

Analyzing long-term data from biological surveys

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Summary

Long-term biological surveys that use a constant sampling regime are rare. This is unfortunate, as understanding complex biological systems often requires long-term studies. A promising source of long-term data could be the biodiversity monitoring schemes that were implemented in many countries some decades ago. However, scientists have criticized biodiversity monitoring programs and other long-term surveys because they often lack well-articulated scientific hypotheses that were formulated prior to data collection. This is probably the main reason why scientists working on functional biology have only rarely used existing data from such monitoring programs, leading to the fact that a huge body of long-term data is still awaiting analysis.

In the first part of this thesis, I aimed to improve methods for analysing long-term survey data. I developed a new method to estimate demographic parameters without the need to individually mark the animals. Using that method, I was able to obtain yearly survival rates of Nightingales (*Luscinia megarhynchos*) that were very similar to the survival estimates obtained from a traditional mark-recapture model applied to the ringing data from the same nightingale population. Since data for traditional mark-recapture analyses are rarely available for large spatial scales, the developed model could open up new possibilities by making the data of long-term surveys available for research on animal demography. I presented such an application by applying the developed model to data on Yellowhammers (*Emberiza citrinella*) from the nation-wide common bird census in Switzerland. I found that territories were colonized at the highest rates in the lowlands. This was in contrast to survival, which was relatively low in the lowlands but tended to increase with altitude. These estimates on demographic rates could not be predicted from the altitudinal patterns of Yellowhammer abundance, which shows highest densities at low altitudes. By providing information on demographic rates,

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our demographic monitoring framework thus considerably broadens the possibilities for biological inference based on data from large-scale bird monitoring programs.

Important benefits from analysing data of long-term surveys are that these data can be used either to generate new hypotheses about the biological system or to test hypotheses that otherwise would have needed a long-running and expensive experiment. In the second part of the thesis, I presented four case studies with such analyses of long-term survey data. I used the survey data on singing activity in male nightingales to formulate hypotheses about the prospecting activity of females. I then tested the predictions in an experimental setup. I found that the timing of female prospecting corresponded to the period of the night when the singing activity of unpaired males was higher than that of paired males. In contrast to females, territory searching males have been shown to prospect territories almost exclusively during the dawn chorus. At dawn, both paired and unpaired males sang at high rates, suggesting that in contrast to nocturnal singing, dawn singing is important to announce territory occupancy to prospecting males. In the nightingale, the sex-specific timing of prospecting thus corresponded to the differential signalling routines of paired and unpaired males, and the temporal patterns in the behaviour of signallers and receivers thus appeared to be mutually adapted.

In two further case studies, I tested the effectiveness of agri-environment schemes (AES) to promote general biodiversity in the agricultural landscape of the canton Aargau, and to reduce homogenization of floristic communities in Swiss grassland. In the first study, I found that in vascular plants and snails, the species richness increased on plots with AES, but not on control plots without AES, whereas in butterflies and birds, no significant differences were found between AES plots and control plots. I concluded that the agri-environment scheme in the canton of Aargau was effective in protecting and promoting biodiversity, but that the effect depended on the group of organisms. However, when I analysed the grassland of entire Switzerland, I found that in the last decade the floristic communities became more and more similar. Thus, I concluded that local-scale changes in land use regimes implemented by agri-environment schemes and other conservation efforts on parts of the grassland area were apparently not yet sufficient to prevent an overall taxonomic homogenization in the Swiss grassland.

Résumé

Des études biologiques à long terme avec un échantillonnage constant sont rares. Cela est regrettable, puisque des suivis à long terme sont souvent nécessaires pour aider à comprendre les systèmes biologiques complexes. Les programmes de suivi de la biodiversité qui ont été impliqués dans certains pays durant les dernières années pourraient donc être une source de données provenant d'études biologiques à long terme intéressante. Toutefois ces programmes de suivi de biodiversité et d'autres études biologiques à long terme ont été critiqués par des scientifiques car souvent des hypothèses scientifiques précises formulées avant la collection de données manquent. Probablement cela est la raison principale pour laquelle des scientifiques travaillant dans le domaine de la biologie fonctionnelle ont jusqu'à présent que rarement travaillé avec des données existantes provenant de tels programmes de suivi de biodiversité. Suite à ce fait, un grand nombre de données provenant d'études biologiques à long terme est encore et toujours en attente d'être analysé.

Dans la première partie de ma thèse de doctorat j'ai essayé d'améliorer les méthodes d'analyse pour des données provenant de suivis à long terme. Dans ce contexte, j'ai développé une nouvelle méthode qui permet d'estimer les données démographiques sans qu'il soit nécessaire de marquer des animaux individuellement. J'ai utilisé cette méthode pour calculer le taux de survie pour une population du Rossignol philomèle (*Luscinia megarhynchos*) ce qui a produit des résultats très similaires aux résultats provenant d'un modèle traditionnel marquage-recapture appliqué à la même population de Rossignols philomèles bagués. Les données nécessaires pour les analyses marquage-recapture traditionnelles sont rarement disponibles pour des régions entières. Le modèle développé pourrait donc viabiliser de nouvelles possibilités en rendant accessibles les données de suivis à long terme pour la recherche concernant la démographie d'animaux. J'ai présenté une telle application ou le modèle à été appliquée aux données du Bruant jaune

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(*Emberiza citrinella*) provenant du monitoring des oiseaux nicheurs répandus de Suisse. Les résultats montraient que les territoires en plaine sont occupés avec le taux le plus élevé alors que le taux de survie a été relativement faible en plaine et semble augmenter avec l'altitude. La prédiction de ces estimations pour des paramètres démographiques ne serait pas possible si seulement la distribution altitudinale du Bruant jaune, qui démontre que les densités les plus élevées sont observées en plaine, serait connue. Notre système de suivi démographique permet donc de nouvelles possibilités d'analyses pour les données provenant de programmes de suivi ornithologiques de grande taille.

L'analyse de données provenant de suivis à long terme a des avantages importants car ces données peuvent être utilisées pour élaborer de nouvelles hypothèses concernant le système biologique ainsi que pour tester des hypothèses existantes dont la vérification aurait autrement nécessité d'une expérience de longue durée et à des coûts élevés. Dans la deuxième partie de ma thèse de doctorat j'ai présenté quatre études exemplaires avec ce type d'analyse avec des données provenant de suivis à long terme. J'ai utilisé les données d'un suivi de l'activité du chant chez des Rossignols philomèles mâles afin de pouvoir formuler des hypothèses concernant la prospection des territoires par les femelles. J'ai en suite testé les prédictions résultants dans une expérience et trouvé que les femelles prospectent les territoires durant la nuit, ce qui est la période dans laquelle les mâles non accouplés chantent plus intensivement que les mâles accouplés. Contrairement aux femelles, les mâles prospectaient des territoires presque exclusivement durant l'aube. Puisque l'aube est la période où tous les mâles – accouplés ou non accouplés – chantent très intensivement cela laisse supposer que le chant durant l'aube est surtout censé aider à défendre les territoires contre les autres mâles contrairement aux objectifs du chant nocturne. Chez le Rossignol philomèle le moment de la prospection de territoires différait donc entre les sexes et correspondait au comportement différent des mâles accouplés et des mâles non accouplés. Le comportement des individus émettant les signaux et des individus qui les perçoivent semble donc être évolué de manière mutuelle.

Dans les deux études suivantes j'ai testé l'efficacité des systèmes agro-environnementaux pour promouvoir la biodiversité dans le paysage agricole du canton d'Argovie ainsi que pour réduire l'uniformisation des communautés floristiques dans les prairies suisses. Dans la première étude j'ai pu démontrer que le nombre d'espèces de plantes vasculaires et de mollusques a augmenté sur les surfaces bénéficiant d'un système agro-environnemental contrairement au nombre d'espèces sur les surfaces sans système

agro-environnemental. Cependant aucun effet significatif n'a pu être démontré pour les papillons diurnes ainsi que pour les oiseaux. De ces résultats j'ai conclu que le système agro-environnemental du canton d'Argovie était efficace pour protéger et promouvoir la biodiversité mais que cet effet dépendait des groupes d'organismes étudiés. L'analyse des prairies de toute la Suisse a relevé une homogénéisation des communautés floristiques lors des dernières dix années. De ce résultat j'ai conclu que les changements impliqués à l'échelle régionale par des systèmes agro-environnementaux et d'autres mesures de conservation ne semblent pas avoir un effet suffisant pour pouvoir stopper l'homogénéisation des communautés floristiques observés dans les prairies à l'échelle nationale Suisse.

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Thesis Introduction

1.1 Long-term surveys in biology

Much of contemporary ecology and conservation biology is concerned with detecting and understanding temporal changes in biological systems, such as changes in the abundance of single species, changes in the compositions of species of a community or the functioning of entire ecosystems (Caughley 1994, Norris 2004, Royle and Dorazio 2008). Yet, temporal changes of biological systems may often be small and difficult to detect; furthermore, we usually have little knowledge concerning the time-lags between a given effect and its related responses (Lepetz et al. 2009, van Strien et al. 2011). Thus, understanding changes in biological systems requires long-term studies on data that are collected using a constant sampling scheme (Yoccoz et al. 2001, Walther et al. 2002, Lepetz et al. 2009, Szabo et al. 2010). An impressive example for the collection of long-term data is the continuous plankton recorder survey (Reid et al. 2003). Analysing the data that were continuously recorded since 1931 has provided important insights into broad study areas and ecological phenomena such as eutrophication, biodiversity and climate change (Reid et al. 2003). The scientific value of the continuous plankton recorder survey is reflected in the number of almost 900 scientific papers that have been published by the end of 2001 (Olson et al. 1966, Reid et al. 2003).

Unfortunately, long-term biological surveys that use a constant sampling regime are rare for several reasons (Wolfe et al. 1987, Magurran et al. 2010). Probably the most important reason is that collecting high-quality data over long periods of time requires considerable investment of time, money and institutional support (Szabo et al. 2010). Furthermore, the usual time lag from the start of data collection until results can be published may refrain scientists from planning and conducting long-term surveys, and funding bodies from supporting such surveys.

In recent decades, however, several biodiversity monitoring schemes have been implemented to assess spatial and temporal trends in biological systems (Yoccoz et al. 2001, Pereira and Cooper 2006, Lindenmayer and Likens 2009). The emphasis of most of these monitoring schemes is on the evaluation of the efficiency of management policies (Yoccoz et al. 2001) and thus, schemes were often implemented for political reasons. Nonetheless, the data obtained from these monitoring schemes can be of high scientific quality. This is because such schemes need to provide highly reproducible, statistically sound data over long time periods to achieve their political goal of evaluating

the efficiency of conservation policies (Weber et al. 2004). Therefore, many biodiversity monitoring schemes may potentially provide long-term survey data on biological systems that could be used by scientists to answer general questions about the functioning of biological systems, beyond simply describing temporal trends in abundance of organisms (Magurran et al. 2010, Couvet et al. 2011).

Recently, however, scientists have criticized biodiversity monitoring programs and other long-term surveys mainly because they often lack well-articulated scientific hypotheses that were formulated prior to data collection (Yoccoz et al. 2001, Nichols and Williams 2006, Lovett et al. 2007, Lindenmayer and Likens 2009). Obviously, collecting data without clear *a priori* hypotheses is in contrast to the common scientific praxis of aiming at strong inference (Platt 1964). Following the praxis of strong inference, conclusions from data are scientifically sound only if i) several *a priori* hypotheses are formulated, ii) experiments are conducted that have several possible outcomes, and iii) the results of an experiment allows to reject at least one of the *a priori* hypotheses. Apparently, this approach cannot be strictly applied to answer functional questions on population biology based on data from monitoring programs that were collected to answer other questions. Therefore, scientists working on functional ecology have only relatively rarely used existing data from such programs, leading to the fact that a huge body of long-term data is still awaiting analysis.

1.2 Outline of the thesis

The main aim of this thesis was to improve biological inference that can be drawn from analysing data from long-term biological surveys. In the first part of the thesis, I developed new statistical tools to analyse the data from long-term surveys. In the second part of the thesis, I conducted several case studies, in which I analysed the data from different long-term surveys and biodiversity monitoring programs.

1.2.1 Part I: Development of new statistical methods to analyse long-term monitoring data

Monitoring programs usually focus on the abundance of the studied species, but the functioning of biological systems is likely to become more explicit when demographic

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parameters such as survival, fecundity or immigration could be obtained from long-term monitoring programs (Saracco et al. 2008). In **chapter 2**, I used the long-term occupancy data on nightingale territories (Amrhein et al. 2002, Amrhein et al. 2004, Amrhein et al. 2007) to develop a new method to estimate demographic parameters from survey data without individual recognition. The developed method on estimating demographic parameters (i.e. local survival and territory colonization) seems promising because it can be applied to large amounts of data that are available from long-term surveys. In **chapter 3**, I refined this method on demographic monitoring and applied it to the data of the common bird census of Switzerland (Kéry and Schmid 2004, Kéry and Schmid 2006).

The singing activity of birds is an important predictor of the detectability (i.e. the probability of detecting a present individual during a survey) that needs to be accounted for in monitoring programs in order to obtain unbiased estimates of the population size of the studied species (Kéry and Schmid 2004, Kéry and Schmid 2006, Amrhein et al. 2007). Therefore, understanding why singing activity may differ between males and why it may change in the course of the season is likely to have important implications for the analysis of data from breeding bird surveys that are usually part of long-term monitoring programs (Link and Sauer 1998, Jiguet et al. 2005, Kéry et al. 2005, Baillie et al. 2009). In **chapter 4**, I used the nightingale singing activity data (Amrhein et al. 2002, Roth et al. 2009) to develop a change-point model in a Bayesian context that is able to account for the different seasonal singing routines of paired males and bachelors (Amrhein et al. 2002, Thomas 2002). Using that model, I analysed the seasonally changing singing activity of paired and unpaired nightingales.

1.2.2 Part II: Analyses of data from long-term surveys

In the second part of the thesis, I analysed the data from different long-term surveys. In **chapter 5**, I used the long-term survey data on singing activity in male nightingales to formulate hypotheses about the prospecting activity of females. The formulation of new hypotheses is a typical product of analysing long-term survey data (Couvét et al. 2011). Long-term surveys thus often create semi-experimental opportunities to built and test hypotheses about the functioning of biological systems (Kerr et al. 2007). Using such a semi-experimental setup, I investigated the diel timing of information gathering of female nightingale searching for males.

A further advantage of long-term surveys is that the data are collected using a standard design, and thus can be used to test hypotheses that were developed long after the sampling scheme has started (Couvét et al. 2011). In the remaining three chapters, I tested such *a posteriori* hypotheses. In **chapter 6**, I tested the effectiveness of an agri-environment scheme in promoting the biodiversity in the agricultural landscape of the canton Aargau. I compared the species richness per study plot at an initial phase of the agri-environment scheme and five years later. The effects of the AES were then tested against the change of species richness in conventionally used agricultural areas.

In recent years, a major concern in conservation biology is that specialist species or species with a restricted range are gradually replaced by range-expanding cosmopolitan species (Devictor et al. 2008, Naaf and Wulf 2010). Thus, locally separated species communities may become more and more similar to each other, a process that has been called biotic homogenization (Olden 2006, Rooney et al. 2007). In **chapter 7**, I tested whether the recent change of land use regimes in part of the Swiss grassland that happened due to the implementation of agri-environment schemes and other conservation efforts was sufficient to prevent the grassland of Switzerland from taxonomic homogenization.

Finally, in **chapter 8**, I tested a common practice in conservation biology, in that indicator species are used as surrogates to identify areas of high conservation value (Noss 1990, Andelman and Fagan 2000). I used data from the Swiss Biodiversity Monitoring Programme and the Swiss breeding bird survey to analyse the use of species from different trophic levels as a surrogate for plant, butterfly and bird species richness.

1.3 The analysed long-term data

1.3.1 The Nightingale project

The study area of the nightingale (*Luscinia megarhynchos*) project is the Petite Camargue Alsacienne in France, about 10 km north of Basel. Within the nightingale project, two different long-term surveys were conducted. For the first long-term survey, each year since 1994, we captured and colour-ringed the owners of about 50 territories as well as their mates, which is around 80% of the individual nightingales that were present each year at the study site.

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For the second long-term survey, each year and every day throughout the entire breeding season, we surveyed the settlement of males at the study site by recording the song posts of males during the hour before sunrise. Similarly, a nocturnal census round was done every night to record the song posts of nocturnally singing males. Given that only unpaired males sing regularly at night (Amrhein et al. 2002, Amrhein et al. 2004), we were able to determine for each male the pairing status and the date of pairing, which is given as the day after which a male was heard singing at night for the last time (Amrhein et al. 2002, Amrhein et al. 2004, Amrhein et al. 2007). During the breeding seasons 1997 to 2003, the mean proportion of unpaired males in the study population was $33 \pm 14\%$; however, in single years, the proportion of unpaired males can be close to 50% (Amrhein and Zwygart 2004, Amrhein et al. 2007).

1.3.2 The monitoring studies

The biodiversity program of the canton Aargau

In 1996, a long-term research project was started to monitor the biodiversity in the whole canton of Aargau (Stapfer 1999, Wagner and Edwards 2001). The sampling scheme is based on a regular grid that covers the entire canton with 516 grid points. The grid points were selected by taking every second point of a 1 km grid based on the national coordinate system. On each study plot at such a grid point, vascular plant, snail, butterfly and bird species were counted. Every year, one fifth of these sample plots are surveyed, and each sample plot is surveyed every five years. The sampling protocol was adapted to the different species groups. Vascular plants species were counted in a circle of 10 m², and on the outer line of the circle in which plant species were counted, eight soil samples were taken during the plant surveys and the number of snail species was estimated from these soil samples. Bird species were estimated from five surveys in a circle with 100 m radius, and for butterflies, 11 surveys were made along a transect of 250 m length (butterflies were recorded within 5 m to each side of the transect line).

The biodiversity monitoring scheme of Switzerland

The Swiss Biodiversity Monitoring scheme (BDM, www.biodiversitymonitoring.ch) was launched in 2001 to monitor Switzerland's biodiversity and to meet the Convention on

Biological Diversity of Rio de Janeiro (Weber et al. 2004). In the BDM scheme, mosses, vascular plants, snails, butterflies and breeding birds are surveyed on two different grids that both cover entire Switzerland but differ in grid density and grain size. The species richness of mosses, vascular plants and snails is investigated on a systematic grid covering 1650 circular 10 m² plots; while the species richness of vascular plants, butterflies and birds is investigated on a systematic grid covering about 500 squares of 1 km². Note that vascular plants are surveyed on both grids. Every year, one fifth of these sample plots from both grids are surveyed – constituting a regularly spaced subsample of all sites – and, each sample plot is surveyed every five years. The field methods for all species groups are highly standardized and are described elsewhere [*mosses*: Bergamini et al. (2006); *snails*: Kobiakka et al. (2010); *vascular plants*: Plattner et al. (2004), Bühler and Roth (2011); *butterflies*: Kéry and Plattner (2007), Kéry et al. (2009); *birds*: Kéry and Schmid (2004), Kéry and Schmid (2006)].

