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The timing of life history events in the presence of soft disturbances

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HIGHLIGHTS

- We introduce a model for the study of the evolutionary stable strategy of timing of life-history events in the presence of a soft disturbance.
- The probability “ p ” of surviving the disturbance and the competition parameter “ a ” of the population are taken into account.
- We prove that the evolutionary stable strategy is unique and we describe it implicitly.
- We analyze the fitness of the population and we prove that it is decreasing with respect to “ a ” and to “ p ”.
- We study the behaviour of the fitness after a sudden climate change.

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ABSTRACT

We study a model for the evolutionarily stable strategy (ESS) used by biological populations for choosing the time of life-history events, such as arrival from migration and breeding. In our model we account for both intra-species competition (early individuals have a competitive advantage) and a disturbance which strikes at a random time, killing a fraction $1-p$ of the population. Disturbances include spells of bad weather, such as freezing or heavily raining days. It has been shown by Iwasa and Levin (1995) that when the disturbance is so strong that it kills any individual present when it strikes (*hard disturbance*, $p=0$), then the ESS is a mixed strategy (individuals choose their arrival date in an interval of possible dates, according to a certain probability distribution). In this case, individuals wait for a certain time and afterwards start arriving (or breeding) every day. In this paper we explore a biologically more realistic situation whereby the disturbance kills only a fraction of the individuals (*soft disturbance*, $p > 0$). We also remove some technical assumptions which Iwasa and Levin made on the distribution of the disturbance. We prove that the ESS is still a mixed choice of times, however with respect to the case of hard disturbance, a new phenomenon arises: whenever the disturbance is soft, if the competition is sufficiently strong, the waiting time disappears and a fraction of the population arrives at the earliest day possible, while the rest will arrive throughout the whole period during which the disturbance may occur. This means that under strong competition, the payoff of early arrival balances the increased risk of being killed by the disturbance. We study the behaviour of the ESS and of the average fitness of the population, depending on the parameters involved. We also investigate how the population may be affected by climate change: namely the occurrence of more extreme weather events, which may kill a larger fraction of the population, and time shifts of the distribution of the disturbance. We show how the ESS and the average fitness change under the new climate and discuss which is the impact of the new climate on a population that still follows the old strategy. In particular, we show that, at least under some conditions, extreme weather events imply a temporary decrease of the average fitness of the population due to an increased mortality. In addition, if the population adapts to the new climate, the population may have a larger fitness.

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1. Introduction

Proper timing of life-history events, like emergence, germination, migration or breeding, is crucial for survival and successful reproduction of almost all organisms. Timing may be set by

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endogenous rhythms or by extrinsic environmental clues (e.g. day length or temperature, Saino and Ambrosini, 2008), but in almost all cases timing seems to have evolved according to two contrasting selective pressures. On the one hand, the first individuals that emerge or arrive at a given site often perform better, because they can profit from the better habitats and benefit from reduced competitions (at least for some time). On the other hand, early individuals may suffer from higher mortality, as they expose themselves to the risk of adverse environmental conditions, which usually are more likely early than late in the season. Autumn migration may seem an exception to this pattern, as the risk of mortality is probably larger for late than early departing individuals. However, in this case, migrants may benefit from a longer stay in their breeding grounds, allowing them e.g. to rise a further brood or to acquire larger fat reserves for migration. At the end, this pattern can be seen as the exact reverse of the process going on in spring, and can therefore be modelled in the same way.

In a seminal work Iwasa and Levin (1995) have provided a first theoretical description of how the risk of incurring in adverse environmental conditions may shape the timing of life history events of a population, as a result of evolution over many generations. Under the assumption that adverse conditions (*disturbance* according to their definition, which we will follow hereafter) strike at a random time and are so strong that no individual incurring in the disturbance can survive, the authors show that (in many cases) the *evolutionarily stable strategy* (ESS from here on) is an asynchronous choice of times in the population. This asynchronicity has been observed in various settings and modelled by several authors (see Bessho and Iwasa, 2012; Calabrese and Fagan, 2004; Post et al., 2001; Richter, 1999; Satake et al., 2001, just to mention a few). In this paper we extend Iwasa and Levin's model to the broader scenario where the disturbance is *soft*, meaning that some individuals survive the disturbance. This condition is biologically more realistic than that assumed by Iwasa and Levin because in many cases some individuals in the population survive even to dramatic adverse conditions. In detail, we are assuming that the disturbance kills each individual with probability $1 - p$, so that the model of Iwasa and Levin can be seen as a particular case of ours when $p = 0$. Clearly if p is close to 0 the disturbance is strong while if p is close to 1 the disturbance is weak. We stress however that a disturbance is not strong or weak *in itself*, but only in relation to the type of population. Hence, a strong disturbance for a population can be perceived as weak by another one.

