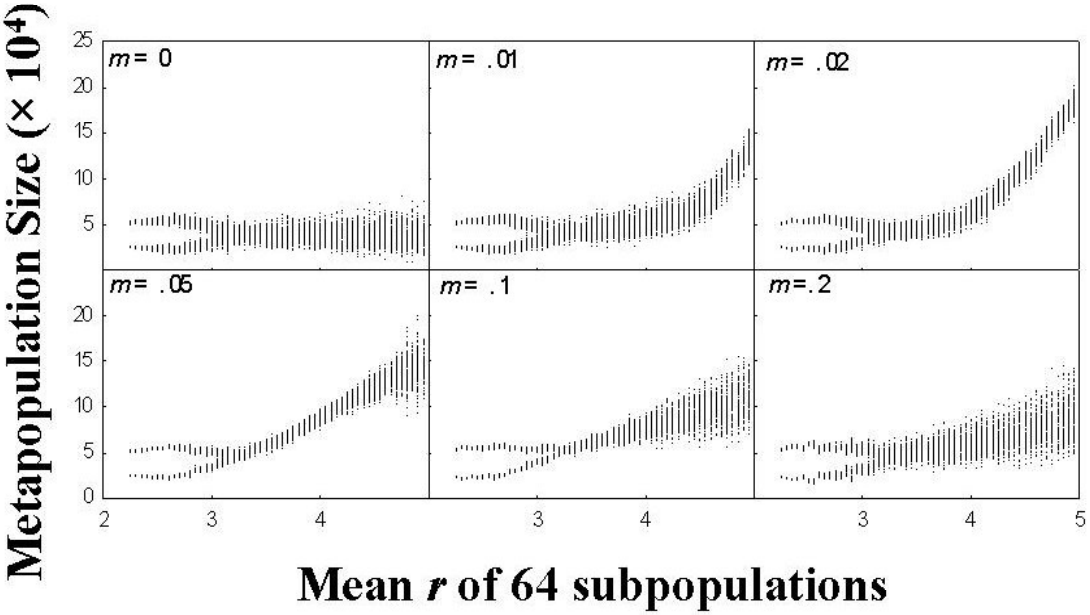

Figure 4.3c. Dynamics of 64-patch metapopulations when migration rate is density-independent, but drawn from a normal distribution of mean *m* and standard deviation of *m*/2. Comparison with fig 4.1 indicates that introducing stochasticity in migration destabilizes the metapopulations, without altering the pattern of maximum stability being attained at intermediate migration rates. See text for further discussion.

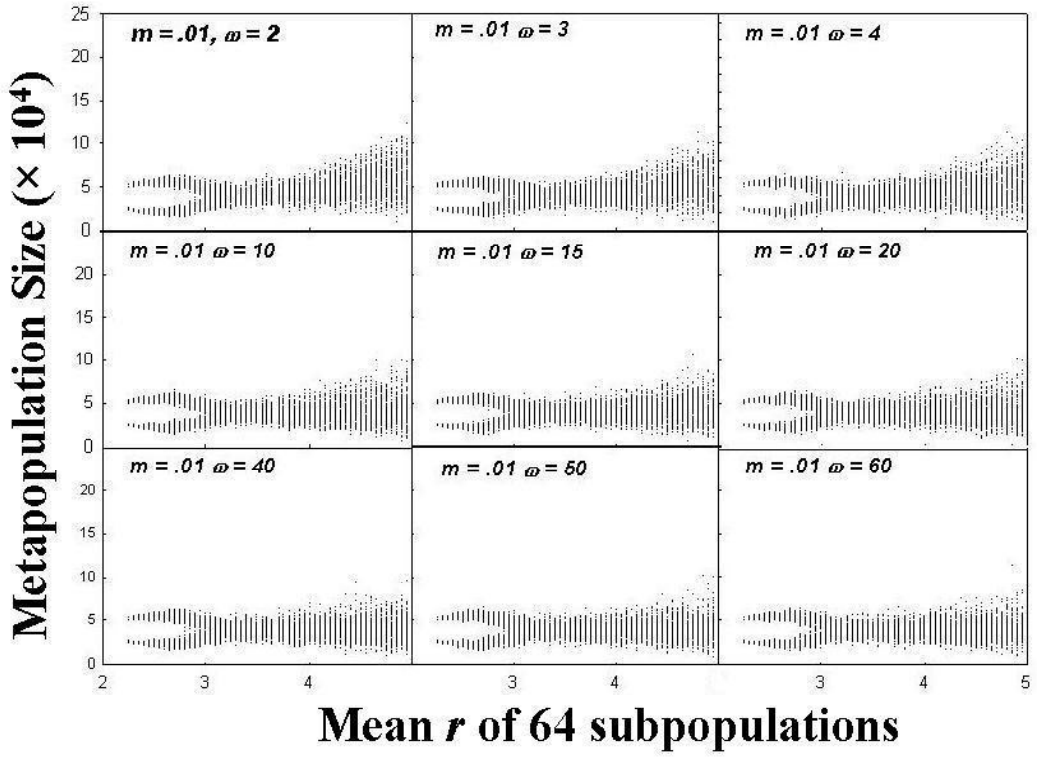

Figure 4.4a. Dynamics of a 64-patch metapopulation when density-independent migration events take place every ω generation at a rate of m = .01When migration events do not take place in every generation, the stabilizing effect of migration is lost. The more infrequent the migrations are (i.e. higher the values of ω) the closer are the pattern of metapopulation dynamics to the zero migration (m = 0) case. See text for further discussion.

Spatial arrangement

No major qualitative differences in patterns of metapopulation stability were observed under the various spatial arrangements considered (linear, alternate, random). This result agrees with a previous study (Dey et al. 2006a) and indicates that the dynamics of metapopulations are reasonably robust to differences in how the subpopulations are arranged in space. This is reassuring from the point of view of metapopulation modeling, as it suggests that the finer details of the precise spatial distribution of heterogeneous subpopulations can be typically safely ignored.

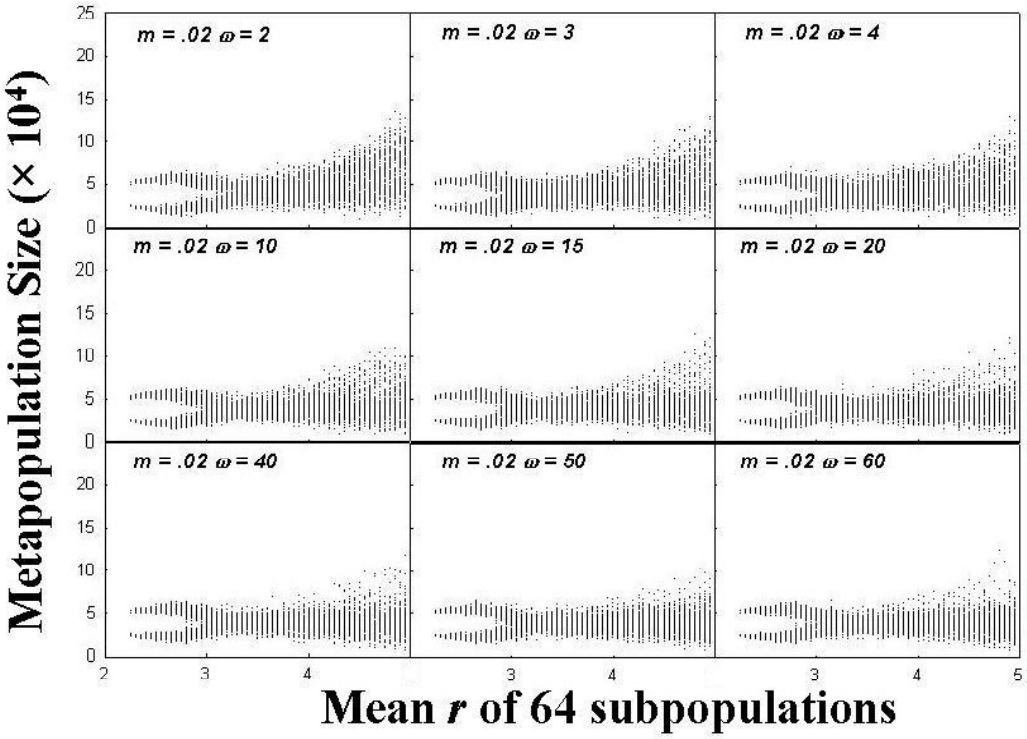

Figure 4.4b. Dynamics of a 64-patch metapopulation when density-independent migration events take place every ω generation at a rate of m = .02.

As there were no major differences between the three spatial arrangements, here I restrict myself to presenting the results of simulations on the linear arrangement of subpopulations (See Methods).

Density-dependent migration rate

Migration rate has been treated as a density-independent constant in most studies on the effects of migration on metapopulation dynamics (Gyllenberg et al. 1993, Hastings 1993, Kendall and Fox 1998, Dey et al. 2006a). However, this is an unrealistic assumption as

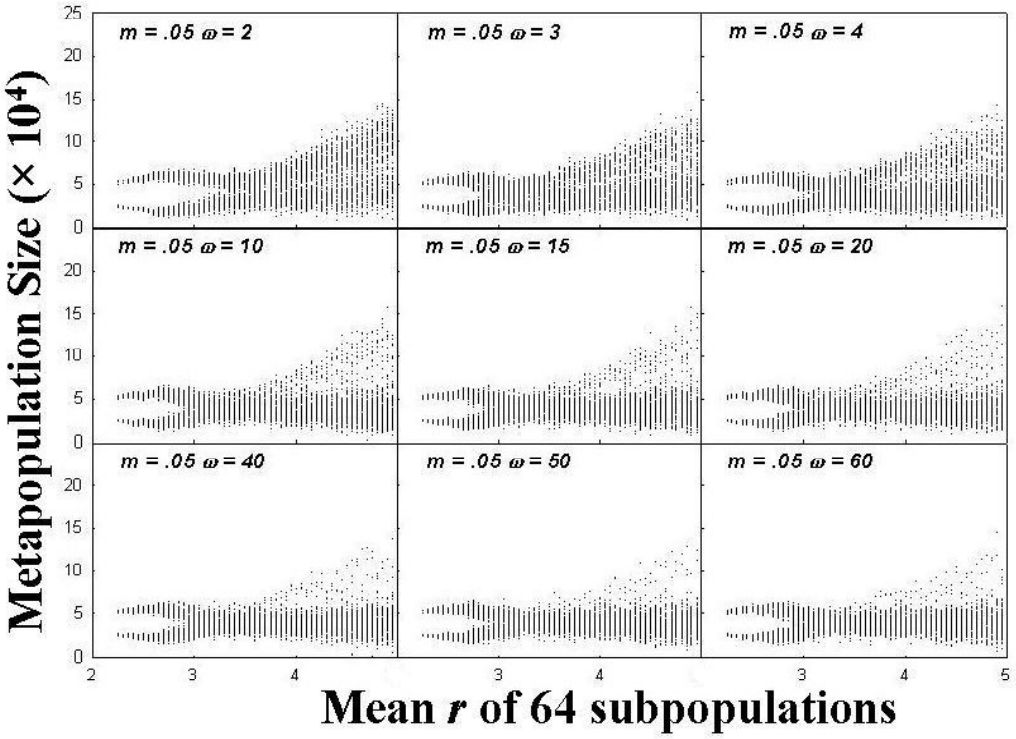

Figure 4.4c. Dynamics of a 64-patch metapopulation when density-independent migration events take place every ω generation at a rate of $m = .05$.

the rate of migration in a given generation and patch is likely to be a function of the present subpopulation density and also subject to stochastic variation. Therefore, I examined the case where migration rate (m) is density-dependent (equation 4) across generations and space (Fig. 4.2). Density-dependent migration (Fig. 4.2) did not lead to any observable qualitative differences from the case when migration rate was density-independent (Fig. 4.1). This suggests that, at least for the formulation of density-dependent migration rate in this study, there is no major difference in the dynamics regardless of whether the migration rate is density-independent or density-dependent. A previous study (Ylikarjula et al. 2000) investigated several different schemes of density-

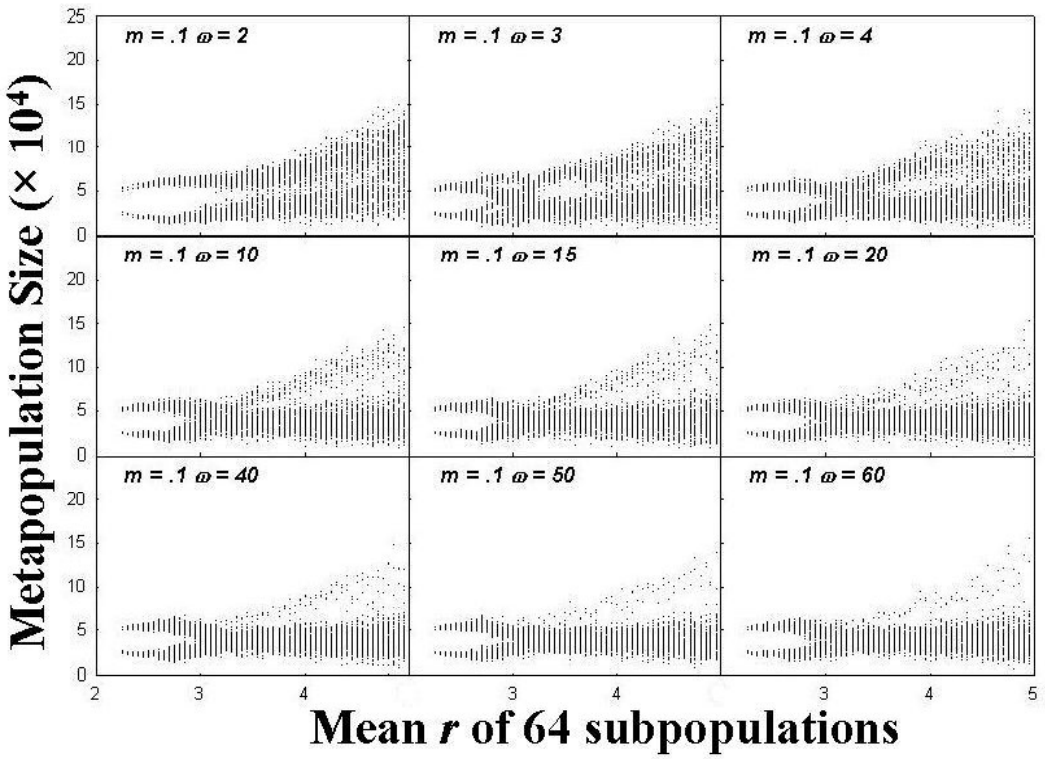

Figure 4.4d. Dynamics of a 64-patch metapopulation when density-independent migration events take place every ω generation at a rate of m = .1.

dependent and density-independent migration, but did not observe any consistent difference in subpopulation synchrony among the different schemes. Unfortunately, Ylikarjula et al. (2000) did not report the behavior of the global dynamics, which makes direct comparison with the current results difficult. It should be noted here that the density-dependent migration scheme used in this work is not one of those used by Yliikarjula et al. (2000). Taking together the results of Yliikarjula et al. (2000), Dey et al. (2006), and the current work, it seems that whether migration rate is density-dependent or density-independent does not make any major differences to the global or local patterns of stability in metapopulations.

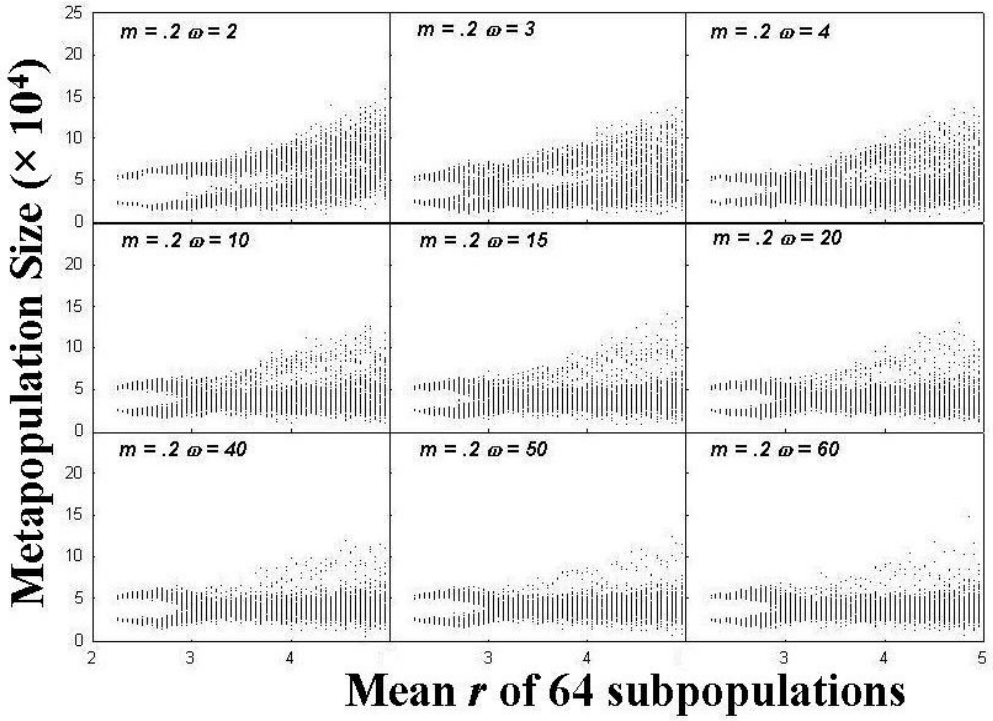

Figure 4.4e. Dynamics of a 64-patch metapopulation when density-independent migration events take place every ω generation at a rate of $m = .2$.

This observation implies that at least for modeling natural metapopulations whose dynamics approximately follow the Ricker map, it might be safe to consider an average density-independent rate of migration, rather than explicitly incorporating a density-dependent function in the model.

Stochastic migration rate

I also studied a scenario where migration is density-independent and occurs every generation, but with rates that are normally distributed around some constant mean and standard deviation. Again, this is a more realistic assumption than the constant rates of

migration assumed by most previous studies. However, just like density-dependent migration rate, stochastic migration rate also did not have any major observable effects on the dynamics of the metapopulations (Fig. 4.3a - 4.3c). As expected, increasing the standard deviation of the distribution of *m* destabilized the metapopulations. Despite this destabilization, the patterns observed in Fig. 4.1 remained unchanged, and maximum stability was obtained for intermediate values of *m*. However, at very high standard deviation (Fig. 4.3c) the maximum stability for high *r*-values was obtained at $m = .02$, rather than at $m = .05$, as in Fig. 4.1. Thus, it appears that at least for the kind of variation in *m* that I considered in this study, it is the mean migration rate that determines the dynamics of the metapopulations. This observation suggests that knowledge of the mean migration rate is probably sufficient to understand the major features of the dynamics of metapopulations and is, therefore reassuring from the point of view of modeling real metapopulations, at least for systems that approximately follow Ricker dynamics.

Periodic migration

When migration is periodic, there is a marked change in the dynamics of the metapopulation (Fig. 4.4, a-e) for all values of *m*. For low values of *m* (.01, .02), even low periodicity (ω) is enough to strongly destabilize the metapopulation (*cf* Fig. 4.1 and first three panels of Fig. 4.4a and 4.4b). Even migration every alternate generation ($\omega = 2$) is not sufficient to stabilize the dynamics at the metapopulation level. As ω increases, the number of migration events taking place within a fixed number of generations goes on decreasing, and the metapopulation dynamics increasingly resembles the situation when there is no migration at all. Thus, for all values of *m*, the three panels at the bottom

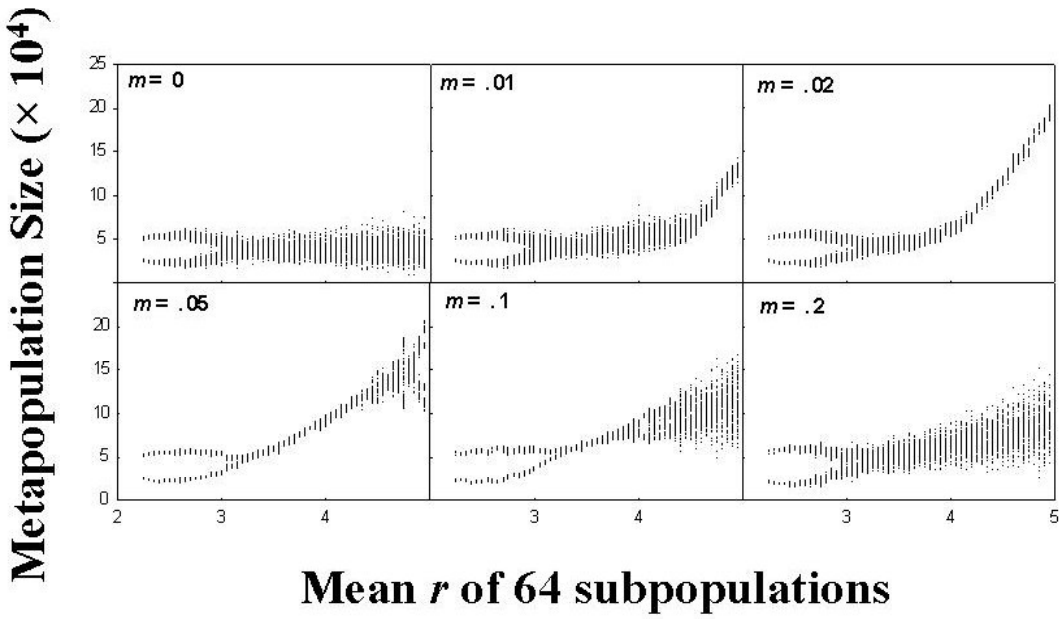

Figure 4.5a. Dynamics of a 64-patch metapopulation when there is a 99% probability of migration taking place in a particular generation for a given subpopulation.

(denoting high values of ω) of Fig. 4.4a - 4.4e are almost identical to the zero migration case of Fig. 1. However, when m is high (.1, .2; Fig. 4.4d and 4.4e), the amplitude of oscillation of metapopulation numbers is greatly increased, particularly for higher values of mean r, thus signifying a greater instability. These behaviors at the metapopulation level can probably be explained if the periodic migration events are thought to be analogous to perturbations in the context of the zero migration case. Thus, low rates of migration (Fig. 4.4a and 4.4b) lead to a smaller degree of perturbation to the metapopulation dynamics as a whole, and hence, the dynamics more or less resemble the case when there is no migration. However, a high rate of migration would mean a greater perturbation to the dynamics of the metapopulation, resulting in a more serious departure from the zero migration scenario. If this conjecture were to be true, then one would expect the rate at which the overall metapopulation dynamics converges to the zero

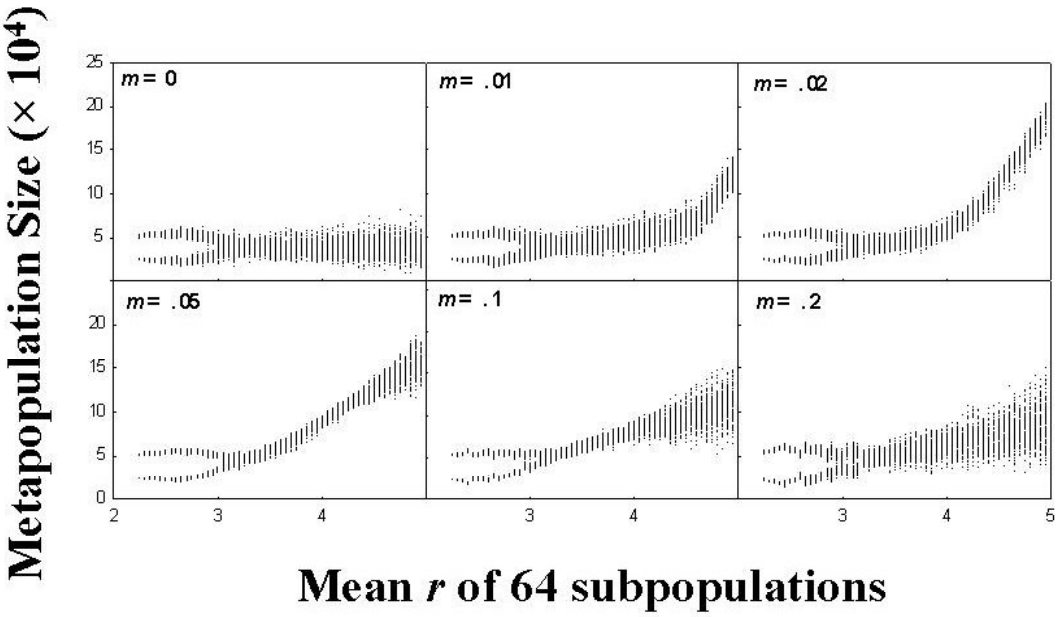

Figure 4.5b. Dynamics of a 64-patch metapopulation when there is a 90% probability of migration taking place in a particular generation for a given subpopulation.

migration case with increase in ω, to be different for different values of m. To be more specific, when m is low, it is expected that the rate of convergence would be high and vice versa. Comparing Fig. 4.4a – 4.4e shows that this indeed is the case, and with increase in m, there is an observable reduction in the speed with which the overall dynamics returns to the zero migration case with increasing ω.