The Common Breeding Bird Survey of Switzerland

The Common Breeding Bird Survey is conducted since 1999 by the Swiss ornithological institute (Schmid et al. 2004, Kéry and Schmid 2006). In the common breeding bird survey, 267 squares of 1 km² are laid out as a grid across the entire country and are surveyed each year using territory mapping methods (Bibby et al. 2000, Zbinden et al. 2005). During each breeding season (15 April – 15 July), three visits (two visits in high altitude squares with less than 10% forest cover) are conducted to each square by highly qualified volunteers. Visits follow an irregular transect route that aims to cover as much as possible of a square and that remains constant during subsequent years. For more details about the methods and results, see for instance Zbinden et al. (2005), Schmid et al. (2004) or Kéry and Schmid (2004).

1.4 Paper outlines

Chapter 2 – Roth, T. and V. Amrhein. 2010. *Estimating individual survival using territory occupancy data on unmarked animals. Journal of Applied Ecology* 47:386-392. Survival estimation forms the basis of much ecological research, and usually requires data on marked animals. In population studies of territorial animals, however, data are often collected on animal territory occupancy without identification of individuals,

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and so far could not be used to estimate demographic parameters such as survival. In this chapter, I developed a hierarchical site-occupancy model for estimating survival from territory occupancy data. To evaluate the model, I used simulated data as well as real data from the long-term nightingale monitoring. I found that estimates of survival from this model were very similar to the estimates obtained from a traditional mark-recapture analyses of the ringing data of the nightingales. Since data collection for mark-recapture analysis is usually invasive and labour intensive, applying my model to territory occupancy data from large-scale monitoring programs could make large amounts of data available for research on animal demography.

Chapter 3 – *Roth, T., M. Kéry, M. Schaub, H. Schmid, and V. Amrhein. In prep. Estimating demographic rates using data on unmarked individuals from bird monitoring programs.*

The effects of management action or of environmental factors would become more explicit when demographic parameters such as survival could be estimated. In this chapter, I developed a demographic monitoring framework to obtain estimates of demographic rates for unmarked individuals. The framework is based on the model that I developed in *chapter 2*. Applying the framework on data of unmarked Yellowhammers (*Emberiza citrinella*) from the common bird census in Switzerland, I found that territories were colonized at the highest rate in the lowlands. In contrast, local survival, which is the probability that an individual survives until the next reproductive period and settles in the same territory again, was relatively low in the lowlands but tended to increase with altitude. I concluded that my demographic monitoring framework considerably broadens the possibilities for inference based on large-scale monitoring programs. Applying my model on data covering large altitudinal or latitudinal ranges could provide estimates on geographic variation in demographic parameters that are urgently needed to understand the effects of climate change on population performance.

Chapter 4 – *Roth, T., P. Sprau, M. Naguib, and V. Amrhein. In prep. Sexually selected signalling in birds: a case for Bayesian change-point analysis of behavioural routines.*

In this chapter, I introduce Bayesian change-point analysis as a promising tool in research on behavioural routines. Using change-point models, it is possible to analyse

data with abrupt changes in the functional relationships, even if the changes are caused by unobserved switches of state in the studied system. Unobserved switches can occur, for example, in the temporal dynamics of populations, in predator-prey interactions and territory defence behaviour, and whenever animals switch from one state to another. The presented model can estimate the position of the change-points and should therefore be of great value in research on animal behaviour. I developed and applied the change-point model in the context of sexually selected signalling of male nightingales. Based on observations of nocturnally singing males, but without empirical data on the presence and behaviour of females, my model provided realistic estimates of the pairing success of males and of the dates of pair formation. Using the change-point model, I was able to detect novel patterns of seasonal trends in singing activity that were obscured when using a traditional generalized linear mixed model.

Chapter 5 – *Roth, T., P. Sprau, R. Schmidt, M. Naguib, and V. Amrhein. 2009. Sex-specific timing of mate searching and territory prospecting in the nightingale: nocturnal life of females. Proceedings of the Royal Society B-Biological Sciences 276:2045-2050.*

In studies on sexual signals like bird song, the receiving side, which is often the females, has long been quite neglected. In nightingales, the diel timing of information gathering strikingly differed between females searching for males and males prospecting for territories. Unpaired females searched for males exclusively at night when mostly unpaired males were singing, while non-territorial males have been shown to search for territories only at dawn, when all males are singing. Furthermore, males that sang with higher intensity around midnight were more likely to attract a female. Taken together, the results suggest that in the nightingale, the singing of males serves mate attraction at night but territory defence at dawn.

Chapter 6 – *Roth, T., V. Amrhein, B. Peter, and D. Weber. 2008. A Swiss agri-environment scheme effectively enhances species richness for some taxa over time. Agriculture Ecosystems & Environment 125:167-172.*

The effectiveness of agri-environment schemes (AESs) in promoting biodiversity was recently debated. One reason for limited effectiveness of AESs may be their application to small and scattered patches of land. The study of this chapter presents the evaluation of a scheme adopted by the canton of Aargau, Switzerland, which seems

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to be unique in its consequent focus on entire farms, aiming at increasing quality and quantity of ecological compensated areas (ECAs). In vascular plants and snails, the species richness increased during a period of five years on plots with AES, but not on control plots without AES. In butterflies and birds, no significant differences were found between AES plots and control plots in the change of species richness over time. While butterfly species numbers generally decreased, bird species numbers increased on both AES plots and control plots. It appears that agri-environment schemes can be effective in protecting and promoting biodiversity, but the effect may depend on the group of organisms

Chapter 7 – *Bühler, C. and T. Roth. 2011. Spread of common species results in local-scale floristic homogenization in grassland of Switzerland. Diversity and Distributions 17:1089-1098.*

In this chapter, I assessed changes in plant species richness and changes in species dissimilarity at local scale in Swiss grassland between the time periods 2001–2004 and 2006–2009. I examined changes in species richness and changes in Simpson dissimilarity index of vascular plants in grassland (meadows and pastures). The results show that species richness of vascular plants in grassland increased during the study period. In contrast, species dissimilarity of plants decreased, suggesting local-scale floristic homogenization of grassland in Switzerland. Floristic homogenization was mostly due to the spread of common species, namely the species that are tolerant to high nutrient levels, the species of low conservation value and the species adapted to moderate temperature levels. Target species for conservation did only marginally affect taxonomic homogenization. In contrast to the predictions from studies of taxonomic homogenization on larger scales, the taxonomic homogenization of grassland at local scale was not explained by the spread of neophytic species. Based on our analyses, I concluded that the biotic diversity of grassland in Switzerland changed considerably between 2001–2004 and 2006–2009. The observed taxonomic homogenization was merely because of the spread of common species. Local-scale changes in land use regimes implemented by agri-environmental schemes and other conservation efforts on parts of the entire grassland area were, apparently, not sufficient to prevent the total grassland from recent taxonomic homogenization.

Chapter 8 – Roth, T. and D. Weber. 2008. Top predators as indicators for species richness? Prey species are just as useful. *Journal of Applied Ecology* 45:987-991.

The use of top predators as surrogates to identify protected areas has been criticized. However, recently a strong positive relationship was found between the presence of top predators and species diversity of several taxa. In this chapter, I used data from the Swiss Biodiversity Monitoring Programme and the Swiss common breeding bird survey to analyse the use of raptor species as a surrogate for plant, butterfly and bird species richness. For each raptor species, I compared species richness in sites where a raptor species was recorded with the remaining sites in which the raptor species was not recorded. For comparison, I conducted the same analyses using tits *Parus spp.* I found little justification for a focus on top predators when identifying conservation areas. For bird and plant species richness, raptors were reasonable surrogates for high species richness, but no raptor species predicted sites with above-average butterfly species richness. The presence of tit species performed equally well as the presence of raptor species to predict sites with high species richness of birds and plants, and performed even better for predicting high butterfly species richness. Based on these results, I concluded that conservation managers using indicator species should be aware that relationships among higher taxa are complex and depend on the species group and the scale of analysis. As shown with the case of raptors, the usefulness of a biodiversity indicator can vary between adjacent areas even if the same species groups are analysed. I recommended the use of more than one indicator species from different taxonomic groups when identifying areas of high biodiversity.

1.5 References

- Amrhein, V., P. Korner, and M. Naguib. 2002. Nocturnal and diurnal singing activity in the nightingale: correlations with mating status and breeding cycle. *Animal Behaviour* 64:939-944.
- Amrhein, V., H. P. Kunc, and M. Naguib. 2004. Seasonal patterns of singing activity vary with time of day in the nightingale (*Luscinia megarhynchos*). *Auk* 121:110-117.

1. THESIS INTRODUCTION

- Amrhein, V., H. P. Kunc, R. Schmidt, and M. Naguib. 2007. Temporal patterns of territory settlement and detectability in mated and unmated Nightingales *Luscinia megarhynchos*. *Ibis* 149:237-244.
- Amrhein, V. and D. Zwygart. 2004. Bestand und Verpaarungstatus von Nachtigallen *Luscinia megarhynchos* im elsässischen Rheintal bei Basel. *Der Ornithologische Beobachter* 101:19-24.
- Andelman, S. J. and W. F. Fagan. 2000. Umbrellas and flagships: Efficient conservation surrogates or expensive mistakes? *Proceedings of the National Academy of Sciences of the United States of America* 97:5954-5959.
- Baillie, S. R., J. H. Marchant, D. I. Leech, A. C. Joys, D. G. Noble, C. Barimore, M. J. Grantham, K. Risely, and R. A. Robinson. 2009. *Breeding Birds in the Wider Countryside: their conservation status 2008*. BTO Research Report. BTO, Thetford.
- Bergamini, A., H. Hofmann, M. Lüth, N. Müller, and N. Schnyder. 2006. Beiträge zur bryologischen Erforschung der Schweiz – Folge 1. *Meylania* 35:31-37.
- Bibby, C.-J., N. D. Burgess, D. A. Hill, and S. H. Mustoe. 2000. *Bird census techniques*. Academic Press, London and San Diego.
- Bühler, C. and T. Roth. 2011. Spread of common species results in local-scale floristic homogenization in grassland of Switzerland. *Diversity and Distributions* 17:1089-1098.
- Caughley, G. 1994. Directions in Conservation Biology. *Journal of Animal Ecology* 63:215-244.
- Couvet, D., V. Devictor, F. Jiguet, and R. Julliard. 2011. Scientific contributions of extensive biodiversity monitoring. *Comptes Rendus Biologies* 334:370-377.
- Devictor, V., R. Julliard, J. Clavel, F. Jiguet, A. Lee, and D. Couvet. 2008. Functional biotic homogenization of bird communities in disturbed landscapes. *Global Ecology and Biogeography* 17:252-261.

- Jiguet, F., R. Julliard, D. Couvet, and A. Petiau. 2005. Modeling spatial trends in estimated species richness using breeding bird survey data: A valuable tool in biodiversity assessment. *Biodiversity and Conservation* 14:3305-3324.
- Kerr, J. T., H. M. Kharouba, and D. J. Currie. 2007. The macroecological contribution to global change solutions. *Science* 316:1581-1584.
- Kéry, M. and M. Plattner. 2007. Species richness estimation and determinants of species detectability in butterfly monitoring programmes. *Ecological Entomology* 32:53-61.
- Kéry, M., J. A. Royle, M. Plattner, and R. M. Dorazio. 2009. Species richness and occupancy estimation in communities subject to temporary emigration. *Ecology* 90:1279-1290.
- Kéry, M., J. A. Royle, and H. Schmid. 2005. Modeling avian abundance from replicated counts using binomial mixture models. *Ecological Applications* 15:1450-1461.
- Kéry, M. and H. Schmid. 2004. Monitoring programs need to take into account imperfect species detectability. *Basic and Applied Ecology* 5:65-73.
- Kéry, M. and H. Schmid. 2006. Estimating species richness: calibrating a large avian monitoring programme. *Journal of Applied Ecology* 43:101-110.
- Kobialka, H., M. Plattner, and J. Rüetschi. 2010. Das Biodiversitätsmonitoring der Schweiz. Methoden und Ergebnisse am Beispiel der Mollusken. *Natur und Landschaft* 85:142-148.
- Lepetz, V., M. Massot, D. S. Schmeller, and J. Clobert. 2009. Biodiversity monitoring: some proposals to adequately study species' responses to climate change. *Biodiversity and Conservation* 18:3185-3203.
- Lindenmayer, D. B. and G. E. Likens. 2009. Adaptive monitoring: a new paradigm for long-term research and monitoring. *Trends in Ecology & Evolution* 24:482-486.
- Link, W. A. and J. R. Sauer. 1998. Estimating population change from count data: Application to the North American Breeding Bird Survey. *Ecological Applications* 8:258-268.

1. THESIS INTRODUCTION

- Lovett, G. M., D. A. Burns, C. T. Driscoll, J. C. Jenkins, M. J. Mitchell, L. Rustad, J. B. Shanley, G. E. Likens, and R. Haeuber. 2007. Who needs environmental monitoring? *Frontiers in Ecology and the Environment* 5:253-260.
- Magurran, A. E., S. R. Baillie, S. T. Buckland, J. M. Dick, D. A. Elston, E. M. Scott, R. I. Smith, P. J. Somerfield, and A. D. Watt. 2010. Long-term datasets in biodiversity research and monitoring: assessing change in ecological communities through time. *Trends in Ecology & Evolution* 25:574-582.
- Naaf, T. and M. Wulf. 2010. Habitat specialists and generalists drive homogenization and differentiation of temperate forest plant communities at the regional scale. *Biological Conservation* 143:848-855.
- Nichols, J. D. and B. K. Williams. 2006. Monitoring for conservation. *Trends in Ecology & Evolution* 21:668-673.
- Norris, K. 2004. Managing threatened species: the ecological toolbox, evolutionary theory and declining-population paradigm. *Journal of Applied Ecology* 41:413-426.
- Noss, R. F. 1990. Indicators for Monitoring Biodiversity - a Hierarchical Approach. *Conservation Biology* 4:355-364.
- Olden, J. D. 2006. Biotic homogenization: a new research agenda for conservation biogeography. *Journal of Biogeography* 33:2027-2039.
- Olson, T. A., T. O. Odlaug, and W. R. Swain. 1966. The Continuous Plankton Recorder: a review of the literature. University of Minnesota Water Research Centre, Minnesota.
- Pereira, H. M. and H. D. Cooper. 2006. Towards the global monitoring of biodiversity change. *Trends in Ecology & Evolution* 21:123-129.
- Platt, J. R. 1964. Strong inference. *Science* 146:347-353.
- Plattner, M., D. Weber, and S. Birrer. 2004. Data quality in monitoring plant species richness in Switzerland. *Community Ecology* 5:135-143.

- Reid, P. C., J. M. Colebrook, J. B. L. Matthews, J. Aiken, and C. P. R. Team. 2003. The Continuous Plankton Recorder: concepts and history, from plankton indicator to undulating recorders. *Progress in Oceanography* 58:117-173.
- Rooney, T. P., J. D. Olden, M. K. Leach, and D. A. Rogers. 2007. Biotic homogenization and conservation prioritization. *Biological Conservation* 134:447-450.
- Roth, T., P. Sprau, R. Schmidt, M. Naguib, and V. Amrhein. 2009. Sex-specific timing of mate searching and territory prospecting in the nightingale: nocturnal life of females. *Proceedings of the Royal Society B-Biological Sciences* 276:2045-2050.
- Royle, J. A. and R. M. Dorazio. 2008. Hierarchical modeling and inference in ecology. Academic Press, Amsterdam, the Netherlands.
- Saracco, J. F., D. F. Desante, and D. R. Kaschube. 2008. Assessing Landbird Monitoring Programs and Demographic Causes of Population Trends. *Journal of Wildlife Management* 72:1665-1673.
- Schmid, H., N. Zbinden, and V. Keller. 2004. Überwachung der Bestandsentwicklung häufiger Bruvögel in der Schweiz. Schweizerische Vogelwarte, Sempach, Switzerland.
- Stapfer, A. 1999. Volkszählung in der Aargauischen Natur? *Umwelt Aargau* 6:5-60.
- Szabo, J. K., P. A. Vesk, P. W. J. Baxter, and H. P. Possingham. 2010. Regional avian species declines estimated from volunteer-collected long-term data using List Length Analysis. *Ecological Applications* 20:2157-2169.
- Thomas, R. J. 2002. Seasonal changes in the nocturnal singing routines of Common Nightingales *Luscinia megarhynchos*. *Ibis* 144:E105-E112.
- van Strien, A. J., C. A. M. van Swaay, and M. Kéry. 2011. Metapopulation dynamics in the butterfly *Hipparchia semele* changed decades before occupancy declined in The Netherlands. *Ecological Applications* 21:2510-2520.
- Wagner, H. H. and P. J. Edwards. 2001. Quantifying habitat specificity to assess the contribution of a patch to species richness at a landscape scale. *Landscape Ecology* 16:121-131.

1. THESIS INTRODUCTION

- Walther, G. R., E. Post, P. Convey, A. Menzel, C. Parmesan, T. J. C. Beebee, J. M. Fromentin, O. Hoegh-Guldberg, and F. Bairlein. 2002. Ecological responses to recent climate change. *Nature* 416:389-395.
- Weber, D., U. Hintermann, and A. Zangger. 2004. Scale and trends in species richness: considerations for monitoring biological diversity for political purposes. *Global Ecology and Biogeography* 13:97-104.
- Wolfe, D. A., M. A. Champ, D. A. Flemer, and A. J. Mearns. 1987. Long-Term Biological Data Sets - Their Role in Research, Monitoring, and Management of Estuarine and Coastal Marine Systems. *Estuaries* 10:181-193.
- Yoccoz, N. G., J. D. Nichols, and T. Boulinier. 2001. Monitoring of biological diversity in space and time. *Trends in Ecology & Evolution* 16:446-453.
- Zbinden, N., H. Schmid, M. Kéry, and V. Keller. 2005. Swiss bird index SBI registered trademark—Kombinierte Indices für die Bestandsentwicklung von Artengruppen regelmässig brütender Vogelarten der Schweiz 199–2004. *Der Ornithologische Beobachter* 102:283-291.

Part I

Development of new statistical methods to analyse data from long-term surveys

2

Estimating individual survival using territory occupancy data on unmarked animals

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2. ESTIMATING INDIVIDUAL SURVIVAL USING DATA ON UNMARKED ANIMALS

Abstract

Aim *Survival estimation forms the basis of much ecological research, and usually requires data on marked animals. In population studies of territorial animals, however, data are often collected on animal territory occupancy without identification of individuals, and so far could not be used to estimate demographic parameters such as survival.*

Location *Petite Camargue Alsacienne, France.*

Methods *We developed a hierarchical site-occupancy model for estimating survival from territory occupancy data without individual identification. We defined survival as the probability that an individual occupying a territory survives until the next reproductive period and settles in the same territory again. To evaluate our model, we used simulated data as well as real data from a long-term study on Nightingales *Luscinia megarhynchos*, from which independent mark-recapture data and territory occupancy data were available.*

Results *When applied to simulated data sets on territory occupancy, with parameter settings that are typical for different monitoring programs (i.e., ten years duration, three or eight visits per season, and 55 or 200 territories surveyed), our model yielded unbiased estimates of survival even if detection of territories was low (i.e., if detection probability during a single visit was $p = 0.3$ or $p = 0.7$). When applied to the data on Nightingale territory occupancy, estimates of survival from our model were very similar to the estimates obtained from a traditional mark-recapture model (Cormack-Jolly-Seber model) applied to independent ringing data from the same nightingale population.*

Main conclusions *Data collection for mark-recapture analysis is usually invasive and labour intensive, and suitable data are rarely available from large-scale monitoring programs covering entire regions or countries. Applying our model to territory occupancy data from such monitoring programs could make large amounts of data available for research on animal demography.*

Keywords: Bayesian analysis, capture recapture, common birds census, robust design, state-space models, territory colonization, territory fidelity, WinBUGS

2.1 Introduction

Research in conservation biology, ecology and evolution often requires knowledge on estimates of survival in individual animals (Stearns 1992, Hoekstra et al. 2001, McCarthy et al. 2008, Ruiz-Gutierrez et al. 2008). In field studies, estimates on survival and other demographic parameters are usually obtained from data on individually marked animals (Lebreton et al. 1992, Sandercock 2006). A major drawback of these methods is that they usually are invasive because individuals need to be captured and marked. This can be stressful for the animals and time- and labour-intensive for researchers (Vögeli et al. 2008).

