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Spatio-temporal dynamics in waterbirds during the non-breeding season: Effects of local movements, migration and weather are monthly, not yearly

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Abstract

Predicting population sizes and dynamics of mobile organisms is important for trend estimation, but this is difficult when the origin of individuals cannot be determined, i.e. residents and migrants are indistinguishable in the field.

Here we examine fluctuations in populations during the non-breeding season (autumn to spring) of seven waterbird species, which co-occur on 122 neighbouring water bodies in south-west Germany. We asked whether site-level abundance patterns can be predicted by weather variables, and whether these effects vary over months and years. We used a spatially explicit hidden Markov model to estimate the effects of local and regional movement on population fluctuations.

Although the species varied in their dynamics, with different amounts of movement estimated between sites, several patterns were common across species: density effects were highly month-specific, but with little variation in the strength of effects over years. The abundance of most species was positively related to temperature, especially in winter.

The common teal *Anas crecca* and common pochard *Aythya ferina* were the most site-fidelic species once they were present in the study area, but also exhibited the strongest regional migration. The mallard *Anas platyrhynchos*, tufted duck *Aythya fuligula* and great crested grebe *Podiceps cristatus* each behaved more like a single population, as individuals more frequently moved between sites and abundance fluctuations at sites were not explained by migratory movements alone.

Our study shows that the strength of population parameters and environmental forces can be decomposed into monthly and yearly effects. Estimating the unknown origin and movement of individuals may show that commensurate populations of mobile species may have different underlying dynamics, while responding similarly to environmental factors.

Zusammenfassung

Die Schätzung von Populationsgrößen und ihrer Dynamik ist von zentraler Bedeutung in Bestandsanalysen. Bei mobilen Organismen wie Wasservögeln erschweren dabei Wanderbewegungen Schätzungen der Bestandsgrößen für ein Gebiet, wobei Wanderbewegungen sowohl innerhalb eines Gebietes als auch als weiträumiger Zu- und Abzug stattfinden können.

Wir untersuchten Populationen von sieben Wasservogelarten in Winterhalbjahren (Herbst bis Frühjahr) von 122 benachbarten Gewässern in Rheinland-Pfalz. Wir untersuchten inwieweit lokale Muster in Abundanzschwankungen und -verbreitung der Arten durch Witterungsbedingungen beeinflusst werden und inwieweit deren mögliche Effekte sich über Jahre oder Monate unterscheiden. Mit Hilfe von räumlich-expliziten Markov-Ketten modellierten wir den Einfluss von lokalen und regionalen Ortswechseln von Vögeln auf deren Abundanzverteilung.

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Obwohl die einzelnen Arten unterschiedliche Abundanzschwankungen und unterschiedlich häufige Ortswechsel aufwiesen, ließen sich artübergreifend gemeinsame Muster feststellen: Die relativen Häufigkeiten von Ortswechseln waren überwiegend monatsspezifisch und zeigten nur geringe Unterschiede über die Jahre. Die Abundanzverteilungen der Vögel wiesen einen positiven Zusammenhang mit den vorherrschenden Temperaturen auf, insbesondere in den Wintermonaten.

Krickente *Anas crecca* und Tafelente *Aythya ferina* zeigten die geringsten Austauschbewegungen mit benachbarten Gewässern, sie wiesen jedoch gleichzeitig die höchsten Zu- und Abwanderungsraten auf. Stockente *Anas platyrhynchos*, Reiherente *Aythya fuligula* und Haubentaucher *Podiceps cristatus* erwiesen sich eher als einheitliche Populationen mit regelmäßigen Ortswechseln zwischen naheliegenden Gewässern und relativ geringerem Einfluss von Zu- und Abwanderungsraten auf lokale Abundanzschwankungen.

Die Studie zeigt, dass sich die Einflüsse von Populationsparametern und Umweltfaktoren auf Abundanzschwankungen sich über zeitliche Dimensionen, wie z.B. Monate und Jahre, auftrennen lassen. Die Abschätzung der Herkunft von Individuen und von Bewegungsmustern kann dabei Aufschluss darüber geben, weshalb mobilen Arten mit ähnlich großen Populationen unterschiedliche Populationsdynamiken zeigen, obwohl sie in ähnlicher Weise auf Umweltfaktoren reagieren.

Keywords: Bird monitoring; Climate forces; Density-dependence; Dispersal; Hierarchical Bayesian model; Lake ecosystems; Markov process; Metapopulation dynamics; Migratory movement; Population networks

Introduction

The distributions of mobile animals, like birds, across sites are determined by complex patterns of local population demography and movements, which link populations from different sites and regions. These movements between sites complicate the investigation of the effects of environmental change on population size of mobile animals (Sæther, Engen, & Lande 1999; Iverson & Esler 2006; Taylor & Norris 2010). Movement can take place over shorter time scales than seasons, so we need to understand these movements if we are to understand the connection between local and regional dynamics. This will tell us both how single local populations behave, and also how the overall regional population behaves: whether it is a structured population, with individuals moving around the region, or whether it can be viewed as a metapopulation, with relatively little movement between populations at different sites. Monitoring populations at a shorter time scale will also let us identify the drivers of regional dynamics such as population change due to migratory movements among regions, and whether these vary throughout a season.

The patterns of movement and mixing of waterbird populations at sites and flyways are affected by environmental conditions, such as cold spells or food depletion (Guillemain, Sadoul, & Simon 2005; Keller, Korner-Nievergelt, & Jenni 2009; Sauter, Korner-Nievergelt, & Jenni 2010). Likewise, the carrying capacities of sites and associated population densities within any area may also respond to variation in local resources or other environmental conditions (Sæther et al. 2008; Murray, Anderson, & Steury 2010). For example, overwintering carnivorous waterbirds can reduce local populations of mussels (Werner, Mortl, Bauer, & Rothhaupt 2005), which can result in density-dependent population declines in the following months as individuals move to other sites. Their search for other resource-rich sites may take place in the same region. Such movements are likely to link subpopulations and this may synchronise population fluctuations (Ranta, Kaitala, Lindström, & Linden 1995; Liebhold, Koenig, & Bjørnstad 2004). In open populations of migratory animals, migration adds another component of population fluctuations across space and time (Esler 2000). However, movements other than the main seasonal migrations, such as within-seasonal population fluctuations at stop-over sites where breeding and overwintering areas of species overlap, are poorly understood and their implication for predicting changes in population size and trends have largely been ignored.

In waterbird species that co-occur but display different foraging and migration behaviour (e.g. over-wintering versus stop-over), we expect abundance fluctuations between autumn and spring to differ between species. We also expect the strength of density and weather effects to differ across months, since species experience large seasonal differences (e.g. relatively mild autumn and spring conditions versus cold winters). On the other hand, some environmental conditions, such as extreme temperatures during winter (i.e. cold spells with frozen water surfaces that limit access to a large range of different resources), may have similar effects on all species regardless of their foraging behaviour.

These issues raise questions about what drives the spatio-temporal dynamics of populations over short time scales. To what extent are individuals sedentary, or moving around the landscape? And can we identify factors which might be driving this movement? Here we use long-term monitoring data on seven sympatric waterbird species in Germany to explore these questions.

In mobile animals with open populations, the provenance of individuals can often not be determined, so it is impossible to distinguish migrants from previously observed resident individuals when unmarked individuals are counted at different times. Migration and dispersal in animal populations have been studied using individual-based approaches such as using genetic markers, stable isotopes, mark-recapture, and ring recovery methods (Webster, Marra, Haig, Bensch, & Holmes 2002; Kelly, Ruegg, & Smith 2005; Boulet, Gibbs,