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Pattern-oriented modelling for estimating unknown pre-breeding survival rates: The case of the Lesser Spotted Woodpecker (*Picoides minor*)

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ABSTRACT

In population viability analysis we are often faced with a lack of knowledge of survival rates in animal populations. In particular, survival of recruits is usually hard to assess. However, data on population structure might be considered as patterns that contain valuable information to estimate missing parameters indirectly. As an example for this pattern-oriented modelling and parameterization, pre-breeding survival rate of the endangered Lesser Spotted Woodpecker (*Picoides minor*) was determined here using data on population structure (e.g. sex ratio) and reproductive success at the population level (e.g. nesting success). Therefore, an individual-based model was developed simulating the population dynamics for two different populations that had been empirically studied at Lake Möckeln, Sweden, and Taunus, Germany. For both populations, a small range for pre-breeding survival rates could be identified wherein all simulated patterns corresponded best to the empirical values. Pre-breeding survival rate was found to be higher in the German scenario than in the Swedish and geographical variation in life-history traits is discussed as a possible reason. It is concluded that the pattern-oriented approach is a valuable method for estimating missing demographic parameters, even when using weak patterns from empirical investigations. Furthermore, it was shown that the use of multiple patterns is necessary for this purpose.

1. Introduction

In applied ecology, stochastic simulation models are increasingly being used to understand the processes involved in population dynamics (Beissinger and Westphal, 1998; Grimm, 1999). Particularly in conservation biology, the use of modelling tools for population viability analysis (PVA) has become important in the last two decades to assess extinction probabilities in populations and to aid management decisions for endangered species (Akcakaya and Burgman, 1995; Brook et al., 2000; Haines et al., 2005; Steifetten and Dale, 2006). Evidently, reliable models of population dynamics require data on demographic parameters, such as mortality and reproduction rates. However, ecologists developing PVAs for decision-making often face uncertainty or lack of data, especially for endangered and, thus, rare species (Beissinger and Westphal, 1998; Wiegand et al., 2003).

One essential and often missing demographic parameter is mortality rate. Reasons for this lack of data can be found in the elusive character of this parameter. Since mortality is rarely observed directly, it is difficult to distinguish between mortality and emigration. Therefore, determining mortality

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rates is particularly difficult in the early, pre-breeding life stage, when most vertebrates become independent and leave the parent's home range. Hence, pre-breeding survival rates for highly mobile animals are scarce or missing completely (Bretagnolle et al., 2004). Nevertheless, since it is assumed to be the major source of individual variation in lifetime reproduction success (Newton, 1989), knowledge of pre-breeding survival rates is essential to investigate population dynamics.

Facing the problem of missing information for a given population, common practice in ecological modelling is the application of data available from other species as well as from other populations or sub-species (Wiegand et al., 1998; Wichmann et al., 2003). However, life-history traits can differ dramatically not only between species but also within the same species between different populations (Frederiksen et al., 2005). In fact, geographical variation in life-history traits is known, due to a gradient in environmental conditions (Murray, 1985; Karr et al., 1990; Griebeler and Böhning-Gaese, 2004) which can be explained by different levels of seasonality of resources (Ashmole, 1963). For example, in birds a trend for increasing clutch size and decreasing survival from the tropics to the poles is generally assumed (Murray, 1985). The inclusion of life-history traits from different sources into PVAs might therefore be misleading, when trying to predict the viability for a certain population.

However, even in cases when demographic parameters are missing, there might be a source of information in data sets that is often not exploited thoroughly. Owing to its importance for population dynamics, pre-breeding survival should have a distinct effect on variables at the population level that might be easier to measure than survival itself. For instance, pre-breeding survival affects the proportion of young individuals in the population and thus the age structure. Furthermore, the proportion of young individuals is likely to affect mean breeding success in the population, since young individuals often have lower reproductive success (Curio, 1983; Saether, 1990; Pyle et al., 2001; Reid et al., 2003). Consequently, age structure or reproductive success observed empirically should include information on the missing pre-breeding survival rate. These variables could be used as "pattern" to calibrate the missing parameter.