However, large data sets from non-invasive monitoring programs or from population studies on single species are available, where animals are not captured and marked and, thus, cannot be individually recognized. For instance, the British Trust of Ornithology (BTO) stores detailed maps of almost a million bird territories, collected during the British common birds census program over more than 40 years (Baillie et al. 2009), and long-term territory occupancy data are available for many individual species (Sergio and Newton 2003). This huge body of data so far could not be used to rigorously estimate demographic parameters such as survival, for lack of a framework to analyse territory occupancy data without individual recognition.

Demographic parameters could not be estimated from territory occupancy data because a territory that is occupied in two successive seasons may be occupied by the same surviving individual, or by two different individuals. In the latter case, the territory owner of the first year may have died or left for some other place, and a new individual may have occupied the territory in the following season. Conceptually, territory occupancy data are thus the result of two different probabilistic events. The first is local survival of a territory owner, which is the probability that a particular individual occupying a territory during one breeding season survives and settles in the same territory during the next breeding season. The second event is territory colonization, which is the colonization of territories by individuals new to the study site, or by individuals that occupied another territory at the same study site during the previous breeding season. Clearly, without individual recognition, local survival of a territory owner cannot be observed directly.

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We developed a model for estimating local survival of territory owners and colonization of territories, using territory occupancy data of unmarked animals. By also estimating the probability of detecting an occupied territory, the model can handle situations where occupied territories are detected imperfectly, i.e. where the probability of detecting an occupied territory is $p < 1$. The parameters of our model can be estimated only if each year, the territories are surveyed more than once, i.e., if data are collected under a robust sampling design (Kendall et al. 1997). Our model builds on the framework of site-occupancy models, which usually estimate the dynamics of the proportion of sites being occupied by a species as a function of local species extinction and species colonization probabilities (MacKenzie et al. 2003, MacKenzie et al. 2006, Royle and Kéry 2007). In our present model on territory occupancy data, we treat territories as concepts that are analogous to the single sites in site-occupancy models. We re-parameterized the dynamic site-occupancy model of Royle & Kéry (2007), to contain parameters for individual survival and colonization probability. We evaluated the performance of our model by using simulated data as well as data from a long-term population study on Nightingales *Luscinia megarhynchos*. We used data on nightingales to obtain survival estimates from territory occupancy data under our model, and then compared those estimates with conventional survival estimates under a Cormack-Jolly-Seber (i.e., mark-recapture) model applied to data from ringed nightingales of the same population. We show that territory occupancy data without individual recognition are useful for estimating demographic parameters such as local survival, which should open up great opportunities for large-scale demographic analyses of animal populations.

2.2 Model structure and notation

2.2.1 Sampling strategy

Suppose that a population of a territorial species is repeatedly sampled for the presence of territory owners in $i = 1, \dots, n$ territories during $t = 1, \dots, T$ breeding seasons. During each breeding season, the territories are surveyed at $j = 1, \dots, J$ visits, yielding observed territory occupancy histories that are based on detection/non-detection data of anonymous territory owners. It is required that $J > 1$; such a sampling design is usually referred to as a robust design (Kendall et al. 1997). Sampling designs with

repeated visits per year are typical for many monitoring programs that use territory-mapping techniques to obtain population estimates of birds and other animals. For instance, in the Common Birds Census of Switzerland, study plots of 1km^2 are selected across the entire country, and each plot is visited 2-3 times within the breeding season of a species and over many years (Kéry and Schmid 2006). During each visit, the position of a detected territory owner, such as a singing male bird, is recorded on a map, yielding observations of occupancy status of territories all over Switzerland.

Denote $y_j(i, t)$ as the observed territory occupancy state, i.e., a territory is observed to be occupied at breeding season t at visit j if $y_j(i, t) = 1$, or is not observed to be occupied if $y_j(i, t) = 0$. We assume that $y_j(i, t)$ are independent and identically distributed for each territory i and breeding season t . Denote $x(i, t)$ as the true territory occupancy state, i.e., a territory i is occupied at time t if $x(i, t) = 1$, or is not occupied if $x(i, t) = 0$. Unlike in traditional site-occupancy models, we modelled the occupancy history conditional on the first observed occupancy: the occupancy history for territory occupied for the first time at $t = f_i$ is the vector $[x(i, t)]_{t=f_i}^T$ with $x(i, f_i) = 1$. Thus, potential territories are considered only from the first time they are occupied by a territorial individual; potential territories that have never been occupied, and territories before first occupation are not considered in the model.

An important point is that the true occupancy state variable $x(i, t)$ is usually not directly observable, i.e., $y_j(i, t)$ is not the same as $x(i, t)$ because a territory owner is not always detected. Our model accounts for this by including a component for the observation process (see below). The observation process links the observations $y_j(i, t)$ with the true occupancy state $x(i, t)$. Thus, observed territory occupancy data can be naturally described as a state-space model (Royle and Kéry 2007).

2.2.2 Demographic territory-occupancy model: the state process

We describe the state process by using two submodels. The first submodel expresses observed territory occupancy dynamics as a function of the probability of individual survival and continued tenancy of a territory by its owner. This is what we define as local survival, because it includes both actual survival and territory fidelity. The second submodel includes the probability that an empty territory is colonized. Note that local survival is not the same as what is usually described as apparent survival when analyzing mark-recapture data with a Cormack-Jolly-Seber model (Lebreton et al. 1992). In

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the context of mark-recapture data, apparent survival is usually the probability that an individual survives and returns to the same study site. Therefore, if surviving individuals do not switch territories between years within the study site, local survival from our present territory occupancy model and apparent survival from a Cormack-Jolly-Seber model will coincide. However, if many individuals switch territories between years within a study site, local survival and apparent survival will diverge.

For the first submodel, let the parameter ϕ_t be the local survival probability of a territory owner from year $t - 1$ to t . Denote the latent (i.e., not directly observable) territory fidelity state $z(i, t)$; if a territory i is occupied at time t by the same individual as at time $t - 1$ then $z(i, t) = 1$, otherwise $z(i, t) = 0$. The latent territory fidelity state $z(i, t)$ is assumed to be Bernoulli distributed with parameter ϕ_t , depending on the true territory occupancy state of the previous year $x(i, t - 1)$. The local survival process (first submodel of the state process) is given by the conditional model

$$z(i, t) | x(i, t - 1) \sim \text{Bernoulli}\left(x(i, t - 1)\phi_t\right) \quad (2.1)$$

for $t = f_i + 1, \dots, T$. In other words, if an individual has occupied a territory at time $t - 1$ (i.e., $x(i, t - 1) = 1$), then its latent territory fidelity state $z(i, t)$ is a Bernoulli random variable with parameter ϕ_t . If no individual was occupying a territory at $t - 1$ (i.e., $x(i, t - 1) = 0$), then $z(i, t)$ is Bernoulli distributed with success probability 0, that is $z(i, t) = 0$ with probability 1.

The second submodel of the state process concerns the probability a currently not occupied territory is colonized by a new individual. Let the parameter be the territory colonization probability. Conditional on the latent territory fidelity state $z(i, t)$, the true territory occupancy state $x(i, t)$ is a Bernoulli random variable with

$$x(i, t) | z(i, t) \sim \text{Bernoulli}\left(z(i, t) + r(1 - z(i, t))\right) \quad (2.2)$$

Thus, if the latent territory fidelity state $z(i, t) = 1$, then the true territory occupancy state is $x(i, t) = 1$ with probability 1, otherwise $x(i, t)$ is a Bernoulli random variable with parameter r . Taking the two submodels eqn 2.1 and eqn 2.2 of the state process together, a territory is occupied at time t if the male occupying the territory at time $t - 1$ survives and returns to the same territory with probability ϕ_t , or if a new male colonizes the territory with probability r . The model assumes the same colonization probability r for territories that were not occupied the previous breeding season (i.e.,

$x(i, t - 1) = 0$), and for territories that were occupied the previous breeding season (i.e., $x(i, t - 1) = 1$) before the territory owner left or died. Thus, in the present model, the territory occupancy state $x(i, t)$ is assumed to be independent of the previous year territory occupancy state $x(i, t - 1)$ given that $z(i, t) = 0$ (i.e., given the territory was previously not occupied, or the former territory owner died or did not return to the same territory).

An alternative way of specifying a territory occupancy model could have been to describe territory occupancy directly in terms of local survival and territory colonization, similarly to Royle & Kéry (2007), who formulated site occupancy of a species as a result of local survival and colonization. Their formulation of a dynamic site occupancy model could also be adapted to territory occupancy data, by treating territories as sites. Here, we preferred a slightly different strategy by using the latent territory fidelity state variable $z(i, t)$ that indicates whether a particular territory owner was occupying the same territory also in the previous breeding season. The inclusion of the latent territory fidelity state into the model is not mathematically necessary, but is biologically relevant: territory owners can acquire fitness benefits from returning to a previously occupied territory, e.g. because they are familiar with the territory (Hoover 2003, Middleton et al. 2006). Having the latent territory fidelity state variable specified, the model directly estimates whether a male present in a territory was there also one year before, and inference on biological differences between returning and colonizing males is straightforward.

2.2.3 Observation process

Usually, not all territories that actually are occupied in a study site are also detected in monitoring programs (Kéry and Schmid 2006, Amrhein et al. 2007, Royle et al. 2007); our model accounts for this imperfect detection by including the observation process. Let the parameter p be the probability of observing a territory owner during a visit given that the territory is occupied. Similarly to the recently developed site occupancy models (MacKenzie et al. 2003, Dorazio et al. 2006, MacKenzie et al. 2006), the detection probability p and the true territory occupancy $x(i, t)$ need to be estimated from repeated visits to the territories each year (i.e., employing a robust design), otherwise the parameters cannot be identified. Conditional on the true territory occupancy state

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$x(i, t)$, the observation $y_j(i, t)$ is given as a Bernoulli random variable

$$y_j(i, t)|x(i, t) \sim \text{Bernoulli}(x(i, t)p) \quad (2.3)$$

Thus, if a territory is occupied (i.e., $x(i, t) = 1$), then it is observed during visit j to be occupied with probability p ; if a territory is not occupied ($x(i, t) = 0$), it is not observed to be occupied with probability 1.

2.3 Bayesian analysis and assessment of model performance

We used a Bayesian analysis of our model based on Markov chain Monte Carlo methods MCMC (Link et al. 2002). We assessed convergence using the Gelman-Rubin diagnostic (Brooks and Gelman 1998). MCMC simulations were conducted using WinBUGS 1.4 (Gilks et al. 1994), executed in R using the R add-on library R2WinBUGS (Sturtz et al. 2005). See Appendix S.2.8, for the WinBUGS implementation of our model.

To explore the performance of our model, we simulated data sets under the territory occupancy model described above. Annual local survival was simulated as normally distributed over the years with an overall mean (ϕ_t) and standard deviation (ϕ_{sd}). See Appendix S.2.9 for an R function to simulate data under our model. For the Bayesian analyses of the simulated data, we assumed conventional diffuse (i.e., $U(0, 1)$) prior distributions for r and p ; the ϕ_t were assigned normal priors on the logit scale with equal, but unknown mean and variance, i.e. $\text{logit}(\phi_t) \sim N(\mu, \tau)$. The parameters μ and τ were then assigned further distributions; we used the conjugate distributions $\mu \sim N(0, 0.67)$ and $\tau \sim \text{Gamma}(100, 100)$. Such a specification leads to rather diffuse priors for ϕ_t ; if instead a conventional diffuse prior distribution was used for μ , the logit-transformation of μ would result in a U-shaped parameter distribution with much of the density near 0 or 1 (Calvert et al. 2009).

The simulations revealed that our model performed well when the sample size was reasonably large and when there were eight visits to the territories per year (i.e., $n = 200$ and $J = 8$, Fig. 2.1, Table 2.1.a). Under such conditions, the model provided estimates for local survival, territory colonization and detection probability that were close to the true values and had relatively narrow credible intervals. None of the estimators of the parameters were biased. When sample size was sparse and detection probability was

2.3 Bayesian analysis and assessment of model performance

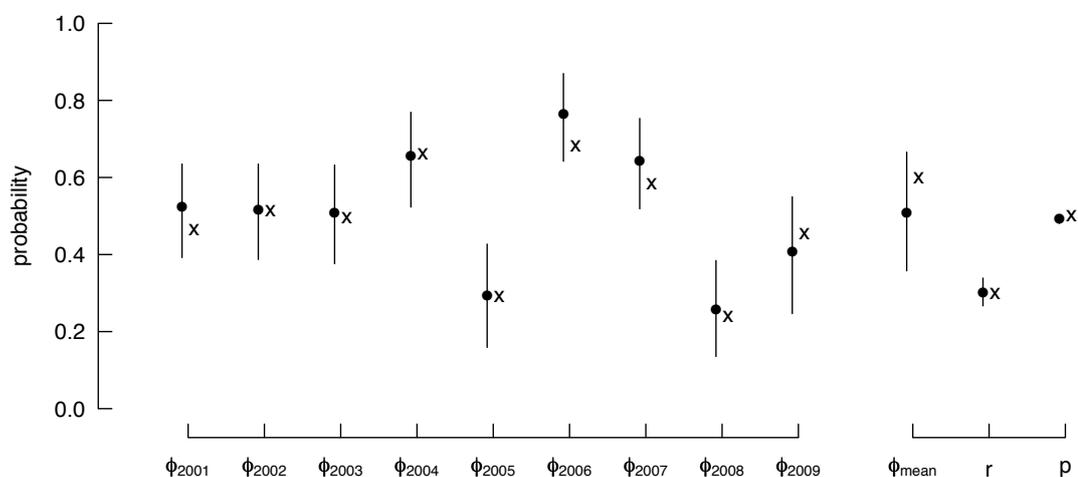


Figure 2.1: Simulation Results - Parameter estimates obtained from analysing a simulated data set with intermediate detection probability ($p=0.5$) and with a relatively large sample size (number of territories $n = 200$; number of study years $T = 10$; number of visits per year $J = 8$). Shown are estimated means and 95% credible intervals of the posterior distribution of the local survival per year ($\phi_{2001} - \phi_{2009}$), the mean of the local survival per year (ϕ_{mean}), the colonization rate (r), and the detection probability (p). Crosses indicate the true parameter values used for the simulation.

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low (i.e., $n = 55$, $p = 0.3$, $J = 8$, Table 2.1.a), the parameter estimators were slightly biased: the model on average slightly overestimated r and slightly underestimated ϕ_t . Biases in parameter estimators were rather strong, however, when low detection probability was coupled with few yearly visits to the territories (i.e., $p = 0.3$, $J = 3$, Table 2.1.b). This is probably because the reduced information in the data resulted in a posterior distribution of the parameters that to some extent was influenced by the prior. Thus, for these small sample situations, the posterior distribution was probably highly skewed, and the posterior median or mode would likely be more appropriate point estimators (Gelman et al. 2004).

2.4 Case study: nightingale data

To further explore our model, we used data collected in a long-term population study on nightingales in the Petite Camargue Alsacienne in the Upper Rhine Valley in France. From 2000 to 2009, we monitored the occupancies of 55 territories by means of daily rounds of inspection following a fixed route covering all 55 territory sites that were occupied at least once during the study period (Amrhein et al. 2002, Amrhein et al. 2007, Roth et al. 2009). Territories occupied by a singing male nightingale were relatively stable across years irrespectively of the identity of the territory holder, because nightingales frequently use the edges of bushes, paths or rivers as territory borders.

Each year, the field season lasted from the day the first male had settled at the study site (mean \pm SD = 9 April \pm 4.7 days; $n = 10$) until the end of May. On average, the males arrived on 18 April (± 2.3 days); no trend in the mean arrival date over the years could be detected (linear regression: year = -0.12, d.f. = 8, $t = 0.44$, $P = 0.67$). In order to remove males from the data set that were present in a territory for a few days only (transients), we defined a territory as being occupied only if a male was heard singing during at least five inspection rounds per year. During the 10 years of the study, the 55 nightingale territories were occupied during 5.2 ± 2.8 years; six of the territories were occupied only once, and four of the territories were occupied each year. Each year, $52.3 \pm 15.0\%$ of the 55 territories were occupied.

The identity of males was ascertained by regular capturing and ringing throughout the field season (Amrhein et al. 2002, Amrhein et al. 2007). In the 10 years of the study, the territorial males were captured and ringed in $62.5 \pm 22.3\%$ of the territories

2.4 Case study: nightingale data

Parameter	Cover	Bias	Length	Cover	Bias	Length	Cover	Bias	Length
(a) Eight visits per study year (J=8), as in the British common birds census (Baillie et al. 2009)									
	p=0.7 n=200			p=0.5 n=200			p=0.3 n=200		
ϕ_{mean}	0.98	0.00	0.36	0.95	-0.02	0.38	0.94	-0.02	0.40
r	0.91	0.00	0.12	0.95	0.01	0.14	0.93	0.01	0.15
p	0.96	0.00	0.03	0.96	0.00	0.04	0.86	0.01	0.04
	p=0.7 n=55			p=0.5 n=55			p=0.3 n=55		
ϕ_{mean}	0.98	0.00	0.41	0.95	-0.04	0.46	0.95	-0.05	0.47
r	0.94	0.01	0.19	0.91	0.02	0.23	0.90	0.03	0.23
p	0.97	0.00	0.06	0.96	0.00	0.07	0.95	0.00	0.07
(b) Three visits per study year (J=3), as in the Swiss common birds census (Kéry & Schmid 2006)									
	p=0.7 n=200			p=0.5 n=200			p=0.3 n=200		
ϕ_{mean}	0.91	-0.02	0.38	0.95	-0.04	0.42	0.80	-0.14	0.53
r	0.90	0.01	0.14	0.93	0.00	0.15	0.96	0.04	0.32
p	0.98	0.00	0.07	0.77	-0.06	0.09	0.50	0.06	0.17
	p=0.7 n=55			p=0.5 n=55			p=0.3 n=55		
ϕ_{mean}	0.95	-0.03	0.46	0.94	-0.07	0.56	0.58	-0.14	0.80
r	0.92	0.02	0.22	0.94	0.06	0.36	0.64	0.04	0.45
p	0.95	0.01	0.11	0.93	0.03	0.20	0.49	0.08	0.28

Table 2.1: Summary of simulation results for the parameters ϕ_{mean} (mean of local survival per year), r (colonization rate) and p (detection probability). Given are credible interval (CRI) coverage (cover: proportion of 100 simulation replicates that the 95% CRI contained the true parameter value), bias (difference between mean estimate minus true value), and CRI length (length: mean length of CRI). True parameter values used for simulation were inspired by the analysis of our nightingale data, with $r = 0.30$, $\phi_{mean} = 0.55$, and $\phi_{sd} = 0.20$. The number of study years was set to $T = 10$. The number of territories was set to cover a relatively large sample size ($n = 200$) and, alternatively, the sample size from our nightingale data ($n = 55$).