These results indicate that at least for systems that approximately follow Ricker dynamics, it is imperative to have very frequent migration among the subpopulations in order to beget stability at the level of the metapopulation. This has possible implications for management and conservation of those animals in which migration plays an important role in stabilizing metapopulation dynamics. However, it is to be noted that even when ω = 2, the total number of migration events that occur in T generations, is $T/2$. In other words, even for the lowest value of ω (= 2) in the present study, a given subpopulation

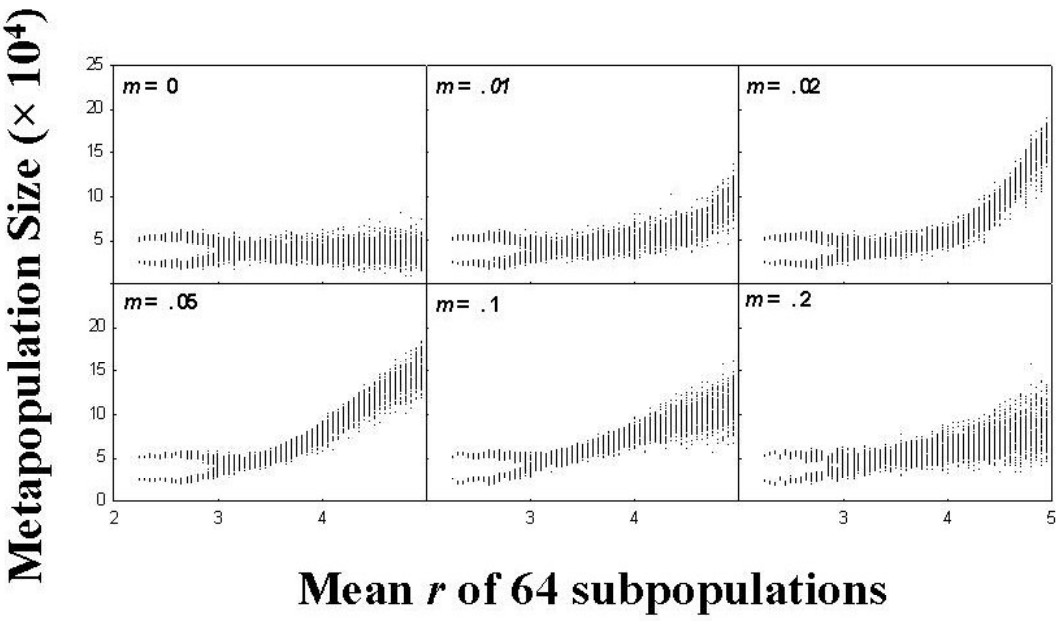

Figure 4.5c. Dynamics of a 64-patch metapopulation when there is a 80% probability of migration taking place in a particular generation for a given subpopulation.

sent out and received migrants only in 250 generations out of 500. This begs the question as to whether this level of occurrence of migration is just too low to maintain stability in the given system, or whether any arbitrarily small departure from the condition of migration every generation would also lead to instability. I deal with this question in the next section.

Stochastic migration events

In this part of the study, migration from a patch in a particular generation was assumed to occur with a certain probability. From Fig. 4.5a it is seen that even when this probability (ψ) is as high as 0.99 (i.e. only in 1/100 generations per subpopulation, on average, does one expect a migration event to *not* occur) there is considerable amount of

destabilization. Limit cycles of low period disappear completely and only high periodicity cycles/chaos are observed. This effect is further magnified at $\psi = 0.9$ and $\psi = 0.8$ (Figs. 4.5b and 4.5c) wherein the range of oscillations in metapopulation size are also increased. Combining the results of this section and the previous one suggests that migration is needed in almost every generation in order to stabilize a Ricker-based metapopulation by migration alone. This result sounds a cautionary note towards efforts to conserve fragmented populations by creating migration corridors between isolated patches. In order to attain stability, it is not only essential that migration occurs at a certain (intermediate) rate, but also that the migration events happen sufficiently regularly.

To summarize, my results suggest that there is no gross difference in the effects of migration rate on metapopulation stability whether migration rate is density-dependent, density-independent, or subject to stochastic variation. However, in order to beget stability by migration alone, it is essential that migration events take place very frequently, preferably every generation. Finally, these results are robust to demographic and spatial heterogeneity among the subpopulations. The Ricker map is known to be a fair descriptor of dynamics of organisms from a large number of taxa, including microbes (Ives et al. 2004) and insects (Cheke and Holt 1993, Sheeba and Joshi 1998, Dey and Joshi 2006b). Therefore, apart from their theoretical implications, these results are expected to be of general importance to empirical ecologists and conservation planners.

CHAPTER 5

EFFECTS OF LOCALIZED PERTURBATIONS

Localized perturbations are unlikely to affect the dynamics of real biological metapopulations.

Dey, S., and Joshi, A. 2007. Local perturbations do not affect stability of laboratory fruitfly metapopulations. PLoS ONE **2**(2): e233.

INTRODUCTION

Simple one-dimensional maps can exhibit a variety of dynamic behaviors ranging from stable points to limit cycles to chaos (May 1974, 1976), and have been extensively used to model the dynamics of single populations. It has been shown that for large ranges of parameter values, the dynamics of such maps can be substantially altered by the addition (McCallum 1992) or removal (Sinha and Parthasarathy 1995, Gueron 1998) of a constant number of individuals every generation. This happens because such perturbations can change the slope of the return map at the equilibrium point, thereby affecting the dynamics of the population (Stone 1993, Stone and Hart 1999). However, such simple models explicitly assume that the individuals in the population are homogeneously distributed in space, whereas many real populations exhibit spatial structuring into metapopulations: groups of local populations (subpopulations) connected by migration. Many methods for stabilizing the dynamics of metapopulations by perturbation have been proposed in the context of both ecological (Güémez and Matías 1993, Stone 1993, Doebeli and Ruxton 1997, Parekh et al. 1998, Stone and Hart 1999) as well as physical (Sepulchre and Bablyonatz 1993, Aranson et al. 1994, Braiman et al. 1995, Grigoriev et al. 1997) systems, and some of these proposed algorithms have been empirically verified in physical (Hunt 1991, Roy and Murphy 1992) or in-vitro physiological systems (Garfinkel et al. 1992, Schiff et al. 1994). However, to the best of my knowledge, there has been no experimental confirmation of stabilization of a real biological metapopulation by constant perturbation.

There are several reasons why experimental studies lag far behind the substantial body of theoretical predictions on the issue of metapopulation stabilization by perturbation. Most theoretical studies on the subject have explicitly concentrated on stability in terms of amelioration of chaos to get stable points or limit cycles (Güémez and Matías 1993, Doebeli and Ruxton 1997, Parekh et al. 1998, Parekh and Sinha 2002). However, since real organisms come in discrete (integer) numbers, no real population can exhibit chaos in the strict sense, although this does not rule out the possibility of complex dynamics (Henson et al. 2001). Moreover, most theoretical treatments assume a large number of subpopulations in an ideal, noise free, zero-extinction environment, which is far from the reality of actual biological metapopulations.

Here I report a 21-generation long experiment on the effects of localized perturbations at the subpopulation level on local and global stability, using two sets of four replicate *D. melanogaster* metapopulations each. Each metapopulation contained 9 subpopulations, represented by single vial cultures, arranged on the periphery of a circle, with 30% migration in each generation to the two nearest neighbors. In the four *pinned* (Parekh et al. 1998) metapopulations, I perturbed the same subpopulation (henceforth, the *pinned subpopulation*) in every generation by adding a fixed number of flies from outside the system, whereas there were no such perturbations in the four *control* metapopulations. I show that although pinning affects the dynamics of the particular pinned subpopulation, it has no measurable effects on metapopulation dynamics. I also show that Ricker-based simulations capture the patterns observed in the data, indicating that my results are generalizable. I further demonstrate, via simulations, that the current findings are robust

to the various assumptions made in the experiment regarding the number of pinned patches per metapopulation, the strength of pinning, and migration rates. Finally, I investigate the effects of the interaction of extinction and pinning in shaping metapopulation dynamics and show that my results generally hold even in the absence of local extinctions. Since I explicitly focus on indicators of stability that are ecologically meaningful and can be measured easily, these results are not only of interest to ecologists but have potential practical implications for a conservation biologist trying to develop schemes for stabilizing a fragmented population.

MATERIALS AND METHODS

Experimental populations

In this experiment I used eight replicate metapopulations of the fruit fly *D. melanogaster*, each consisting of nine subpopulations. Four of these metapopulations were subjected to pinning and the other four acted as controls. The seventy-two subpopulations, each represented by a single-vial culture, were derived from a long-standing, outbreeding laboratory population (JB-1) of *D. melanogaster*, whose ancestry and maintenance regime has been described elsewhere (Sheeba et al. 1998). Each subpopulation was initiated by placing exactly 20 eggs in a 30 ml glass vial containing ~1 ml of banana-jaggery medium. The flies that came out of these eggs were designated as generation 0, and no direct control was exercised on the egg density in a vial from that point onwards. Once the adults started eclosing around day 8-9 after egg lay, they were collected daily in

corresponding holding vials containing ~3 ml of medium. The adults were transferred to fresh holding vials every alternate day, until day 18 after egg collection. Extreme care was taken to ensure one-to-one correspondence between egg vials and adult collection vials. On day 18, the flies were supplied with excess live-yeast paste for three days, to enhance their fecundity. On the 21st day after collection of eggs, the adult flies were sexed, censused, subjected to migration (see below), and allowed to lay eggs for 24 hours in vials containing ~1 ml banana-jaggery medium. After oviposition, the adults were discarded while the eggs formed the next generation. This maintenance regime (low larval and high adult food levels) has been extensively studied and is known to induce large amplitude periodic oscillations in population numbers (Mueller and Huynh 1994, Sheeba and Joshi 1998, Mueller et al. 2000, Prasad et al. 2003).

Migration and pinning

Following an earlier study (Dey and Joshi 2006b), the subpopulations (single vial *D. melanogaster* cultures) were arranged on the periphery of a circle, with each of them sending out and receiving migrants to and from the two nearest neighbors. This arrangement can also be visualized as a one-dimensional linear array with periodic boundary condition in terms of migration. Such one-dimensional systems can be found in nature on the shores of lakes or on forest edges. Migration (30%) was imposed by manually removing the required number of flies from a subpopulation and distributing them equally to the two neighboring vials, just prior to reproduction in every generation. Only mated females were migrated, as the dynamics of the population of a sexually

reproducing organism is chiefly governed by the number of females. In order to calculate the number of migrant females, the total count in a vial was halved (i.e. a sex ratio of 1:1 is assumed) and rounded upwards in case of fractions. This number was multiplied by 0.3 (i.e. the migration rate) and rounded off to the nearest even integer, to give the total number of female migrants. There were frequent extinctions in the subpopulations during the course of the experiment. Upon extinction, a vial remained empty until it was recolonized by migrants from a neighboring vial.

Pinning was imposed on four metapopulations by introducing eight mated females every generation to a designated (pinned) subpopulation just before the census. The flies required for this purpose were generated from backup vials that had excess (~ 6 ml) food for larvae and yeast supplement for the adults, and were run in parallel with the experimental vials. It should be noted that for a particular metapopulation, the same subpopulation was pinned in every generation. The average subpopulation size in these experiments was found to be ~26 flies. Thus, the strength of pinning used in this experiment is ~33% of the average population size. Given that only mated females were migrated, this represents a fairly strong perturbation. Since the pinning flies were introduced prior to the census, a 30% migration rate ensured that at least one female was migrated to each of the neighboring vials. Thus, the pinning strength can also be described as six flies to the pinned vial and one each to the two immediate neighbors. The remaining four metapopulations experienced 30% migration but no pinning and, thus, served as controls.

Measuring stability and synchrony

I considered a population whose size fluctuates with higher amplitude across time to be less stable than one that has lower amplitude of fluctuation ("constancy" attribute of stability, *sensu* Grimm and Wissel 1997). I measured the constancy stability using the fluctuation index (FI) (Dey and Joshi 2006b), which is given by:

$$\mathrm{FI} = \frac{1}{T\overline{N}} \sum_{t=0}^{T-1} \mathrm{abs}\,(N_{t+1} - N_t)\ ,$$

where N_t is the population size at time t and $\overline{N}$ is the mean population size over T generations. Thus, FI measures the average one-step fluctuation in population size across generations, scaled by the mean population size. Since it is a dimensionless quantity, FI can be used to compare the dynamics of populations even if they vary widely in size. I measured synchrony as the cross-correlation at lag zero of the first differenced time series of log abundance [ln (N_{t+1}) - ln (N_t), where N_t is the population size at time t] of the nearest neighboring subpopulations in a metapopulation (Bjørnstad et al. 1999).

Statistical analysis

All data were subjected to a two-way nested mixed model analysis of variance (ANOVA), treating replicate metapopulation as a random factor nested within treatment

(control/pinned; fixed factor). All statistical analyses were performed using the commercially available software, STATISTICA ® v 5.0 (Statsoft Inc).

Simulations

The simulation study was designed to be as close to the experimental system as possible. The subpopulation dynamics were modeled using the Ricker model [$n_{t+1} = n_t \exp (r(1 - n_t / K))$] (Ricker 1954), where n_t represents the subpopulation size at time t, and r and K refer to the intrinsic per capita growth rate of the subpopulation and carrying capacity of the patch, respectively. A metapopulation consisted of nine linearly arranged subpopulations, with nearest neighbor migration under periodic boundary condition (Dey et al. 2006a, Dey and Joshi 2006b). The carrying capacity, K (=25) and the initial subpopulation size (=20) were kept invariant for all the simulations. All the subpopulations in a given run had the same value of r with a noise term ε ($0 < \varepsilon < 0.2$; uniform random distribution) added to r for each subpopulation at every generation, to simulate stochastic variation in population growth rates. I simulated the experimental system for r-values of the subpopulations ranging from 2.0 to 4.0 in increments of 0.1 and for each value of r, I plotted the means and standard errors of 10 independent runs. Estimates of r (mean 2.9; SD .33) and K (mean 25.1; SD 7.2) were derived by fitting the Ricker map to the subpopulation time series from the experimental controls (see *Parameter estimation* below). Thus, the chosen parameter range includes the biologically relevant range for my laboratory populations of *D. melanogaster*.

Coupled map lattices can have very long transients (supertransients) lasting for thousands of iterations (Kaneko 1998), and the behavior of the system during this transient phase can be very different from the equilibrium behavior (Hastings and Higgins 1994). Although most theoretical studies on coupled map lattices concentrate on the equilibrium dynamics (eg. Güémez and Matías 1993, von Bremen and Udwadia 2002), I calculated the various metrics estimated in the experiment using data from only the first 100 iterations, thus concentrating explicitly on the transients. I consider this to be a closer approximation to my experiment, which lasted for 21 generations. Moreover concentrating on transient dynamics is also more meaningful ecologically as any real population is unlikely to experience a constant environment or, for that matter, even survive for thousands of generations in nature (Hastings 2004).

In the simulations seeking to imitate the experimental conditions, the rate of migration was kept constant at 30%. Pinning was modeled by adding 8 individuals to the pinned subpopulation, in every generation, prior to migration. Since a Ricker map does not take zero values, I stipulated extinction probabilities that were estimated from the time series of the controls (Fig. 5.1). For this, I calculated the frequency of extinction (absence of at least 1 male and 1 female, before migration) in the next generation (t+1), when the population sizes were low (< 10), medium (≥ 10 and <70) or high (≥ 70) in the parent generation (t). At an r-value of 2.8, this set of extinction probabilities predicted an average of 5.02 out of 9 subpopulations going extinct per generation, which was higher than the corresponding estimate from the experimental controls (3.69). I also computed the extinction probability profile from the experimental data for bin sizes of <5, 5-70, and

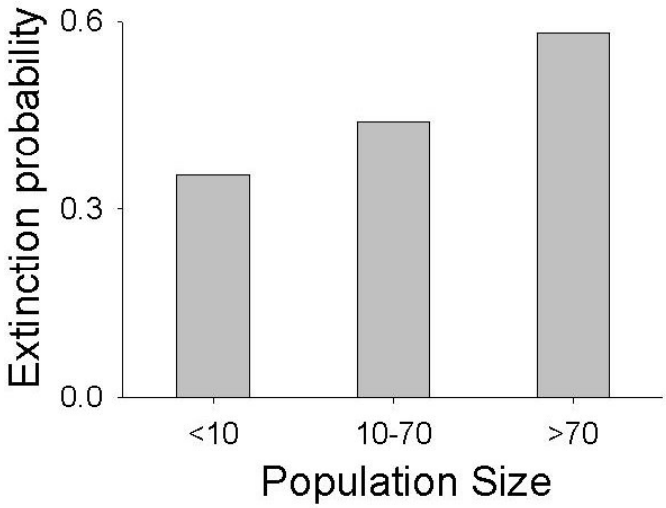

Figure 5.1. Empirically observed extinction probabilities at different population sizes. This shows the fraction of times a population went extinct in generation $t+1$, when the population size in generation t fell within a particular range in the controls.

>70, and repeated all the simulations with these values of extinction probabilities (data not shown). This predicted an average subpopulation extinction rate of 3.3 out of 9 per generation, but did not lead to any qualitatively different predictions at the subpopulation or metapopulation level from those shown in figures 5.3-5.6. This suggests that my simulation results are robust to the way in which the extinction probabilities are computed.

I then studied the effects of pinning different numbers of subpopulations (1, 2, 3, 4, 5, 7, 9), pinning strengths (0, 2, 4, 8, 12, 16 individuals per generation) and migration rates (10%, 20%, 30%, 40%) on the metapopulation dynamics. Since it is known that the distribution of pinned patches can affect the dynamics (Doebeli and Ruxton 1997), for a given level of number of pinned patches (i.e. 1, 2, 3, 4, 5, 7 or 9), the spatial arrangement

of the pinned patches was kept similar in all simulations. In all the simulations described in this paragraph, the default values of parameters not under investigation were kept constant at levels described for the simulations mimicking the experiments. Thus, for example, in the simulations on the effects of pinning different numbers of subpopulations, the pinning strengths and migration rates were kept constant at 8 individuals and 30%, respectively, and so on.

Parameter estimation

The least-squares estimates of the parameters r and K were obtained using the in-built Quasi-Newton algorithm of STATISTICA ® v 5.0 (Statsoft Inc) and, on an average, the model was able to explain ~40% of the variation in the data. While this fraction does appear to be somewhat low, note that the subpopulations were also undergoing migration in every generation, a fact that was ignored during the modeling procedure, when individual subpopulation time series data were fit to the model. Moreover, the sources of noise in my model are a) white noise in the parameter r, and b) experimentally derived extinction probabilities, whereas a model that explicitly incorporates demographic stochasticity (Drake 2005) might be better suited to model extinction prone populations. While it would be interesting to compare the parameter estimates derived from such detailed models with the estimates obtained in the present study, such an exercise is clearly beyond the scope of this thesis.

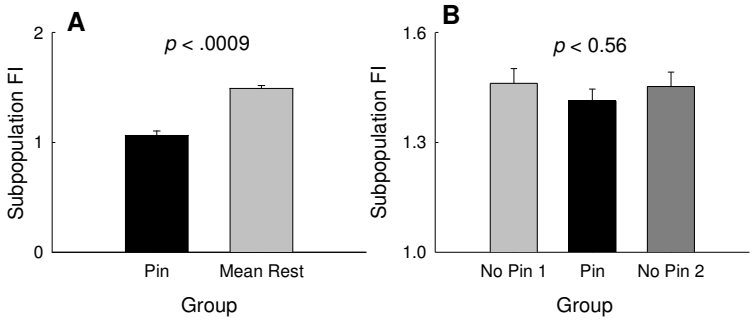

Figure 5.2. Experiment: effect of pinning at the subpopulation level, averaged over four replicate metapopulations. (**A**) The mean FI of the pinned subpopulation was significantly less than the mean of the remaining eight subpopulations. (**B**) There was no difference in the average FI of the pinned group (the pinned subpopulation and its two immediate neighbors) and the two neighboring groups on either side (No Pin1 and No Pin 2). This suggests that the stabilized subpopulation could not stabilize the dynamics of the pinned group vis-à-vis the two neighboring groups. Error bars indicate standard errors around the mean in this and all subsequent figures in this chapter.

RESULTS AND DISCUSSION

Experiment

The mean fluctuation index, FI (Dey and Joshi 2006b), of the pinned subpopulations was significantly lower ($F_{1,3}$= 180.95, $p < 0.0009$) than the mean FI of the remaining eight subpopulations in the pinned metapopulations (Fig. 5.2A). This indicates that constant addition of flies every generation from outside the metapopulation stabilized the pinned subpopulation by reducing the fluctuation in its population size over time. I then sought to check if this stabilized subpopulation (i.e. the pinned subpopulation) was in turn able to affect the dynamics in its neighborhood or not. For this, I divided the pinned metapopulation into three groups; each consisting of three subpopulations. The *pinned*

group contained the pinned subpopulation and its two immediate neighbors, while the other two groups (*No Pin 1* and *No Pin 2* in Fig. 5.2B) were comprised of the three neighboring subpopulations to the right and left of the pinned group respectively. There was no significant difference ($F_{2,6}$ = .64, p = 0.56) between the average FI of the pinned group and the neighboring groups (Fig. 5.2B) thus indicating that the reduced FI of the pinned subpopulation does not translate into significant stabilization of the pinned group vis-à-vis the neighboring non-pinned groups.

I then measured the various attributes of metapopulation dynamics (see Materials and methods), like metapopulation stability (Fig. 5.3A), subpopulation stability (Fig. 5.3B), synchrony among nearest neighboring subpopulations (Fig. 5.3C), and average subpopulation size (Fig. 5.3D), but did not observe any significant difference between the control and the pinned metapopulations. Another commonly used measure of population stability, namely the coefficient of variation (CV) of population size, was also found to be similar in both treatments at the metapopulation ($F_{1,6}$ = .32, p < 0.59) and subpopulation ($F_{1,6}$ = 1.13, p < 0.33) level. When an extinct patch was defined as one that remained empty during breeding after migration had taken place, the total number of subpopulation extinctions over 21 generations was considerably less in the pinned metapopulations (39) than in the controls (69). However, this is an artifact of the experimental protocol, as all three subpopulations in the pinned group of the pinned metapopulation were, by design, receiving flies from outside every generation (see Materials and methods) and hence they were never scored as extinct. When I considered pre-migration extinction, in the form of absence of at least one breeding pair (i.e. 1 male + 1 female) in a subpopulation, there

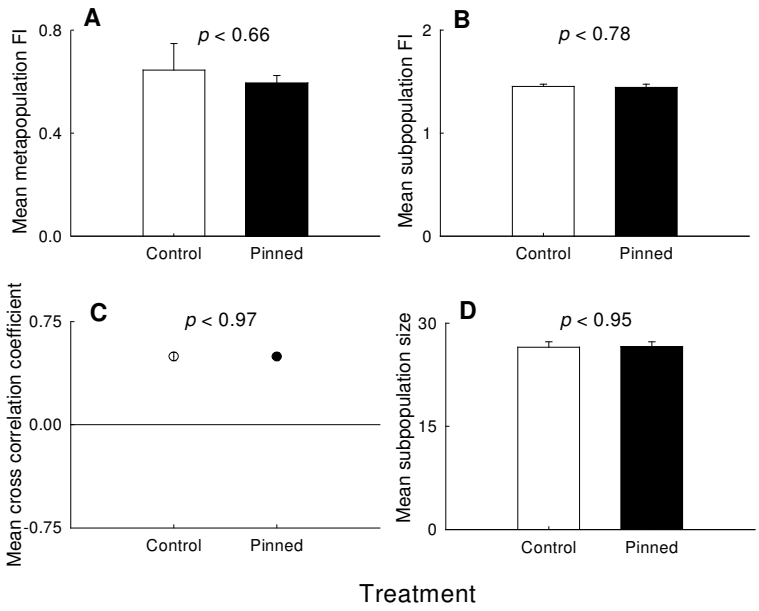

Figure 5.3. Experiment: effect of pinning at the metapopulation level, averaged over four replicate metapopulations. (**A**) Metapopulation stability and (**B**) subpopulation stability were measured as the fluctuation index (FI) over 21 generations. (**C**) Synchrony among nearest neighbors was measured as the cross-correlation at lag zero of the first differenced ln-transformed values of population sizes. Due to the high rates of migration, the subpopulations were found to be in synchrony, as demonstrated by the positive cross correlation coefficients. (**D**) Average subpopulation size. There was no difference among the pinned and the control metapopulations in any of the panels, indicating that pinning had no detectable effect on metapopulation dynamics.

was no difference in number of extinctions per generation between the pinned and control metapopulations ($F_{1,6}$ = .009, p < 0.93), indicating that pinning did not affect the persistence of subpopulations. Together, these observations suggest that pinning had no effects on stability or, indeed, on any of the other measured attributes of the metapopulation.