Before going into the details of our model, we have to mention that it focuses on the long time behaviour of a very large population. Indeed we implicitly assume that when the existence of mutants with better fitness is theoretically possible, then such mutants will appear and spread across the population. This is what in population biology is called *infinite population size assumption*, which is a standard assumption in ESS theory (see for instance Maynard Smith, 1972). This assumption implies that we do not take into account the disappearance (in finite populations) of certain alleles by mere random factors, a phenomenon which can be studied by means of mathematical population genetics (see for instance Ewens, 2004). Long time behaviour of finite populations can also be studied through spatial models, namely *interacting particles systems*. Space not only adds complexity (Durrett and Levin, 1994), but may also be interpreted as “type”, that is the location of one or more individuals can be seen as representing their genotype. For the simplest among this models, the *branching random walk*, much has been done: for instance in Bertacchi and Zucca (2008, 2009, 2012), Müller (2008), Stacey (2003), and Zucca (2011) one finds characterization of the persistence/disappearance of genotypes (seen as locations for the model), on general space structures; the same can be found, for some random graphs, in

Bertacchi and Zucca (2015) and Pemantle and Stacey (2001). Stochastic modelling and interacting particle systems have been successfully applied to biology and ecology (see Belhadji et al., 2010; Bertacchi et al., 2011, 2007; Champagnat et al., 2008; Chan et al., 2009; Kang and Lanchier, 2012; Lanchier, 2011; 2013; Lanchier and Neuhauser, 2006; Méléard, 1990; Garet et al., 2012; Zucca, 2014; just to mention a few). Although stochastic modelling is very interesting and complex, here we will assume that over many generations, our populations have been sufficiently large (thus in some sense “close” to an infinite population) to justify the use of a model where stochasticity appears only in the random time at which the disturbance strikes.

While developing the present work we focus on migratory birds and their time of arrival to the breeding grounds. This choice should not be considered a reduction in the scope of this paper, since our modelling approach is very broad, as it applies to the investigation of the timing of any life-history event when the benefits from being early and the risk of incurring in a soft disturbance are in conflict. Migratory birds are a well studied biological system where timing is crucial for the fitness of individuals, and where a long record of adverse conditions killing or impairing the reproduction of individuals exists (see e.g. Newton, 2007). Currently the interest in the timing of recurrent biological events (phenology) is very strong among biologists after that several studies have consistently observed an advancement in spring phenology supposedly as a consequence of climate change. Birds are the taxon on which the vast majority of studies on the impact of climate change on biological systems focus (see Both et al., 2004; Cotton, 2003; Walther et al., 2002 and also Møller et al., 2010 and the references therein.). Climate change not only implies warming temperatures, but also higher frequency and intensity of extreme meteorological events (see IPCC, 2012). This increased weather unpredictability may severely affect migrant birds, because warmer springs prompt birds towards earlier arrivals, while more frequent unseasonable weather increases the risk of mass mortality events (see Schinazi, 2005 for a stochastic model for random catastrophes striking a spatially structured population). It is widely accepted that climate change is endangering migrant populations (see Saino and Ambrosini, 2011). Ornithologists therefore strongly need models investigating the contrasting forces affecting the timing of bird migration to improve their understating of the ongoing ecological processes and to plan better conservation strategies for declining migrant populations. We point out that even if our primary interest here are evolutionarily stable strategies arising in large populations after many generations of stable climate (an equilibrium situation), our study also allows us to analyze some effects of a sudden climate change (an off-equilibrium dynamics). Indeed our results not only describe the ESS (Theorem 3.5) but also the effects of the climate change on the fitness of a population not yet adapted to the change (Propositions 3.7–3.9).

Here is a short outline of the paper. In Section 2 we introduce the model and the notation. We describe the meaning of an ESS and we discuss the easiest cases where either there is no competition or every individual survive with probability 1, i.e. the disturbance has no effect whatsoever (Remark 2.1). Section 3 contains our main results. Theorem 3.5 extends previous results by Iwasa and Levin (1995, Appendix A) and shows that there is only one possible ESS for the population in response to a fixed disturbance distribution. We discuss how the ESS and the fitness of the individuals change when the strength of the disturbance or of the competition change. As an example, we describe the case where the disturbance strikes according to a uniform distribution (see Section 3.1). The effects of climate change are studied in Section 3.2. The main questions discussed here are the following. How does the ESS change after a climate modification? What happens if a population would keep

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