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that were occupied in a given year. Between 2000 and 2008, we captured 99 different males; males that were caught in 2009 for the first time were excluded from the analyses, as those males could not provide information on survival.

We analysed the nightingale territory occupancy data with our model, including year effects on local survival (ϕ_t), and assuming a constant territory colonization (r) and detection probability (p). For the Bayesian analyses, we assumed conventional diffuse [i.e. $U(0, 1)$] prior distributions for the parameters. To test how the model would perform when analysing results from a conventional breeding bird monitoring scheme, in which usually no more than eight to ten visits are being made to a given territory (Baillie et al. 2009), we applied the model to a subset of the at least 40 daily visits we made at the study site each year. This subset included observed nightingale territory occupancy data from eight arbitrarily chosen visits (observed territory occupancies from the visits made every fifth day from 15 April to 20 May). The results on local survival from our model were then compared with the yearly apparent survival (ϕ_t , which is the probability an individual survives between two years and returns to the same study site), obtained from analysing the data on captured individuals with a state-space formulation of the traditional Cormack-Jolly-Seber model (CJS, i.e. a mark-recapture model, Royle 2008). The CJS model also included a constant capturing probability (p). For the Bayesian analyses of the CJS model, we assumed conventional diffuse [i.e. $U(0, 1)$] prior distributions for all ϕ_t and p .

The results from analysing the nightingale data showed parallel fluctuations of the local survival calculated from territory occupancy data under our model, and of apparent survival estimated from mark-recapture data (Fig. 2.2); the posterior means of the yearly estimates were strongly correlated (Pearson's correlation: $r = 0.82$, $t = 3.77$, d.f. = 7, $P = 0.007$).

2.5 Discussion

We developed and illustrated a new model for estimating local survival from a demographic site-occupancy model applied to territory occupancy observations without individual recognition of animals. Similar to the recently developed site occupancy models (MacKenzie et al. 2003, Dorazio et al. 2006, MacKenzie et al. 2006), our model can cope with imperfect detection of the occupied territories. Unless data were

very scarce, our simulation results revealed that parameter estimates were reliable also when some occupied territories are not detected due to a low detection probability or due to a small number of visits per territory. This is important, because territory occupancy data from monitoring schemes or population studies of single species are usually obtained by visiting the potential territories during only few visits per year, and because territory owners are not always detected (Kéry and Schmid 2006, Amrhein et al. 2007, Royle et al. 2007).

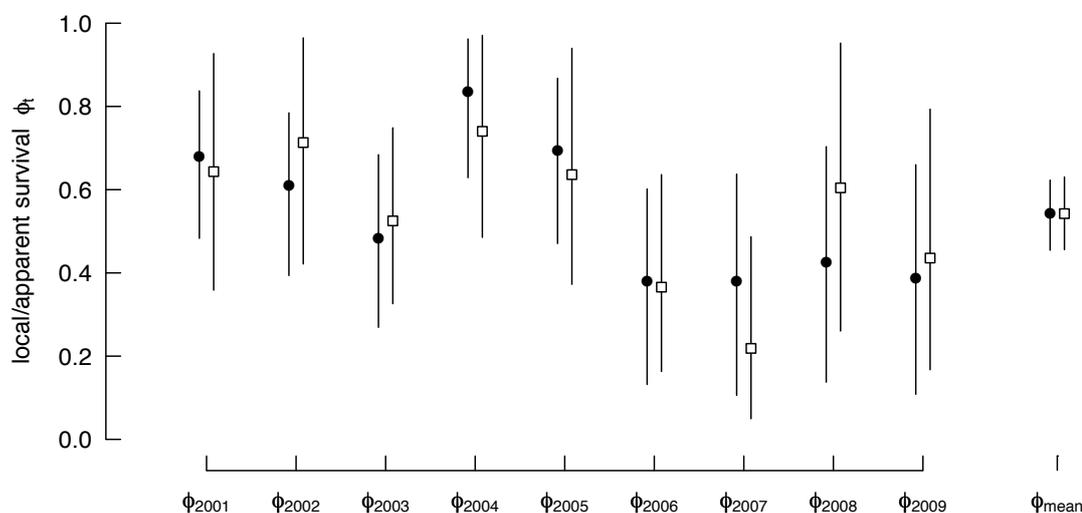


Figure 2.2: Local survival and apparent survival of the studied nightingales - Local survival estimates obtained from territory occupancy data under our model, compared to apparent survival estimates obtained from ringing data. Given are estimated values of local apparent survival per year ($\phi_{2001} - \phi_{2009}$), and the mean local apparent survival (ϕ_{mean}). Our present territory occupancy model was used to analyse eight visits per territory and year (black dots), and a traditional Cormack-Jolly-Seber model was applied to the mark-recapture data from ringed nightingales (open squares). Shown are means and 95% credible intervals of the posterior distributions.

An important condition for applying our model is that territories can be monitored accurately in all years of a study. Arguably, the size and shape of territories may change between years depending on social and environmental variables (Pärt and Gustafsson 1989, Pons et al. 2008). However, in many species, the locations of territories remain relatively stable from year to year, because territory owners often defend areas that include rare but spatially stable resources such as isolated habitat patches, nest cavities,

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or food resources (Newton 1998). If the locations, but not the shape or size of the territories remain stable between years, accurate territory occupancy data may still be obtained. Indeed, high quality territory occupancy data are available for many species, e.g. from national monitoring schemes (Sergio and Newton 2003).

A benefit of the hierarchical model formulation that we used for our model is its great flexibility and ease with which the model can be adapted to different situations (Royle and Dorazio 2008). The present model contained local survival probabilities that varied between years, but constant territory colonization and detection probabilities. If appropriate, however, dynamic effects could also be considered for temporally changing colonization and detection probabilities. Further, the hierarchical modelling approach also allows covariates to be included (Royle and Dorazio 2008). For example, our models could be used to investigate how the variation in local survival or territory colonization correlates with characteristics of the territories, or with characteristics of the territory owners such as measures of sexually selected traits or of pairing status. Such information could provide a deeper understanding of the populations and individuals under study (for the integration of covariates in hierarchical models in a Bayesian framework, see for instance Kéry and Royle 2008). Our model could also be used for large-scale investigations of demographic parameters, to compare local survival and colonization rates among regions in entire countries.

In most species, only males are surveyed in monitoring programs, because they often are more conspicuous than females and actively advertise their territories (Andersson 1994). When using data from monitoring programs, our model thus is likely to estimate only local survival of males. However, the advantage of territory occupancy data is that they can easily be collected or, in the case of many national monitoring programs (Kéry and Schmid 2006, Baillie et al. 2009), often already are available. Furthermore, in the case of certain endangered species or of species that are difficult to capture, researchers may prefer not to mark individuals. Under such circumstances, observed territory occupancies might be the only data available.

In the case study on nightingales, the survival estimates obtained from our territory occupancy model corresponded very well with the survival estimates obtained from a mark-recapture model, suggesting that our territory occupancy model is generally reliable. Note, however, that local survival as estimated from our model and apparent survival as estimated from mark-recapture models are expected to coincide only if

between years, individuals do not switch territories within the study site. If such switches do occur, they are not usually detected in studies on territory occupancy of unmarked birds, leading to underestimation of true survival when applying our model. As in other bird species (Harvey et al. 1979, Beletsky and Orians 1987, Pärt and Gustafsson 1989), a moderate proportion of male nightingales at our study site do switch territories from one year to the next (unpublished data). Because the birds at our study site are part of a larger nightingale population in the Upper Rhine Valley, several males that switched territories may have selected new territories outside our study site. In such cases in which individuals emigrate from a study site, both the estimates on local survival of unmarked animals and the estimates on apparent survival of marked animals will be similarly biased due to territory switches, which may explain why in our nightingale study, both models yielded similar estimates.

Estimating demographic parameters from survey data without individual recognition seems to be a promising new tool, but its potential for general application needs to be further explored. More studies are needed that apply the model to other territorial species and compare the results with traditional estimates of demographic parameters using marked individuals. Additionally, further development of our model may contribute to the advancement of integrated population models that combine different sources of demographic data (Schaub et al. 2007). Thus, mark-recapture data and territory occupancy data may be combined to obtain more precise estimates of the parameters described in this study, or of estimates of additional parameters. In conclusion, we suggest that adopting hierarchical mark-recapture models to territory occupancy data can make large amounts of data available for research on animal demography.

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2.7 References

- Amrhein, V., P. Korner, and M. Naguib. 2002. Nocturnal and diurnal singing activity in the nightingale: correlations with mating status and breeding cycle. *Animal Behaviour* 64:939-944.
- Amrhein, V., H. P. Kunc, R. Schmidt, and M. Naguib. 2007. Temporal patterns of territory settlement and detectability in mated and unmated Nightingales *Luscinia megarhynchos*. *Ibis* 149:237-244.
- Andersson, M. 1994. *Sexual selection*. Princeton University Press, Princeton.
- Baillie, S. R., J. H. Marchant, D. I. Leech, A. C. Joys, D. G. Noble, C. Barimore, M. J. Grantham, K. Risely, and R. A. Robinson. 2009. *Breeding Birds in the Wider Countryside: their conservation status 2008*. BTO Research Report. BTO, Thetford.
- Beletsky, L. D. and G. H. Orians. 1987. Territoriality among male Red-winged Blackbirds. 1. Site-fidelity and movement patterns. *Behavioral Ecology and Sociobiology* 20:21-34.
- Brooks, S. P. and A. Gelman. 1998. General methods for monitoring convergence of iterative simulations. *Journal of Computational and Graphical Statistics* 7:434-455.
- Calvert, A. M., S. J. Bonner, I. D. Jonsen, J. M. Flemming, S. J. Walde, and P. D. Taylor. 2009. A hierarchical Bayesian approach to multi-state mark-recapture: simulations and applications. *Journal of Applied Ecology* 46:610-620.
- Dorazio, R. M., J. A. Royle, B. Soderstrom, and A. Glimskar. 2006. Estimating species richness and accumulation by modeling species occurrence and detectability. *Ecology* 87:842-854.
- Gelman, A., J. B. Carlin, H. S. Stern, and D. B. Rubin. 2004. *Bayesian Data Analysis*. Second Edition edition. Chapman & Hall/CRC, London.
- Gilks, W. R., A. Thomas, and D. J. Spiegelhalter. 1994. A language and program for complex Bayesian modelling. *Statistician* 43:169-178.

- Harvey, P. H., P. J. Greenwood, and C. M. Perrins. 1979. Breeding area fidelity of Great Tits (*Parus major*). *Journal of Animal Ecology* 48:305-313.
- Hoekstra, H. E., J. M. Hoekstra, D. Berrigan, S. N. Vignieri, A. Hoang, C. E. Hill, P. Beerli, and J. G. Kingsolver. 2001. Strength and tempo of directional selection in the wild. *Proceedings of the National Academy of Sciences of the United States of America* 98:9157-9160.
- Hoover, J. P. 2003. Decision rules for site fidelity in a migratory bird, the prothonotary warbler. *Ecology* 84:416-430.
- Kendall, W. L., J. D. Nichols, and J. E. Hines. 1997. Estimating temporary emigration using capture-recapture data with Pollock's robust design. *Ecology* 78:563-578.
- Kéry, M. and J. A. Royle. 2008. Hierarchical Bayes estimation of species richness and occupancy in spatially replicated surveys. *Journal of Applied Ecology* 45:589-598.
- Kéry, M. and H. Schmid. 2006. Estimating species richness: calibrating a large avian monitoring programme. *Journal of Applied Ecology* 43:101-110.
- Lebreton, J. D., K. P. Burnham, J. Clobert, and D. R. Anderson. 1992. Modeling survival and testing biological hypotheses using marked animals - a unified approach with case studies. *Ecological Monographs* 62:67-118.
- Link, W. A., E. Cam, J. D. Nichols, and E. G. Cooch. 2002. Of BUGS and birds: Markov chain Monte Carlo for hierarchical modeling in wildlife research. *Journal of Wildlife Management* 66:277-291.
- MacKenzie, D. I., J. D. Nichols, J. E. Hines, M. G. Knutson, and A. B. Franklin. 2003. Estimating site occupancy, colonization, and local extinction when a species is detected imperfectly. *Ecology* 84:2200-2207.
- MacKenzie, D. I., J. D. Nichols, J. A. Royle, K. H. Pollock, L. L. Bailey, and J. E. Hines. 2006. *Occupancy Estimation and Modeling. Inferring Patterns and Dynamics of Species Occurrence.* Elsevier Inc., Burlington.
- McCarthy, M. A., R. Citroen, and S. C. McCall. 2008. Allometric scaling and Bayesian priors for annual survival of birds and mammals. *American Naturalist* 172:216-222.

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- Middleton, H. A., C. A. Morrissey, and D. J. Green. 2006. Breeding territory fidelity in a partial migrant, the American dipper *Cinclus mexicanus*. *Journal of Avian Biology* 37:169-178.
- Newton, I. 1998. *Population Limitation in Birds*. Academic Press, London, UK.
- Pärt, T. and L. Gustafsson. 1989. Breeding dispersal in the Collared Flycatcher (*Ficedula albicollis*) - Possible causes and reproductive consequences. *Journal of Animal Ecology* 58:305-320.
- Pons, P., J. M. Bas, R. Prodon, N. Roura-Pascual, and M. Clavero. 2008. Territory characteristics and coexistence with heterospecifics in the Dartford warbler *Sylvia undata* across a habitat gradient. *Behavioral Ecology and Sociobiology* 62:1217-1228.
- Roth, T., P. Sprau, R. Schmidt, M. Naguib, and V. Amrhein. 2009. Sex-specific timing of mate searching and territory prospecting in the nightingale: nocturnal life of females. *Proceedings of the Royal Society B-Biological Sciences* 276:2045-2050.
- Royle, J. A. 2008. Modeling individual effects in the Cormack-Jolly-Seber model: A state-space formulation. *Biometrics* 64:364-370.
- Royle, J. A. and R. M. Dorazio. 2008. *Hierarchical modeling and inference in ecology*. Academic Press, Amsterdam, the Netherlands.
- Royle, J. A. and M. Kéry. 2007. A bayesian state-space formulation of dynamic occupancy models. *Ecology* 88:1813-1823.
- Royle, J. A., M. Kéry, R. Gautier, and H. Schmid. 2007. Hierarchical spatial models of abundance and occurrence from imperfect survey data. *Ecological Monographs* 77:465-481.
- Ruiz-Gutierrez, V., T. A. Gavin, and A. A. Dhondt. 2008. Habitat fragmentation lowers survival of a tropical forest bird. *Ecological Applications* 18:838-846.
- Sandercock, B. K. 2006. Estimation of demographic parameters from live-encounter data: a summary review. *Journal of Wildlife Management* 70:1504-1520.

- Schaub, M., O. Gimenez, A. Sierro, and R. Arlettaz. 2007. Use of integrated modeling to enhance estimates of population dynamics obtained from limited data. *Conservation Biology* 21:945-955.
- Sergio, F. and I. Newton. 2003. Occupancy as a measure of territory quality. *Journal of Animal Ecology* 72:857-865.
- Stearns, S. C. 1992. *The Evolution of Life histories*. Oxford University Press, Oxford.
- Sturtz, S., U. Ligges, and A. Gelman. 2005. R2WinBUGS: A Package for Running WinBUGS from R. *Journal of statistical Software* 12:1-16.
- Vögeli, M., P. Laiolo, D. Serrano, and J. L. Tella. 2008. Who are we sampling? Apparent survival differs between methods in a secretive species. *Oikos* 117:1816-1823.

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S.2.8 WinBUGS model specification

WinBUGS model specification for the demographic site-occupancy model. The model includes constant colonization rate r , constant detection probability p and yearly local survival ϕ_t .

```
# MODEL DEFINITION OF THE TERRITORY OCCUPANCY MODEL
#
# The following data should be provided:
# y[i,m] = observations, Matrix with n rows and J*T columns, with
# m = ((t-1)*J)+j for the jth visits in year t
# nter = number of territories (n)
# nyears = number of years (T)
# visits = number of yearly visits (J)
# first[i] = vector with year of first occupation for each territory
#
# Parameters to be estimated:
# phi[t] = yearly local survival
# r = territory colonization
# p = detection probability
#
# Latent state variables:
# x[i,t] = true territory occupancy state
# z[i,t] = territory fidelity state

for(i in 1:nter){
  x[i,first[i]] ~ dbern(1)
  for(j in 1:visits) {
    y[i,(first[i]-1)*visits+j] ~ dbern(p)
  }
  for(t in (first[i]+1):nyear) {
    # first submodel of state process
    mu1[i,t] <- phi[t] * x[i,t-1]
```

S.2.8 WinBUGS model specification

```
z[i,t]    dbern(mu1[i,t])
# second submodel of state process
mu2[i,t] <- z[i,t] + r * (1-z[i,t])
x[i,t]    dbern(mu2[i,t])
# Observation process
mu3[i,t] <- p * x[i,t]
for(j in 1:visits) {
y[i,((t-1)*visits+j)]  dbern(mu3[i,t])
}
}
}
```

2. ESTIMATING INDIVIDUAL SURVIVAL USING DATA ON UNMARKED ANIMALS

S.2.9 R code for the simulation function

R code for the function to simulate data for testing the territory occupancy model.

The yearly local survival ϕ_t is simulated with $\phi_t \sim N(\phi_t, \phi_{sd})$.

```
# FUNCTION TO SIMULATE TERRITORY OCCUPANCY DATA
sim.set <- function(x1_lambda, nyear, n_ter, visits, phi_mean, phi_sd, r, p) {
### The following parameters should be given to the function:
### x1_lambda = probability a territory is occupied at t=0
### nyear = number of study years (T)
### n_ter = number of territories (n)
### visits = number of visits each year (J)
### phi_mean = mean yearly local survival
### phi_sd = sd of yearly local survival
### r = territory colonization
### p = detection probability
### Define matrix x (true territory occupancy state)
### Note: x includes a column for t=0
x <- matrix(rep(0, (nyear+1)*n_ter), ncol=(nyear+1))
x <- as.data.frame(x)
names(x) <- paste("t", 0:nyear, sep="")
### Define the matrix y that contains the observations, the first J
### columns will contain observed occupancy states for the first year on
### the 1...J visits, the J+1 column will contain the observations of
### the first visit in the second year...
y <- matrix(rep(0, nyear*n_ter*visits), ncol=(nyear*visits))
y <- as.data.frame(y)
### Simulate the yearly local survival
### Note 1: make sure that 0 <= phi <= 1
### Note 2: phi[1] is the local survival from t=0 to t=1, it will not
### be possible to estimate phi[1] with the territory occupancy model
phi <- rnorm(nyear, phi_mean, phi_sd)
phi[phi<0] <- 0; phi[phi>1] <- 1
```

S.2.9 R code for the simulation function

```
### Simulate territory occupancies at t=0 (each territory is occupied at
### t=0 with probability x1_lambda)
x$t0 <- rbinom(n_ter, 1, x1_lambda)
### Simulate x and y from t=1 to t=nyear
### BE AWARE: t = year+1 (because x contains occupancy state for t=0)
for(i in 1:n_ter) {
  for(t in 2:(nyear+1)) {
    x[i,t] <- rbinom(1,1,x[i,t-1]*phi[t-1])
    x[i,t] <- rbinom(1,1,max(x[i,t],r))
    for(j in 1:visits) {
      y[i,((t-2)*visits)+j] <- rbinom(1,1,x[i,t]*p)
    }
  }
}
### Return observed territory occupancy matrix, i.e. the observations
as.matrix(y)
}
```

2. ESTIMATING INDIVIDUAL SURVIVAL USING DATA ON UNMARKED ANIMALS

3

Estimating demographic rates using data on unmarked individuals from bird monitoring programs

Manuscript in preparation:

Roth, T., M. Kéry, M. Schaub, H. Schmid, and V. Amrhein. In prep. Estimating demographic rates using data on unmarked individuals from bird monitoring programs.