The above experimental observations could have arisen due to two possible reasons: either pinning, at least at the levels used here, genuinely does not affect the dynamics of

metapopulations, or there are some unique features of *D. melanogaster* life-history or ecology in the laboratory that ameliorate the effects of pinning. In case the second hypothesis were true, these results are not likely to be generalizable to other species and, hence, would be of limited interest. One way to distinguish between these competing hypotheses is to simulate my experimental system with a biologically relevant model of population dynamics that is broadly applicable to several species and does not include any specific features of *D. melanogaster* life-history or laboratory ecology. If such a model were able to capture at least the general features seen in the experimental data, then one would expect these results to be valid for a wide spectrum of organisms.

Simulations

Experimental system

It has been analytically demonstrated that populations with a random spatial distribution and scramble competition follow the Ricker dynamics (Brännström and Sumpter 2005). Since laboratory cultures of *D. melanogaster* exhibit both features, I modeled the subpopulation dynamics by the Ricker model (Ricker 1954), a simple one-dimensional model of population dynamics, whose qualitative behavior is solely determined by the intrinsic growth rate parameter, *r* (May and Oster 1976). The Ricker model has been shown to be a good descriptor of the dynamics of various types of organisms like microbes (Ives et al. 2004), fishes (Ricker 1975) and insects (Cheke and Holt 1993), including *D. melanogaster* (Sheeba and Joshi 1998, Dey and Joshi 2006b). Thus, this

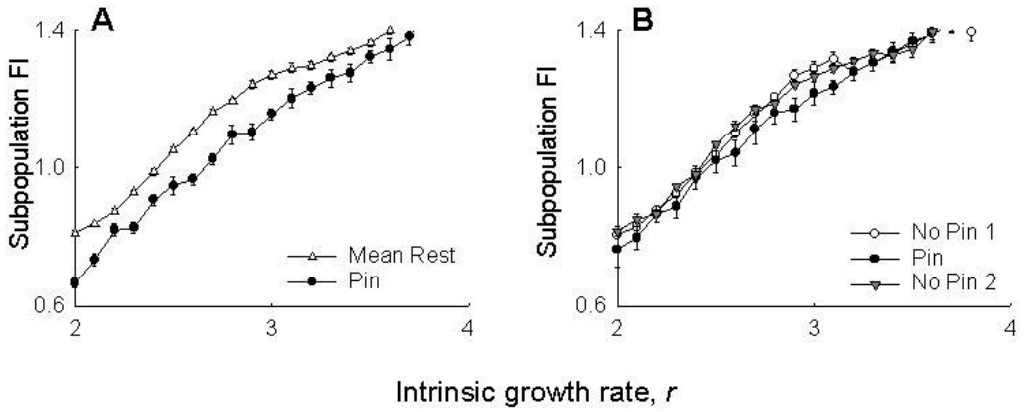

Figure 5.4. Simulations mimicking experiment: effect of pinning at the subpopulation level. (**A**) The FI of the pinned subpopulation was lower than the mean of the remaining eight subpopulations, over a substantial range of the intrinsic growth rate parameter, *r*. (**B**) There was no difference in the average FI of the pinned group and its two neighboring groups. These observations agree with the experimental results (*cf.* Fig 5.1), implying that the experimental findings are not specific to *D. melanogaster*. All data points in this and subsequent simulation figures represent average of 10 independent runs. See text for details of simulations.

model satisfies the criteria of being biologically relevant, not specific to *D. melanogaster*, and widely applicable.

The simulation results were seen to support the experimental observations. The FI of the pinned subpopulation in the simulations was found to be lower than the mean of the remaining eight subpopulations for a range of *r*-values (Fig. 5.4A), while the mean FI of the pinned group was found similar to or, for some values of *r*, slightly lower than the other groups (Fig. 5.4B). As in the experiments, there were no observable differences in the metapopulation FI (Fig. 5.5A), subpopulation FI (Fig. 5.5B) or subpopulation synchrony (Fig. 5.5C) between control and pinned metapopulations in the simulations. The model predicted a slight decrease in subpopulation size (Fig. 5.5D) in the pinned metapopulations, at least for lower values of intrinsic growth rate *r*, which was not observed in the experiments. Overall, these results agree well with the experimental data,

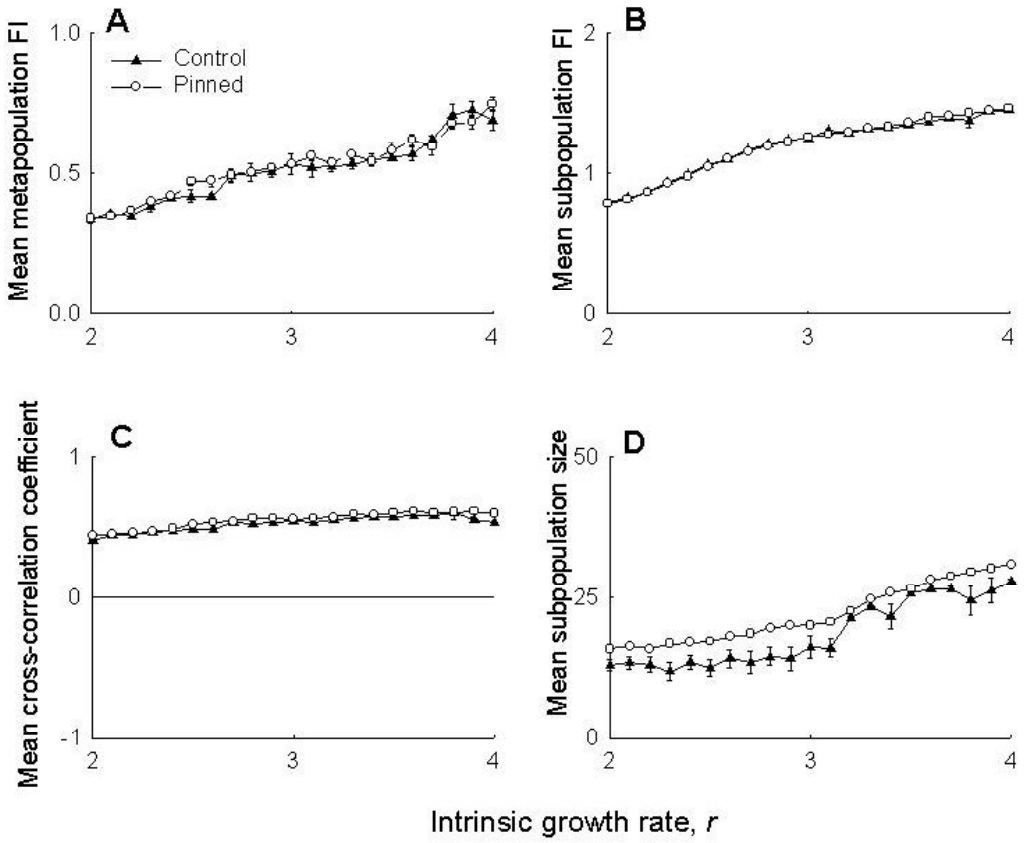

Figure 5.5. Simulations mimicking experiment: effect of pinning at the metapopulation level. Ricker based simulations predicted no difference in (**A**) metapopulation stability, (**B**) subpopulation stability, and (**C**) synchrony amongst nearest-neighbors, between the control and pinned metapopulations. (**D**) The simulations suggested a slight decrease in subpopulation size for low values of *r*, which was not picked up by the experiment. Overall, these results agree with the corresponding experimental findings (Fig 5.2), indicating that they are likely to be applicable to other species.

suggesting that the experimental observations are unlikely to be specific to *D. melanogaster*. It is important to note here that these results do not invalidate previous theoretical studies on using regular perturbations to stabilize chaotic systems to get limit cycles or stable points (Doebeli and Ruxton 1997, Parekh et al. 1998), as those studies investigated a different kind of stability altogether. The findings of this study merely suggest that, all else being equal, the effects of localized perturbations are unlikely to be measurable at the metapopulation level in real biological populations.

Relaxing experimental assumptions

Studies on laboratory systems generally entail a higher degree of accuracy in measurement and better control over noise than is possible in nature. Thus, failure to observe an effect of pinning under controlled laboratory conditions indicates that, at least under conditions similar to the experiment, pinning is expected to be of limited importance in controlling the dynamics of real populations. However, earlier theoretical studies have shown that the number of patches pinned, the magnitude of pinning, and the migration rate can affect the dynamics of the metapopulation (Doebeli and Ruxton 1997, Parekh et al. 1998, Parekh and Sinha 1999, 2002). Since I conducted the experiments under a fixed set of conditions — pinning one patch with 8 females in each generation, under 30% migration rates — it is natural to ask whether these results would have been altered if one or more of these conditions had been different. Moreover, in this study, I used unstable *D. melanogaster* subpopulations that had a high rate of extinction, which can also possibly influence the dynamics. Although the ideal way to address these issues would have been to conduct more experiments under appropriate conditions, logistic constraints prevented me from doing so. Since this and earlier studies (Dey and Joshi 2006b) have indicated that Ricker-based coupled map lattices are good surrogates for *D. melanogaster* metapopulations, I used the same simulation framework described above to investigate the effects of departures from the experimental conditions.

Increasing the proportion of pinned patches did not change the metapopulation FI, at least for values of $r < 3$ (Fig. 5.6A). For higher values of r, which signifies the chaotic zone in

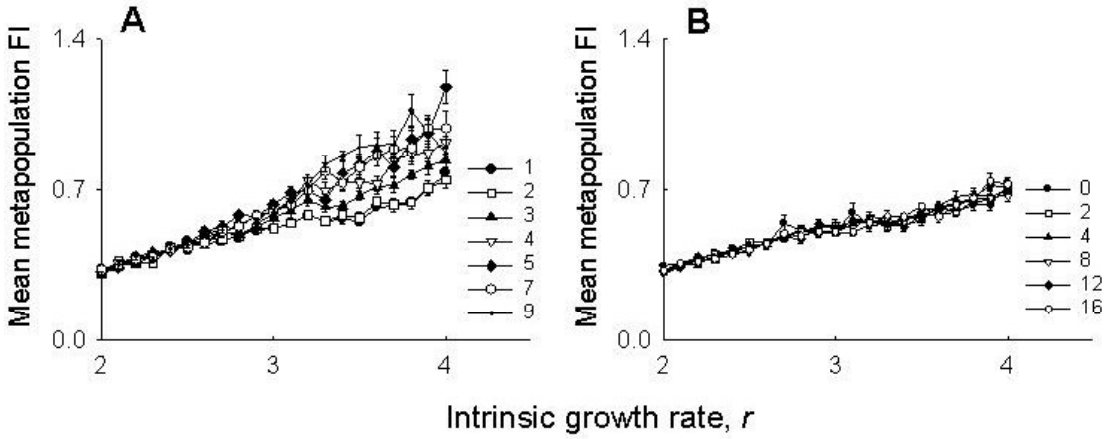

Figure 5.6. Simulations relaxing experimental assumptions: effect of pinning density and magnitude on stability. (**A**) There was no effect on metapopulation FI due to pinning greater number of patches for $r < 3$. When $r > 3$, increasing the proportion of pinned patches generally increased FI, although there were no consistent patterns. (**B**) Varying the magnitude of pinning had no effects on metapopulation stability. These suggest that the empirical results are robust to departures from the conditions of the experiment.

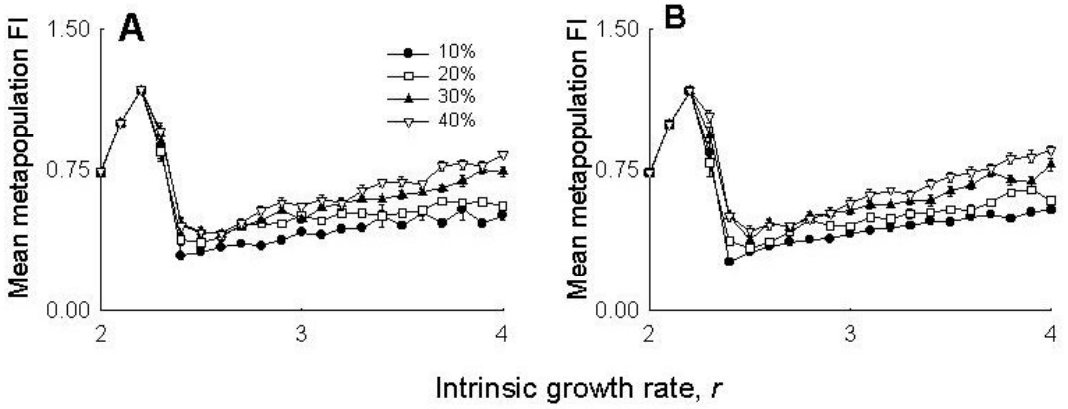

Figure 5.7. Simulations relaxing experimental assumptions: effect of migration rate on stability. Various rates of migration did not have a differential effect on the stability of the (**A**) control and (**B**) pinned metapopulation, again indicating the robustness of the experimental findings.

case of the Ricker model, increasing the number of pinned patches generally increased the metapopulation FI (hence instability), although there were no distinct patterns.

Altering the pinning strength failed to produce any observable change in the metapopulation dynamics (Fig. 5.6B). It has been shown earlier that low and high rates of migration reduce and enhance the metapopulation FI, respectively (Dey and Joshi 2006b). While similar patterns were observed in my simulations, there was no observable difference between the control (Fig. 5.7A) and the pinned (Fig 5.7.B) metapopulations. Together, these observations suggest that the experimental results are robust and no significant changes in the outcome would have been expected, even if the experiments were to have been conducted under different conditions of pinning or migration rates.

Absence of extinction

Like most of their natural counterparts, the experimental metapopulations experienced frequent local extinctions followed by recolonization from neighboring patches. This immediately raises the question as to whether the observed effects of pinning were modulated by subpopulation extinctions. I investigated this issue by repeating all the above-described simulations in the absence of any extinctions. When there were no extinctions, the FI of the pinned subpopulation was found to be slightly less than the mean of the remaining eight subpopulations (Fig. 5.8A) for $r < 2.6$. However, for $r > 2.6$, the pinned subpopulation had a higher FI, which agrees with the findings of a previous study that used an individual based model without any local extinction (Solé and

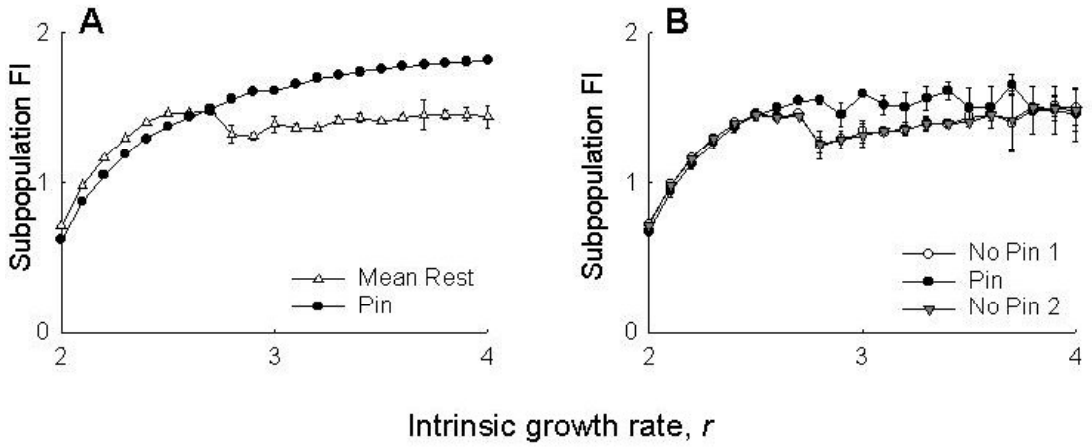

Figure 5.8. Simulations with no extinctions: effect of pinning at the subpopulation level. (**A**) The FI of the pinned subpopulation was higher than the mean of the remaining eight subpopulations only for $r > 2.6$. (**B**) The average FI of the pinned group tended to be higher than the two neighboring groups for $r > 2.6$, although this difference was significant only for a comparatively narrow parameter range. Both these results were contradictory to the observations from the experiments (Fig 5.1) and the simulations mimicking the experiments (Fig 5.3), indicating that the effect of pinning at the subpopulation level interacts with the extinction probability.

Gamarra 1999) but is contrary to the experimental data (Fig. 5.2A) and the earlier simulation (Fig. 5.4A). The FI of the pinned group was also higher than the two neighboring groups (*cf* Fig. 5.8B and Fig. 5.4B) for $r > 2.6$. These observations indicate that in the absence of extinction, the effect of pinning on subpopulation dynamics interacts with the intrinsic growth rate of the subpopulations. However, in the presence of local extinctions, pinning uniformly stabilizes the subpopulation dynamics.

These differences at the subpopulation level, however, did not lead to major changes in the results at the metapopulation level (Fig. 5.9A) compared to the case when extinction probabilities were explicitly incorporated into the simulations (Fig. 5.5A). Thus, although there seemed to be an effect of pinning on the shape of the metapopulation FI profile (*cf*

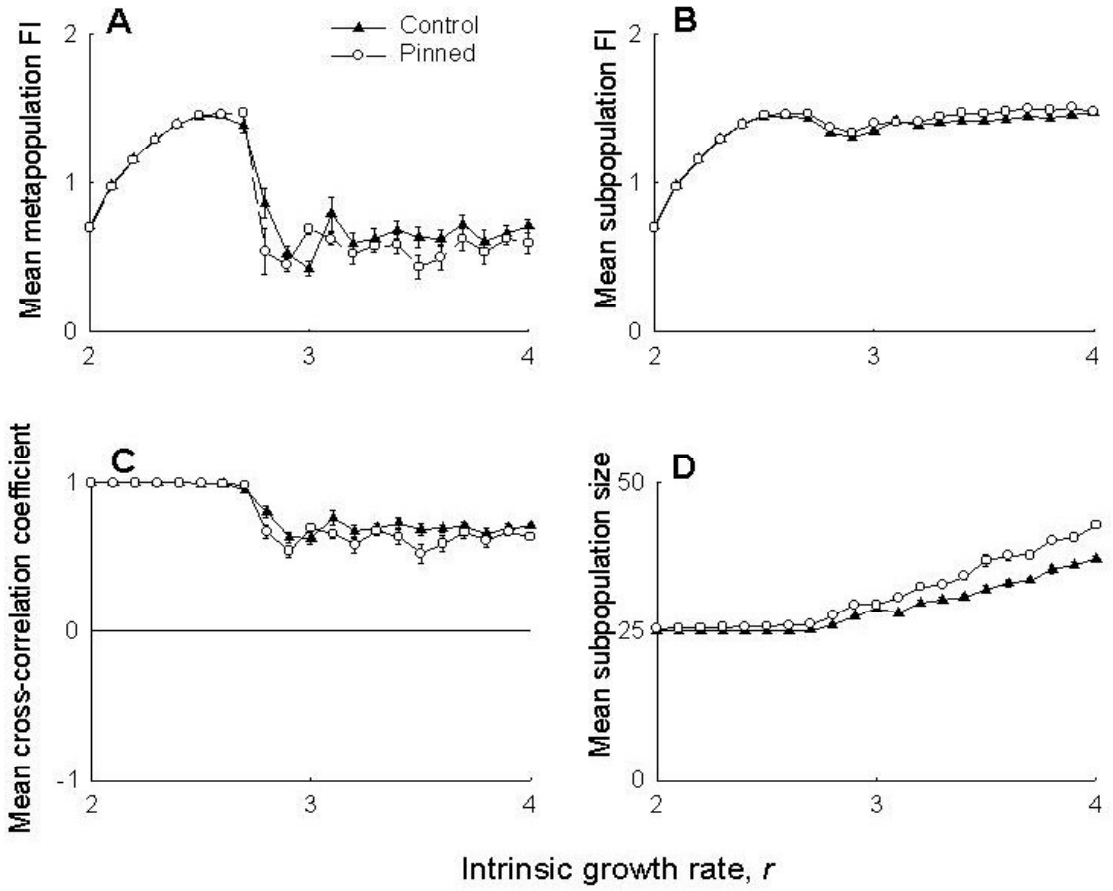

Figure 5.9. Simulations with no extinctions: effect of pinning at the metapopulation level. Although there were qualitative differences in the shapes of the profiles compared to the case when extinction probabilities were incorporated (Fig 5.4), there were no systematic differences between the control and the pinned treatments in terms of (**A**) metapopulation FI, (**B**) subpopulation FI, and (**C**) subpopulation synchrony. However, the average subpopulation size (**D**) of the pinned subpopulations was predicted to be similar to the controls for $r < 3$, which agrees with the experiments (Fig 5.2D), but not the earlier simulations (Fig 5.4D). Taken together it can be said that even in the absence of extinctions, pinning is unlikely to affect metapopulation dynamics.

Fig. 5.9A and Fig. 5.5A), there were no systematic differences in the FI of the control and the pinned metapopulations. The subpopulation FI (Fig. 5.9B) and the nearest neighbor cross-correlation coefficient (Fig. 5.9C) were also seen to be similar in the control and pinned metapopulations. Under no extinction, the model predicted an increase in average subpopulation size of the pinned metapopulations (Fig. 5.9D) for high values of r (> 3.2),

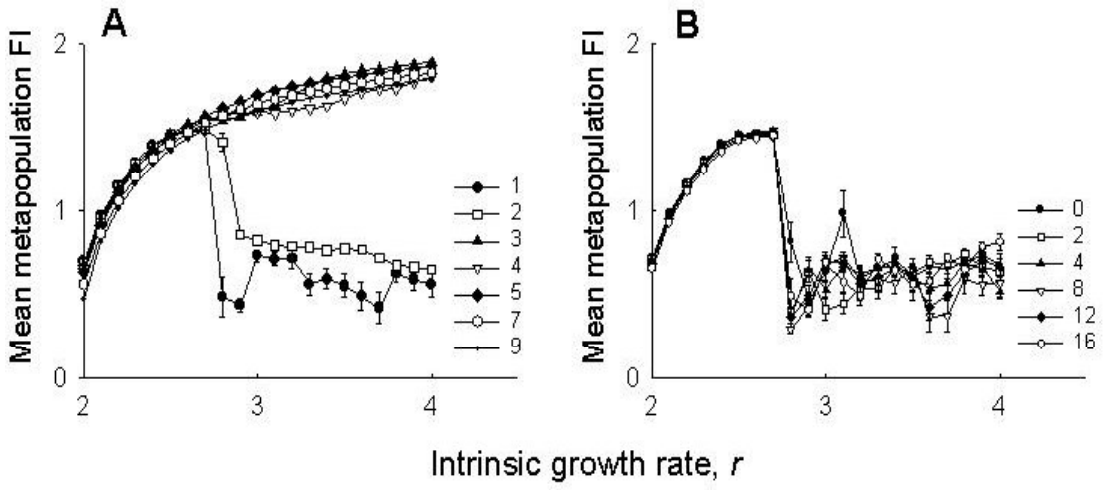

Figure 5.10. Simulations with no extinctions: effect of pinning density and magnitude on stability. (**A**) When there are no extinctions, increasing the number of pinned patches was generally found to destabilize the metapopulation dynamics, similar to the experimental scenario (5.5A). (**B**) Changing the strength of pinning, however, did not affect the metapopulation stability, although there was a change in the FI profile relative to the earlier simulations incorporating extinctions (*cf*. Fig 5.5B).

which was again different from the effects under extinction (Fig. 5.5D). Together, these observations suggest that while the subpopulation level dynamics under pinning might be affected by the presence/absence of extinction, this difference is unlikely to have a major global impact at the metapopulation level.

