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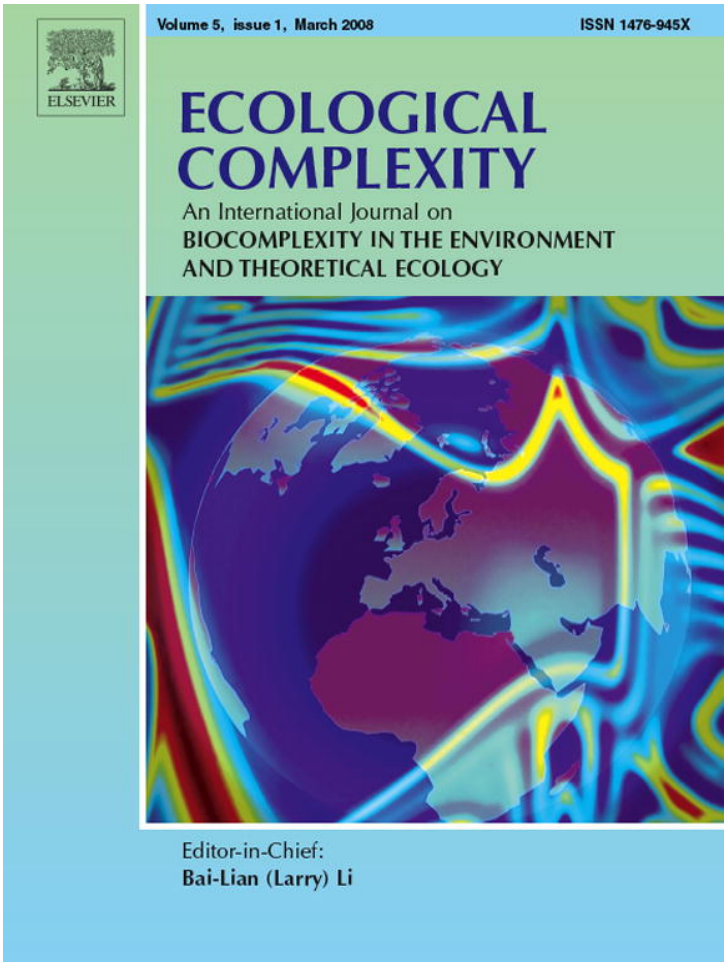

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Short note

When similar ecological patterns in time emerge from different initial conditions: equifinality in the breeding performance of animal populations

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ABSTRACT

In many behavioural, ecological and evolutionary trade-offs, patterns and trends, the same/similar outcomes are often expected from the different initial conditions. One of the most frequently encountered problems in ecology is how to disentangle two or more different hypotheses possibly explaining the emergence of an ecological pattern based on limited data that would fit both. Using previously published interaction patterns between floaters and breeders of an eagle population (Penteriani et al., 2006), it was possible to detect and to find an explanation to the singular case of the emergence of a similar ecological pattern under two very different scenarios, that is when different factors are affecting the intrinsic dynamic of a population.

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1. Introduction

Population ecologists are interested in the mechanisms behind any observed pattern and pattern formation can play a very important role in ecological and evolutionary systems. However, we can be recurrently confronted to complicated dynamics and fuzzy distribution patterns (Savill and Hogeweg, 1999; Nowak and May, 1992; Nowak and Sigmund, 2000). In fact, one of the most frequently encountered problems in ecology is how to disentangle two or more different hypotheses possibly explaining the emergence of an ecological pattern based on limited data that would fit both. On one hand, the analysis of the spatio-temporal patterns in population dynamics calls for a large amount of data, which are seldom available (Sundell et al., 2004). On the other, several examples in the scientific literature show that frequently several distinct factors, as well as their interaction, may determine similar patterns that made interpreting patterns difficult (e.g. Bolker and Pacala, 1997; Ranta et al., 1998; Bjørnstad et al., 1999; Ruetz et al., 2005; Heath, 2006).

Equifinality is a concept strictly related to inferential fallacy (Alker, 1969), quite relevant to, but probably often overlooked by, analyses on animal population dynamics and regulation when they deduce individual processes from wide patterns. Not surprisingly, mistakes may arise from inferring processes or patterns at one level of analysis from those occurring at another level.

Equifinality has been invoked in many fields, e.g. biophysics (Bartsev and Bartseva, 2002), geosciences (Haines-Young and Petch, 1983; Schulz et al., 1999; Savenije, 2001; Sleewaegen

