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Original Research Article

# Stabilizing the dynamics of laboratory populations of *Drosophila melanogaster* through upper and lower limiter controls

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ABSTRACT

Although a large number of methods exist to control the dynamics of populations to a desired state, few of them have been empirically validated. This limits the scope of using these methods in real-life scenarios. To address this issue, we tested the efficacy of two well-known control methods in enhancing different kinds of stability in highly fluctuating, extinction-prone populations of *Drosophila melanogaster*. The upper limiter control (ULC) method was able to reduce the fluctuations in population sizes as well as the extinction probability of the populations. On the negative side, it had no effect on the effective population size and required a large amount of effort. On the other hand, lower limiter control (LLC) enhanced effective population size and reduced extinction probability at a relatively low amount of effort. However, its effects on population fluctuations were equivocal. We examined the population size distributions, with and without the control methods, to derive biologically intuitive explanations for how these control methods work. We also show that biologically realistic simulations, using a very general population dynamics model, are able to capture most of the trends of our data. This suggests that our results are likely to be generalizable to a wide range of scenarios.



## 1. Introduction

Over the last two decades, several methods have been suggested in control theory (Chernousko et al., 2008) and theoretical nonlinear dynamics (Andrievskii and Fradkov, 2003, 2004; Schöll and Schuster, 2008) to stabilize unstable non-linear dynamical systems. Several of these methods have been proposed for system where the underlying dynamics are well-characterized and stability is achieved by perturbing system parameters in real time to attain desired behaviours like stable points or simple limit cycles (Garfinkel et al., 1992). Unfortunately, for even fairly simple biological populations, the exact equations underlying the dynamics are often unknown. Moreover, when available, the parameters of such equations (e.g., carrying capacity or intrinsic growth rate) can often only be estimated *a posteriori* through model fitting and thus are not available for real-time perturbations. Finally, due to the ubiquity of noise in biological systems, it is not only impossible to attain stable points or limit cycles in the strict mathematical sense, it also becomes very difficult to distinguish such behaviours from chaotic dynamics (although see Desharnais et al., 2001). Thus, a different class of control methods and observables are needed in the context of biological populations.

The choice of method also critically depends upon the desired goal of control. There are two major, typically mutually exclusive, motivations for stabilizing biological populations. The first is in the context of economically exploited species (e.g., fishes) where the aim is to maximize the yield over a long period of time and reduce the uncertainty of the yield (Lande et al., 1997). The second aim seeks to reduce the amplitude of fluctuation in sizes or increase the long-term probability of persistence of populations (Gusset et al., 2009; Hilker and Westerhoff, 2007). Not surprisingly, stabilizing the yield of harvested populations has received far more theoretical and empirical attention (Milner-Gulland and Mace, 1998) than stabilizing threatened species. Part of the problem with the latter is that conservation efforts are usually directed towards charismatic species of mammals and birds. The dynamics of such species typically cannot be captured by the simple models that have been often used to investigate the various control methods (e.g., Dattani et al., 2011; Sah et al., 2013). However, it should be

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noted that a simple model like the Ricker map (Ricker, 1954) does provide fairly accurate descriptions of the dynamics of taxonomic groups including bacteria (Ponciano et al., 2005), fungi (Ives et al., 2004), ciliates (Fryxell et al., 2005), insects (Sheeba and Joshi, 1998) and fishes (Denney et al., 2002). Together, such taxa account for a huge fraction of the total biodiversity on earth, at least some part of which have already been recorded to be extinct (Baillie and Butcher, 2012). Therefore, there is a need to study the methods that can stabilize the dynamics of such 'non-charismatic' taxa.

A major hindrance in applying the insights gained from theoretical studies in controlling endangered populations is the fact that few of the proposed methods have been empirically validated even under laboratory conditions (however see Desharnais et al., 2001; Dey and Joshi, 2007; Sah et al., 2013), let alone in nature. Given that survivals of threatened species are at stake, it is understandable when practitioners of conservation are unwilling to try out untested methods in the field. On the other hand, new methods have to be validated somehow in order to assess their suitability for a given scenario. A reasonable way out of this impasse is to validate these methods under laboratory conditions. The success of a method to stabilize laboratory populations allows us to verify our understanding about how the method works. Unfortunately, it does not guarantee the method's success under field conditions but merely increases the confidence that can be placed on its success. On the other hand, the failure of a method under laboratory conditions would typically suggest lack of understanding regarding some crucial aspect of the biology of the system.