When there were no extinctions, increasing the number of pinned subpopulations had no effects at low values of *r* but, in general, destabilized the metapopulations by increasing the FI for high values of *r* (Fig. 5.10A). Although there was a distinct change in the profile, and an increase in the overall magnitude of metapopulation FI (*cf* Fig. 5.10A and Fig. 5.6A), the basic observation that increasing the proportion of pinned subpopulations generally increased the metapopulation FI remained unchanged. The prediction that increasing the density of pinned subpopulations might lead to an observable change in the

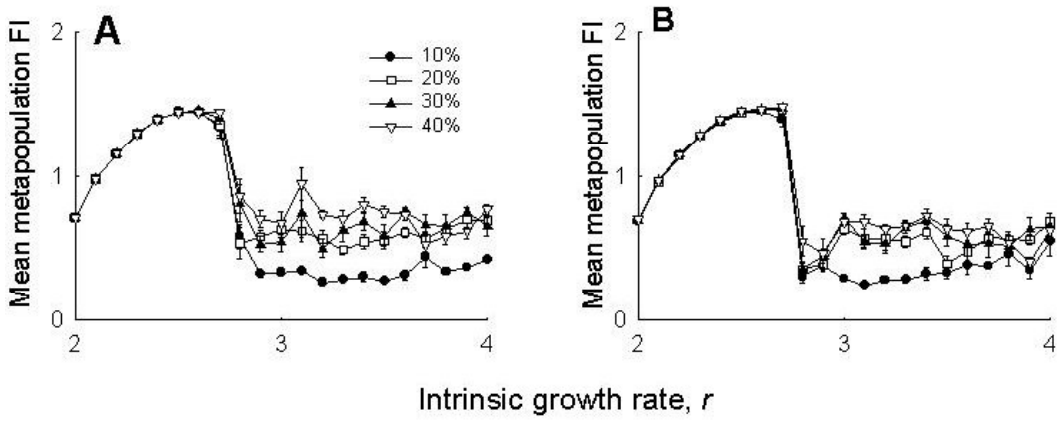

Figure 5.11. Simulations with no extinctions: effects of migration rate on stability. In the absence of extinctions, there were no major differences in the FI of the (A) control and (B) pinned metapopulations. However, there was a change in the profile of the metapopulation FI (*cf.* Fig 5.6), indicating that migration rate can interact with the levels of extinction, although it is not expected to interact with pinning to alter the empirically observed patterns of metapopulation stability.

global dynamics, at least for a sizable range of *r*-values, agrees well with previous results (Parekh et al. 1998). Different strengths of pinning (Fig. 5.10B) or different rates of migration (Fig. 5.11) did not predict any change in the dynamics, although again there was an overall increase in the magnitude of FI. Considering all these observations together, it is clear that although extinction plays a crucial role in determining subpopulation dynamics, it is not expected to interact with the effects of pinning at the metapopulation level, except when there is variation in the density of pinning.

CONCLUSIONS

Pinning has been suggested as a possible method for stabilizing populations living in a fragmented habitat (Doebeli and Ruxton 1997, Parekh and Sinha 2002). However, my

experiments indicate that, under realistic scenarios, constant localized addition of individuals from the outside is not expected to have a major impact on the metapopulation dynamics, and my simulations suggest that these experimental observations are generalizable. I show that although pinning might interact with extinctions in producing the observed dynamics at the subpopulation level, this is unlikely to affect the metapopulation dynamics. I predict that when there are no local extinctions, increasing the number of pinned subpopulations is likely to destabilize the metapopulation in terms of increased fluctuation in metapopulation size. This result is of potential interest to conservation biologists planning re-introduction of species into natural habitats to boost an extant population, or agricultural scientists trying to eradicate a pest. However, I would like to explicitly point out that the results of the present study were derived from simulations based on the Ricker model and it is possible that metapopulations of species whose dynamics are not well approximated by the Ricker might respond differently to pinning (Parekh and Sinha 1999).

CHAPTER 6

EFFECTS OF LIFE-HISTORY EVOLUTION

Although population stability can evolve as a correlated response to selection on traits unrelated to demography, the evolution of one stability property does not necessarily guarantee the evolution of other stability properties.

Dey, S., Prasad, N. G., Shakarad, M. and Joshi, A. 2007. Population stability does evolve – or does it? Manuscript under preparation

INTRODUCTION

Theoretical studies of simple population growth models predict increasing destabilization of the dynamics above a threshold value of intrinsic per capita growth rate (May 1974, 1976, May and Oster 1976). All else being equal, natural selection should favor the evolution of increased intrinsic growth rate, a close correlate of fitness, suggesting that real populations should often exhibit unstable dynamics. On the other hand, empirical evidence indicates that many natural and laboratory populations tend to exhibit relatively stable dynamics (Hassell et al. 1976, Turchin and Taylor 1992, Ellner and Turchin 1995). This apparent discrepancy has prompted questions about the proximal mechanisms that stabilize population dynamics, and how these mechanisms may evolve in response to natural selection at the individual and group levels (reviewed in Mueller and Joshi 2000, Mueller et al. 2000).

Traits affecting the value of population growth parameters, and hence population stability, have been shown to be genetically variable (Mueller and Ayala 1981a) and, therefore, likely to respond to selection at the individual level. However, it is hard to imagine how natural selection acting at the level of individuals could lead to the evolution of population stability through a decrease in population growth rates, as this would require an evolutionary reduction in key fitness components like fecundity or survivorship (Mueller and Joshi 2000, Mueller et al. 2000). Theoretical explanations for the evolution of population stability include group selection acting through long-term persistence, individual selection acting directly on demographic parameters, and the evolution of stability as a by-product of life-history evolution (Mueller et al. 2000).

In the group selectionist view, less stable populations are expected to go extinct more frequently than their more stable counterparts. The resulting empty patches would then be recolonized by individuals from more stable neighboring patches, eventually leading to the evolution of stability (Thomas et al. 1980, Berryman and Millstein 1989). Such theories assume that differences in stability properties among populations are largely genetic, and lead to differential rates of extinction. However, if among-population variation in stability properties were largely environmental, this mechanism would not work. Generally, the set of conditions under which population stability could evolve by group selection is fairly restrictive and lacks empirical support (Mueller and Joshi 2000).

It has also been suggested that population stability can evolve through direct selection on stability determining demographic parameters such as growth rate components, or their sensitivity to density (Hansen 1992, Ebenman et al. 1996). Mueller et al. (2000) put this hypothesis to test by rearing 20 populations of *Drosophila melanogaster* on food regimes that induced large and regular fluctuations in population numbers. However, they failed to notice any evolutionary change in stability, or in stability determining demographic parameters such as the sensitivity of female fecundity to increasing adult density, even after 65 generations. Lack of genetic variability in the populations was clearly not a limiting factor, since non-demographic traits, such as larval feeding rate, evolved rapidly in response to the increased larval density in the experiment within the first 20 generations (Joshi et al. 2003).

The view that stability could evolve as a by-product of life-history evolution suggests that tradeoffs among demographic parameters are crucial to the evolution of population stability (Turelli and Petry 1980, Mueller and Ayala 1981b, Stokes et al. 1988). For example, reanalysis of blowfly population data from Nicholson (1957) suggested that the apparent stability in the latter half of that experiment might be explained by the evolution of the ability of severely protein-deprived females to lay some number of eggs, albeit at the cost of reductions in survivorship and maximal fecundity (Stokes et al. 1988). It was, therefore, conjectured that population stability probably evolves as a correlated response to selection on life-history traits that are not demographic parameters per se (Mueller et al. 2000). This hypothesis was empirically supported by Prasad et al. (2003), using populations of *D. melanogaster* selected for faster development and early reproduction, and their corresponding ancestral controls. Using a 20 generation long time series of small (single vial) populations derived from these selected and control populations, it was shown that the selected populations had evolved increased stability (indicated by a lower coefficient of variation, CV, of population size). The stability of the selected populations was attributed to their lower preadult survivorship (~78%) and fecundity (~65%) compared to the controls; traits that had evolved as correlated responses to selection for rapid development over about 125 generations. This study (Prasad et al. 2003) provided the first clear experimental evidence in support of any hypothesis pertaining to the evolution of population stability.

Any discussion of the evolution of population stability, however, is complicated by the context specificity of the notion of stability in population ecology: over 163 definitions of

stability are found in the ecological literature, pertaining to about 70 concepts and more than 40 different measures (Grimm and Wissel 1997). Most of these definitions fall under one of six 'stability properties', based on the particular aspect of the dynamics under consideration in the given population (Grimm and Wissel 1997). Thus, *sensu* Grimm and Wissel (1997), the study of Prasad et al. (2003) based on the CV of population size, was an investigation into the "constancy" (staying essentially unchanged) property of the population, whereas theories of the evolution of stability by group selection (Thomas et al. 1980, Berryman and Millstein 1989) focused on the "persistence" (not going extinct over time) property of the population.

This explicit distinction between the various types of population stability leads me to the interesting issue of correlated evolution of different stability properties and raises questions as to how evolution of one kind of stability property in a population might affect the other stability properties of the same population. Here, I examine this issue by analyzing a 36-generation data set, generated from a continuation of the experiment reported by Prasad *et al* (2003). I look at the evolution of constancy and persistence by examining the dynamics of population size in 64 small (single vial) populations that were derived from large populations of *D. melanogaster* selected for faster development and early reproduction, and their corresponding control populations. I directly measure the relevant life-history traits (pre-adult survivorship, female fecundity) in these small populations, and also estimate demographic parameters (intrinsic rate of growth, r) by fitting a simple model of population dynamics to the census data. I then show (a) how constancy and persistence evolve independently as correlated responses to selection on

development time, (b) the interplay between these two stability properties, and (c) how the manifestation of a stability property can be altered by seemingly trivial details of the environment or rearing protocol.

MATERIALS AND METHODS

Experimental Populations

This study used eight long-standing, large (~1800 individuals), outbred populations of *D. melanogaster*. Four of these populations (FEJ_{1-4}) had been selected for faster development and early reproduction for *ca*. 125 generations at the start of this study. The other four populations (JB_{1-4}) were matched ancestral controls, the details of whose maintenance regime have been described elsewhere (Prasad et al. 2000, Prasad et al. 2001). The JBs are maintained at moderate densities of 60-80 eggs/~6 ml food at 25^{o}C under constant light on a 21 day discrete generation cycle, with no conscious selection on pre-adult development time. The FEJs are maintained at similar egg densities, but are under selection for faster pre-adult development. Only the first ~20% of FEJ flies eclosing in a vial are transferred to population cages for breeding. The flies are immediately supplied with yeast paste and the eggs for initiating the next generation are collected after three days. Thus, the reproduction of an FEJ fly is conditional upon (a) being among the first 20% of flies to eclose in the vial, and (b) its fecundity on day three of adult life. Neither the FEJs nor the JBs are under differential direct selection for any stability determining demographic trait, or its sensitivity to population density, as they are maintained at constant moderate larval and adult densities (Prasad et al. 2003). Moreover,

in the discrete generation maintenance regimes used in these experiments, development time is unlikely to have a major effect on population dynamics, although it can be an important demographic parameter in overlapping generation cultures of *D. melanogaster* (Prasad et al. 2003).

Population Dynamics Experiment

From each replicate FEJ and JB population, I derived eight small populations, each represented by a single vial culture, as in Sheeba and Joshi (1998). For this, eight mated females per vial were allowed to lay eggs for 24 hours. The adults were then discarded and these eggs formed the founder generation. Once the flies started eclosing in the vials, they were transferred daily into parallel adult collection vials till day 18 after egg lay, with food changes every alternate day. Thereafter, the adults were put into conditioning vials (see Food Regime, below) for three days. On day 21 after egg lay, all the surviving adults were allowed to oviposit in fresh food vials for 24 hours and these eggs constituted the next generation. The adults were then collected, censused and discarded. Thus, the population dynamics experiment featured small (single vial) populations that were kept on a 21-day discrete generation cycle with no control imposed on egg or adult densities. The experiment was terminated after 36 generations, and a preliminary report from the first 20 generations of data has been published previously (Prasad et al. 2003).

Food Regime

Of the eight small populations derived from each replicate FEJ and JB population, four were subjected to a food regime where larval food was limiting (~2 ml per vial) and the adults were supplied with excess live yeast paste for three days prior to oviposition (hereafter, the destabilized or the LH regime). The other four small populations were subjected to a food regime where larval food was not limiting (~6 ml per vial) and the adults were not supplied with live yeast paste during the conditioning period (henceforth, the stabilized or the HL regime). Thus, there were a total of 32 small populations in each food regime (LH/HL), 16 each from FEJs and JBs. The LH regime is known to produce high amplitude two-point cycles in population numbers, whereas the HL regime tends to reduce the fluctuations in population numbers and does not induce limit cycles (Mueller and Huynh 1994, Sheeba and Joshi 1998, Mueller and Joshi 2000, Mueller et al. 2000, Prasad et al. 2003).

Extinctions and Restarts

In this study, an extinction was said to occur when not even one fly eclosed in a vial during the entire adult collection period. There were no extinctions in the HL regime during the entire course of the experiment, but the small populations in the LH regime became extinct frequently and had to be restarted in order to continue the experiment. To restart a small population that had gone extinct in the population dynamics experiment, four females from any of the remaining three small populations from the same selection × replicate large

population × food regime combination were used, after the females had oviposited in their own vials for 24 hours.

Measures of Dynamics and Stability Properties

Following Joshi et al. (2001), differences in the gross dynamics of the FEJ- and JB-derived small populations, as reflected in the return maps (plots of N_{t+1} versus N_t), were examined by treating N_{t+1} as the dependent variable, and assessing whether N_{t+1} values for a given range of N_t (low: $N_t < 5$, 70; medium: $5 \leq N_t < 55$, $70 \leq N_t < 210$; high: $N_t \geq 5$, 70; for LH and HL, respectively) differed between the FEJs and JBs. Since mean and variance for population size differed considerably between nutritional regimes (data not shown), separate three-way mixed model analyses of variance (ANOVA) were carried out for the data from the LH and HL regimes, respectively. In these ANOVAs, pairs of replicate FEJ and JB populations were treated as random blocks (1-4, representing ancestry of the FEJ and JB populations: FEJ_i was derived from JB_i), whereas selection regime (FEJ / JB) and N_t range (low / medium / high) were treated as fixed factors, crossed among themselves and with block.

Constancy stability, (*sensu* Grimm and Wissel, 1997) of the FEJ- and JB-derived small populations was measured by the fluctuation index, FI (Dey and Joshi 2006b), defined as

$$\mathrm{FI} = \frac{1}{T\overline{N}} \sum_{t=0}^{T-1} \mathrm{abs}\,(N_{t+1} - N_t) \ ,$$

where $\overline{N}$ is the mean population size over T generations and N_t is the population size in generation t. Thus, the higher the FI, the lower the constancy of the population, and vice

versa. The FI data were subjected to three-way mixed model ANOVA treating selection regime and food regime (LH / HL) as fixed factors, crossed with each other, and with random blocks, representing ancestry of the FEJ and JB populations. The FI values from the four small populations within each block × selection regime × food regime combination were treated as replicate within-cell observations. Constancy stability was also estimated using two commonly used measures of stability, the coefficient of variation (CV) of population size (Prasad et al. 2003) and the S-index, standard deviation of $\log_{10}$-transformed population size (Lewontin 1966, Turchin 2003).

Following Leigh (1981) and Goodman (1987), three different indices were used to estimate the persistence stability (*sensu* Grimm and Wissel, 1997) of a small population in the population dynamics experiment: 1) the overall probability of extinction in the small population over the span of 36 generations, calculated as the total number of extinctions divided by the number of generations, 2) the probability of independent extinctions in a small population over the time course of the experiment (i.e. considering all consecutive extinctions in a small population as a single extinction event spanning a single generation; see Discussion for further details and rationale), and 3) the number of generations before a small population became extinct for the first time. Populations going extinct more often, undergoing a higher number of independent extinctions, or exhibiting a lower time to first extinction, were deemed to be relatively less stable with regard to persistence stability. Since all extinctions took place only in the LH food regime, the ANOVA model comprised of selection (fixed factor) crossed with block (random factor), with the corresponding

persistence index for each of the four small populations in a selection × block combination acting as within-cell replications.

Life-History Assays

In order to ascertain whether the earlier observed differences in life-history traits of the FEJs and JBs (Prasad et al. 2000, Joshi et al. 2001, Prasad et al. 2001) still persisted after 36 generations of the population dynamics experiment, pre-adult survivorship and fecundity on day 21 from egg lay were assayed on individuals from all FEJ- and JB-derived small populations in the LH food regime. Flies for the assays were generated by mixing all the four small populations derived from each replicate FEJ or JB population and allowing them to oviposit in a population cage. The progeny of these flies underwent another generation of cage rearing under identical JB-like conditions to eliminate non-genetic parental effects, and the eggs collected from these flies were then used for the various assays.

For measuring pre-adult survivorship, 10 vials, each containing exactly 50 eggs/~6 ml food, were set up and the proportion of flies eclosing in each vial was recorded. The flies eclosing in these vials were collected and maintained exactly as in the population dynamics experiment till day 18, when they were conditioned in the presence of yeast (similar to the LH regime). The fecundity of these flies was then measured on day 21 (their normal day of egg lay in the population dynamics experiment) by setting up 20 vials per population, each containing one male and one female, and counting the number of eggs laid in each vial over a period of 24 hours. The survivorship (after arcsine square

root transformation) and fecundity data were subjected to separate two-way mixed model ANOVAs with selection regime and block crossed with each other, and the corresponding vial values as the replicate within cell observations.

Estimation of Intrinsic Growth Rate

The per capita intrinsic growth rate parameter r was estimated by fitting the Ricker (1954) model to the census data. This is a widely used and thoroughly studied model of population dynamics, given by

$$N_{t+1} = N_t \exp (r (1 - N_t / K)),$$

where N_t is the population size at time t, and r and K refer to the intrinsic rate of per capita growth and carrying capacity, respectively (May 1976, Mueller and Joshi 2000). It has been shown analytically that populations with individuals randomly distributed in space and experiencing scramble competition follow Ricker dynamics (Brännström and Sumpter 2005). Moreover, this model is known to fit well to time series data from insect populations in general (e.g. Cheke and Holt 1993) and single vial cultures of *D. melanogaster* in particular (Sheeba and Joshi, 1998).

The zero values in the small population size data (extinctions) posed a problem in estimation of r as it is biologically impossible for a population to grow after it has become extinct, although the model predicts the highest realized growth rate when $N_t = 0$. Therefore, although the size of a small population *in* the generation in which it went extinct was taken as zero, the size of the parent small population for the generation *following* an extinction

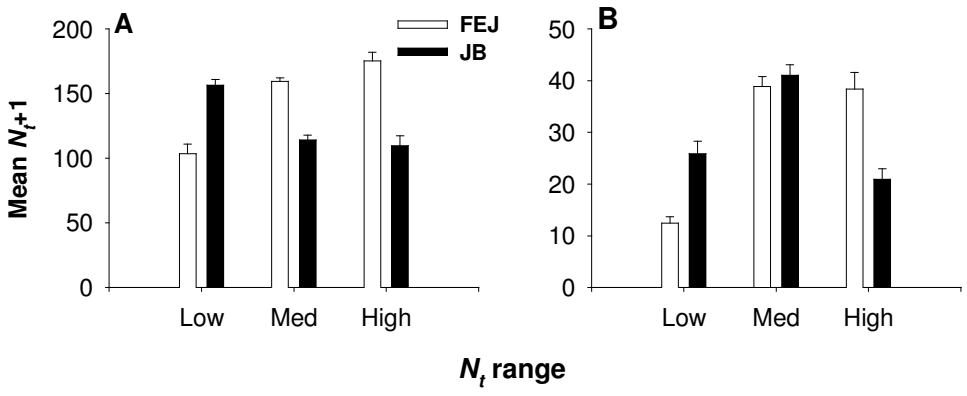

Figure 6.1. Summary of data from the return maps showing mean (± s.e.) N_{t+1} attained by FEJ- and JB-derived small populations for different ranges of N_t-values in (**A**) stabilized regime, and (**B**) destabilized regime. In both nutritional regimes, the mean N_{t+1} of the FEJs is lower in the low N_t range, but higher in the high N_t range, indicating that they have a lower growth rate and a higher carrying capacity than the JBs.

was considered to be four, to account for the fact that the small populations were restarted with four females after an extinction event. All model fitting was done using the in-built Quasi-Newton algorithm of Statistica® (Release 5.0 B, Statsoft Inc.). The ANOVA model used to analyze the *r*-value data was essentially similar to the one used in case of the fluctuation index. All multiple comparisons for the various traits subjected to ANOVAs were carried out using Tukey's HSD test (Sokal and Rohlf 1995).

RESULTS

The summary data on mean N_{t+1} from the return maps in the LH and HL regimes (Fig. 6.1) clearly show that the FEJ-derived populations maintained a lower N_{t+1}, on average, than

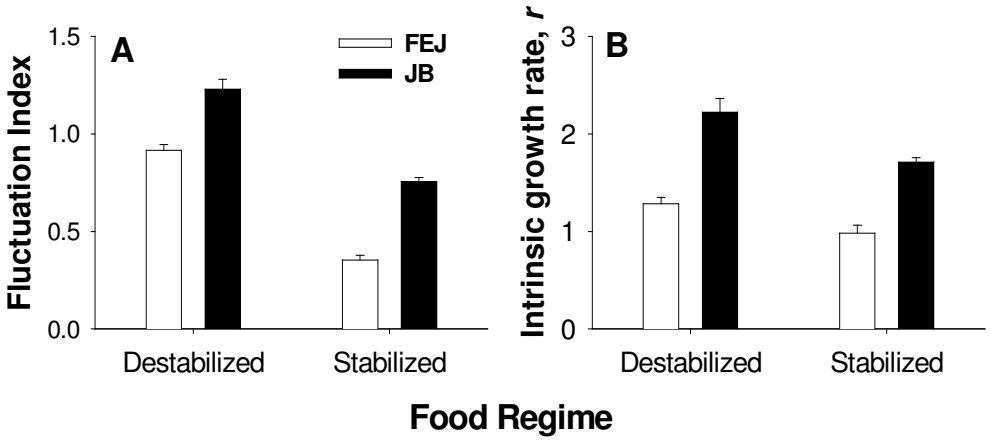

Figure 6.2. (**A**) Mean (± s.e.) constancy stability, as measured by the fluctuation index, of the FEJ- and JB-derived small populations. (**B**) mean (± s.e.) estimated intrinsic growth rate *r* of the FEJ- and JB-derived small populations. Compared to the JBs, the FEJs were more stable in both regimes, and had a lower intrinsic growth rate, *r*.

their JB-derived counterparts, when N_t was low. However, mean N_{t+1} in the FEJs was higher than JBs when N_t was relatively high. This pattern indicates that the FEJs had a lower intrinsic growth rate and higher carrying capacity than the JBs. The ANOVAs revealed significant selection regime × N_t range interactions for both the HL ($F_{2,6} = 23.95$, $p < .01$) and LH ($F_{2,6} = 10.58$, $p < .05$) regimes. Multiple comparisons revealed that all three pair wise differences between JBs and FEJs were significant ($p < .05$) in the HL regime, whereas in the LH regime, only the FEJ-JB difference for high N_t was significant at the $p = .05$ level. The FEJ-JB difference at low N_t in the LH regime was, however, marginally significant ($.05 < p < .1$), and in a direction consistent with the interpretation of a lower intrinsic growth rate in the FEJs.

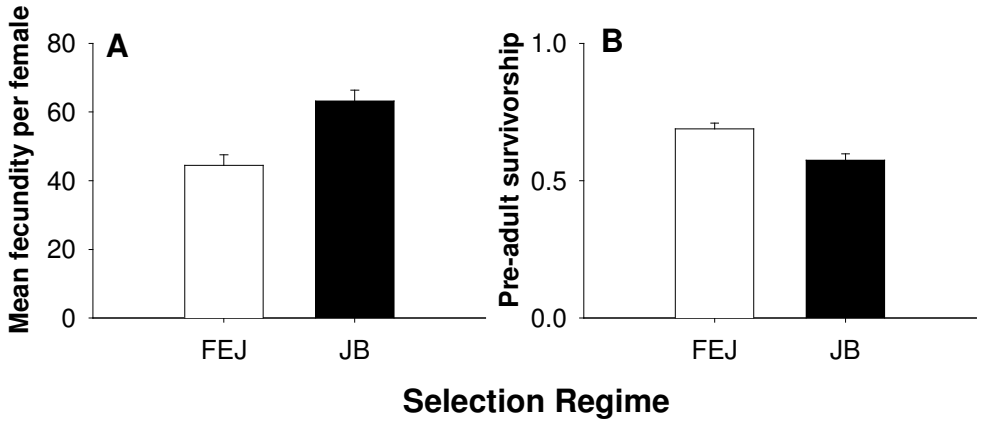

Figure 6.3. (**A**) Mean (± s.e.) fecundity and (**B**) mean (± s.e.) pre-adult survivorship of the FEJ- and JB-derived small populations. The lower growth rate of the FEJs could be attributed to the lower mean fecundity, which had evolved as a result of selection for faster pre-adult development and early reproduction. The pre-adult survivorship of the FEJs was found to be marginally higher than the JBs, although this difference was statistically insignificant. See text for possible explanation.