Patterns are characteristic, clearly identifiable structures in nature itself or in data extracted from nature (Grimm et al., 1996). They contain "hidden" information about the processes generating them (Wiegand et al., 2003). This information can be used for several purposes in ecological modelling: guiding model design (Thulke et al., 1999; Grimm and Railsback, 2005; Grimm et al., 2005), testing alternative theories (Railsback and Harvey, 2002), validating model output (Ferrer et al., 2004; Tews et al., 2004), or calibrating uncertain parameters via indirect parameterisation (Wiegand et al., 2003). Indirect parameterisation by pattern-oriented modelling (also called "inverse modelling") is well known in some disciplines, e.g. hydrology (Grimm et al., 2005). In ecology, however, case studies applying this method are rare (Wiegand et al., 1998, 2003, 2004; Kramer-Schadt et al., 2004; Revilla et al., 2004). In these studies, usually entire sets of unknown parameters were determined simultaneously by calibrating the model to a set of more or less striking patterns, for example long-term time series or spatial patterns. But what if such striking patterns are not available?

The aim of this study is to demonstrate that a set of observed population-level variables can be used for calibrating a missing parameter that is needed for conducting a PVA. The study organism is the endangered Lesser Spotted Woodpecker (*Picoides minor*), a species that was investigated in two field studies conducted at Lake Möckeln in Sweden (Olsson, 1998; Wiktander, 1998) and in a low mountain range near Frankfurt/Main, Germany (Höntsch, 2005; Rossmanith, 2005). In these studies, data about the most important demographic parameters could be collected; only information on the fate and survival rate of fledged young is still missing. In a pattern-oriented modelling approach, this study aims to assess pre-breeding survival rates indirectly for both Lesser Spotted Woodpecker populations using data on population structure and reproductive success at the population level. Based on the general hypothesis of geographical variation of survival rates in birds, it is expected that survival rate in the southern (German) population is higher than in the northern (Swedish) population.

2. Background

2.1. Lesser Spotted Woodpecker

The Lesser Spotted Woodpecker is distributed over the entire Palaearctic region, from Great Britain and Northwest Africa to Kamtschatka (Cramp, 1985). The species is in general socially monogamous and forms lifelong pair bonds (Glutz von Blotzheim and Bauer, 1994; Wiktander et al., 2000). Pairs that bred together in previous years, start to breed earlier within the season (Wiktander et al., 2001a; Rossmanith, 2005). Due to changes in food availability within the breeding season, an earlier onset of breeding translates into higher breeding success (Wiktander et al., 2001b; Rossmanith, 2005). Lesser Spotted Woodpeckers are single-brooded and do not relay when the first clutch fails.

Over the last few decades, Lesser Spotted Woodpecker populations have suffered a dramatic decline in several countries (Tiainen, 1985; Nilsson et al., 1992; Mikusinski and Angelstam, 1997). Reasons for the decline remain unclear, although habitat loss is discussed (Nilsson et al., 1992). This development has stimulated two studies that provide the empirical data basis for the presented model investigation.

2.2. Two field studies

The first empirical study was conducted between 1989 and 1998 on the subspecies *P. minor minor* in southern Sweden (56° 40′N, 14° 10′E) (Olsson, 1998; Wiktander, 1998). About half of the study area was covered by water of Lake Möckeln and the land area was mostly forested, interspersed with both agricultural land and marshland areas (Wiktander et al., 2001c). The second study was carried out between 1996 and 2003 on *P. minor hortorum* in a German low mountain range (Taunus) near Frankfurt/Main (50°09′N, 8°27′E) (Höntsch, 2005; Rossmanith, 2005). The study area consisted of a mosaic of different forest types, old orchards as well as grassland and settlement areas.