3. DEMOGRAPHIC MONITORING USING DATA OF BIRD MONITORING PROGRAMS

Abstract

Aim Large-scale monitoring programs are mostly designed to survey population sizes of unmarked animals. However, the effects of management action or of environmental factors would become more explicit when demographic parameters such as survival could be estimated. Here, we developed a demographic monitoring framework for exploring the spatial configuration of occupied territories detected in nation-wide bird monitoring programs, to obtain estimates of demographic rates for unmarked individuals.

Location Switzerland.

Methods To test the performance of our model, we simulated eight years of territory mapping, with parameter settings that are typical for bird monitoring programs (five visits per season, 100 territories surveyed).

Results We found that our method is able to obtain realistic estimates of demographic rates. Bias was low provided that territories were fairly stable over years and that between visits, movements of birds were low to intermediate. Applying our framework on data of unmarked Yellowhammers *Emberiza citrinella* from the nation-wide common bird census in Switzerland, we found that territories were colonized at the highest rate in the lowlands. In contrast, local survival, which is the probability that an individual survives until the next reproductive period and settles in the same territory again, was relatively low in the lowlands but tended to increase with altitude.

Main conclusions We conclude that our demographic monitoring framework considerably broadens the possibilities for inference based on large-scale monitoring programs. Applying our model on data covering large altitudinal or latitudinal ranges could provide estimates on geographic variation in demographic parameters that are urgently needed to understand the effects of climate change on population performance.

Keywords: Bayesian analysis, breeding bird survey, site-occupancy, state-space model, territory colonization, territory fidelity, WinBUGS

3.1 Introduction

Nation-wide animal monitoring programs usually focus on estimating temporal variation in population trends of selected species (Link and Sauer 1998, Yoccoz et al. 2001). Such trend estimates are key instruments to inform resource managers and policy makers and to improve the management of ecosystems and of natural resources (Norris 2004, Gaston and Fuller 2008). For example, trend estimates of population size revealed that recent climate change affects animal populations (Gregory et al. 2009). However, there is often a lag from the time when environmental conditions change until a population responds by changing its size (Desante et al. 2001). Such a time lag can occur, for example, because immediately after a deleterious event, non-breeding individuals from other areas may immigrate into the population, thus resulting in apparent stability of local breeding densities despite decreasing fecundity (Newton 1992, van Strien et al. 2011).

The effects of management action or of environmental factors would become more explicit when demographic parameters such as survival, fecundity or immigration could be directly estimated from large-scale monitoring programs (Saracco et al. 2008). The estimation of demographic rates often needs data from individually marked animals (Lebreton et al. 1992, Sandercock 2006). However, the collection of data of marked individuals is often invasive and labor intensive and rarely applied to a large spatial scale (but see the Constant Effort Ringing Programs in birds, e.g. Saracco et al. 2010). Therefore, the development of methods to estimate demographic rates that do not rely on trapping and marking individuals and that make use of the huge amounts of data that have been collected for many decades during non-invasive monitoring programs are highly desirable (Greenwood and Robinson 2006, Manning and Goldberg 2010). Recently, a statistical model was proposed for estimating local survival (which is the probability that an individual occupying a territory survives until the next reproductive period and settles in the same territory again) based on territory occupancy data that are obtained without marking individuals (Roth and Amrhein 2010). Note that we define a territory as a patch of habitat that could be occupied by the studied species. The model can be applied to small spatial scales to estimate local survival and territory colonization probabilities for an intensively surveyed study population of a single

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songbird species. The model assumes that each individual can be assigned to a territory without error and that the number of territories is known. Here, we developed new methods for estimating the demographic parameters local survival and territory colonization from data on unmarked birds that are collected during nation-wide bird monitoring programs. From all available studies on the varying abundance of animals, bird monitoring programs have probably covered the largest spatial and temporal scales worldwide (Robbins et al. 1989, Julliard et al. 2006, Baillie et al. 2009). Bird monitoring programs often use territory mapping techniques, by recording the positions of territorial males during several visits to a study site for each breeding season (Kéry and Schmid 2006). However, the data collected from those monitoring schemes usually do not directly deliver territory occupancy data that could be used for estimating local survival and territory colonization (*sensu* Roth and Amrhein 2010). Instead they provide maps, where the location of recorded individuals at each visit is indicated. These locations could be also summarized with coordinates. The territory-mapping methods for analyzing data from large-scale monitoring do provide the number of occupied territories per breeding season, but so far they do not provide information on the potential number of territories that would be available for occupation. This can be illustrated with the following example. Consider a territory mapping study revealing 10 occupied territories in each of two consecutive breeding seasons. This could mean the study site contains 10 territories that were occupied during both breeding seasons. However, this could also indicate that the study site contains 20 territories, with the first half of territories being occupied during the first breeding season, and the second half during the second breeding season. But even more refined, in both cases the study site may contain an additional but unknown number of territories that were occupied in neither of the two breeding seasons. Thus, without accounting for the spatial configuration of territories, a long-term territory mapping study would not provide territory occupancy data.

The main obstacle for obtaining territory occupancy data from large-scale monitoring programs is that defining the locations of territories from the huge amounts of data is simply unfeasible when done by hand. A formal framework is thus needed to explore the spatial configuration of the occupied territories in consecutive years, and to automatize the calculation of territory occupancy data. In the present study, we develop a formal framework for obtaining territory occupancy data from existing bird monitoring

programs and a statistical model to analyze the obtained data for estimating local survival and territory colonization. We use simulated data to test the performance of our procedures, and we analyze data on the Yellowhammer *Emberiza citrinella* obtained from a large-scale bird monitoring program, the Swiss common bird census (Kéry and Schmid 2006).

The strength of our approach is that the effect of ecologically important covariates on local survival and territory colonization can now be investigated on large spatial and temporal scales. We provide an example of such an application by including altitude as a covariate for local survival and territory colonization in our model on the Yellowhammer. Altitude is likely to be an important predictor for demographic rates, as it is for the distribution of birds (Maggini et al. 2011). Studies examining demographic parameters over larger altitudinal ranges are so far hardly available (Chamberlain et al. 2012); however, they are important to understand how bird populations are affected by locally changing temperatures, and thus are useful models to predict responses of populations to a warming climate (Kim and Donohue 2011). Because high mountains are likely to be particularly vulnerable to climate change, there is a need to understand the demographic mechanisms that dictate future altitudinal shifts in the distributions of birds and of other organisms (Chamberlain et al. 2012).

3.2 Demographic monitoring framework

3.2.1 Assigning multi-year bird detections to unique territories to obtain territory occupancy data

Bird monitoring programs using territory-mapping data are usually designed for providing the number of occupied territories C_t for each breeding season $t = 1, \dots, T$. The main goal in bird monitoring program is to infer temporal trends in the number of occupied territories C_t . However, usually it is not analyzed from bird territory-mapping which of the C_t territories that were occupied in breeding season t were the same territories as those occupied in the next breeding season $t + 1$, and which of the territories were only occupied in one of the breeding seasons. Consequently, the total number of territories that were occupied at least once (N) is not known. Note that N is not necessarily the total number of territories in the study site because it does not include those territories that were never occupied during the survey. We will account later

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for the territories that were never occupied during the survey, but for the present we assume that N is the total number of territories available in the study site. To obtain territory occupancy data the number of territories (N) is essential, and the occupied territories C_t that are observed during territory mapping need to be allocated to the $i = 1, \dots, N$ territories.

Let define the occupied territories that were observed during territory mapping during the entire study with a unique id $p = 1, \dots, P$, where $P = \sum C_t$. We propose a algorithm to allocate the $p = 1, \dots, P$ occupied territories observed during territory mapping during the entire study to the $i = 1, \dots, N$ territories. Let define the allocation state variable $A_p \in \{1, \dots, N\}$ that contains the information to which of the territories $i = 1, \dots, N$ an occupied territory p that was observed during territory mapping belongs. For instance $A_{13} = 5$ would mean that during territory mapping the territory $i = 5$ was observed to be occupied and this observation of an occupied territory got the id-number $p = 13$ that is unique over all breeding seasons. If the same territory was observed to be occupied during an other breeding season, then this observation of an occupied territory would get an other unique id, say $p = 24$, and the allocation to the territory would be $A_{24} = 5$.

The aims of our territory-alignment algorithm are to derive the unknown number of territories N and the allocation stat variable A_p . One of the assumptions of the territory-alignment algorithm is that in a given breeding season, a territory can be occupied only once. Thus, if for example the observations of occupied territories with id-number $p = 1$ and $p = 2$ were recorded during the same breeding season, then $A_1 \neq A_2$. The second assumption is that if two observations of occupied territories (for example $p = 3$ and $p = 4$) are located further away than a threshold distance D , they are always considered as belonging to two different territories also if they were not recorded during the same year (thus $A_3 \neq A_4$). The threshold distance D is the maximal possible distance between two observations of a male that is occupying the same territory. The choice of D can be informed by the territory mapping data (e.g., from observations of simultaneously singing males), from a preliminary study, from telemetry data or from the literature. Later, we will use simulation to gauge the effects of different choices of D on the estimators of the demographic parameters.

We let the territory-alignment algorithm start with the starting values $N = P$ and $A_p = p$, thus all occupied territories that were observed during territory mapping over

3.2 Demographic monitoring framework

the entire study (i.e. $p = 1, \dots, P$) are allocated to different territories. The algorithm is then formulated as follows:

1. Select the two observations of occupied territories $a \in \{1, \dots, P\}$ and $b \in \{1, \dots, P\}$ with the shortest distance, i.e. $\min(\text{distance}[a \longleftrightarrow b])$ with $a \neq b$.
2. If the shortest distance between two 'occupied territories' is larger than D , i.e. $\min(\text{distance}[a \longleftrightarrow b]) > D$, then stop the algorithm.
3. If all observations of occupied territories that were previously allocated to territory a and b (i.e. all observations of occupied territories with $A_p = a$ or $A_p = b$) were recorded in different years, then fuse these territories (i.e. set $A_p = a$ for all p with $A_p = b$) and remove one territory from the available territories (i.e. set $N = N - 1$); otherwise, if at least two observations of occupied territories that were previously allocated to territory a and b were recorded in the same year, set the distance between the two territories a and b to a value larger than D (i.e. set $\min(\text{distance}[a \longleftrightarrow b]) = D + 1$).
4. If the total number of territories N equals the maximum number of occupied territories identified by territory mapping in one year, stop the algorithm; otherwise go to step 1 of the algorithm.

On completion of the territory-alignment algorithm, we obtain the number of territories N and the allocation vector A_p . Note, however, that at this stage the number of territories N is biased low since it does not yet contain the territories that were never occupied during the study period. We will account for this bias in the territory-occupancy model below. From the number of territories N and the allocation state variable A_p , it is now straightforward to derive the observed territory occupancy data. Denote the observed territory occupancy data $Y_{i,t} \in 0, 1, \dots, J$ as the number of times a territorial male was observed in territory $i = 1, \dots, N$ during the J visits and during breeding season $t = 1, \dots, T$. These observed territory occupancy data $Y_{i,t}$ are the data that are analyzed using the model that is described next. See Appendix S.3.7 in the Supplementary information for an implementation of the territory-alignment algorithm written in R software.

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3.2.2 Territory occupancy model to estimate demographic rates from territory occupancy data

Our model is based on that of Roth and Amrhein (2010) and allows us to estimate local survival and territory colonization from data obtained from bird monitoring programs using our method of territory alignment. Note, however, that the territory-alignment algorithm as described above yields estimated territory occupancy data $Y_{i,t}$. We have currently no way to gauge the associated estimation error and our territory occupancy model assumes that no error is made in the assignment of bird locations to territories over all years of study. This will introduce bias to the degree that the assignments of birds to territories are not perfect over the years (see simulations below).

Roth and Amrhein (2010) model is a robust-design site-occupancy model, treating the territories as concepts that are analogous to the single sites in site-occupancy models (Kendall et al. 1997, MacKenzie et al. 2003, MacKenzie et al. 2006, Royle and Kéry 2007). The territory-occupancy model also contains a parameter for the detection probability, which is the probability that the territory holder of an occupied territory is observed during one visit to the territory during a monitoring survey. In contrast to Roth and Amrhein (2010), we here also aimed to use the number of available territories as an indication of habitat availability and, therefore, aimed to estimate the number of territories that were never observed to be occupied during the entire study period. From the concept, the proposed extension of the Roth and Amrhein (2010) model is similar to the extension of a mark-recapture model to estimate survival (e.g. Cormack-Jolly-Seber model) to a mark-recapture model that simultaneously estimates survival, recruitment and population size (e.g. Jolly-Seber model, Lebreton et al. 1992, Link and Barker 2005). The Roth and Amrhein (2010) territory-occupancy model, for which the number of available territories was not in focus, conditioned on the breeding season the territory was observed to be occupied for the first time, whereas here we developed an unconditional model, thus all occupancy data were analyzed from the first breeding season. Thus, we added a new parameter Ψ , which is the occupation probability of a territory during the first breeding season. Denote as the true territory occupancy state $X_{i,t}$, i.e. $X_{i,t} = 1$ if territory i is occupied during season t , and $X_{i,t} = 0$ otherwise. We assume that the true territory occupancy state $X_{i,t}$ of territory i during the first

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breeding season is given as a Bernoulli trial with probability ψ

$$X_{i,1} \sim \text{Bernoulli}(\psi) \quad (3.1)$$

We further assume that the true territory occupancies $X_{i,t}$ in later seasons evolve according to a Markov process as a function of two demographic processes. The first process is the probability an individual will survive and will continue to occupy the same territory (ϕ_i). We term this local survival, because it is the product of the probabilities of survival and territory fidelity (Roth and Amrhein 2010). The second process is represented by the probability that an empty territory is colonized (r_i). The latent territory occupancy state $X_{i,t}$ for the breeding seasons $t = 2, \dots, T$ can be described by

$$Z_{i,t} \sim \text{Bernoulli}(\phi_i X_{i,t-1}) \quad (3.2)$$

$$X_{i,t} \sim \text{Bernoulli}(Z_{i,t} + r_i(1 - Z_{i,t})) \quad (3.3)$$

Eqn 3.2 describes the local survival of the male in territory i from one breeding season to the next. The state variable $Z_{i,t}$ denotes the territory fidelity of a male in territory i : if territory i is occupied during breeding season t by the same male as during breeding season $t - 1$ then $Z_{i,t} = 1$, otherwise $Z_{i,t} = 0$. Note that the territory fidelity state during the first breeding season ($Z_{i,t}$) can not be estimated since the latent territory occupancy state $X_{i,0}$ before the first breeding season is not known. eqn 3.3 describes the colonization of territory i with probability r_i if the territory was not reoccupied by the male from the previous breeding season ($Z_{i,t} = 0$); if the territory is occupied by the same male as in the previous season, then $Z_{i,t} = X_{i,t} = 1$.

Our model accounts for imperfect detection of a territory in a breeding season by assuming that the number of detections of territory i during breeding season t is a binomial random variable with index J (corresponding to the number of surveys).

$$Y_{i,t} \sim \text{Binomial}(J, pX_{i,t}) \quad (3.4)$$

In the Roth and Amrhein (2010) model, the local survival ϕ was assumed to be year specific, whereas the territory colonization probability r and the detection probability p were assumed to be constant. Because territories are likely to differ in quality, we here allowed the demographic parameters local survival ϕ_i and territory colonization r_i

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to vary among territories (Hoover 2003, Howlett and Stutchbury 2003). We formulated both parameters on the logit scale as Normal random effects,

$$\text{logit}(\phi_i) \sim \text{Normal}(\mu_\phi, \sigma_\phi^2) \quad (3.5)$$

$$\text{logit}(r_i) \sim \text{Normal}(\mu_r, \sigma_r^2) \quad (3.6)$$

where μ_ϕ is the mean (over territories) and σ_ϕ^2 the among-territory variance of the logit transform of local survival probability; and μ_r is the mean and σ_r^2 the among-territory variance of the logit transform of territory colonization probability.

The parameter space of our model is not fixed, because the number of territories that were never occupied is not known. We therefore used data augmentation (Royle et al. 2007) and Markov chain Monte Carlo methods (MCMC) to obtain Bayesian estimates of all parameters in our territory-occupancy model. We added to the observed territory occupancy data $Y_{i,t}$ m hypothetical territories with all 0 detection histories. The dimension of $Z_{i,t}$ and $X_{i,t}$ in the augmented data set is then fixed to M territories, where M is the sum of the number of territories that were occupied at least once (N) plus m . To analyze the augmented data, we fit a re-parameterized version of the territory occupancy model. We added one hierarchical layer by defining a binary variable w_i to indicate whether territory i in the augmented list of M territories is available for occupation ($w_i = 1$) or not ($w_i = 0$). We defined w_i such that $w_i \sim \text{Bernoulli}(\omega)$. Let define the total number of available territories, including territories that were never occupied, as H . It can be calculated as a derived quantity with $H = \sum w_i$, and can be interpreted as habitat availability for the study species. For more details about the territory occupancy model formulation and the analyses of the model using WinBugs (Gilks et al. 1994, Lunn et al. 2009), we refer the reader to Roth and Amrhein (2010).

3.3 Applications

3.3.1 Simulation study

In our previous work (Roth and Amrhein 2010), we showed that a territory occupancy model similar to the model introduced above is able to recover unbiased estimates of local survival and territory colonization when the territory occupancy data are observed

data. Here, however, we apply the model to territory occupancy data that were derived using our territory-alignment algorithm for data from bird monitoring programs. It is likely that the untreated uncertainty in the derived territory occupancy data will lead to biased estimates of the target parameters. We conducted a simulation study to investigate some of the likely biases induced by errors in the territory alignment process. See Appendix S.3.8 of the supplementary material for R code to simulate territory occupancy data.