The mean FI of FEJs was significantly lower than that of the JBs ($F_{1,3} = 67.5$, $p < .01$), and that in the HL regime was significantly lower than in the LH regime ($F_{1,3} = 203.91$, $p < .001$) (Fig. 6.2A). This indicates that in terms of constancy, the FEJ selection regime and the HL food regime were more stable than the JB and LH respectively, which corroborates the earlier findings of Prasad et al. (2003). The selection × food regime interaction was not significant ($F_{1,3} = 0.920$, $p = 0.408$), suggesting that there was no differential effect of food regime on the dynamics of the FEJ and the JBs. The FEJs were significantly more stable than the JBs in terms of two other measures of constancy, namely CV ($F_{1,3} = 14.977$, $p < .05$) and S-index ($F_{1,3} = 26.305$, $p < .05$). Similarly, the constancy stability of HL was found to be significantly lower than LH using both CV ($F_{1,3} = 1096.302$, $p < .001$) and S-index ($F_{1,3} = 507.884$, $p < .001$), indicating that my results are robust to the measures of constancy used.

The estimated *r*-values of the JBs were found to be significantly higher than the FEJs ($F_{1,3}$ = 62.08, $p < .01$), those in the LH regime higher, but not signficantly, than in the HL regime ($F_{1,3}$ = 9.384, $p = .054$), with no significant selection × food regime interaction ($F_{1,3}$ = 1.889, $p = .263$) (Fig. 6.2B). These findings can probably be attributed to the significantly higher ($F_{1,3}$ = 25.837, $p < .05$) mean fecundity of the JBs, as compared to the FEJs, on day 21 after egg lay (Fig. 6.3A). There was, however, no significant difference between the pre-adult survivorship of FEJs and JBs ($F_{1,3}$ = 1.909, $p = .261$) (Fig. 6.3B). Surprisingly, the preadult survivorship of the FEJs was found to be marginally higher than the JBs, a result that is contrary to earlier observations on these populations (Prasad et al. 2001).

The persistence of the JBs was higher than the FEJs when assessed by the overall extinction probability (Fig. 6.4A; $F_{1,3}$ = 0.522, p = 0.522). On the other hand, the probability of independent extinctions in the JBs was greater, implying lower persistence, than in the FEJs, (Fig. 6.4C; $F_{1,3}$ = 1.227, p = 0.349). Similarly, the mean number of generations to first extinction in the FEJs was found to be larger than the JBs, again suggesting that the JBs were less persistent (Fig. 6.4B; $F_{1,3}$ = 1.298, p = 0.337). However, none of these differences in persistence measures between the FEJs and JBs was statistically significant.

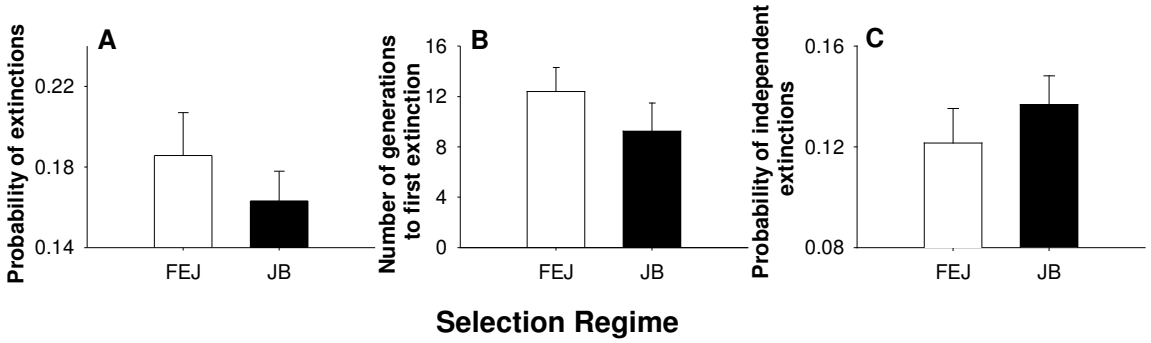

Figure 6.4. Persistence stability of the FEJ- and JB-derived small populations. (**A**) Mean (± s.e.) proportion of extinctions per generation in each small population. (**B**) Mean (± s.e.) number of generations till first extinction in each small populations. (**C**) Mean (± s.e.) proportion of extinctions per effective generation in each small population, treating each series of consecutive extinctions as one extinction event, accounting for one generation, when calculating the proportion of extinctions. None of the differences were statistically significant.

DISCUSSION

Constancy

The observed increase in constancy stability of the FEJs (Fig. 6.2A) is presumably a result of the change in life-history traits during 125 generations of selection for faster development and early reproduction. Although the FEJs and the JBs are maintained under moderate larval densities in their respective selection regimes, the small populations derived from FEJs and JBs were often under high levels of crowding in the population dynamics experiment. It is known that larval crowding prolongs the pre-adult development time of *D. melanogaster* (Bierbaum et al. 1989). Hence, the FEJs, being selected for faster development, would be intuitively expected to have an advantage under crowded culture conditions, relative to the JBS, by having an increased likelihood of eclosing by the 18thday, when adult collection was stopped, an advantage likely to be further magnified by the higher *K* of the FEJs (Joshi et al. 2001). Any such advantage would be expected to contribute to an increase in the growth rate

of the FEJs, thus destabilizing their dynamics. Moreover, the mean effective population size of the FEJs was higher than that of the JBs in both food regimes (data not shown), suggesting that the JBs were likely to have undergone more drift-induced inbreeding depression, another factor that could contribute to a relatively higher growth rate in the FEJs. Yet, despite these two factors, the FEJs were found to have higher constancy stability than the JBs, underscoring the conservative nature of my results, and suggesting a fundamental difference in the dynamics of the FEJs and JBs, consistent with the return map data summarized in figure 6.1.

Although Prasad et al. (2003) invoked lower preadult survivorship of the FEJs as one of the probable factors leading to their reduced intrinsic growth rate, the present study showed that the preadult survivorship of the FEJs was, if anything, slightly higher than the JBs, although the difference was not statistically significant (Fig. 6.3B). This result not only contradicts previous findings on these populations (Prasad et al. 2000, Prasad et al. 2001), but also does not match with very recent observations (after 235 generations of selection) showing that the FEJs have a lower pre-adult survivorship than the JBs (Shampa Ghosh, K. M. Satish and Amitabh Joshi *unpublished data*). This anomaly can probably be attributed to the fact that selection for faster development on the FEJs had been relaxed under the conditions of the population dynamics experiment, a scenario expected to lead to reverse evolution (Teotónio and Rose 2001) in the FEJs, which could have led to an increase in their pre-adult survivorship. Moreover, the pre-adult survivorship was measured on flies that were derived from the LH regime, an environment that is characterized by low population sizes and frequent bottlenecks. Given the lower effective population size of the JBs, the possibility of

greater random genetic drift in the JBs leading to a decrease in their survivorship relative to the FEJs also cannot be ruled out. In the present study, the increased constancy stability of the FEJs appears to be largely driven by a reduced intrinsic growth rate (Fig. 6.2B), which is, in turn, largely due to reduced fecundity of the FEJ females (Fig. 6.3A).

Persistence

As noted previously, all extinctions occurred only in the LH regime and, hence, the discussion in this section focuses solely on that regime. Generally, populations with a low intrinsic growth rate are expected to go extinct at a higher frequency than those with higher growth rates (Pimm et al. 1988). This is because such populations would require a longer time to recover from a trough in population density and hence would be more vulnerable to extinction due to chance factors during those stages (Pimm 1991). This prediction seems to be borne out in this experiment as the FEJs undergo more extinctions than the JBs. However, on the other hand, this argument stands true only if the population size falls below some critical threshold size, at which point environmental or demographic stochasticity becomes a powerful enough factor to drive the population to extinction. This is more likely to happen for those populations that either have a very low size or fluctuate to a greater degree or both (Pimm et al. 1988, Pimm 1991). Although there is not much difference between the mean population sizes of FEJs and JBs in the LH regime, the fact that FEJ population size undergoes smaller fluctuations than the JBs makes it unlikely that they would be going below a threshold population size as many times as the JBs. Thus, the higher probability of extinction in the FEJs (Fig. 6.4A) appears to be somewhat counter-intuitive.

However, a clear pattern emerged while looking at the sequence of extinctions in the FEJs and JBs. Extinct subpopulations in the experiment were restarted using flies from any of the three small populations in the same selection × block × food regime combination, after the females had already oviposited for 24 hours for the parent vial. This means that the FEJ females, with a lower fecundity (Fig. 6.3A), could probably lay fewer eggs in the subsequent 24 hours, compared to the JBs. It has been observed that very low egg densities can also drastically reduce larval survivorship, as the medium tends to dry out and become unsuitable for the larvae (*personal observation*). Thus, under such a situation, the extinctions in a single vial population over time no longer remain independent of each other and, hence, one would expect more sets of consecutive extinction events in the FEJs compared to the JBs. When the number of extinctions was recalculated by treating two or more extinctions in consecutive generations as a single extinction event, the FEJs turned out to have a lower probability of extinctions than the JBs (Fig. 6.4C). The contention that the FEJs have a lower tendency to go extinct than the JBs is also supported by the fact that the FEJ-derived small populations, on an average, took a larger number of generations to go extinct for the first time (Fig. 6.4B). Taken together, these observations suggest that the FEJs have a relatively lower inherent tendency to go extinct, than the JBs. However, owing to an interaction between their life-history and the food regime described in this study, they end up as less persistent than the JBs in terms of overall extinction probability. This finding exemplifies the possibility that the manifestation of a stability property may not be independent of the environment in which it is expressed.

This study also highlights the fact that evolution of one kind of stability property (here, constancy) does not necessarily guarantee the evolution of another type (here, persistence). As I show in this study, reduced fluctuation in population numbers does not necessarily mean that the chances of the same population going extinct are reduced. Therefore, particularly in real world scenarios, due caution must be exercised in judging the relevance of the measured stability property to the problem at hand.

CONCLUSION

I show that constancy stability can evolve as a correlated response to selection on life history traits not directly related to the demography of the population. I also show that although constancy has evolved as a correlated response in the selected populations, persistence has not, with selected populations undergoing a greater number of extinctions than the controls. I further show that this result is likely to be an artifact of an interaction between food regime and how extinctions were dealt with in the maintenance protocol, underscoring the context-specificity of stability attributes of populations. Any statement about stability, therefore, should be qualified with a suite of conditions and interpreted and extrapolated with due caution.

CHAPTER 7

EFFECTS OF ADULT MORTALITY

In populations with discrete generations, increasing the rate of adult mortality leads to increased stability, via the reduction of growth rates.

Dey, S. and Joshi, A. Increased rates of adult mortality stabilize the dynamics of laboratory populations of *D. melanogaster*. Manuscript under preparation

INTRODUCTION

Although theoretical studies on the dynamics of populations often assume an ideal, noise-free environment (e.g. Mueller 1988, McCallum 1992), real populations typically face varied and frequent perturbations. These perturbations might take the form of environmental variation (e.g. fluctuations in temperature, humidity etc.), different biotic factors (e.g. predators, pathogens or parasites), behavioral factors (migration), or, particularly for economically important species, harvesting. Due to obvious practical implications, the effects of harvesting on the dynamics of populations have been widely investigated theoretically (e.g. Lande et al. 1995, Engen et al. 1997, Gueron 1998, Jonzén et al. 2002), through laboratory experiments (Nicholson 1957, Cameron and Benton 2004, Fryxell et al. 2005), and in field studies (e.g. Solberg et al. 1999, Milner et al. 2007), and a large corpus of knowledge exists on the subject (see Getz and Haight 1989)).

The effects of perturbation on population dynamics can be very complex and may depend, among other things, on stage structure (Cameron and Benton 2004), age-structure (Brauer 1983), environmental noise (Jonzén et al. 2002) and the strategies of harvesting (Lande et al. 1995, Fryxell et al. 2005). Due to the application-oriented context of harvesting, most empirical studies on the effects of mortality on population dynamics (Nicholson 1957, Cameron and Benton 2004, Fryxell et al. 2005) have considered overlapping generation populations, with a distinct age- and/or stage-structure. However, the ecology of an overlapping-generation population can be very

different from a discrete generation one, owing to the temporal separation of the various life-stages in the latter (Mueller and Joshi 2000). When adults and juveniles coexist and share the same resources, culling a fraction of the adults immediately increases the resources available to the juveniles, which in turn may increase their survivorship, and hence the growth rate (Cameron and Benton 2004). On the other hand, when the adults and the juveniles are separated from each other, the effect of reducing the adult numbers in a given generation, on the adult numbers of the next generation, involves a much longer time delay, potentially leading to a different kind of dynamics. While there have been a few theoretical investigations on the effects of mortality in discrete generation systems using different kinds of models (Gueron 1998, Jonzén et al. 2002), the predictions from these studies have not been tested empirically.

Here, I first study the effects of different rates of mortality on population stability via Ricker-based deterministic and stochastic simulations under discrete generation systems. I then verify the predictions from the simulations, using data from a 27-generation experiment on replicated laboratory populations of the fruit fly *D. melanogaster*, subjected to three different levels of adult mortality. Although the experiment originally included a fourth treatment with no mortality (i.e. controls), unforeseen circumstances rendered the control data unusable. Therefore, this study concentrates solely on the effects of three different rates of mortality on the dynamics of *D. melanogaster* populations.

MATERIALS AND METHODS

Simulations

The effects of mortality were studied by iterating the expression:

$$N_{t+1} = (1\text{-}m).\, N_t \exp\,(r\,(1 - N_t / K))$$

where, N_t represents the subpopulation size at time t, r and K refer to the intrinsic per capita growth rate and carrying capacity of the population, respectively, and m ($0 \leq m \leq 1$) represents the fraction of the adult population that was removed prior to reproduction. This expression is derived from the Ricker model, $N_{t+1} = N_t \exp\,(r\,(1 - N_t / K))$ (Ricker 1954), which has been extensively studied theoretically (May and Oster 1976). Here, I investigated the effects of m-values ranging from 0 to 0.8 at steps of 0.01. The initial population size was kept constant ($N_0 = 20$) for all the simulations. For each value of m, the above expression was iterated for 100 time steps, and the CV (McArdle et al. 1990) and FI (Dey and Joshi 2006b) were computed from the time series. In the deterministic simulations, the values of r and K were fixed at 1.8 and 125, respectively, for the simulations representing the stabilized regime and at 2.8 and 26 for those representing the destabilized regime. These values were chosen based on previous estimates of these parameters in the stabilized and destabilized regime from other experiments (see chapters 6,8). In the stochastic simulations, a noise term ε ($0 < \varepsilon < 0.2$; uniform random distribution) was added to r in every generation, to simulate stochastic variation in

population growth rates, and a 50% probability of extinction in generation t+1 was stipulated, if the population size in generation t was below 4. I also repeated the deterministic and stochastic simulations for different values of r in the relevant ranges for the stabilized and destabilized populations, but did not observe any major qualitative differences in the results from those presented here.

Experimental system

60 single-vial populations of *D. melanogaster* were set up from a large, outbreeding laboratory population (MGB_1), the details of whose maintenance regime and ancestry have been described elsewhere (Sharmila Bharathi et al. 2007). Each population was initiated by placing exactly 50 eggs in a vial and the eclosing adults constituted generation 0. Half of these populations were placed in a nutritional regime where the larvae received ~1 ml of food and the adults were given live yeast paste for three days prior to laying eggs, while in the remaining cultures, the larvae received ~6 ml of food and the adults did not get any yeast supplement. It is known that the former nutritional regime (LH / destabilized) leads to high growth rates and regular, high amplitude oscillations in population numbers, while the dynamics of the latter regime (HL / stabilized) is characterized by low growth rates and no periodic oscillations (Mueller and Huynh 1994, Sheeba and Joshi 1998, Mueller and Joshi 2000, Mueller et al. 2000, Prasad et al. 2003). The populations were maintained on 21-day discrete generation cycles following the maintenance protocol of earlier studies (Sheeba and Joshi 1998, Prasad et al. 2003, Dey and Joshi 2006b, Dey and Joshi 2007).

Mortality and extinctions

The 30 replicate populations in a nutritional regime (stabilized / destabilized) were distributed equally among three mortality treatments — low, medium and high — representing 20%, 40% and 60% adult mortality, respectively. In each generation, the adults were sexed and censused just prior to reproduction. The required fraction (.2, .4 or .6) of males and females (separately) were removed manually and the remaining individuals formed the breeding population for the next generation. There were several extinctions, scored as the absence of at least one male-female pair, in the destabilized regime. In case of extinction, the populations were reset using four males and four females from the pool of flies that were removed during the imposition of mortality.

Analysis

The constancy stability (Grimm and Wissel 1997) of the populations was measured as the coefficient of variation, CV (McArdle et al. 1990) and fluctuation index, FI (Dey and Joshi 2006b) of population size over time. The persistence stability of a given mortality treatment (low / medium / high) was measured as the number of populations that went extinct in each generation, out of the 10 replicate populations in that treatment. The parameters of the Ricker model (r and K) were estimated via non-linear regression of the untransformed time-series data, using the in-built Quasi-Newton algorithm of the commercially available software STATISTICA® v5.0 (Statsoft Inc.). All data, except

when specifically stated otherwise, were subjected to two-way ANOVA with two levels (stabilized / destabilized) of nutritional regime crossed with three levels (low, medium and high) of mortality. Post-hoc tests of significance were performed using Tukey's honest significance difference (HSD) test (Sokal and Rohlf 1995).

RESULTS AND DISCUSSION

Simulations

In the stabilized regime, the deterministic simulations suggest that increasing the mortality rates in the range used in our experiment would lead to a minor decrease followed by a slight increase in CV (Fig. 7.1A), which agrees with previous theoretical results based on stochastic models (Jonzén et al. 2002). On the other hand, the FI is expected to decrease monotonically with increasing mortality rates in the experimental range. However, the magnitude of change in CV or FI is so low (note the Y-axis scale in Fig. 7.1A), that this level of difference in the stabilized regimes would be almost impossible to detect in experiments, due to the inherent noise in a real population. The change in stability with increase in mortality rates is very low in the stabilized regime, probably because the magnitude of mortality-induced stabilization depends upon the *r*-value of the populations being considered. The Ricker model exhibits a damped oscillatory approach to a stable point equilibrium as long as $r < 2$. Thus, any mortality-induced decrease in the *r*-value in the stabilized regime ($r = 1.8$) is not expected to lead to

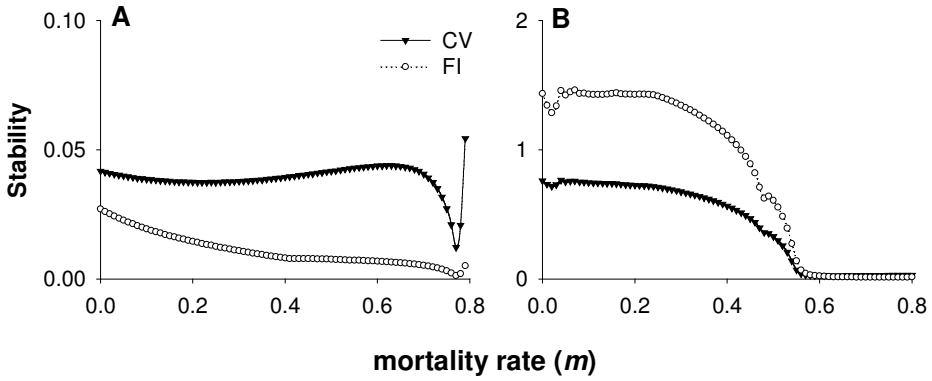

Figure 7.1. Deterministic simulations of the effects of different rates of mortality on the CV and FI of single populations in (**A**) stabilized regime, $r = 1.8$, and (**B**) destabilized regime, $r = 2.8$. When mortality rate (m) is increased, there is very little effect on stability in the stabilized regime, but a much greater effect on stability in the destabilized regime (note the difference in Y-axis scale between the two panels). See text for possible explanations.

a change in the pattern of the equilibrium dynamics and hence should not result in any major change in CV or FI.

When $2 < r < 2.69$, the Ricker model exhibits limit cycles of increasing amplitude with increasing r, which in turn leads to increased CV and FI. Since, in the destabilized regime, the r-values are above 2, the mortality-induced reduction in CV and FI via the reduction in the value of r should be significant enough to be detectable in experiments (Fig. 7.1B). Figure 7.1B predicts that in the destabilized regime, there would be a relatively minor reduction in the magnitude of the CV on increasing mortality from 20% to 40%, and a more discernible reduction in CV when mortality increases from 40% to 60%. The reason for this can be understood when one calculates the r-value, after the mortality has been imposed. When the growth rate under no mortality is 2.8, the values of r under 20%, 40% and 60% mortality are 2.58, 2.28 and 1.88, respectively, which in turn represent equilibrium behaviors of 4-point limit cycles, 2-point limit cycles, and stable

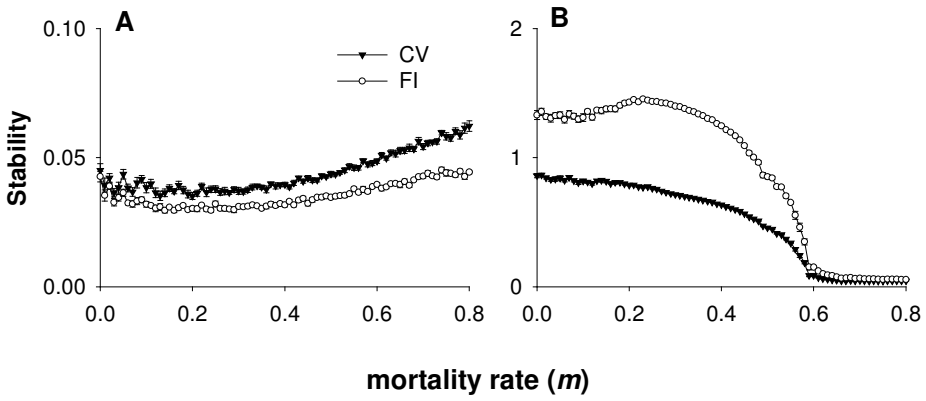

Figure 7.2. Stochastic simulations of the effects of different rates of mortality on the CV and FI of single populations in (**A**) stabilized regime, $r = 1.8$, and (**B**) destabilized regime, $r = 2.8$. The noise was added every generation in the form of a 50% probability of extinction when the population size falls below 4, and a random noise ε ($0 < \varepsilon < .2$) to the r-value. Each point represents the average of ten independent runs and the error bars denote the standard error around the mean. There are no major changes in the stability patterns on the addition of noise (*cf* figure 7.1).

point equilibrium for the Ricker model. From the bifurcation diagram of the Ricker model (see Fig. 8, May and Oster 1976), it is seen when r decreases from 2.58 to 2.28, there is slight decrease in the range over which the population sizes oscillate, which explains the reduction in CV in this range. However, when the r-value is 1.88, the population quickly reaches stable point equilibrium, and hence shows very low CV.

Since the above simulations are all deterministic, it is natural to ask if these observations would hold even in the presence of noise in the dynamics, or population extinctions and resets, both of which are expected to be present in laboratory populations of *D. melanogaster*, particularly under high growth rates. In order to answer this question, I repeated the simulations shown in Fig. 7.1, with random noise added to the growth rate, and a 50% probability of extinction when population size becomes too low (see section: Materials and methods for details). All the observations made in case of the deterministic

simulations in general, continued to hold for the stochastic simulations (Fig. 7.2) as well, indicating that adding noise to the system does not change the effects of mortality rate in stabilizing the populations.

Note that the precise quantitative relationship with mortality rates differs between the two measures of stability and, moreover, depend on the *r*-values of the populations (Fig. 7.1, 7.2). Consequently, the pattern of which pair-wise differences among mortality levels turn out to be statistically significant is likely to vary among nutritional regimes and stability measures. However, the general premise that adult mortality reduces the growth rates of the populations should remain valid at all values of *r*, at least in the context of the Ricker model.