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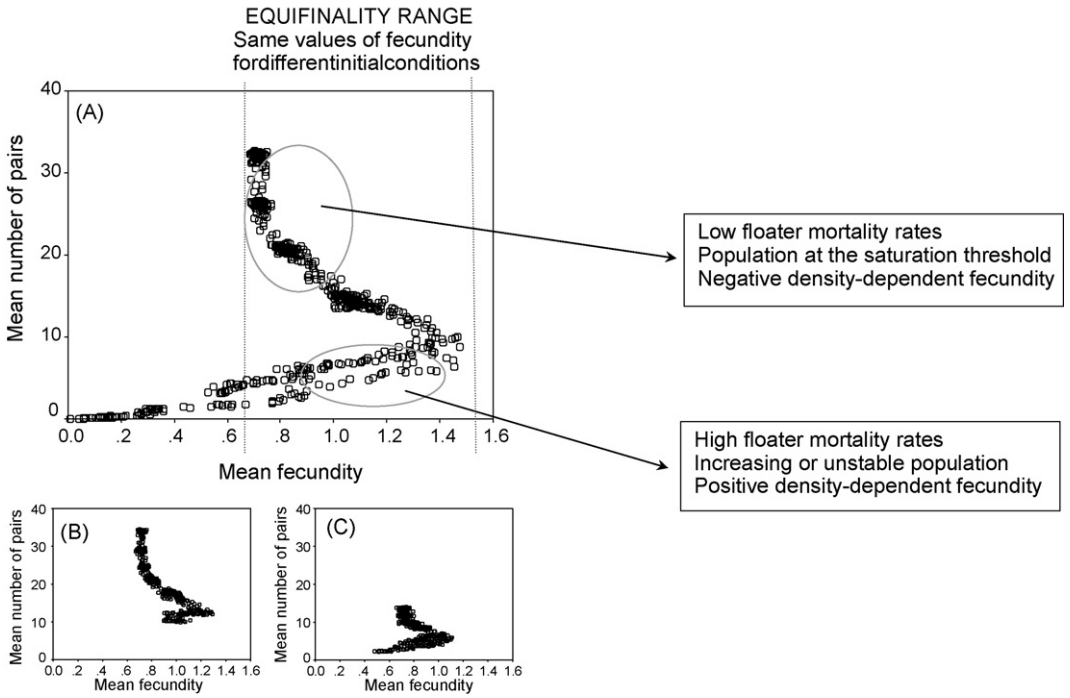

Fig. 1 – Equifinality in breeding performance, that is, different departure conditions of a breeding population can determine similar breeding performances. The examples (patterns of breeder fecundity under different levels of floater mortality; from Penteriani et al., 2006) highlight that the same values of mean fecundity can appear in the same breeding population under extremely different situations (e.g. saturated and stable population vs. increasing or unstable population), due to variations of levels of floater mortality within settlement areas. Circles in (A) indicate two of the most extreme cases, in which the population shows the same fecundity at very different population densities (more than 20 pairs vs. less than 10 pairs). (B) (population with the age at first reproduction of 3 years and 20 breeding pairs) and (C) (population with the age at first reproduction of 5 years and 10 breeding pairs) show two additional cases in which similar patterns in breeding performance may arise under different biological scenarios, i.e. when simulating different ages at first reproduction and population thresholds.

et al., 2003; Wilby, 2005), the life cycles of parasites (Gulyaev, 1997), physiology (Popescu and Rymer, 2000; Hinder and Milner, 2003; Feldman and Latash, 2005), psychology (Santoro et al., 1997; Mathieu et al., 2005) and zooarchaeology (Marean et al., 1992). For all these field, the concept of equifinality was associated to the idea that both: (a) a pattern, a trend or a shape can have different origins, i.e. can be the result of different causes, combinations of parameters, factors or pressures and (b) the end result is the same independently of the causes or stimuli that engendered it (e.g. movement end points are unaffected by either different perturbations or by variations in the starting point of the motion; Popescu and Rymer, 2000). Similarly, human medicine appeals to equifinality when the same symptomatic or syndromatic clinical diagnostic individual can represent different initial conditions that lead to the same clinical endpoint (Avissar and Schreiber, 2002). As an end result, and as recently highlighted by Beven (2006), the concept of equifinality allows us to focus our attention on the potential risk that "*... there are many acceptable representations that cannot be easily rejected and that should be considered in assessing the uncertainty associated with predictions*". For example, in the field of geomorphology (Beven, 2006), the term equifinality indicates that similar landforms might arise as a result of quite different sets of processes and histories.

Recently, the effects of the mortality of floaters (i.e. dispersing individuals able to enter as breeders in the reproductive population when a breeding territory or a potential mate – owner of a suitable breeding territory – becomes available) on the stability of a breeding population of Spanish imperial eagle *Aquila adalberti* were analysed by individually-based simulation models simulations (Penteriani et al., 2005a,b, 2006). In particular, when analysing how different rates (from 5 to 30%) of floater mortality could affect the mean fecundity of a breeding population under two different scenarios (i.e. when the gradient of the age at first reproduction varied from 3 to 5 years and for population thresholds of 10, 15 and 20 breeding pairs), the patterns shown by the density-dependent fecundity (see Penteriani et al., 2006 for more details) highlighted the occurrence of a singular phenomenon within the breeding population. In fact, fecundity showed similar values for different rates of floater mortality (i.e. different pressures acting on the population; Fig. 1, grey circles). This means that such similar values of fecundity can be the result of (at least) two different factors acting on the population: (a) a density-dependent effect due to population saturation (upper circle of Fig. 1) or (b) high mortalities acting on floaters (lower circle of Fig. 1). That is, two very different initial conditions (i.e. a stable and saturated population or high rates of floater mortality

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determining a decrease in the population) may determine similar patterns (i.e. the same values of mean fecundity) in a population. That is, equifinality (*sensu* von Bertalanffy, 1950) appears to be an intrinsic property of the breeding performance of animal populations. To my knowledge, this is the first time that equifinality has been detected in the breeding performance of animal populations. This result was supported by non-significant statistical outputs (see Penteriani et al., 2006), since no statistical analysis can distinguish between processes that are truly equifinal (von Bertalanffy, 1950).

Such an example shows us that we need to carefully take into consideration all the possible processes that can be responsible of the patterns that we observe in animal population, equifinality being able to engender mistakes in our perception of population dynamics. Above all, the possibility that equifinality could represent a new bias in our understanding of the dynamics of animal populations needs to be considered as the opportunity to move further and further in our analyses on animal populations, which could engender the opportunity to discover unsuspected factors (both intrinsic and extrinsic to a population) determining the patterns that we observe.

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