We aim to simulate the positions of territorial males that are observed during several years of territory mapping, and start with simulating the positions of the H territories that are available for occupation. These positions of territories are fixed during the entire study period. If a male occupies a territory, the simulation routine assumes that the male has a activity center within the territory that is fixed during a given breeding season, but is subject to variation between breeding seasons. The center of activity might reflect the song post or the nesting site of the territorial male, and the song post or the nesting site may be fixed in a given breeding season but may change from breeding season to breeding season, irrespectively of whether it is the same male that occupies the territory in the two breeding seasons. Further, the observed positions of territorial males during territory mapping are subject to variation within breeding seasons. This is simply because territorial males may change their positions between the J visits that are conducted during the single breeding seasons. Note, that it is variation within breeding seasons that determines what is usually considered as territory size. The number of territorial males that were observed during the study depends on local survival, territory colonization and detection probability, and was simulated under the territory occupancy model described above. In summary, our simulation routine can be described in four steps:

1. Determine the location of each territory in the study site by using a uniform distribution of patch coordinates and a minimal distance between territories.
2. Simulate the activity centers of the males that occupy the territories ('between year variation of activity centers').
3. Given the position of the activity centers in one year, simulate for each visit the positions of the male that occupies the territory ('between visit variation of positions of males').

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4. Given local survival ϕ_i , territory colonization r_i and detection probability p , simulate the number of times a male in territory i and breeding season t is observed.

See Appendix S.3.9 of the supplementary material for an R-function to simulate territory-mapping data with the described simulation routine. We considered three scenarios to investigate the bias and precision of the parameter estimates. First, we simulated ‘stable territories’ with no between-year variation of activity centers (i.e. $\sigma^{year} = 0$, see Appendix S.3.8) and with little movement of territorial males between visits ($\sigma^{ind} = 10$, see Appendix S.3.8). Second, we simulated ‘rather stable territories’ with little between-year variation of activity centers (i.e. $\sigma^{year} = 10$) and with intermediate movement of territorial males between visits ($\sigma^{ind} = 20$). Third, we simulated ‘unstable territories’ with large between-year variation of activity centers (i.e. $\sigma^{year} = 20$) and with large movement of territorial males between visits ($\sigma^{ind} = 30$). See Fig. 3.1 for example data that were simulated under the three scenarios.

We aimed to simulate a realistic study of a songbird in a study site of 3km x 3km. We used the following specification for each of the 100 performed simulations for each of the three scenarios. The specification was used to reflect a typical field study using territory mapping technique (Kéry and Schmid 2006, Baillie et al. 2009, Roth and Amrhein 2010). The study lasted for $T = 8$ breeding seasons. Each breeding season, the study site was visited $J = 5$ times for mapping territorial males, and territorial males were detected with a probability of $p = 0.5$. We assumed that within the study site and during the entire study, there were $H = 100$ territories available for occupation with at least 100m distance between the territories. During the first study year, the territories were occupied with a probability of $\psi = 0.6$. Thereafter, each breeding season, some territorial males settled in the same territory as in the previous breeding season, with an average local survival probability of $\bar{\phi} = 0.6$ (Howlett and Stutchbury 2003, Roth and Amrhein 2010). Empty territories were colonized with an average probability of $\bar{r} = 0.3$ (Roth and Amrhein 2010). Both local survival and territory colonization varied among territories on the logit-scale, with $\phi_{SD} = r_{SD} = 0.2$. For running the territory-alignment algorithm, we used for each simulation a threshold distance $D = 200$ that was twice the minimal distance between territories (we tested the effect of the threshold distance on estimates of demographic parameters in a further simulation study, see below). For the Bayesian analyses of the territory occupancy

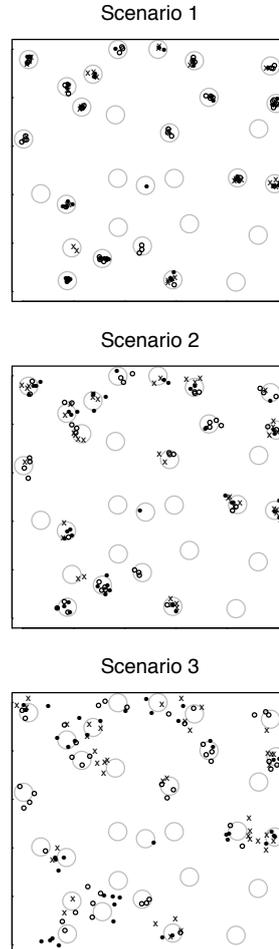


Figure 3.1: The three simulation scenarios - Example simulations showing the data of three years of territory-mapping, simulated according to three scenarios: stable territories with no between-year variation of activity centers and with little movement of territorial males between visits (Scenario 1, upper panel), rather stable territories with little between-year variation of activity centers and with intermediate movement of territorial males (Scenario 2, panel in the middle) and unstable territories with large between-year variation of activity centers and with large movements of territorial males between visits (Scenario 3, lower panel). The open circles, closed circles and the crosses indicate the observed positions of territorial males during territory mapping in the first, second and third study year, respectively. The large grey circles are the territories that need to be estimated using the described demographic monitoring routine. The data are simulated under the described simulation routine (see Appendix S.3.8) for $N = 30$ territories, with average local survival $\bar{\phi} = 0.6$, average territory colonization $\bar{r} = 0.3$, and with detection probability of $p = 0.5$. See text for further specification of the simulation.

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model, we assumed conventional diffuse prior distributions [i.e. $U(0,1)$ for ψ , $\bar{\phi}$, \bar{r} , p and ω ; $U(0.01,2)$ for ϕ_{SD} and r_{SD}].

	Bias	Coverage	CRI-length
<i>a) Scenario 1</i>			
$\bar{\phi}$	-0.03	0.96	0.21
\bar{r}	0.04	0.84	0.15
p	0.00	0.95	0.05
<i>b) Scenario 2</i>			
$\bar{\phi}$	-0.04	0.92	0.22
\bar{r}	0.04	0.79	0.15
p	0.00	0.94	0.05
<i>c) Scenario 3</i>			
$\bar{\phi}$	-0.12	0.48	0.25
\bar{r}	0.06	0.57	0.14
p	0.00	0.98	0.05

Table 3.1: Summary of 100 simulations according to each of three scenarios: a) stable territories with no between-year variation of activity centers and with little movement of territorial males between visits, b) rather stable territories with little between-year variation of activity centers and with intermediate movement of territorial males and c) unstable territories with large between-year variation of activity centers and with large movements of territorial males between visits. Given are the results for the parameters $\bar{\phi}$ (average local survival), \bar{r} (average colonization probability) and p (detection probability). Given are credible interval (CRI) coverage (the proportion of 100 simulation replicates that the 95% CRI contained the true parameter value), bias (difference between mean estimate minus true value), and CRI length (mean length of CRI). See text for the true parameter values used for simulation.

The results of our simulation studies demonstrated that our method of demographic monitoring (i.e. application of our model to data obtained in our territory-alignment method) is able to recover realistic estimates of local survival and territory colonization from data of unmarked individuals in bird monitoring programs, provided that territories are fairly stable over years and within-territory movement of males was low to intermediate only. Local survival tended to be biased low with little bias in the first two scenarios and intermediate bias in the third scenario (Table 3.1). Territory

colonization tended to be biased high with little bias in the first two scenarios and only slightly higher bias in the third scenario (Table 3.1). Detection probability was unbiased in all three scenarios. Therefore, our method of demographic monitoring may be applied mainly to species with territories that remain relatively stable from year to year. Such species with stable territories include species that defend areas including rare but spatially stable resources such as isolated habitat patches, nest cavities, or food resources.

In a second simulation study, we aimed to investigate the effect of the chosen threshold distance D on the parameter estimates. The threshold distance D is the maximum possible distance between two observations of a male that is occupying the same territory. We simulated data under scenario 2 above and used different values of D . Results show that except for very low values of D , estimates of local survival were unaffected by D (Fig. 3.2). In contrast, the estimates of territory colonization depended on the threshold distance D that was used for the analyses, and the bias slightly increased with increasing D (Fig. 3.2).

In a third simulation study, we investigated how the number of available territories (H) at the study site would affect the estimates of the demographic parameters. We simulated data under scenario 2 above and varied the number of available territories H . We found no effect of the number of territories (H) on the estimates of local survival or territory colonization. The bias in estimates of both demographic parameters remained constant (Fig. 3.3).

3.3.2 Analysis of Yellowhammer data

As a case study for our approach to demographic monitoring, we analyzed data from the long-term monitoring program on the common birds in Switzerland, the ‘Monitoring Häufige Brutvögel’ MHB (Kéry and Schmid 2004, Schmid et al. 2004). Launched in 1999, 267 squares of 1km^2 are laid out as a grid across the entire country and are surveyed each year using territory-mapping methods. Every square is visited 2-3 times in each breeding season. We analyzed a subsample of 100 squares for 2004-2009 and digitized the coordinates of each observed individual bird. We chose data from the Yellowhammer *Emberiza citrinella*, which is widespread in Switzerland in open landscapes (Schmid et al. 1998). The Yellowhammer has fairly well recognizable territories and should therefore not pose too many problems in terms of our model

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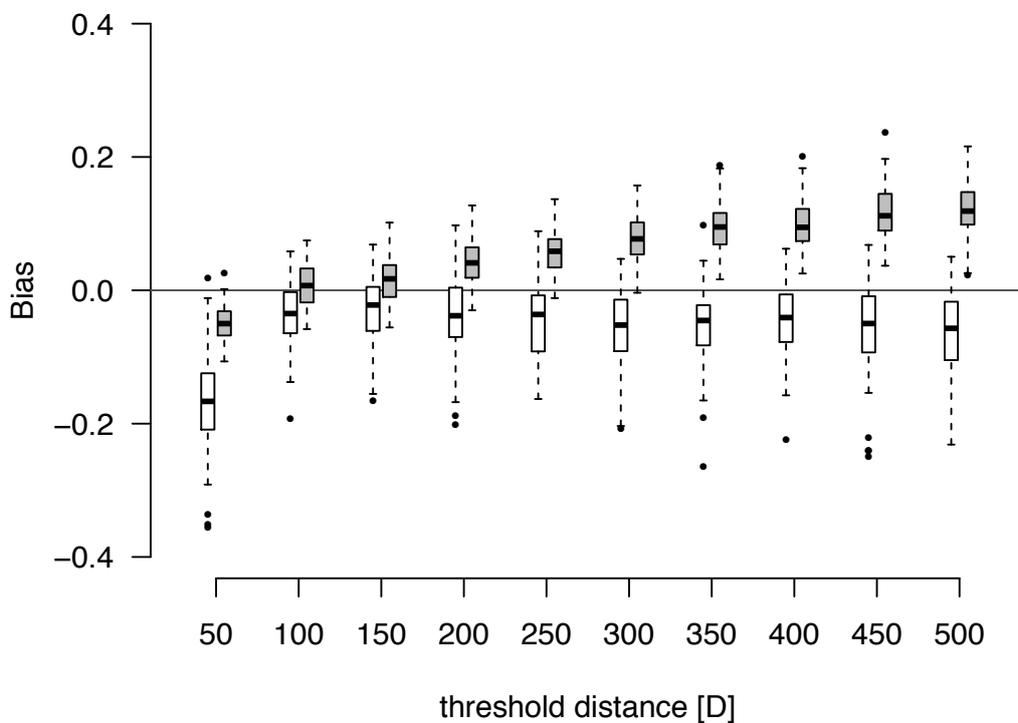


Figure 3.2: Effects of the threshold distance - The effects of the threshold distance (D) on the estimates of local survival (white boxes) and territory colonization (grey boxes). The threshold distance D is the maximal possible distance between two observations of a male that is occupying the same territory and needs to be defined to run the algorithm to obtain territory occupancy data from bird monitoring programs. Shown are boxplots of the bias for 100 simulations under scenario 2 (see text).

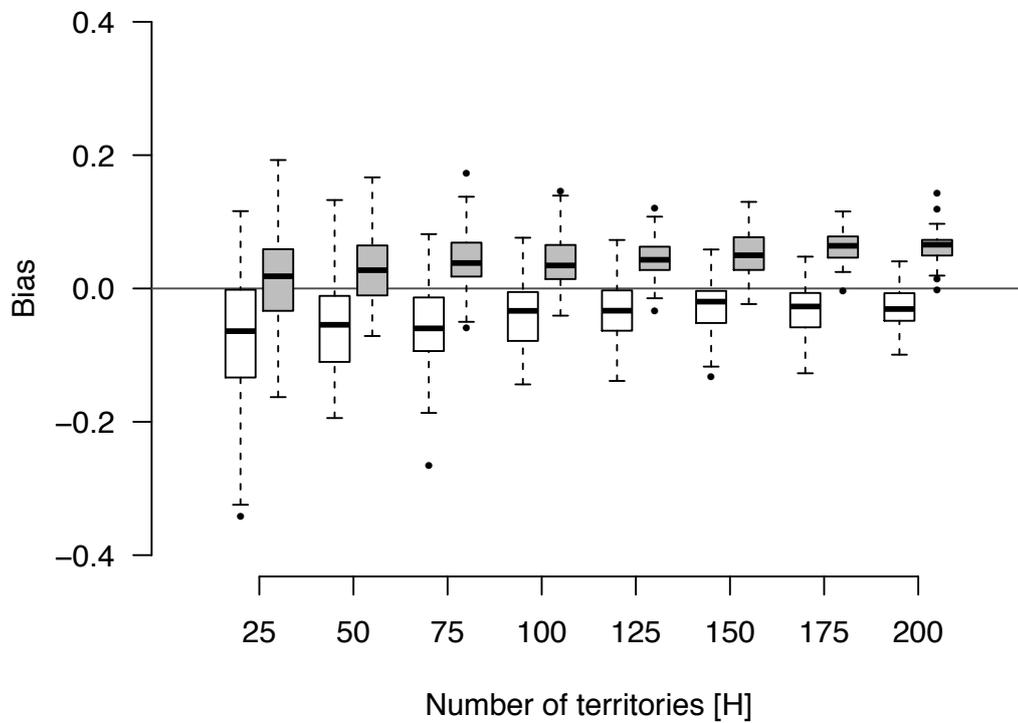


Figure 3.3: Effects of the number of territories - The effects of the number of territories (H) on the estimates of local survival (white boxes) and territory colonization (grey boxes). Shown are boxplots of the bias for 100 simulations under scenario 2 (see text).

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assumptions. Yellowhammers were observed in 58 squares, in which the mean \pm SD number of occupied territories per square and year was 4.0 ± 0.2 . We used our territory alignment algorithm to deduce territory occupancy data using a threshold distance $D = 200m$ to each of the 100 squares. The choice of the threshold distance D was based on a preliminary analysis of the five squares with the highest density of Yellowhammers where the maximal distance between two observations of a male that were presumably occupying the same territory was about 200m. We augmented the observed data in each square with 10 potential territories (see Data augmentation in earlier section).

We then aimed to analyze the territory occupancy data of the $k = 1, \dots, 100$ squares with the described territory occupancy model. Up to now, the territory occupancy data was formulated for a single study site, but now yellowhammer data are from 100 different sites. Therefore, we had to add an additional hierarchical layer to the occupancy model. We fitted a model where the average local survival of a square and the average territory colonization of a square, μ_ϕ and μ_r , respectively, were both related to the elevation (linear and squared; alt_k and alt_k^2) of square k and to its number of territories occupied at least once (N_k) according to

$$\text{logit}(\mu_{\phi,k}) = \alpha_0 + \alpha_1 alt_k + \alpha_2 alt_k^2 + \alpha_3 N_k \quad (3.7)$$

$$\text{logit}(\mu_{r,k}) = \beta_0 + \beta_1 alt_k + \beta_2 alt_k^2 + \beta_3 N_k \quad (3.8)$$

In eqn 3.7, α_0 is the intercept, α_1 is the linear, and α_2 the quadratic effect of altitude, and α_3 is the linear effect of the number of territories observed in square k . Similarly in equation 3.8, β_0 is the Intercept β_1 is the linear, and β_2 the quadratic effect of altitude, and β_3 is the linear effect of the number of territories observed in square k . Furthermore, the first-year occupancy probability was assumed to be different for each square k , i.e. Ψ_k . Likewise, the probability ω_k that a territory in the augmented list is part of the territories that are available for occupation was assumed to be different for each square.

The specification of the model was as follows: the study lasted for $T = 6$ breeding seasons (2004-2009). Each breeding season, the studied 100 squares were visited $J = 3$ times (except for high altitude squares with $J = 2$ visits). As in the simulation study, we adopted a Bayesian analysis of our territory-occupancy model using Markov chain Monte Carlo methods (MCMC; Link et al. 2002). We assumed conventional diffuse prior distributions [i.e. $U(0,1)$ for ψ_k , $\bar{\phi}_k$, \bar{r}_k , p and ω_k ; $U(0.01,2)$ for ϕ_{SD} and r_{SD} ;

Norm(0,1) for α_1 , α_2 , α_3 , β_1 , β_2 and β_3]. See Appendix S.3.10 for a description of the model in the BUGS language.

3.3.3 Results on the Yellowhammer

We found that local survival of Yellowhammers tended to increase with altitude (linear effect of altitude [α_1]: mean=0.79, 95%-credible interval CI=-0.17 – 1.66; quadratic effect of altitude [α_2]: mean=0.51, CI=-0.24 – 1.32; left panel of Fig. 3.4). In contrast, the probability of a Yellowhammer territory to be colonized decreased linearly with altitude, and thus territories were colonized at the highest rates in the lowlands (linear effect of altitude [β_1]: mean=-0.38, CI=-0.70 – -0.05; quadratic effect of altitude [β_2]: mean=0.05, CI=-0.29 – 0.29; right panel of Fig. 3.4). Thus, average local survival at the squares was negatively correlated with the average territory colonization of the squares ($r=-0.79$, $df=98$, $t=12.57$, $p<0.001$). The number of observed territories in a square may explain this negative correlation of local survival and territory colonization: local survival tended to decrease with the number of territories (α_3 : mean= -0.10, CI=-0.21 – 0.04), whereas territory colonization increased with the density of territories (β_3 : mean= 0.12, CI= 0.08 – 0.16).

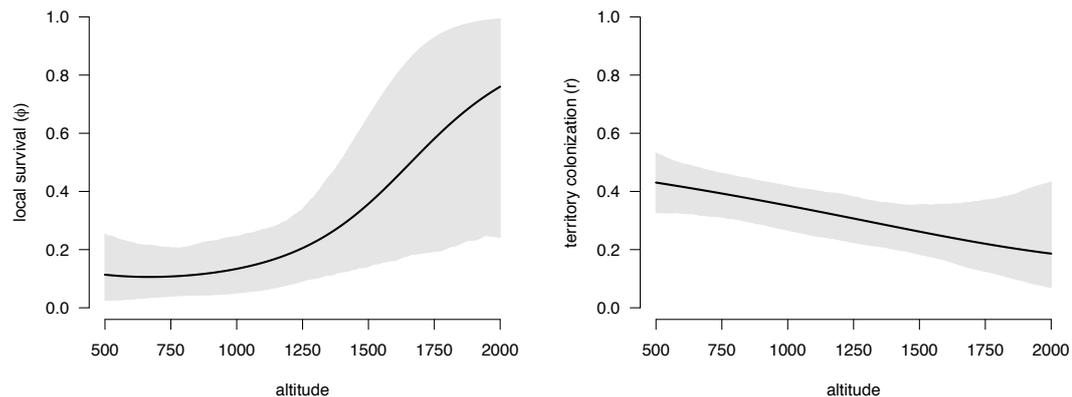


Figure 3.4: Results of the Yellowhammer study - Estimates of local survival (left panel) and territory colonization (right panel) over different altitudes obtained from territory mapping data of Yellowhammer from the Swiss Common Bird Census (MHB). Shown are the regression lines (bold lines) and the 95% credible interval of the regression lines (grey shade) for squares with 10 territories that are available for occupation..