Experiment

Stability

As expected, there was a significant main effect of nutritional regime on CV ($F_{1,54}$ = 638.05, $p << .001$), and the CV in the destabilized regime was higher than that in the stabilized regime (Fig. 7.3). The main effect of mortality on CV was also found to be significant ($F_{1,54} = 4.13$, $p < .02$), with the only significant difference being between CV under low and high mortality treatments ($p < .016$). The interaction between nutritional regime and mortality rate was also significant ($F_{2,54} = 12.41$, $p << .01$) and a clear

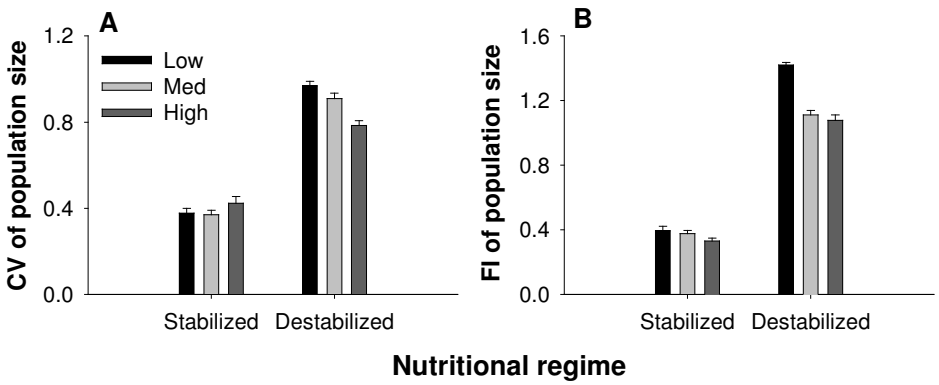

Figure 7.3. Stability of the populations under three different adult mortality treatments: low (20%), medium (40%) and high (60%). In this, and subsequent figures of this chapter, each bar represents the mean of 10 replicate populations and the error bars represent SE around the mean. (**A**) Coefficient of variation (CV) and (**B**) Fluctuation index (FI). As anticipated from the simulations, there were no significant effects of different mortality rates on the stability in the stabilized regime. In the destabilized regime the CV and the FI behaved differently with increasing mortality rates.

difference between the nutritional regimes was observed with respect to the effects of mortality rate on CV (Fig. 7.3). Post hoc tests indicated that none of the pair-wise differences in the stabilized regime were significant at the $p = 0.05$ level (Fig. 7.3A). In the destabilized regime, on the other hand, all but one (low-medium; $p = .49$) of the pair-wise differences were found to be significant ($p < .01$), and the rank order in terms of magnitude of CV was low > medium > high (Fig. 7.3A). The simulations had predicted that in the stabilized regime, changes in the CV of population size with increasing mortality would be negligible (Figs. 7.1A, 7.2A), and this prediction is corroborated by the experimental data (Fig. 7.3A). Since, even in the absence of mortality, the estimated *r*-values of the stabilized regime populations are generally below 2 (see chapters 6, 8), the mortality-induced reduction in *r*-values is not expected to lead to any difference in the dynamics or the CV. However, in the destabilized regime, one expects to see a monotonic decrease in CV, with a greater reduction in magnitude when going from 40% mortality to

60% mortality, than between 20% mortality and 40% mortality (Figs. 7.1B, 7.2B), and the data are consistent with this prediction (Fig. 7.3B).

Unfortunately, the only other laboratory study that systematically investigated the effects of different mortality rates on the dynamics of population size (Fryxell et al. 2005), did not report the change in variability of population size over time, and hence it is not possible to compare their results with the current findings. Another study on stage-structured populations of soil mites reported an increase in standard deviation on culling the adults, accompanied by an increase in growth rates (Cameron and Benton 2004). Although Cameron and Benton (2004) did not investigate the effects of systematic variation of mortality rates, the fact that adult mortality increased variability of population size in their study, is at odds with the empirical observations and simulations of the present study. The reason for this discrepancy is most likely the use by Cameron and Benton (2004) of an overlapping generation system in which adults and juveniles competed for the same food resource. Thus, a reduction in adult number would not only reduce adult competition, but also the competition among larvae, which would have an immediate effect of increasing the population growth rate. However, in the present study, I used a discrete generation system in which the adults and the larvae do not co-exist, and hence do not compete for the same resources. This ensures that culling the adults in a given generation does not directly increase the growth rate of the population and, thus, mortality in my experiment tends to reduce variability in population size. The differences between my results and those of Cameron and Benton (2004) underscores the fact that the effect of adult mortality on population variability might depend crucially on the relative

delays in the feedback loops acting on the various life-history stages (McNair 1995, Mueller and Joshi 2000).

In the case of FI, the broad pattern of results was similar to those for CV (Fig. 7.3). There was a significant main effect of nutritional regime ($F_{1,54}$ = 1667.59, $p << .001$) and, expectedly, FI in the destabilized regime was greater than in the stabilized regime (Fig. 7.3B). As with the CV, the main effect of mortality was significant ($F_{1,54}$ = 36.89, $p << .001$), as was the nutritional regime × mortality interaction ($F_{2,54}$ = 21.56, $p << .001$). As noted earlier for CV, the very low levels of differences between the predicted FI-values at the three mortality rates in the stabilized regime precludes the possibility of finding significant differences in an experiment. Thus, not surprisingly, none of the pair-wise differences in FI among mortality rates within the stabilized regime were significant at the p = 0.05 level. In the destabilized regime, the rank order of the FI-values (low > medium > high; Fig. 7.3B) was as expected from the simulations (Figs. 7.1B, 7.2B), and post hoc tests indicated that all but one (medium-high; p =.93) of the pair-wise differences were significant at the $p < .01$ level. Overall, the experimental results (Fig. 7.3) are consistent with the gross prediction from the simulations that, all else being equal, increasing the mortality rates would enhance the stability of populations under discrete generations.

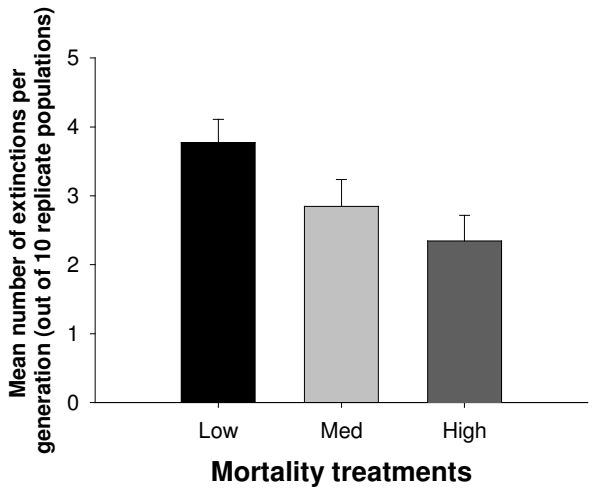

Figure 7.4. Effects of mortality rates on extinctions. As mortality rates increased, the persistence of the populations were also increased, presumably due to the reduction in amplitude of fluctuations in population size (*cf* Fig. 7.3).

Extinction

Since there were no extinctions in the stabilized regime, the discussion in this section pertains solely to the dynamics of populations in the destabilized regime. All else being equal, a population with greater amplitude of fluctuation in population size across generations is expected to hit lower population sizes more often, and therefore, be more prone to extinctions, than one with smaller amplitude of fluctuation. Thus, populations with higher FI are expected to be less persistent than those with lower FI. This intuitive reasoning seemed to be supported by the experimental data, where the rank order of persistence was low < medium < high (Fig. 7.4). Single-factor ANOVA showed a significant main effect of mortality ($F_{2,75} = 3.91$, $p < .02$) and post-hoc tests suggested that the high treatment was significantly more persistent than the low treatment ($p < .02$), while none of the other differences were significant at the $p = .05$ level. Thus, in

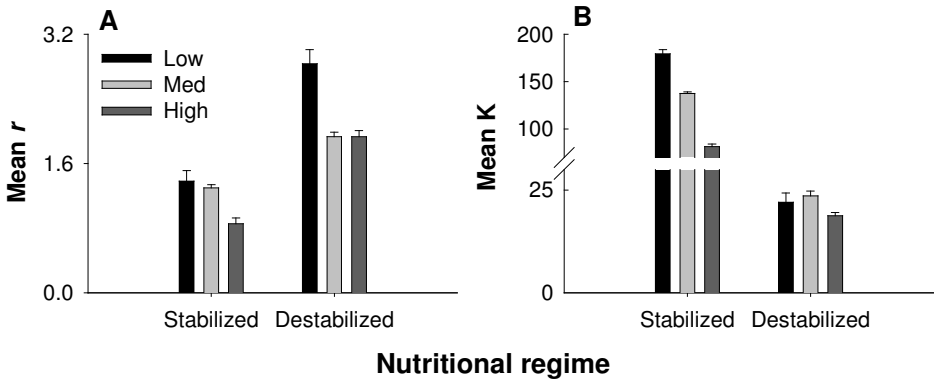

Figure 7.5. Parameter estimates derived by fitting the Ricker model to the time series of each population. (**A**) Intrinsic growth rate (r), and (**B**) carrying capacity (K). These estimates show that increased rates of mortality monotonically reduce both r and K in the stabilized regime, but the relationship is more complicated in the destabilized regime.

populations with high growth rates, high mortality rates can enhance persistence by reducing the growth rate and, thus, the amplitude of fluctuation in population size.

Growth rates

ANOVA on the estimated Ricker r-values (Fig. 7.5A) indicated that there was a significant effect of nutritional regime ($F_{1,54}$ = 157.84, $p << .001$), mortality ($F_{2,54}$ = 25.17, $p << .001$) and a significant interaction between the two ($F_{2,54}$ = 7.95, $p << .001$). As expected, the estimated r-values were higher in the destabilized regime than in the stabilized regime. Post-hoc tests indicated that in the stabilized regime, the r-value of the high-mortality treatment was significantly ($p < .05$) lower than the medium and the low mortality treatments (Fig. 7.5B), which however did not translate into a significant difference in terms of CV or FI, between these treatments (Fig. 7.3). In the destabilized

regime, the mean *r*-value of the low mortality treatment was significantly ($p < .05$) higher than the two other treatments, which is consistent with the patterns observed for CV and FI.

The mean *K* of the stabilized regime was higher than the destabilized regime ($F_{1,54} = 3015.1$, $p << .001$), and the main effect of mortality was significant ($F_{2,54} = 211.16$, $p << .001$). Post-hoc tests indicated that all pair-wise differences in the stabilized regime were significant ($p << .001$) while none were significant at $p = .05$ level in the destabilized regime.

CONCLUSIONS

In discrete generation populations with high growth rates, increasing the rate of adult mortality reduces the growth rates, and, thus, reduces the variability in population size, resulting in greater stability in terms of both consistency and persistence (*sensu* Grimm and Wissel 1997). However, the conclusions reached about the precise degree of relative stability under different mortality rates is likely to depend on the measure of stability used. In populations with low growth rates, the adult-mortality induced differences in stability tend to be marginal, and difficult to detect experimentally. Although the increased stability in terms of reduced fluctuation in population size with increasing rates of adult mortality translated into increased persistence of the populations in this experiment, this may not always be the case, as shown in chapter 6. This highlights the

fact that the concordance between measures of different aspects of stability is likely to depend critically on the underlying mechanism by which the stability is attained in a particular ecological context.

CHAPTER 8

EFFECTS OF NUTRITIONAL REGIME

Varying the quantity / quality of nutrition available to the larvae / adults can alter the dynamics of small populations of D. melanogaster by modulating the relative strengths of different density-dependent feedback loops.

Dey, S., Rajamani, M. and Joshi, A. Effects of different nutritional regimes on the dynamics and stability of laboratory populations of *D. melanogaster*. Manuscript under preparation

INTRODUCTION

Drosophila melanogaster has been a favorite model organism since the early days of population ecology (Pearl 1927) and the laboratory ecology of this species has been extensively studied (Sang 1949, Chiang and Hodson 1950, Bakker 1961, Prout and McChesney 1985), resulting in a rich body of information on the effects of various density-dependent factors on the population dynamics of lab cultures (reviewed by (Mueller 1985, Mueller and Joshi 2000). For example, it is known that increased larval density reduces pre-adult survival (Sang 1949, Chiang and Hodson 1950, Bakker 1961, Prout and McChesney 1985), and adult body weight (Chiang and Hodson 1950, Robertson 1957, Prout and McChesney 1985, Rodriguez 1989), which in turn reduces adult fecundity (Chiang and Hodson 1950, Robertson 1957, Prout and McChesney 1985). If the larval crowding is high, the mean amount of food available per larva is reduced. As a result, a large proportion of larvae are unable to attain the critical body mass needed for successful pupation, thus increasing the larval mortality (Bakker 1961). The mean size of the surviving larvae at pupation is also reduced in a crowded culture. Since the body size (and hence fecundity) of the adults depends mainly on the amount of resources gathered during the larval stage, the adults emerging out of crowded cultures are generally small in size and exhibit low fecundity (Chiang and Hodson 1950, Robertson 1957, Prout and McChesney 1985). Adult fecundity is also reduced with increasing density of adults in a culture (Pearl 1932, Chiang and Hodson 1950, Rodriguez 1989) and this is generally attributed to increased interference with egg laying (Pearl 1932). Interestingly, this negative effect of adult density on fecundity can be ameliorated by supplying the adults

with excess amount of live yeast paste (Mueller and Huynh 1994). Since survival and fecundity are the major factors affecting the growth rate of a population, it seems plausible that these three density-dependent feedback loops — effects of larval crowding on larval survivorship and adult fecundity, and effects of adult crowding on adult fecundity — can play a major role in determining the dynamics and stability of *D. melanogaster* populations in the laboratory (Mueller and Joshi 2000).

Several recursion functions for dynamics of *D. melanogaster* laboratory cultures have been proposed that incorporate one or more of these density-dependent feedback mechanisms (Mueller and Ayala 1981b, Prout and McChesney 1985, Rodriguez 1989). Mueller (1988) explicitly incorporated all three density-dependent feedback mechanisms into a single recursion as:

$$n_{t+1} = ½ \, . \, G(N_t). \, F(Vn_t). \, W(Vn_t). \, V.n_t$$

where n_t and N_t represent the number of eggs and adults in generation t, respectively, 1- V is the density-independent probability of larval mortality, $W(Vn_t)$ and $F(Vn_t)$ are the functions representing the effects of larval density on larval survivorship and adult fecundity, respectively, and $G(N_t)$ is the function reflecting the effect of adult density on adult fecundity. This model remains the most detailed abstraction of *D. melanogaster* dynamics in the literature and gave rise to several interesting predictions that were subsequently verified empirically (Mueller et al. 1991, Mueller and Huynh 1994, Sheeba and Joshi 1998). One of the most interesting predictions was that the dynamics of *D.*

melanogaster populations could be stabilized or destabilized by altering the strength of these three feedback loops. More specifically, it was predicted (Mueller 1988) and demonstrated (Mueller and Huynh 1994, Sheeba and Joshi 1998, Mueller et al. 2000, Prasad et al. 2003) that a combination of low food available to the larvae and addition of live yeast paste to the food available to the adults can lead to regular oscillations in adult numbers from generation to generation. On the other hand, excess food available to the larvae, together with no yeast supplement for the adults, stabilizes the dynamics and reduces the intrinsic growth rate of the populations (Mueller and Huynh 1994, Sheeba and Joshi 1998). These observations clearly demonstrate that manipulating the quantity/quality of food provided to the larvae/adults can alter the gross dynamics of the *D. melanogaster* populations.

Here I report a 49-generation experiment that systematically investigates the effects of four different types of nutritional regimes on the dynamics of single laboratory populations of *D. melanogaster*. I assess the stability properties of these populations and investigate the nature of the dynamics via autocorrelations and phase plots of the time series at different lags. I also fit two different population dynamics models and a suit of response surfaces of different orders, to the population time series and estimate different parameters. Based on these, I show that in three of the four food regimes, there is no apparent effect of density in generation t-1 on the population size at generation t+1. I also propose possible mechanisms for some of the findings of the present study that contradict existing observations in the literature.

MATERIALS AND METHODS

Experimental system

Thirty-two single vial *D. melanogaster* cultures were set up from one large outbreeding population (JB_1). Each culture was initiated (generation 0) with eight male and eight female flies, and then maintained on a 21-day discrete generation cycle, similar to that mentioned in chapter 6. Of these 32 cultures, eight each were subjected to one of the following food regimes — LL, HH, LH, HL — where the first letter denotes the quantity of food provided to the larvae whereas the second letter stands for a qualitative difference in the adult nutrition. The L and H, in the context of larval food quantity, refer to ~2 ml and ~6 ml of food per 8 dram vial, respectively. In case of adults, the L and H denote the absence and presence of live yeast paste during the three-day conditioning period, respectively. Thus, as in chapter 6, the LH regime denotes ~2 ml food for the larvae and live yeast paste for the adults, the HL regime refers to ~6 ml food for the larvae and no yeast paste for the adults, and so on. Two of these regimes (LH and HL) have been studied earlier in some detail (Mueller and Huynh 1994, Sheeba and Joshi 1998, Mueller and Joshi 2000, Mueller et al. 2000, Prasad et al. 2003), whereas population dynamics under the HH regime has been examined in only one earlier study (Mueller and Huynh 1994). There has been no previous study of population dynamics under the LL regime.

Analysis

The constancy stability (Grimm and Wissel 1997) of the populations was measured using FI (Dey and Joshi 2006b) and CV (Mueller and Joshi 2000, Prasad et al. 2003), whereas the nature of the dynamics was assessed by correlograms. All differences among food regimes, except when specifically noted otherwise, were tested using single factor ANOVA, and Tukey's HSD (Sokal and Rohlf 1995) was used for post-hoc comparisons. Phase-diagrams (N_{t+1} or the ln-transformed growth rate [$\ln(N_{t+1}/N_t$] against N_t) were plotted for exploratory data analysis. The Ricker model (Ricker 1954) and an extension of it (Turchin 1990; see below) were directly fit to the time series using the in-built Quasi-Newton algorithm of the commercially available software STATISTICA® (Statsoft Inc. v5.0). The goodness-of-fit measures achieved by non-linear regression techniques are often lower than those observed using linear regression on ln-transformed data (Turchin 2003). However, it is also known that such a process leads to severe under-estimation of the parameter values (Morris 1990), and hence it was not attempted here.

Model

The Ricker model (Ricker, 1954)

$$N_{t+1} = N_t \exp (r (1 - N_t / K))$$

assumes that the population density in a given generation is a function of the population density in the previous (parental) generation (lag 1). However, it has been shown earlier that incorporating higher lags in the Ricker model can significantly improve its fit to time

series of natural insect populations (Turchin 1990). Thus, it is conceivable that the population density in the grand-parental or great-grand parental generations (i.e. higher lags) might influence *D. melanogaster* dynamics, at least under certain food regimes. I investigated this possibility in two ways. First, I fit the model (Turchin 1990, Kaitala et al. 1996):

$$N_{t+1} = N_t \exp (r - sN_t - l\, N_{t-1})$$

to the time series data. Note that when $l = 0$, this reduces to the Ricker model with $s = r / K$. Thus, the estimated magnitude of l, relative to estimated s, should provide a crude reflection of the relative magnitude of the effect of density at generation t-1 vis-à-vis the density at generation t, on the population size at t+1.

I also investigated the effects of the grand-parental generation using the nonlinear time-series modeling (NLTSM) approach proposed by Turchin (2003). This involves fitting linear autoregressive (AR) polynomial models of various orders (p) to the data, and selecting the appropriate AR model via sequential-blocks cross-validation. Note that this approach only suggests the appropriate process order (i.e. how many generations should be incorporated in a model for the time series) and not the actual, biologically relevant, model. The NLTSM analysis was carried out using the NLTSM software of Peter Turchin, available at http://www.eeb.uconn.edu/people/turchin/NLTSM.htm.

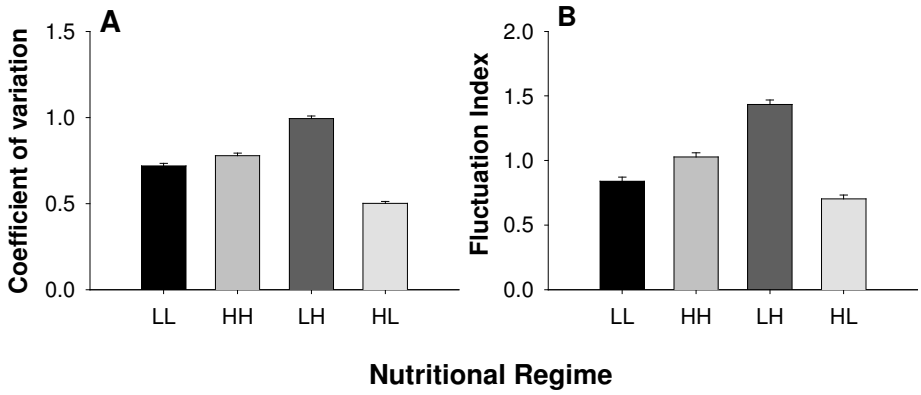

Figure 8.1. Constancy stability in the four regimes as reflected by (**A**) CV and (**B**) FI. Each bar represents the mean of eight replicate populations in a regime, and error bars represent SE around the mean.. Both indices suggested that the populations in the HL regime were the most stable while those in the LH regime were the least stable. All pair-wise comparisons are significant.

RESULTS AND DISCUSSION

Stability

In terms of both CV and FI, the constancy stability of the four regimes was significantly different (CV: $F_{3,28} = 212.17$, $p < .01$; FI: $F_{3,28} = 98.41$, $p < .01$) with post-hoc tests indicating that all pair-wise differences were significant at the $p < .05$ level). The order of stability in the four regimes was found to be HL > LL > HH > LH (Fig. 8.1), consistent with earlier observations that the HL regime leads to more stable dynamics than the LH regime in terms of constancy (Mueller and Huynh 1994, Sheeba and Joshi 1998, Mueller and Joshi 2000, Mueller et al. 2000, Prasad et al. 2003). However, the dynamics in the HH regime were found to be less stable than in the HL regime, which contradicts an earlier observation (Mueller and Huynh 1994) that the stability of HL and

HH (as reflected by the stability determining eigen values) are not different. Possible explanations for this discrepancy are discussed later in this section.

Previous theoretical studies predict that the per-capita food available to the larvae, as well as the sensitivity of adult fecundity to density, have major effects on the dynamics of the populations (Mueller 1988, Mueller and Joshi 2000). In the present study, the first factor was directly manipulated via the level of food available to the larvae, while the second was indirectly modulated via presence/absence of live yeast paste to the adults. I analyzed the effects of larval and adult food level on population stability by treating them as two fixed factors, each with two levels (L and H), crossed with each other in a two-way ANOVA. In case of CV, there were significant main effects of both larval ($F_{1,28}$ = 240.04, $p < .01$) and adult food level ($F_{1,28}$ = 396.47, $p < .01$), but the interaction was not significant ($F_{1,28}$ = .008, $p < .93$). With respect to FI, the main effects of larval ($F_{1,28}$ = 71.97, $p < .01$) and adult food level ($F_{1,28}$ = 205.34, $p < .01$) were significant, and so was the interaction ($F_{1,28}$ = 17.93, $p < .01$). These two results, as in the previous chapter (chapter 7), again highlight the fact that CV and FI measure two different aspects of constancy stability, and hence need not necessarily lead to same conclusions about stability properties of a population.

Autocorrelations

The correlograms of the time series in the four regimes provided several interesting observations (Fig. 8.2). As expected from previous studies (Mueller and Huynh 1994,

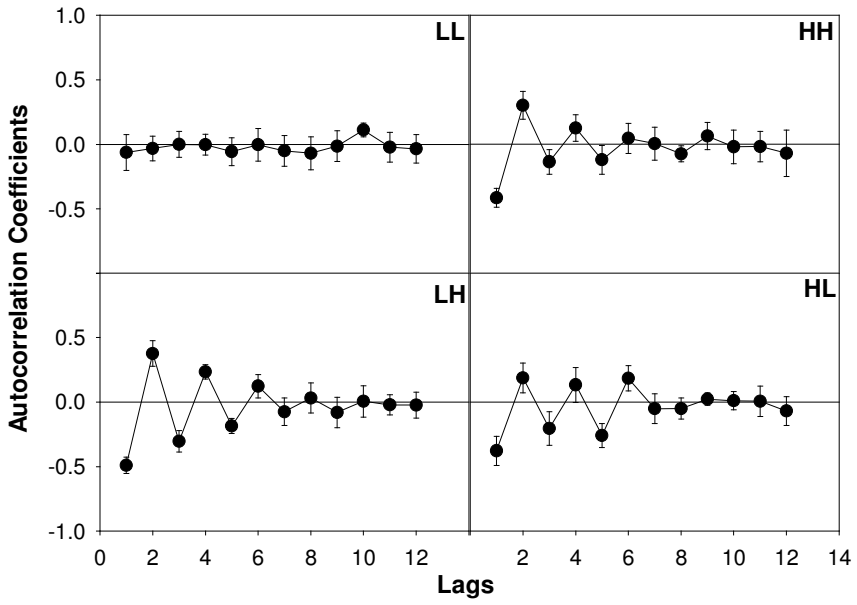

Figure 8.2. Correlograms of time series in the four regimes, each averaged over the eight replicate populations. Error bars represent 95% CI around the mean. As expected, the LH showed alternating negative and positive lags, which indicates two-point limit cycles. Unexpectedly, the HL and HH regime also showed the same trend. While there are some possible reasons for this observation in the case of HH (see text), currently we have no explanation for the two-point limit cycles in HL. No particular trend was observed in the LL dynamics.