In this context, a well-investigated class of methods are the so-called limiter control methods, which seek to stabilize a population by implementing different kinds of thresholds in population sizes (Corron et al., 2000; Zhou, 2006). Extensive mathematical (Franco and Hilker, 2013, 2014), numerical (Sah and Dey, 2014; Sah et al., 2013) and empirical (Sah et al., 2013) studies suggest that at least for one method of this class – the so-called adaptive limiter control or ALC – the theoretical predictions match the empirical data rather well. In this study, we investigate the stabilizing properties of two other limiter control methods, namely upper limiter control (ULC) and lower limiter control (LLC) (Hilker and Westerhoff, 2005), using unstable laboratory populations of the common fruitfly *Drosophila melanogaster*. For each of these control methods, we investigate two different arbitrarily chosen values of the controlling parameter. We chose these two methods over many such available culling/restocking schemes (e.g., Dattani et al., 2011; Liz and Franco, 2010) primarily because they have been extensively investigated theoretically and numerically (Hilker and Westerhoff, 2005, 2006; Tung et al., 2014). This means that a number of predictions already exist in the literature for verifying against our empirical data. Therefore, the main focus of this paper was on an intuitive understanding of how these two methods affect the dynamics.

Here we show that ULC reduces temporal fluctuations in population sizes, as well as the extinction probability of populations. However, it is unable to enhance the effective population size and has high effort magnitude. On the other hand, the efficacy of LLC in reducing the fluctuations in population sizes is equivocal. In spite of that, the method is able to cause significant reduction in extinction probability and increased effective population size. Most importantly, the effort magnitude required to stabilize the populations is much less compared to ULC. We provide biologically intuitive explanations of how these control methods stabilize the populations. We also experimentally verify several theoretical predictions from the literature and show that our empirical results agree well with biologically realistic simulations.

## 2. Methods

### 2.1. Maintenance regime of the flies

In this study, we used individuals from a large (breeding size of ~2400) laboratory population of *D. melanogaster* called $DB_4$. The detailed maintenance regime and ancestry of this population has been described elsewhere (Sah et al., 2013). From this population, we derived 30 single vial cultures, each of which represented an independent population. Each of these populations was initiated by placing exactly 10 eggs on 1.1 ml of banana–jaggery medium in a 30-ml plastic vial. The vials were placed in an incubator at 25 °C under constant light conditions. Once eclosion started, the freshly emerged adults of a population were daily transferred to a corresponding adult-holding vial, containing approximately 6 ml of banana–jaggery medium. This process continued till the 18$^{th}$ day after egg collection, after which the egg vials were discarded. The adult flies were then supplied with excess live yeast paste for three days to boost up their fecundity. On the 21$^{st}$ day after egg collection, the adults were counted and culling or restocking of flies was imposed as per the prescribed control regimes (see Section 2.2). Since the dynamics of a sexually reproducing species is primarily governed by the number of females, culling or restocking was implemented only on the female flies (Dey and Joshi, 2006; Dey and Joshi, 2007). The adults were then allowed to oviposit in a vial containing 1.1 ml of medium for 24 h. After oviposition, the adults were rejected and the eggs formed the next generation. The experiment was run over 14 generations. Theoretical (Mueller, 1988) and empirical (Dey and Joshi, 2006; Mueller and Huynh, 1994; Sah et al., 2013) studies have shown that a combination of low levels of larval food (1.1 ml here) and excess live yeast paste destabilizes the populations by inducing large amplitude oscillations in the time series. This nutritional regime thus allowed us to study the stabilizing effect of various control methods on populations whose dynamics were otherwise unstable.

### 2.2. Control methods

Upper limiter control (ULC) involves culling to a fixed threshold, i.e., the population size is not allowed to go beyond an upper value (Hilker and Westerhoff, 2005). Mathematically, this is written as $N_t' = \min(N_t, U)$, where $N_t$ and $N_t'$ refer to the population sizes before and after the application of the control method, $U$ is the pre-determined value of the upper threshold and $\min(x,y)$ is the minimum operator. To impose ULC experimentally, we culled the number of females in a population to the arbitrarily set levels of 15 (U1) or 10 (U2). When the number of females in a population was less than the threshold, the population was left unperturbed. Note that for ULC, lower values of U represent more stringent control and therefore U2 is a stronger control than U1.

Lower limiter control (LLC) is achieved by restocking the population to a fixed number, i.e., the population size is never allowed to fall below a fixed limit ($L$). Mathematically, this is given as $N_t' = \max(N_t, L)$, where $L$ stands for the fixed lower threshold and $\max(x, y)$ is the maximum operator. For experimental implementation, we chose two arbitrary lower thresholds of 4 (L1) and 10 (L2) females, where L2 represents a stronger control than L1. Following an earlier protocol (Dey and Joshi, 2006), the flies were counted, the number was multiplied by half (i.e., assuming equal sex ratio) and rounded up to estimate the number of females in the population. If this number was greater than the pre-determined value of $L$ (i.e., 4 or 10), then the population was left untouched, else the shortfall was made up by adding the required number of females from outside. Thus, we explicitly incorporated some degree of noise in terms of application of LLC (see Section 4.2 for the rationale of the same).