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3.4 Discussion

We presented and tested a new framework for exploring the spatial configuration of occupied territories provided by bird monitoring programs to obtain estimates on local survival and territory colonization of the studied species. Applying our framework on the data of unmarked Yellowhammers from the nation-wide common bird census in Switzerland, we found that territories were colonized at the highest rate in the lowlands, while local survival increased with altitude. These estimates on demographic rates could not be predicted from the altitudinal patterns of Yellowhammer abundance, which shows highest densities at low altitudes (Maumary et al. 2007). By providing information on demographic rates, our demographic monitoring framework thus considerably broadens the possibilities for inference based on data from large-scale bird monitoring programs.

Habitats with the highest densities of a species are usually assumed to be optimal for that species. However, local survival might be considered as reflecting habitat quality more directly than overall abundance. This is because individuals often use their own reproductive performance at a site to assess the current and expected future quality of the habitat, and respond by returning or not returning to the same site (Hoover 2003, Howlett and Stutchbury 2003, Sergio and Newton 2003). Thus, high local survival should indicate habitats of high quality. The analysis on the Yellowhammer, however, revealed that average local survival was low in lowlands, where territory colonization rate and density of Yellowhammers were highest. Such a pattern could potentially be explained if lowland habitat were to function as ecological trap, in which individuals preferentially settle despite its relatively low quality (Robertson and Hutto 2006). In Switzerland, ecological compensated areas have been mainly implemented in the intensively used agricultural land in the lowlands, and they provide new habitat in which Yellowhammers prefer to establish their territories (Herzog et al. 2005, Birrer et al. 2007). Whether or not ecological compensated areas could act as ecological traps for Yellowhammers could be explored in experimental studies (Robertson and Hutto 2006).

Survival rates are usually obtained from capture-recapture data on individually marked animals (Lebreton et al. 1992, Sandercock 2006). However, marking individuals and reencounter them is often invasive and labor intensive and is rarely used in the frame of large-scale monitoring programs (but see Saracco et al. 2010). Most of the

currently known non-invasive methods to estimate demographic rates rely on individual recognition based on morphological characters (Meekan et al. 2006) or songs and calls (Vögeli et al. 2008), or based on hair samples using genetic techniques (Kéry et al. 2011). In our new demographic monitoring framework, the spatial locations of territories can be seen as a new way to identify individuals (Manning and Goldberg 2010). Such a spatial recognition of territory holders is of course prone to error, because different individuals may occupy different territories during consecutive breeding seasons. Traditional capture-recapture models are based on the assumption that there are no errors in recognition of individuals, and could thus not be used in our framework. In contrast, our territory occupancy model accounts for imperfect recognition of individuals by including the territory colonization probability: errors in individual recognition could occur when an individual occupies a territory that was previously occupied by another individual. Thus, the territory colonization probability as estimated from our model can be regarded as the nuisance parameter accounting for imperfect recognition of territory holders, allowing for estimates of local survival that are corrected for imperfect individual recognition.

In most territorial species, it is usually the males that are more conspicuous than the females and the males actively advertise their territories (Andersson 1994). Therefore, mainly the males are surveyed in monitoring programs, and our model is likely to estimate only local survival of males (Roth and Amrhein 2010). However, the advantage of applying our demographic monitoring framework to national bird monitoring programs is that bird monitoring programs have probably covered the largest spatial and temporal scales worldwide (Robbins et al. 1989, Julliard et al. 2006, Baillie et al. 2009). Thus, local survival can now be investigated on large spatial and temporal scales.

Much effort is currently focused on predicting the impact of climate change on populations of animals and plants (Walther et al. 2002, Parmesan 2006). It is therefore necessary to understand how the demographic parameters of a population are affected by variation in ambient temperatures. Studies on intraspecific variation in demographic parameters across altitudes offer a particularly useful tool for predicting population responses to a warming world, and demographic studies across multiple ranges of altitude are urgently needed (Kim and Donohue 2011). At least for birds, however, few studies

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have considered variation in demographic parameters in relation to altitude (Chamberlain et al. 2012). Our territory occupancy model for analyzing the Yellowhammer data was parameterized using a hierarchical modeling approach (Gelman and Hill 2007) to provide estimates on 100 different sites (1km squares) from Switzerland. Under the hierarchical modeling approach, we were able to obtain altitude-specific estimates on local survival and on territory colonization for the Yellowhammer by combining all of the data within a single model. Thus, applying our hierarchical territory occupancy model on data from bird monitoring programs covering large altitudinal (Kéry and Schmid 2006) or latitudinal ranges (Baillie et al. 2009) could provide estimates on geographic variation in demographic parameters that are urgently needed to understand the effects of climate change on population performance. We thus hope that the presented demographic monitoring framework will help to inform resource managers and policy makers by providing information on large-scale demographic rates.

3.5 Acknowledgements

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3.6 Literature Cited

- Andersson, M. 1994. Sexual selection. Princeton University Press, Princeton.
- Baillie, S. R., J. H. Marchant, D. I. Leech, A. C. Joys, D. G. Noble, C. Barimore, M. J. Grantham, K. Risely, and R. A. Robinson. 2009. Breeding Birds in the Wider Countryside: their conservation status 2008. BTO Research Report. BTO, Thetford.
- Birrer, S., M. Spiess, F. Herzog, M. Jenny, L. Kohli, and B. Lugin. 2007. The Swiss agri-environment scheme promotes farmland birds: but only moderately. *Journal of Ornithology* 148:S295-S303.

- Chamberlain, D. A. N., R. Arlettaz, E. Caprio, R. Maggini, P. Pedrini, A. Rolando, and N. Zbinden. 2012. The altitudinal frontier in avian climate impact research. *Ibis* 154:205-209.
- Desante, D. F., M. P. Nott, and D. R. O'Grady. 2001. Identifying the proximate demographic cause(s) of population change by modelling spatial variation in productivity, survivorship, and population trends. *Ardea* 89:185-207.
- Gaston, K. J. and R. A. Fuller. 2008. Commonness, population depletion and conservation biology. *Trends in Ecology & Evolution* 23:14-19.
- Gelman, A. and J. Hill. 2007. *Data Analysis Using Regression and Multilevel/Hierarchical Models*. Cambridge University Press, Cambridge.
- Gilks, W. R., A. Thomas, and D. J. Spiegelhalter. 1994. A language and program for complex Bayesian modelling. *Statistician* 43:169-178.
- Greenwood, J. J. D. and R. A. Robinson. 2006. *General census methods. Ecological Census Techniques*. 2nd edition. University Press, Cambridge.
- Gregory, R. D., S. G. Willis, F. Jiguet, P. Vorisek, A. Klvanova, A. van Strien, B. Huntley, Y. C. Collingham, D. Couvet, and R. E. Green. 2009. An Indicator of the Impact of Climatic Change on European Bird Populations. *Plos One* 4.
- Herzog, F., S. Dreier, G. Hofer, C. Marfurt, B. Schupbach, M. Spiess, and T. Walter. 2005. Effect of ecological compensation areas on floristic and breeding bird diversity in Swiss agricultural landscapes. *Agriculture Ecosystems & Environment* 108:189-204.
- Hoover, J. P. 2003. Decision rules for site fidelity in a migratory bird, the prothonotary warbler. *Ecology* 84:416-430.
- Howlett, J. S. and B. J. M. Stutchbury. 2003. Determinants of between-season site, territory, and mate fidelity in hooded warblers (*Wilsonia citrina*). *Auk* 120:457-465.
- Julliard, R., J. Clavel, V. Devictor, F. Jiguet, and D. Couvet. 2006. Spatial segregation of specialists and generalists in bird communities. *Ecology Letters* 9:1237-1244.

3. DEMOGRAPHIC MONITORING USING DATA OF BIRD MONITORING PROGRAMS

- Kendall, W. L., J. D. Nichols, and J. E. Hines. 1997. Estimating temporary emigration using capture-recapture data with Pollock's robust design. *Ecology* 78:563-578.
- Kéry, M., B. Gardner, T. Stoeckle, D. Weber, and J. A. Royle. 2011. Use of Spatial Capture-Recapture Modeling and DNA Data to Estimate Densities of Elusive Animals. *Conservation Biology* 25:356-364.
- Kéry, M. and H. Schmid. 2004. Monitoring programs need to take into account imperfect species detectability. *Basic and Applied Ecology* 5:65-73.
- Kéry, M. and H. Schmid. 2006. Estimating species richness: calibrating a large avian monitoring programme. *Journal of Applied Ecology* 43:101-110.
- Kim, E. and K. Donohue. 2011. Demographic, developmental and life-history variation across altitude in *Erysimum capitatum*. *Journal of Ecology* 99:1237-1249.
- Lebreton, J. D., K. P. Burnham, J. Clobert, and D. R. Anderson. 1992. Modeling survival and testing biological hypotheses using marked animals - a unified approach with case studies. *Ecological Monographs* 62:67-118.
- Link, W. A. and R. J. Barker. 2005. Modeling association among demographic parameters in analysis of open population capture-recapture data. *Biometrics* 61:46-54.
- Link, W. A., E. Cam, J. D. Nichols, and E. G. Cooch. 2002. Of BUGS and birds: Markov chain Monte Carlo for hierarchical modeling in wildlife research. *Journal of Wildlife Management* 66:277-291.
- Link, W. A. and J. R. Sauer. 1998. Estimating population change from count data: Application to the North American Breeding Bird Survey. *Ecological Applications* 8:258-268.
- Lunn, D., D. Spiegelhalter, A. Thomas, and N. Best. 2009. The BUGS project: Evolution, critique and future directions. *Statistics in Medicine* 28:3049-3067.
- MacKenzie, D. I., J. D. Nichols, J. E. Hines, M. G. Knutson, and A. B. Franklin. 2003. Estimating site occupancy, colonization, and local extinction when a species is detected imperfectly. *Ecology* 84:2200-2207.

- MacKenzie, D. I., J. D. Nichols, J. A. Royle, K. H. Pollock, L. L. Bailey, and J. E. Hines. 2006. *Occupancy Estimation and Modeling. Inferring Patterns and Dynamics of Species Occurrence.* Elsevier Inc., Burlington.
- Maggini, R., A. Lehmann, M. Kéry, H. Schmid, M. Beniston, L. Jenni, and N. Zbinden. 2011. Are Swiss birds tracking climate change? Detecting elevational shifts using response curve shapes. *Ecological Modelling* 222:21-32.
- Manning, J. A. and C. S. Goldberg. 2010. Estimating population size using capture–recapture encounter histories created from point-coordinate locations of animals. *Methods in Ecology and Evolution* 1:389-397.
- Maumary, L., L. Vallotton, and P. Knaus. 2007. *Die Vögel der Schweiz. Schweizerische Vogelwarte, Sempach and Nos Oiseaux.*, Montmollin.
- Meekan, M. G., C. J. A. Bradshaw, M. Press, C. McLean, A. Richards, S. Quasnichka, and J. G. Taylor. 2006. Population size and structure of whale sharks *Rhincodon typus* at Ningaloo Reef, Western Australia. *Marine Ecology-Progress Series* 319:275-285.
- Newton, I. 1992. Experiments on the limitation of bird numbers by territorial behavior. *Biological Reviews of the Cambridge Philosophical Society* 67:129-173.
- Norris, K. 2004. Managing threatened species: the ecological toolbox, evolutionary theory and declining-population paradigm. *Journal of Applied Ecology* 41:413-426.
- Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology Evolution and Systematics* 37:637-669.
- Robbins, C. S., J. R. Sauer, R. S. Greenberg, and S. Droege. 1989. Population Declines in North-American Birds That Migrate to the Neotropics. *Proceedings of the National Academy of Sciences of the United States of America* 86:7658-7662.
- Robertson, B. A. and R. L. Hutto. 2006. A framework for understanding ecological traps and an evaluation of existing evidence. *Ecology* 87:1075-1085.

3. DEMOGRAPHIC MONITORING USING DATA OF BIRD MONITORING PROGRAMS

- Roth, T. and V. Amrhein. 2010. Estimating individual survival using territory occupancy data on unmarked animals. *Journal of Applied Ecology* 47:386-392.
- Royle, J. A., R. M. Dorazio, and W. A. Link. 2007. Analysis of multinomial models with unknown index using data augmentation. *Journal of Computational and Graphical Statistics* 16:67-85.
- Royle, J. A. and M. Kéry. 2007. A bayesian state-space formulation of dynamic occupancy models. *Ecology* 88:1813-1823.
- Sandercock, B. K. 2006. Estimation of demographic parameters from live-encounter data: a summary review. *Journal of Wildlife Management* 70:1504-1520.
- Saracco, J. F., D. F. Desante, and D. R. Kaschube. 2008. Assessing Landbird Monitoring Programs and Demographic Causes of Population Trends. *Journal of Wildlife Management* 72:1665-1673.
- Saracco, J. F., J. A. Royle, D. F. DeSante, and B. Gardner. 2010. Modeling spatial variation in avian survival and residency probabilities. *Ecology* 91:1885-1891.
- Schmid, H., R. Luder, B. Naef-Daenzer, R. Graf, and N. Zbinden. 1998. Schweizer Brutvogelatlas. Verbreitung der Brutvögel in der Schweiz und im Fürstentum Liechtenstein 1993-1996. Schweizerische Vogelwarte, Sempach, Switzerland.
- Schmid, H., N. Zbinden, and V. Keller. 2004. bewachung der Bestandsentwicklung hufiger Bruvögel in der Schweiz. Schweizerische Vogelwarte, Sempach, Switzerland.
- Sergio, F. and I. Newton. 2003. Occupancy as a measure of territory quality. *Journal of Animal Ecology* 72:857-865.
- van Strien, A. J., C. A. M. van Swaay, and M. Kéry. 2011. Metapopulation dynamics in the butterfly *Hipparchia semele* changed decades before occupancy declined in The Netherlands. *Ecological Applications* 21:2510-2520.
- Vögeli, M., P. Laiolo, D. Serrano, and J. L. Tella. 2008. Who are we sampling? Apparent survival differs between methods in a secretive species. *Oikos* 117:1816-1823.

3.6 Literature Cited

- Walther, G. R., E. Post, P. Convey, A. Menzel, C. Parmesan, T. J. C. Beebee, J. M. Fromentin, O. Hoegh-Guldberg, and F. Bairlein. 2002. Ecological responses to recent climate change. *Nature* 416:389-395.
- Yoccoz, N. G., J. D. Nichols, and T. Boulinier. 2001. Monitoring of biological diversity in space and time. *Trends in Ecology & Evolution* 16:446-453.

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S.3.7 R-function for estimating territory occupancy data

R-function for estimating territory occupancy data from bird monitoring programs using territory mapping methods. The following arguments should be provided to the `align()`-function:

<code>obs.data</code>	data.frame with two columns that contains the observed positions of territorial males
<code>put.ter</code>	id of the occupied territory (p in the manuscript) for all positions of territorial males in <code>obs.data</code> .
<code>year</code>	year for all positions of territorial males in <code>obs.data</code>
<code>D</code>	The threshold distance D that is the maximal possible distance between two observations of a male that is occupying the same territory.

The `align()`-function returns the following results:

<code>Y[i,t]</code>	Observed territory occupancy data for territory i and year t
---------------------	--

```
# R-FUNCTION FOR ESTIMATING TERRITORY OCCUPANCY DATA
align <- function(obs.data, put.ter, year, D) {
### Estimate the centres of the occupied territories and count the total
### number of observations in that territory
ter <- data.frame(list(
terID = names(tapply(obs.data[,1], put.ter, mean)),
year = tapply(year, put.ter, mean),
x = tapply(obs.data[,1], put.ter, mean),
y = tapply(obs.data[,2], put.ter, mean),
obs = table(put.ter)
))
ter$terID <- as.integer(ter$terID)
ter <- ter[order(ter$terID),]

### Calculate the distances between all territories.
dist <- data.frame(matrix(NA, nrow=nrow(ter), ncol=nrow(ter)))
x <- ter$x
```

S.3.7 R-function for estimating territory occupancy data

```
y <- ter$y
for(t.y in 2:nrow(ter)) {
  for(t.x in 1:(t.y-1)) {
    ### Note: if territories are recorded during the same year the distance
    ### between these territories remains 'NA'
    if(ter$year[t.y] != ter$year[t.x]) dist[t.y,t.x]
    <- sqrt((x[t.x]-x[t.y])*(x[t.x]-x[t.y]) + (y[t.x]-y[t.y])*(y[t.x]-y[t.y]))
  }
}

### Prepare a list; in that list we will note all the occupied territories
### from territory mapping in the different years that belong to the same
### territory.
terlist <- list()
for(t in 1:nrow(ter)) terlist[t] <- ter$terID[t]

### Calculate the maximum number of occupied territories per year and set
N
ex <- max(apply(table(ter$year, ter$terID)>0, 1, sum))
N <- nrow(ter)

### Start alignment algorithm
while(ifelse(sum(!is.na(dist))==0, FALSE, min(dist, na.rm=T) < D & N>ex))
{
  ### Get the two territories with minimal distances
  fuse <- which(dist==min(dist, na.rm=T), arr.ind=T)[1,]
  ### get all the putative territories that are already allocated to these
  ### two territories
  to_fuse_ter <- c(unlist(terlist[min(fuse)]),unlist(terlist[max(fuse)]))
  ### Make sure that the territories that should be fused are all from
  ### different years
  ausw <- rep(FALSE, nrow(ter))
  for(ii in to_fuse_ter) ausw[ter$terID==ii] <- TRUE
}
```

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```
fuseOK <- sum(table(ter$year[ausw])>1)==0
### Fuse territories if all territories are from different years
if(fuseOK) {
  terlist[[min(fuse)]] <- to_fuse_ter
  ter$terID[ter$terID == max(fuse)] <- min(fuse)
  dist[unlist(terlist[[max(fuse)]]),] <- NA
  dist[,unlist(terlist[[max(fuse)]])] <- NA
  for(k in 2:length(unlist(terlist[[min(fuse)]]))) {
    dist[min(fuse), ter$year==ter[terlist[[min(fuse)]] [k], "year"]] <- NA
    dist[ter$year==ter[terlist[[min(fuse)]] [k], "year"], min(fuse)] <- NA
  }
}
### If territories should not be fused set distance between the two
### territories to 'NA'
if(!fuseOK) {
  dist[unlist(terlist[[max(fuse)]]),] <- NA
  dist[,unlist(terlist[[max(fuse)]])] <- NA
  if(length(unlist(terlist[[min(fuse)]]))>1) {
    for(k in 2:length(unlist(terlist[[min(fuse)]]))) {
      dist[min(fuse), ter$year==ter[terlist[[min(fuse)]] [k], "year"]] <- NA
      dist[ter$year==ter[terlist[[min(fuse)]] [k], "year"], min(fuse)] <- NA
    }
  }
}

### Make observed territory occupancy data (Y[i,t])
ter$terID <- as.integer(factor(ter$terID))
Y <- data.frame(matrix(0, nrow=length(unique(ter$terID)), ncol=max(ter$year)))
for(t in 1:max(ter$year)) Y[ter[ter$year==t, "terID"], t] <- ter[ter$year==t,
"obs.Freq"]