Mueller and Joshi 2000), the LH populations showed a clear signature of a two-point cycle. However, unexpectedly, the populations in the HL and the HH regime also seemed to exhibit two-point cycles, which contradicts an earlier study (Mueller and Huynh 1994), which found none of the autocorrelation lags in these regimes to be significantly different from zero. One of the possible reasons for this discrepancy might be the short duration (12 generations) of the previous study (Mueller and Huynh 1994), as a short time series can complicate the estimation of higher lag autocorrelation coefficients. The observed difference in the dynamics in case of the HH regime can also be possibly attributed to the difference in maintenance regime of the populations (bottle cultures on a 28-day cycle) in the previous study (Mueller and Huynh 1994) compared to the present one (21-day

cycle). A greater age of the adults at the time of egg lay in a 28-day cycle would reduce the per-capita fecundity of the females on the day of egg collection, as compared to the females in a 21-day cycle culture. Consequently, the growth rates of populations under a 28-day cycle is expected to be lower than those under a 21-day cycle, thus giving rise to more stable dynamics. Given that supplying yeast is expected to destabilize the dynamics of *D. melanogaster* cultures, it is intuitive to expect that the HH regime would lead to more destabilized dynamics than the HL regime. It is interesting to note here that although it did not show up in correlograms, the HH time series of Mueller and Huynh do show regular oscillations (see Fig. 4 of (Mueller and Huynh 1994), and the stability determining eigen values estimated by Mueller and Huynh (1994) were not significantly different between the HH and the LH regime. However, the anomalous limit cycles observed in the case of the HL regime of the present study contradict several earlier studies that have noted the lack of periodicity in HL dynamics (Mueller and Joshi 2000, Mueller et al. 2000, S. Dey unpublished data), and currently there is no explanation for this discrepancy.

Phase Plot

The plot of N_{t+1} vs. N_t (Fig. 8.3) suggested that the nature of the dynamics was similar in the HL and the LL regimes whereas the LH dynamics resembled that in the HH regime. In other words, the nature of the phase plot was being determined by the type of adult nutrition, i.e. the sensitivity of female fecundity to adult crowding. The HH and the LH phase plots had the characteristic L-shape indicative of two-point limit cycles. However,

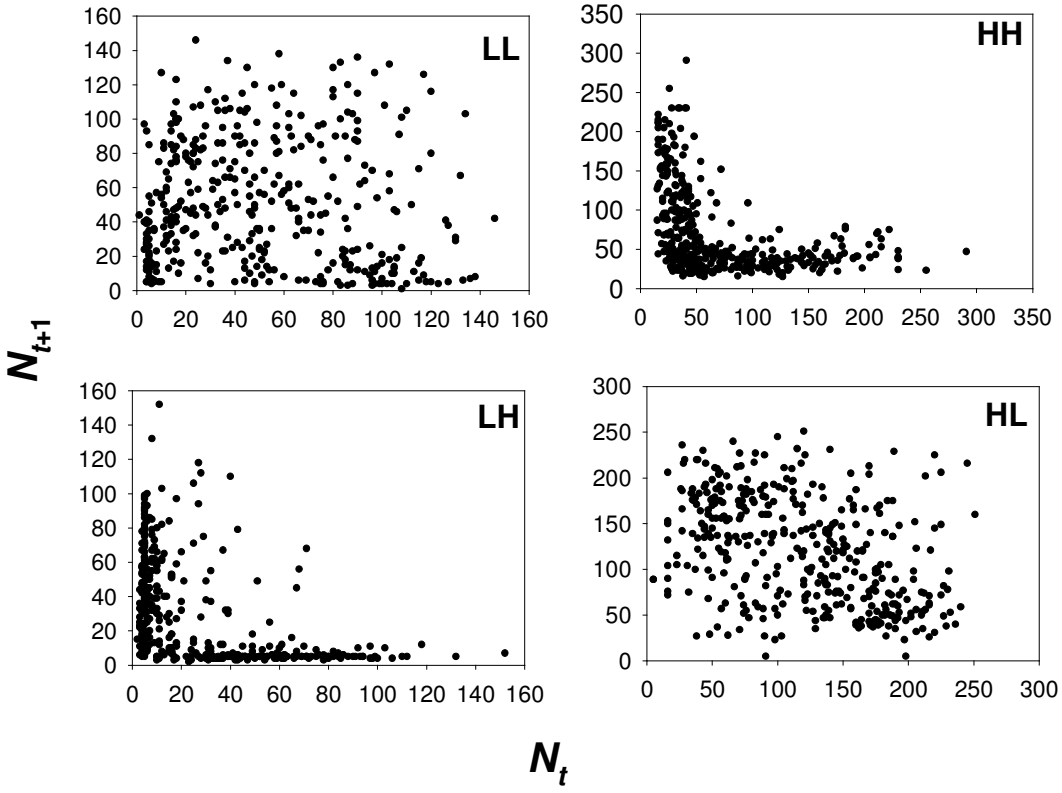

Figure 8.3. Phase plots of N_{t+1} vs. N_t for the four nutritional regimes, each pooled over the eight replicates in a regime. The HH and LH plots indicate regular oscillations in population size, while no clear patterns are observable in case of the LL and HL. This suggests that the main determinant of the dynamics in these populations was the adult density-dependent feedback on female fecundity, which was modulated in the current study via the presence/absence of live yeast paste, leading to a contrast between the L and H regimes experienced by adults but not larvae.

there were no observable patterns in the LL and HL plots, suggesting the presence of either considerable noise or a higher order dynamics, or both. In the case of the LL and HL data, there was a linear decrease in ln $[N_{t+1})/N_t)]$ with increasing N_t (Fig. 8.4), implying that a first order exponential function might be suitable for modeling these data (Box and Draper 1987, Turchin 1991). The linear relationship of ln (N_{t+1}) with N_t also indicates that the lack of any apparent relationship between the N_{t+1} and N_t for the LL and HL regimes (Fig. 8.3) was probably due to the presence of noise in the dynamics. The slight curvature in the plots, particularly in the case of LH and HH (Fig. 8.4), suggested

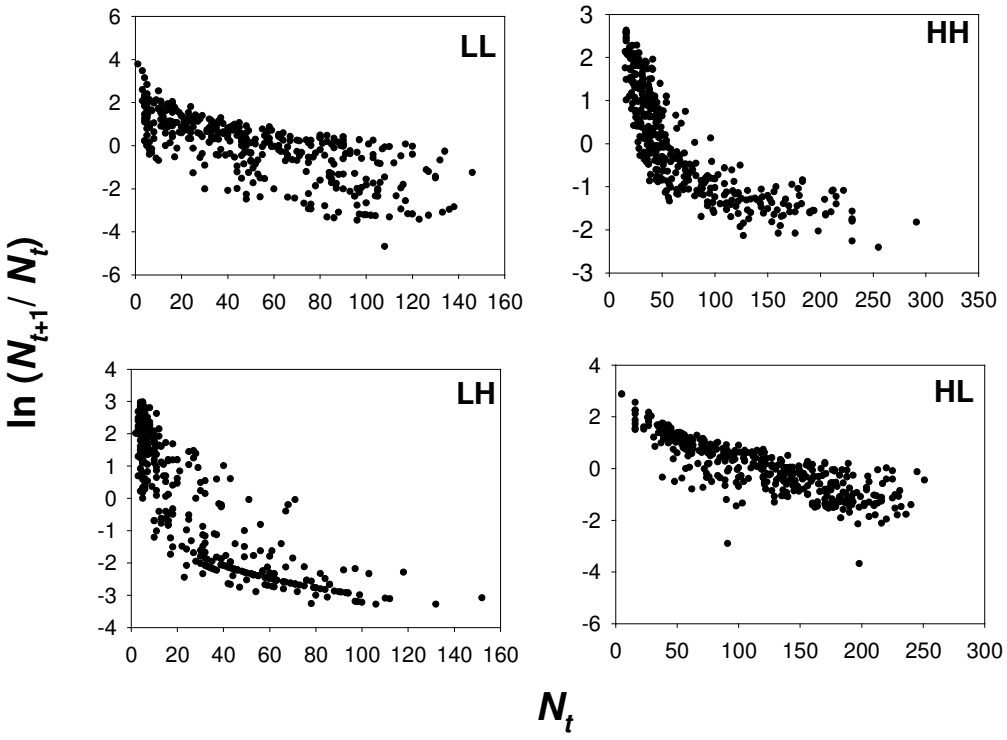

Figure 8.4. Phase plots of ln $[N_{t+1}/N_t]$ vs. N_t for the four nutritional regimes, each pooled over the eight replicates in a regime. The LL and HL plots are linear and monotonically decreasing, indicating that a first order exponential model might be suitable for these data. A slight curvature in the LH and HH plots indicated that fitting a theta-Ricker model might improve the fit in these cases. However, preliminary data-fitting exercises ruled out the possibility of using a theta-Ricker (see text).

that a theta-Ricker model (Thomas et al. 1980) with $\theta < 1$ might improve the fit to the data (Turchin 2003). However, during the parameter estimation process of the theta-Ricker model, the minimizing algorithm either failed to converge or sometimes led to absurd values, particularly in the HH regime. Therefore, I limited the model-fitting endeavors to the Ricker map and its extension.

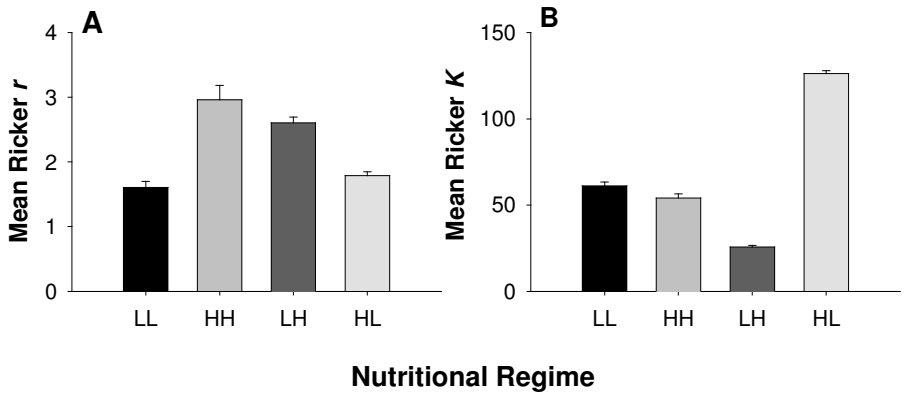

Figure 8.5. Estimates of (**A**) *r* and (**B**) *K*, obtained by fitting the Ricker model to individual time series. Each bar represents the mean of eight replicate populations in a regime, and error bars represent SE around the mean. The *r*-values of HH and LH were significantly greater than those in LL and HL. This suggests that it is the adult nutrition, which chiefly determines the growth rates of these populations. The *K*-value of the HH regime was found to be significantly lower than that of the HL regime, which contradicted a previous study (see text for possible explanations).

Parameter estimation

There were significant differences among the estimated Ricker-*r* values among populations from the four nutritional regimes ($F_{3,28}$ = 24.22, p < .01) and post-hoc comparisons indicated that LL~HL < HH~LH (p < .01, Fig. 8.5A). This is consistent with the observation that it is the type of adult nutrition that seems to be the major determinant of the dynamics in these populations (Fig. 8.3). Moreover, the estimated *r*-values in the HL regime were in the range that predicts damped oscillations in population numbers (May 1976). This result agrees with a previous analysis (Turchin 1991) of dynamics of *D. melanogaster* populations (Rodriguez 1989) maintained on a regime similar to the HL regime of this study.

Although there was no significant difference between the *r*-values in the HH and LH regimes (Tukey's HSD, $p = .24$), the FI in the HH regime was significantly lower than that in the LH regime (Fig. 8.1B). This highlights the fact that the correspondence between *r* and FI is not very good in the region of high *r*-values, where there is a transition from low-periodicity limit cycles to high-periodicity limit cycles or chaos. This is because, by virtue of its formulation, the FI of a population undergoing a two-point limit cycle within a particular upper and lower bound, will be more than the FI of a population undergoing a higher periodicity limit cycle within the same upper and lower bounds of population size.

The estimated *K*-values of the populations in the four regimes were also found to be significantly different from each other ($F_{3,28} = 490.25$, $p < .01$, Fig. 8.5B) and all pair-wise differences were also significant ($p < .01$), except the one between LL and HH which was marginally non-significant ($.05 < p < .06$). This contradicts an earlier observation by Mueller and Huynh (1994), who had found the carrying capacity of HH cultures to be greater than HL cultures. This discrepancy might be explained by the above-mentioned differences between their study and the present one.

I also fit an extension of the Ricker map (see section: Materials and methods), involving an extra lag, to the population time series from the four regimes (Fig. 8.6 A). The values of estimated *r* from the extended model were significantly different from each other ($F_{3,28} = 9.73$, $p < .01$), again showed the same rank order (LL~HL < HH~LH) as in the case of the Ricker estimated *r*-values, and the relevant differences were statistically significant at

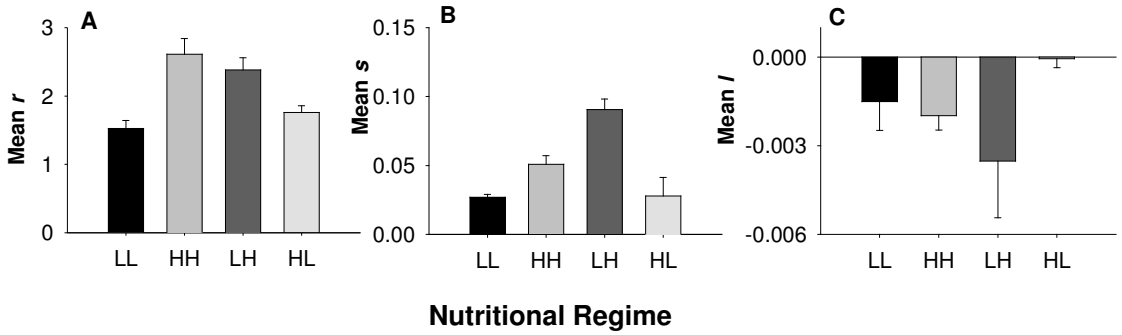

Figure 8.6. Estimates of (**A**) *r* and (**B**) *s*, and (C) *l*, obtained by fitting an extension of the Ricker model to individual time series. Each bar represents the mean of eight replicate populations in a regime, and error bars represent SE around the mean. The estimates of *r* again showed the same relationship, LL~HL significantly less than HH~LH, as with the Ricker *r*. The magnitudes of the l-values were very low, relative to the *s*-values, suggesting that the role of the density of the grand parental generation (N_{t-1}) in determining the size of the offspring generation (N_{t+1}) is probably negligible.

$p < .01$. The values of *s*, the coefficient of the first lag, showed a significant main effect ($F_{3,28} = 12.44$, $p < .01$, and the post-hoc tests indicated that the *s*-value in the LH regime was significantly greater ($p < .01$) than those in all other regimes, with none of the other differences being significant (Fig. 8.6 B). This suggests that the density-dependent effects of the population size of the parental generation (i.e. N_t) were maximal in the LH regime as compared to the other regimes. This is intuitively expected due to the high fecundity of the LH regime females, and the intense competition for food among the LH larvae, which makes the effects of addition/subtraction of each extra female much more substantial for the dynamics, compared to the other regimes, where either the female fecundity is lower (LL) or the larval competition is less (HH), or both (HL).

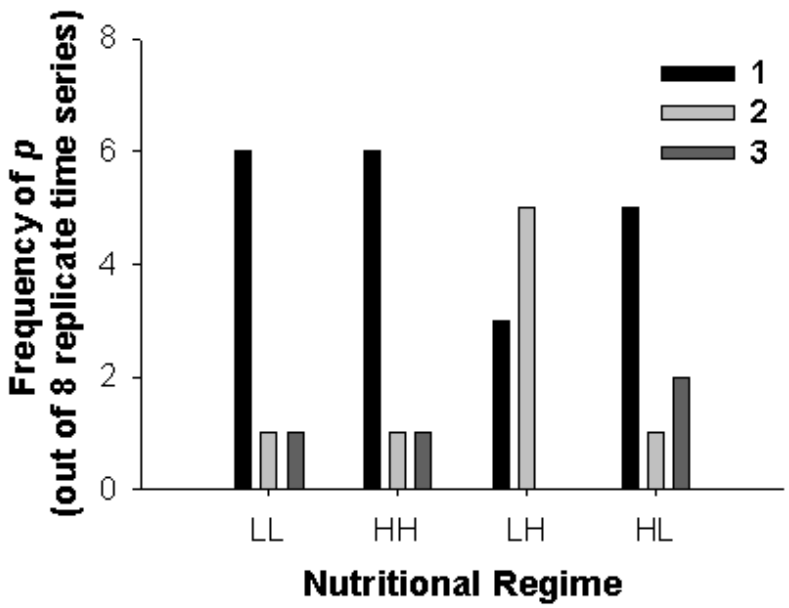

Figure 8.7. Frequency of the estimated process order, *p*, from the NLTSM analysis. The LL, HH and HL regimes clearly show a dominance of $p = 1$, suggesting that a first order model would be sufficient to model these data. However, the LH regime shows a preponderance of $p = 2$, suggesting that the population size at generation *t*-1 plays a greater role in determining the dynamics of these populations.

The values of *l*, i.e. the coefficient of the second lag (N_{t-1}) were not significantly different from one another ($F_{3,28} = 1.66$, $p < .20$; Fig. 8.6c) and more importantly, the *l*-values were about an order of magnitude less than the corresponding *s*-values, (*cf* Fig. 8.6B and 8.6C). The increase in goodness-of-fit with the extended Ricker model (mean $R^2 = .22$) was also found to be marginal when compared to the Ricker model (mean $R^2 = .19$). Taken together, these two observations suggest that the effects of incorporating an extra lag in the Ricker model is negligible, which in turn indicates that the density in the grand-parental generation (N_{t-1}) is unlikely to significantly affect the population size of the offspring generation (N_{t+1}), and agrees with previous findings on data from laboratory cultures of *D. melanogaster* (Turchin 1991). This observation was also supported by the NLTSM analysis, which indicated that in case of the LL, HH and HL, considering the

population size of the parental generation should be sufficient for the purpose of modeling the time series (Fig. 8.7). This is evident by the highest frequency of the first order (p = 1) for these three regimes. However, in case of the LH regime there was predominance of p = 2, suggesting that incorporating a second lag might be called for. Although the extended Ricker model did not do a better job in fitting the LH data, it is interesting to note that the magnitude of l was the highest in the LH regime (Fig. 8.6), again indicating that there seems to be a fundamental change in the dynamics of these populations mediated by the different food regimes.

The observation that the extended Ricker model does not improve the fit to data is in contrast with a previous study in which parameters of this model were estimated for natural insect populations, and the coefficients of the second lag were seen to be of similar magnitude, or sometimes even greater than, the coefficients of the first lag (Turchin 1990). One possible reason for this might be the fact that natural populations generally have overlapping generations and, hence, the effects of the grand-parental generation tends to linger longer and affect the dynamics more than it would be in a discrete generation culture. In fact, in laboratory *D. melanogaster* populations maintained with overlapping generations, it has been shown that the adult density in a particular generation can affect the fecundity of the flies two generations later (Shorrocks 1970). I also note here that formal methods, like the Akaike Information Criteria (AIC) and Bayesian Information Criteria (BIC), exist for choosing the best model among a suite of models with different numbers of parameters (Draper and Smith 1998, Johnson and Omland 2004). However, in this study, the improvement of goodness-of-fit with the

extended Ricker model was so marginal compared to the Ricker model, that I did not perform explicit model selection tests. The values of R^2 obtained for the Ricker are actually poor, particularly given that the data represents dynamics of laboratory populations. This indicates that either there was a large amount of noise in the system, which reduced the fit between the model and the data, or, that the Ricker model is not a good descriptor of *D. melanogaster* dynamics. High degree of noise is expected in the present study as small, single-vial cultures are liable to have greater demographic variation as compared to the larger populations used in previous studies (Rodriguez 1989, Mueller and Huynh 1994). However, in spite of this, there was a good correspondence between the parameters estimated by fitting the Ricker model and the qualitative behavior expected in those parameter zones, suggesting that the Ricker model was a fair descriptor of the fly dynamics in the present study.

CONCLUSIONS

Varying the quantity / quality of nutrition available to the larvae / adults can alter the dynamics of small populations of *D. melanogaster* by modulating the relative strengths of different density-dependent feedback loops. The empirical data suggests that of the three major density-dependent feedback loops in *D. melanogaster*, the effect of adult density on adult fecundity seems to be the main determinant of the qualitative nature of the dynamics. Model-fitting exercises indicate that the population size at generation t-1 does not play a major role in determining the population size at generation t+1, and hence can

probably be ignored while modeling the dynamics of *D. melanogaster* populations maintained on discrete generation cycles.

CHAPTER 9

EFFECTS OF MICRO-ENVIRONMENTAL CONDITIONS

Variation in micro-environmental conditions can systematically bias the measurement of life-history traits, and act as a source of stochasticity in the experiments.

Dey, S., Dey, S., Mohan, J., and Joshi, A. 2006. Micro-environmental variations in pre-assay rearing conditions can lead to anomalies in the measurement of life-history traits. *Journal of Genet*ics **85**, 53-56.

INTRODUCTION

Experiments in ecology and evolution often involve the measurement of traits related to the life-history, such as fecundity, stress resistance and duration of various life stages. Since any such trait is expected to exhibit some variance around the mean, a meaningful point estimate can only be derived by taking an average over a large number of replicate measurements. Although all replicates within a treatment should ideally be identical to each other in every respect, it is often impossible to realize this in practice. For example, if one needs to measure the fecundity of a large number of adults, it might not be feasible to procure/generate all of them from a single source/batch such that they share a common environment during pre-assay rearing. The effects of such pre-assay variation in macro-environmental factors on life-history traits have been well studied empirically in laboratory systems such as *Drosophila* (Mueller 1985, Service and Rose 1985, Chippindale et al. 1993, Borash and Ho 2001, Prasad et al. 2003). However, such variation is not expected to be a severe problem under laboratory conditions, as it is possible to exercise strict control over most known sources of macro-environmental variation, such as temperature, light and food, across batches. Nevertheless, one still needs to address possible effects on assayed traits of differences across batches in micro-environmental factors, which include all those elements that cannot possibly be controlled by an experimenter. For example, in case of a *Drosophila* system in the laboratory, this might include, *inter alia*, density of microflora on the food or minor differences in the space available to the flies; factors that are normally ignored as of trivial import.

In this study, I directly examine the possible effects of micro-environmental variation while generating experimental organisms on the measurement of a life-history trait. I assay fecundity in the fruit fly *Drosophila melanogaster* by allowing replicate single pairs (one male and one female) to lay eggs for varying lengths of time. I find that the temporal pattern of cumulative fecundity is anomalous when all flies in a particular egg-lay duration treatment are derived from a single vial. I conduct another experiment to show that the anomalous patterns tend to disappear as a consequence of differences due to micro-environmental variation getting averaged out when the flies subjected to a particular egg-lay duration treatment are derived from different vials. I compute an index that reflects this parent vial specific effect, and use it to generate predictions about the expected number of eggs laid over time. I then perform a third experiment to independently verify these predictions and find good agreement between the predicted and observed values. These results demonstrate the importance of randomizing across pre-assay micro-environmental conditions before assaying any life-history related trait.

MATERIALS AND METHODS

Derivation of the flies

All experiments were conducted on a large outbred population of *D. melanogaster*, the so-called JB_1 that has been maintained in the laboratory on a three week discrete generation cycle for more than 200 generations. Details of the maintenance protocol of

these flies have been described elsewhere (Sheeba et al. 1998) and are not relevant to the present study. Eggs were collected from the JB_1 population by placing a petri plate containing banana-jaggery medium in the population cage for 24 hours. The eggs were then distributed into 16 vials, each containing 70-80 eggs in ~ 6 mL of media. The medium in each vial was obtained from a single cooked batch. The adult flies eclosing in these vials were transferred to fresh media vials on day 12, 14 and 16, post egg collection. All flies that eclosed from a particular vial were collected together and strict one-to-one correspondence was maintained between the egg vials and the adult collection vials. On day 18 after egg collection, the flies were put into vials containing ~ 6 mL of media, for three days. Eight of the 16 vials were supplied with excess live yeast paste to boost female fecundity, while the remaining eight vials did not get any nutritional supplement. Thus, all flies in a particular vial (henceforth, parent vial) ultimately came from the same egg vial and presumably experienced similar micro-environmental conditions during their pre-adult and adult stages, especially during the three day conditioning period. On day 21 after egg collection, these flies were distributed into fecundity vials for measuring the number of eggs laid over different durations of egg-laying window.

Experiment 1

Twenty fecundity vials, each containing one male and one female fly in ~2 ml of medium, were derived from each of the eight unyeasted parent vials. The flies were then allowed to lay eggs in these vials for durations of 1, 2, 3, 4, 5, 6, 7 or 8 hours. All 20

fecundity vials that were set up from a particular parent vial were allotted to the same egg-lay duration treatment. At the end of the assigned time, the adults were discarded and the number of eggs laid in each vial was counted manually under a binocular microscope. A similar protocol was followed for measuring the fecundity of flies from the yeasted parent vials, with the exception that only ten fecundity vials were set up from each parent vial.

Experiment 2

In this experiment, sixteen egg vials, each containing 200-300 eggs were set up, and the flies were handled as explained above (see Derivation of flies) until day 21 after egg-lay. For both unyeasted and yeasted treatments, seven fecundity vials containing 1 male and 1 female each, were obtained from each parent vial. Seven different durations of egg-lay window, between one to seven hours, were studied in this experiment. Eight fecundity vials, one from each parent vial, were allotted to each egg-lay duration in the case of both unyeasted and yeasted treatments. As before, the number of eggs laid in each vial during the egg-lay duration was recorded, after discarding the adults. Thus, experiment 2 differed from experiment 1 in that parent vial was not confounded with egg-lay duration but crossed with it.

Performance Index

Using the data from experiment 2, I calculated a statistic that I call the performance index, in the following way:

$$S_i = \frac{1}{T}\left[\sum_{t=1}^{T} \frac{f_{i,t}}{N_t}\right]$$

Here, S_i denotes the performance index of the i^{th} parent vial, T is the total number of egg-lay window durations studied (7 in experiment 2), $f_{i,t}$ is the number of eggs in the fecundity vial belonging to i^{th} parent vial and t^{th} egg-lay duration window, and N_t is the mean number of eggs laid in the t^{th} egg-lay window, averaged across all fecundity vials in that window. This statistic, calculated separately for each parent vial, gives us an estimate of the relative fecundity of the pairs of flies that belonged to a particular parent vial vis-a-vis flies from other parent vials. When a particular value of S_i is multiplied by any N_t, I get a prediction for E[$f_{i,t}$,], the expected number of eggs laid by the flies from the i^{th} parent vial over an egg-lay duration window of t hours. A third experiment was conducted simultaneously to test these predictions arising out of experiment 2.

Experiment 3

The design of this experiment was similar to that of experiment 1 in that all the fecundity vials in a given egg-lay window were derived from a single parent vial. However, there were two major differences: (a) the sixteen parent vials used in this experiment were the same ones that were used in experiment 2, and (b) each egg-lay duration treatment

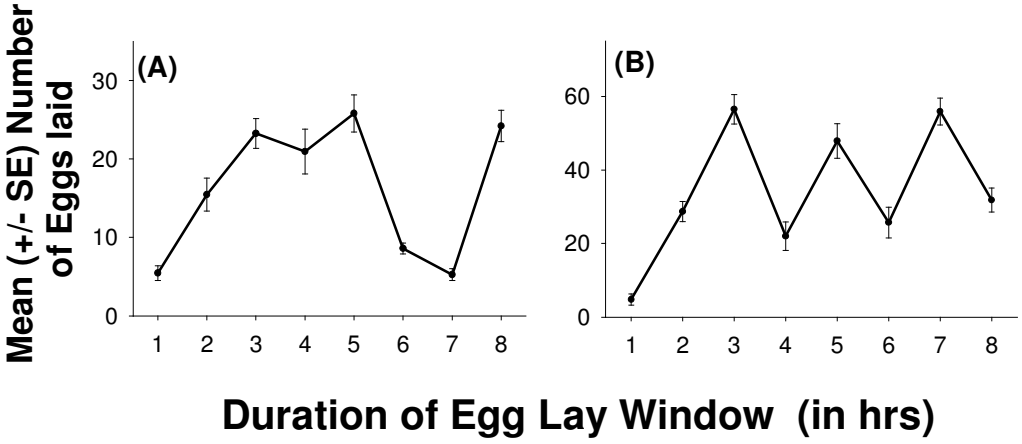

Figure 9.1. The mean number of eggs laid across successive lengths of time in the two treatments, (**A**) Unyeasted and (**B**) Yeasted, in experiment 1. Since this number is cumulative, the observed trends are unexpected. See text for possible explanations.

consisted of ten fecundity vials in both the unyeasted and yeasted treatments. The number of egg-lay window durations studied was seven, as in experiment 2.

RESULTS AND DISCUSSION

Experiment 1

In this experiment, I was measuring the number of eggs laid by single *D. melanogaster* females over an increasing duration of egg-lay. Intuitively, one would expect this number to increase up to a certain point of time and then plateau out. However, under no circumstances would one anticipate a reduction in the cumulative number of eggs laid over successively increasing lengths of time, as seen in this experiment (Fig. 9.1). Here I note that there almost seems to be a regular oscillation (two-point cycle) in the mean

fecundity of the yeasted flies (Fig. 9.1B). However, this is most probably a coincidence, as all the means arising out of different egg-lay duration are independent of each other by design in this experiment. Such anomalous results can possibly arise if there is large variation in fecundity among individuals, or alternatively in the presence of some random environmental noise affecting the fecundity vials. These explanations, nevertheless, are unlikely in the present case, as the standard errors across the mean (fecundity) were found to be small (Fig. 9.1) and macro-environmental factors were strictly controlled. The observed pattern of cumulative fecundity (Fig. 9.1) could also potentially result from micro-environmental variation leading to a systematic increase or decrease in the fecundity of all pairs of flies that came from a particular parent vial. Experiments 2 and 3 were specifically designed to test this hypothesis.

Experiment 2

In this experiment, each fecundity vial in a particular egg-lay window was derived from a different parent vial. Therefore, in terms of the mean number of eggs laid in a given duration, any major parent vial specific variation, if present, is expected to be smoothed by averaging across parent vials within egg-lay window durations. On the other hand, in case there was major among-individual variation in fecundity, one could anticipate some anomalous pattern, as observed in experiment 1. The same argument applies to any random environmental noise affecting the fecundity vials differently, although such an event is unlikely in the controlled laboratory conditions under which the experiments were run.

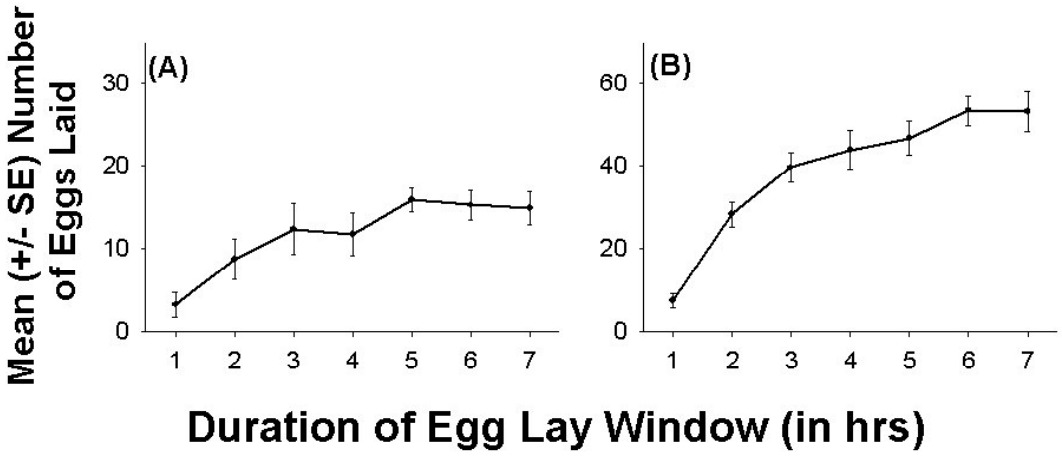

Figure 9.2. The mean number of eggs (N_t) laid across successive lengths of time in the two treatments, (**A**) Unyeasted and (**B**) Yeasted, in experiment 2. These curves are closer to the intuitive expectations and thus rule out individual variations and random noise as causes of the observed patterns in experiment 1.

In experiment 2, the mean number of eggs laid over successively longer durations of time increased initially up to ~ 4 hours and then leveled off (Fig. 9.2). This result rules out individual variation or random environmental noise as potential causes of anomaly in experiment 1, but does not directly implicate micro-environmental variation among parent vials for the same. To prove that micro-environmental variation can indeed lead to systematically aberrant cumulative fecundity patterns, I calculated the performance index (S_i) as mentioned above (see Materials and methods: Performance Index). This statistic is an average score for the fecundity of flies that came from the same parent vial, relative to the fecundity of flies from other parent vials. Thus, S_i is expected to reflect the component of variation due to parent vial specific differences in micro-environment. Since the same parent vials were used in experiment 2 and 3, I was able to generate independent predictions for the mean number of eggs in a time-window in experiment 3. For this, I used the product of S_i and N_t (from experiment 2) for the corresponding egg-lay window of t hours in which the i^{th} parent vial was tested in experiment 3.

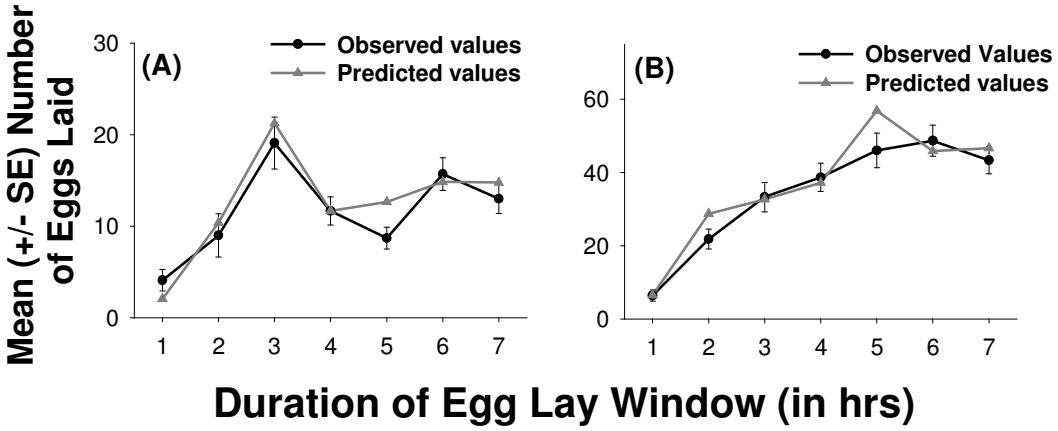

Figure 9.3. The mean number of eggs across successive lengths of time in the two treatments (**A**) Unyeasted, and (**B**) Yeasted in experiment 3, along with the corresponding predictions from experiment 2. There are no significant differences between the predicted and observed numbers of eggs.

Experiment 3

There was considerable agreement between the predicted and the observed values of mean fecundity across different egg-lay window durations (Fig. 9.3) and a chi-square test detected no significant difference between the two in either regime (unyeasted, $\chi^2_{(6)} = 3.93$, $p = 0.69$; yeasted, $\chi^2_{(6)} = 4.24$, $p = 0.64$). This ability of S_i to successfully predict the mean fecundity in experiment 3, indicates that micro-environmental variations can systematically affect life-history traits of organisms. It is worth noting that by mimicking the design of experiment 1, I again confront some anomalous patterns in the unyeasted regime (Fig. 9.3A). However, no such clear aberrations are observable in the yeasted regime (Fig. 9.3B), which most probably happens to be a fortuitous event.

CONCLUSIONS

This study demonstrates the artifactual anomalies that can potentially arise due to non-random sampling across the micro-environmental conditions over which the experimental organisms have been reared before an assay of life-history related traits. Unfortunately, this aspect is not always taken care of while setting up experiments in ecology or evolution, and most often not reported clearly in the literature. Similar artifactual results might arise while measuring other life-history related traits too, as fecundity is known to be correlated with a host of life-history attributes (Prasad and Joshi 2003). It is noteworthy that this study was conducted in the laboratory under constant temperature, humidity and light, and all flies were treated similarly as far as practicable. It is difficult, if not impossible, to maintain such rigorous standards of control in field or quasi-natural studies. Thus, one cannot over emphasize the need for randomization across pre-assay micro-environments before assigning individuals to different experimental treatments for measuring trait values.

CHAPTER 10

CONCLUSIONS

This thesis examined several issues in single-species population and metapopulation dynamics, using a combination of simulations and experiments on small laboratory populations of *D. melanogaster*. While stability remained the main focus of attention in most chapters, I also addressed other issues like synchrony in spatially structured populations and effects of minor variations in assay conditions on life-history traits important to population dynamics.

My simulations indicate that the effects of migration rate on metapopulation stability do not depend upon the precise spatial arrangement of the subpopulations in the lattice, suggesting that metapopulation models are robust to variation in spatial arrangement of patch quality (Dey et al. 2006a; chapter 2). I also show that for any given arrangement of the patches, maximum stability occurs when the migration levels are intermediate, a result that agrees well with previous studies on two-map coupled map lattices (Gyllenberg et al. 1993, Hastings 1993, Kendall and Fox 1998). I further demonstrate that these patterns of metapopulation stability at different migration rates are not altered by migration being density-dependent or density-independent (chapter 4). In both cases, maximum metapopulation stability is attained at intermediate migration rates (5%) whereas lower or higher migration rates lead to instability. This pattern is consistent even when migration rates are made stochastic, although there is an overall destabilization of the metapopulations. Even a 1% probability of migration events not occurring in every generation is enough to promote metapopulation instability. Importantly, all these results were found to be robust to demographic and spatial heterogeneity among patches.

The above simulations, and previous theoretical results on two-map coupled map lattices (Gyllenberg et al. 1993, Kendall and Fox 1998), suggested that the amplitude of fluctuation of metapopulation sizes is reduced under low migration rates (5-10%) but not under higher migration rates. I verified this prediction using replicate laboratory metapopulations of *D. melanogaster* subjected to different migration rates. Low migration stabilized metapopulation dynamics, while promoting unstable subpopulation dynamics, by inducing asynchrony among neighboring subpopulations (Dey and Joshi 2006b; chapter 3). On the other hand, as predicted, high migration synchronized subpopulation dynamics, thereby destabilizing the metapopulations. Contrary to some theoretical predictions (Hanski and Zhang 1993, Ives et al. 2004), increased migration did not affect average population size. I also simulated the experimental system using a simple non-species specific population growth model (Ricker model), and was able to recover most of the features of the empirical data. This suggests that the experimental results were not caused by some unique aspect of *D. melanogaster* biology, but can be attributed to the effects of migration. The Ricker model is known to be a good descriptor of the dynamics of several kinds of organisms. Moreover, a subsequent simulation study using other widely used models of population dynamics like the Hassell model or the Maynard Smith - Slatkin model, corroborated the observation that low migration rates lead to asynchrony among neighboring subpopulations (Ranta and Kaitala 2006). Thus, the phenomenon of low migration rates promoting metapopulation stability seems to be applicable to a large number of systems.

This leads to an important question: why does low migration promote asynchrony among subpopulations? Ranta and Kaitala (2006) proposed that the observed asynchrony in my experiments was due to a fortuitous choice of initial population sizes interacting with stochasticity that is inherent in any biological system. Their hypothesis implied that asynchrony among subpopulations arose as a matter of chance, and hence was at odds with the statistically significant asynchrony observed in my experiments. This apparent anomaly can be resolved by noting that Ranta and Kaitala's (2006) arguments are based on simulations of a 2-patch system whereas I had used 9-patch metapopulations for both my simulations and experiments. Using a 9-patch metapopulation simulation, I then showed that in the presence of noise, asynchrony among subpopulations is an extremely likely event, even if there are no differences in the initial population sizes (Dey and Joshi 2006a; chapter 3). Thus, real metapopulations, which are generally noisy and extinction-prone, are very likely to exhibit asynchrony under low migration rates. Although these results reinforce the generality of the finding that low migration rate stabilizes metapopulation, at least under the conditions of the experiments and the simulations, it is yet unclear as to what causes this asynchrony. Currently, I have no answer to this question, and must propose this as an interesting avenue for further work. It would also be interesting to perform these experiments on populations undergoing overlapping generations, as that would be a closer approximation of many natural systems. Simulation studies indicate that migration and spatial correlation interact with each other to produce different patterns of population synchrony (Kendall et al. 2000), and it would be interesting to test these predictions using the kinds of experiments described in chapter 3.

Several studies in the past had predicted that it would be possible to alter the dynamics of metapopulations by localized perturbations to the subpopulations (Doebeli and Ruxton 1997, Parekh et al. 1998, Solé and Gamarra 1999). However, my experiments on *D. melanogaster* metapopulations suggested that constant addition of individuals to a particular subpopulation in every generation stabilizes that population locally, without any detectable effect on metapopulation dynamics and stability (Dey and Joshi 2007); chapter 5). Ricker-based simulations of the experimental system corroborated the experimental observations, thus suggesting that the results were not *D. melanogaster* specific. Further simulations investigating the effects of perturbing a larger number of subpopulations, increasing the strength of perturbations, and varying the rate of migration, suggested that the empirical results were robust to changes in any of these conditions. One reason for the discrepancy between the predictions of previous theoretical studies and my results could be the presence of local extinctions in my experimental populations. However, I also showed that the main results of my study are robust to the presence of local extinctions in the metapopulation. What then led to the apparent differences between the predictions of the previous theoretical studies and the current work? One possible reason might be the fact that, in all previous studies, stabilization of a population consisted of the dynamics changing from chaotic to simpler limit cycles or even single-point equilibria. However, owing to the short length of ecological time series, coupled with the inherent noise in any real population, it is almost impossible to figure out whether a given empirical time series is chaotic, or stable with some amount of noise. Thus, from a purely pragmatic point of view, I found it more worthwhile to measure stability in terms of coefficient of variation (CV), or fluctuation

index (FI), and thus my results, strictly speaking, do not invalidate the previous studies. The simulations presented in this study of constant localized perturbations (Dey and Joshi 2007) lead to several interesting observations, which might be worthwhile to investigate in more detail in the future. However, several of these theoretical results hold only for values of intrinsic growth rate that are difficult to obtain using a *Drosophila* system. Thus, one would need to work with a system with a much higher growth rate, say microbes or protozoa, in order to validate these predictions.

Several theories had been proposed to explain the mechanism of evolution of population stability by natural selection (Mueller and Joshi 2000). All these theories remained empirically untested, till it was shown that selection on traits not directly related to demography could promote population stability by reducing the growth rate (Prasad et al. 2003). A more detailed analysis of an extended time-series from the same experiment (Prasad et al. 2003), along with direct measurements of fecundity and survivorship, corroborated the earlier findings (chapter 6). The analysis also showed that evolution of one type of stability (in this case, reduced amplitude of fluctuation of population size), does not necessarily lead to manifestation of another kind of stability (namely, persistence). This sounds a cautionary note for population management practitioners, that it might be dangerous to consider one kind of stability as a surrogate for another.

Experiments in population ecology are often performed on organisms with overlapping generations. While being closer to the real conditions experienced by most species, a population with overlapping generations has more complex dynamics due to the

juxtaposition of different age / stage classes. Thus, it is possible that the model predictions derived for systems with continuous generations might be very different from those obtained for models under discrete generations. This intuitive reasoning was borne out in a study of effects of different rates of mortality on the dynamics and stability of populations undergoing discrete generation cycles (chapter 7). Ricker-based simulations suggested that with increasing mortality rates, the growth rates of the populations would be reduced, and hence the stability would increase. The empirical data generally supported these predictions, although the inferences on stability differed depending on the measure of stability being used (namely, CV or FI). These observations differed from the predictions of overlapping generation systems that mortality would enhance growth rates and destabilize populations (Cameron and Benton 2004), thereby highlighting the difference between the dynamics of populations undergoing overlapping and discrete generations. Interestingly, the persistence stability of the populations undergoing different rates of mortality was in the same rank order as the constancy stability of these populations. However, as noted above, this may not always be the case and it would probably be wiser not to substitute one stability measure for another.

Many earlier studies, both theoretical and empirical, had shown that the dynamics and stability of *D. melanogaster* populations would be affected by the quantity and quality of food provided to the larvae and the adults, respectively (Mueller and Huynh 1994, Sheeba and Joshi 1998, Mueller and Joshi 2000, Mueller et al. 2000, Prasad et al. 2003). I investigated this issue in detail by studying the dynamics of single populations under four different kinds of nutritional regimes (chapter 8). The empirical results broadly

conformed to the findings of previous studies, and model-fitting exercises indicated that under a discrete generation system, the population size in generation *t*-1 does not play a major role in determining the population size at generation *t*+1. This is again at variance with previous studies on natural populations with overlapping generations, where population sizes at up to four earlier lags were shown to be of importance for modeling the dynamics of serial-transfer systems (Mueller 1985). One potential avenue of future work is to consider models other than the Ricker, and their corresponding extensions into higher time lags, and fit them to the time-series data generated from the present experiment. It would be interesting to investigate if these other models also lead to the same observation that the effects of generation *t*-1 on the population size at generation *t*+1 are minimal.

Chapter 9 was a slight digression from the main theme of population dynamics and stability, and was concerned with the measurement of life-history traits in the presence of micro-environmental variation in culture conditions: minor variation in environmental conditions that are impossible to control and generally judged to be too small to have any effects on the measurement of traits. However, I found that micro-environmental conditions could actually systematically bias the measurement of traits like fecundity, and hence act as an hitherto unappreciated source of stochasticity in experiments (Dey et al. 2006b). Thus, it is recommended that micro-environmental factors should be averaged out as far as practicable, by judicious experimental design.

In conclusion, the work reported in this thesis has verified several existing predictions using a laboratory system and, in some cases, shown that these predictions are likely to be generalizable across a wide range of conditions. On the other hand, the simulations and the experiments of this study have also led to some new observations, which remain unexplained as of now, but hopefully, would succumb to the inquisitive attention of ecologists in the near future.

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Experimental and Theoretical Investigation of the Dynamics and Stability of Single Populations and Metapopulations of *Drosophila melanogaster* in the Laboratory

A Thesis Submitted for the Degree of

Doctor of Philosophy

by

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2007

This thesis is dedicated to my family —

My parents, ***Shree Tapan Kanti Dey*** *and* ***Smt Sabita Dey****,*

and my brother, ***Punyatirtha Dey*** *—*

who always had faith in me even in those trying

moments of life when I had lost all of it.

Contents

Declaration

I declare that the matter presented in my thesis entitled "Experimental and Theoretical Investigation of the Dynamics and Stability of Single Populations and Metapopulations of *Drosophila melanogaster* in the Laboratory" is the result of studies carried out by me at the Evolutionary and Organismal Biology Unit of the Jawaharlal Nehru Centre for Advanced Scientific Research, Bangalore, India, under the mentorship of Prof. Amitabh Joshi, and that this work has not been submitted elsewhere for any other degree.

In keeping with the general practice of reporting scientific observations, due acknowledgement has been made wherever the work described has been based on the findings of other investigators. Any omission, which might have occurred by oversight or error of misjudgment, is regretted.

Place: Bangalore, India **Sutirth Dey**

Date: April 5, 2007

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CERTIFICATE

This is to certify that the work described in the thesis entitled "**Experimental and theoretical investigation of the dynamics and stability of single populations and metapopulations of *Drosophila melanogaster* in the laboratory**" is the result of investigations carried out by Mr. Sutirth Dey in the Evolutionary and Organismal Biology Unit of the Jawaharlal Nehru Centre for Advanced Scientific Research, Jakkur, Bangalore 560 064, under my supervision, and that the results presented in the thesis have not previously formed the basis for the award of any other diploma, degree or fellowship.

Amitabh Joshi, Ph.D.
Associate Professor

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List of publications

1. Prasad, N. G., **Dey, S**., Shakarad, M. and Joshi, A. 2003. The evolution of population stability as a by-product of life-history evolution. *Proceedings of the Royal Society of London: Biological Sciences* (*Supplement: Biology Letters*) **270**: S84-S86; DOI: 10.1098/rsbl.2003.0020.

2. **Dey, S**., Dabholkar, S., and Joshi, A. 2006. The effect of migration on metapopulation stability is qualitatively unaffected by spatial structuring of among patch variation. *Journal of Theoretical Biology* **238**, 78-84.

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4. **Dey, S.,** and Joshi, A. 2006. Stability via asynchrony in *Drosophila* metapopulations with low migration rates. *Science* **312**, 434-436.

5. **Dey, S.,** and Joshi, A. 2006. Response to comment on " Stability via asynchrony in *Drosophila* metapopulations with low migration rates." *Science* **314**, 420b.

6. **Dey, S.,** and Joshi, A. 2007. Local perturbations do not affect stability of laboratory fruitfly metapopulations. PLoS ONE **2**(2): e233.