### Return results
```

S.3.7 R-function for estimating territory occupancy data

```
list(ter=ter, Y=Y)  
}
```

3. DEMOGRAPHIC MONITORING USING DATA OF BIRD MONITORING PROGRAMS

S.3.8 Description of the simulation

In this supplement, we developed a model to simulate data from a bird monitoring program using territory-mapping techniques. We will use that model to simulate data and test our procedures for demographic monitoring described in the main body of the manuscript.

Description of simulation model

Suppose that a population of a territorial species is sampled using territory mapping methods (Bibby et al. 2000) during $j = 1, \dots, J$ visits within a breeding season. During each visit, the location of every visual or acoustic contact with a territorial (i.e. usually singing) male of the surveyed species is mapped. The observed positions of territorial males from all visits during a given year are combined and clustered to territories based on the knowledge of species-specific territory size and the clustering of observations (Kéry and Schmid 2006, Gottschalk and Huettmann 2011). Let assume that within the study site, $i = 1, \dots, N$ territories are available for occupation, and N remains constant over the entire study. Let further assume that each territory has a position (i.e. the centre of the territory) within the study site that is fixed during the entire study. Furthermore, let assume that each male occupying a territory has an activity center where the male is most likely to be observed. The activity center of a male is not necessarily in the center of its territory, and the position of the activity centers of the males may also change from breeding season to breeding season. Denote the centers of the territories $S(x/y - coordinates)_i$ as the two-dimensional matrix that contains the x- and y-coordinates of the centres of the $i = 1, \dots, N$ territories. Further, denote the activity centres $A(x/y - coordinates)_i$ as the three-dimensional matrix that contains the x- and y-coordinates of the male that occupies territories i during breeding season $t = 1, \dots, T$. We assume that the activity centres $A(x/y - coordinates)_{i,t}$ of the males vary from the centers of the territories $S(x/y - coordinates)_i$ with a Normal distribution and standard deviation σ^{year} . Furthermore, the positions of the territorial males vary around the activity centers $A(x/y - coordinates)_{i,t}$ with a normal distribution and standard deviation σ^{ind} .

For the data simulation, we first assume that all N territories were occupied during the entire study of T breeding seasons and were always detected during the J visits.

S.3.8 Description of the simulation

We therefore simulate $V = N \times T \times J$ observations of territorial males. Denote the observations $P(x/y - coordinates)_v$ as the two-dimensional matrix that contains the x- and y-coordinates of all $v = 1, \dots, N \times T \times J$ positions of territorial males. Then the observations $P(x/y - coordinates)_v$ are given by

$$A(x/y - coordinates)_{i,t} \sim Norm(S(x/y - coordinates)_i, \sigma^{year}) \quad (3.9)$$

$$P(x/y - coordinates)_v \sim Norm(A(x/y - coordinates)_{i,t}, \sigma^{ind}) \quad (3.10)$$

Since territories are not always occupied and males of occupied territories are not always detected, we now describe which of all the possible observations $P(x/y - coordinates)_v$ were indeed observed. The simulation routine has to account for two different patterns. First, it is only possible to observe a territorial male when the territory is occupied, and whether a territory is occupied depends on the demography of the population. Second, also if a territory is occupied, the male of the territory may be not observed. Denote $X_{i,t}$ as the true territory occupancy state of territory $i = 1, \dots, N$ during the breeding seasons $t = 1, \dots, T$. If territory i during breeding season t is occupied, then $X_{i,t} = 1$; otherwise $X_{i,t} = 0$. We assume that during the first breeding season of the study, a territory i is occupied with probability ψ , thus

$$X_{i,1} \sim Bernoulli(\psi) \quad (3.11)$$

We assume that the territory occupancies after the first breeding season are the result of two demographic processes. The first is the probability of individual survival and continued tenancy of a territory by its owner, which we define as local survival, because it includes both actual survival and territory fidelity (Roth and Amrhein 2010). The second process includes the probability that an empty territory is colonized. Let the parameter $\phi_{i,t}$ be the local survival probability of a territory owner in territory i from breeding season $t - 1$ to t , and let $r_{i,t}$ be the colonization probability of a territory i in breeding season t given that the territory is not occupied. Then the territory occupancy $X_{i,t}$ for the breeding season $t = 2, \dots, T$ is described in two steps

$$Z_{i,t} \sim Bernoulli(\phi_{i,t}X_{i,t-1}) \quad (3.12)$$

$$X_{i,t} \sim Bernoulli(Z_{i,t} + r_{i,t}(1 - Z_{i,t})) \quad (3.13)$$

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Eqn 3.12 describes the survival of a male from one breeding season to next breeding season. The state variable $Z_{i,t}$ denotes the territory fidelity of a male: if territory i is occupied at time t by the same male as at time $t - 1$ then $Z_{i,t} = 1$, otherwise $Z_{i,t} = 0$. Eqn 3.13 describes the colonization of the territory if the territory was not reoccupied by the male from the previous breeding season.

In the simulation model, we also acknowledge that territories may differ in quality (Hoover 2003, Howlett and Stutchbury 2003), and thus local survival $\phi_{i,t}$ and territory colonization $r_{i,t}$ may vary between territories. We assumed that the variation among territories is described by a normal distribution with a correlation ρ between local survival $\phi_{i,t}$ and territory colonization $r_{i,t}$. In real world data, would may expect the correlation ρ between local survival $\phi_{i,t}$ and territory colonization $r_{i,t}$ to be positive because an individual in a territory of high quality will be more likely to return to the same territory than an individual in a territory of low quality, and similarly a territory of high quality is more likely to be colonized by a new individual than a territory of low quality.

$$\phi_{i,t} \sim Norm(\bar{\phi}, \Sigma) \quad (3.14)$$

$$r_{i,t} \sim Norm(\bar{r}, \Sigma) \quad (3.15)$$

$$\text{with } \Sigma = \begin{pmatrix} \phi_{SD}^2 & \rho\phi_{SD}r_{SD} \\ \rho\phi_{SD}r_{SD} & r_{SD}^2 \end{pmatrix} \quad (3.16)$$

We now have described the generation of the territory occupancy data $X_{i,t}$ that depends on the demographic parameters local survival $\phi_{i,t}$ and the colonization probability $r_{i,t}$. When applying territory-mapping methods, the location of a territorial male can be observed only if a territory is occupied, i.e. if $X_{i,t} = 1$. However, even if the territory is occupied, in some instances the territorial male may be overlooked and thus its position is not recorded. Denote I_v as a logical variable indicating whether one of all the $v = 1 \dots, N \times T \times J$ possible observation $P(x/y - \text{coordinates})_v$ was indeed observed (i.e. $I_v = 1$) or remains a potential observation (i.e. $I_v = 0$). Let define p as the probability that an individual of an occupied territory is detected, then

$$I_v \sim Bernoulli(pX_{i,t}) \quad (3.17)$$

Thus, the data of territory mapping methods are all potential observations $P(x/y - \text{coordinates})_v$ with $I_v = 1$. In Appendix S.3.9, we give a function written

in the software R (R Development Core Team 2010) that simulates data using the described data model.

Literature Cited

- Bibby, C.-J., N. D. Burgess, D. A. Hill, and S. H. Mustoe. 2000. Bird census techniques. Academic Press, London and San Diego.
- Clark, J. S. and O. N. Bjornstad. 2004. Population time series: Process variability, observation errors, missing values, lags, and hidden states. *Ecology* 85:3140-3150.
- Gottschalk, T. K. and F. Huettmann. 2011. Comparison of distance sampling and territory mapping methods for birds in four different habitats. *Journal of Ornithology* 152:421-429.
- Hoover, J. P. 2003. Decision rules for site fidelity in a migratory bird, the prothonotary warbler. *Ecology* 84:416-430.
- Howlett, J. S. and B. J. M. Stutchbury. 2003. Determinants of between-season site, territory, and mate fidelity in hooded warblers (*Wilsonia citrina*). *Auk* 120:457-465.
- Kéry, M. and H. Schmid. 2006. Estimating species richness: calibrating a large avian monitoring programme. *Journal of Applied Ecology* 43:101-110.
- R Development Core Team. 2010. R: A language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
- Roth, T. and V. Amrhein. 2010. Estimating individual survival using territory occupancy data on unmarked animals. *Journal of Applied Ecology* 47:386-392.

3. DEMOGRAPHIC MONITORING USING DATA OF BIRD MONITORING PROGRAMS

S.3.9 R-function to simulate data

R-function to simulate data under the simulation routine described in Supplement S.3.8

The following arguments should be provided to the `sim()`-function

N	The fixed number of available territories in the study site.
T	The number of studied breeding seasons.
J	The number of visits per breeding season.
psi1	The probability that a territory is occupied in the first breeding season.
phi_mean	The average local survival.
phi_sd	The standard deviation of the variation in local survival between territories.
r_mean	The average territory colonization.
r_sd	The standard deviation of the variation in territory colonization between territories.
roh	The correlation between local survival and territory colonization.
p	The detection probability.
sd_year	The variation (SD) of activity centres around the 'hyper territory centres'.
sd_ind	The variation (SD) of potential observations around the activity centres.
min_dist	The minimal distance between the 'hyper territory centres'.
size_site	The size of the (squared) study site in meter.

```
# R-FUNCTION TO SIMULATE DATA
sim <- function(N, T, J, psi1, phi_mean, phi_sd, r_mean, r_sd, roh, p, sd_year,
sd_ind, min_dist, size_site) {

### Load libraries
library(MASS)
```

S.3.9 R-function to simulate data

```
### Define data structures
S <- array(NA, dim=c(N,2))
A <- array(NA, dim=c(N,T,2))
P <- array(NA, dim=c(N*T*J,2))
X <- array(NA, dim=c(N,T))
Z <- array(NA, dim=c(N,T))
I <- rep(NA, N*T*J)
year <- rep(NA, N*T*J)
putative_ter <- rep(NA, N*T*J)

### Simulate positions of centres of territories in study site
S[1,1] <- runif(1, 0, size_site)
S[1,2] <- runif(1, 0, size_site)
i <- 2
while(i <= N) {
  x_next <- runif(1,0, size_site)
  y_next <- runif(1,0, size_site)
  if(f_min_dist(S[1:(i-1),1],S[1:(i-1),2],x_next, y_next)>min_dist) {
    S[i,1] <- x_next
    S[i,2] <- y_next
    i <- i+1
  }
}

### Simulate activity centres of males for all years
for(t in 1:T) {
  A[,t,1] <- rnorm(N, S[,1], sd_year)
  A[,t,2] <- rnorm(N, S[,2], sd_year)
}

### Simulate all possible observations and make a territory index c for each
### observation that is unique for each activity centre
counter <- 1
```

3. DEMOGRAPHIC MONITORING USING DATA OF BIRD MONITORING PROGRAMS

```
territory_index <- 1
for(i in 1:N) {
  for(t in 1:T) {
    for(j in 1:J) {
      P[counter,1] <- rnorm(1, A[i,t,1], sd_ind)
      P[counter,2] <- rnorm(1, A[i,t,2], sd_ind)
      putative_ter[counter] <- territory_index
      counter <- counter + 1
    }
    territory_index <- territory_index +1
  }
}

### Simulate phi and r for each territory
COV <- roh * phi_sd * r_sd
lphi_mean <- log(phi_mean/(1-phi_mean))
lr_mean <- log(r_mean/(1-r_mean))
var.cov.matrix <- matrix(c(phi_sd*phi_sd, COV, COV, r_sd*r_sd),2,2)
temp.dat <- mvrnorm(n=N, mu=c(lphi_mean, lr_mean), Sigma=var.cov.matrix)
phi <- exp(temp.dat[,1])/(1+exp(temp.dat[,1]))
r <- exp(temp.dat[,2])/(1+exp(temp.dat[,2]))

### Simulate territory occupancies
X[,1] <- rbinom(N, 1, psi1)
for(t in 2:T) {
  Z[,t] <- rbinom(N, 1, X[,t-1]*phi)
  X[,t] <- rbinom(N, 1, Z[,t]+(1-Z[,t])*r)
}

### Simulate logical vector that indicates whether the location of a
### potential observation is observed
counter <- 1
for(i in 1:N) {
```

```

for(t in 1:T) {
for(j in 1:J) {
I[counter] <- rbinom(1, 1, X[i,t]*p)
year[counter] <- t
counter <- counter + 1
}
}
}

### Return true observations data, i.e. all P[v] with I[v]==1, as well as
the
### year in which a true observation was observed, an Index to which of the
### occupied territory an observation belongs to and the true territory
### occupancy data X[i,t]
list(obs.data=P[I==1,], year=year[I==1], put.ter=putative_ter[I==1], X=X,
S=S)
}

### Help-function to get minimum distance from one point (xpoint,ypoint)
to
### all other points (xkoord, ykoord)
f_min.dist <- function(xkoord, ykoord, xpoint, ypoint) {
res <- numeric()
for(i in 1:length(xkoord)) {
res[i] <- sqrt((xkoord[i]-xpoint)*(xkoord[i]-xpoint)
+ (ykoord[i]-ypoint)*(ykoord[i]-ypoint))
}
min(res)
}

```

3. DEMOGRAPHIC MONITORING USING DATA OF BIRD MONITORING PROGRAMS

S.3.10 WinBUGS model description

WinBUGS model description to estimate the demographic parameters from the observed territory occupancy data of Yellowhammer (*Emberiza citrinella*).

```
# TERRITORY OCCUPANCY MODEL FOR YELLOWHAMMER-DATA
model {

### Define Priors
###-----
phi ~ dunif(0,1)
alpha0 <- logit(phi)
alpha1 ~ dnorm(0,1)
alpha2 ~ dnorm(0,1)
alpha3 ~ dnorm(0,1)
phi_sd.i ~ dunif(0.01,2)
phi_prec.i <- 1/(phi_sd.i*phi_sd.i)

r ~ dunif(0,1)
beta0 <- logit(r)
beta1 ~ dnorm(0,1)
beta2 ~ dnorm(0,1)
beta3 ~ dnorm(0,1)
r_sd.i ~ dunif(0.01,2)
r_prec.i <- 1/(r_sd.i*r_sd.i)

p ~ dunif(0,1)
lp <- logit(p)
p_sd.i ~ dunif(0.01,2)
p_prec.i <- 1/(p_sd.i*p_sd.i)

# Square specific priors
for(k in 1:K) {
```

S.3.10 WinBUGS model description

```
psi1[k] ~ dunif(0,1)
omega[k] ~ dunif(0,1)
}

### Define parameters
###-----
# Site level
for(k in 1:K) {
# local survival
lphi_k[k] <- alpha0 + alpha1*alt1[k] + alpha2*alt2[k] + alpha3*(nter[k]-10)
# territory colonization
lr_k[k] <- beta0 + beta1*alt1[k] + beta2*alt2[k] + beta3*(nter[k]-10)
}
# Territory level
for(i in 1:M) {
# local survival
lphi_i[i] ~ dnorm(lphi_k[site[i]], phi_prec_i)I(-100,100)
logit(phi_i[i]) <- lphi_i[i]
# territory colonization
lr_i[i] ~ dnorm(lr_k[site[i]], r_prec_i)I(-100,100)
logit(r_i[i]) <- lr_i[i]
# detection probability
lp_i[i] ~ dnorm(lp, p_prec_i)I(-100,100)
logit(p_i[i]) <- lp_i[i]
}

### Model definition
###-----
for(i in 1:M){
w[i] ~ dbern(omega[site[i]])
mu1[i,1] <- w[i] * psi1[site[i]]
X[i,1] ~ dbern(mu1[i,1])
mu3[i,1] <- p_i[i] * X[i,1]
```

3. DEMOGRAPHIC MONITORING USING DATA OF BIRD MONITORING PROGRAMS

```
Y[i,1] ~ dbin(mu3[i,1], J[i])
for(t in 2:T) {
mu1[i,t] <- phi_i[i] * X[i,t-1]
Z[i,t] ~ dbern(mu1[i,t])
mu2[i,t] <- Z[i,t] + ((1-Z[i,t])*r_i[i]*w[i])
X[i,t] ~ dbern(mu2[i,t])

mu3[i,t] <- p_i[i] * X[i,t] Y[i,t] ~ dbin(mu3[i,t], J[i])
}
}
}
```

4

Sexually selected signalling in birds: a case for Bayesian change-point analysis of behavioural routines

Manuscript in preparation:

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4. CHANGE-POINT ANALYSIS OF BEHAVIOURAL ROUTINES

Abstract

Aim Responses of organisms to environments or conspecifics may abruptly change once the organism changed its state. For example, the expression of sexually selected signals often depends on the pairing status of the sender. A likely change in signalling routines at the event of pair formation should thus be taken into account when investigating a sexually selected trait like birdsong.

Location Petite Camargue Alsacienne, France.

Methods We developed a change-point model in a Bayesian context to analyse the seasonally changing singing activity in male nightingales, *Luscinia megarhynchos*, for which the pairing status was assumed to be unknown. We used our change-point singing activity model to estimate the pairing success of the males as well as the dates of pair formation.

Results We obtained results on pairing success and date of pair formation that were consistent with our capturing data and with earlier studies. We also found that the peak in nocturnal and dawn singing activity was after the period of female arrival and was later in the season in unpaired males than in paired males. Those seasonal patterns of singing activity were obscured when using generalized linear mixed models, which are traditionally used to analyse seasonal patterns of behavioural routines.

Main conclusions Based on our analyses, we argue that change-point models are powerful analytical tools for many fields of research and may be used whenever animals abruptly switch behavioural routines.

Keywords: female arrival, *Luscinia megarhynchos*, model-based approach, piecewise regression, state-space models, switch-point analyses

4.1 Introduction

Responses of organisms to environments or conspecifics may abruptly change once a threshold has been crossed or once the organism changed its state. Abruptly changing responses may occur in space; for instance, the population size of a species in a particular region may abruptly decrease when a threshold of available habitat is reached (Swift and Hannon 2010). Likewise, abrupt responses may occur in time; for instance, an individual advertising to attract a mate may instantly change its behaviour after pair formation (Krebs et al. 1981, Nemeth 1996, Staicer 1996, Amrhein et al. 2002). The exact time or threshold when such abrupt changes in responses take place are usually called change-points (Thomson et al. 2010). Accurate estimation of the change-points is important, as subsequent estimation of ecological quantities depends on the position of the change-points, and not accounting for the change-points may lead to misleading results (Beckage et al. 2007).

Birdsong has evolved under both inter- and intrasexual selection, and the males' song mostly serves to attract females and to repel rival males (Catchpole and Slater 2008). Singing activity was often shown to change depending on the stages of breeding cycle of the female; such stages are the fertile period of the female before the first egg is laid, the egg-laying period, or the incubation period. Singing activity in birds is a case where not accounting for change-points has possibly led to contradicting results in the published literature. Møller (1991) reviewed studies on male singing activity that mostly did not account for change-points between the individual stages of the breeding cycle; he concluded that more than 70% of the studied bird species showed a peak of singing activity during the time of the year when females are fertile. Gil et al. (1999), however, reviewed studies on singing activity that were mostly based on analyses that did account for the change-points between the individual stages of the breeding cycle. The authors concluded that in most species, the males did not show a peak of singing activity during the fertile period of their mates. We argue that the contradicting conclusions in the reviews by Møller (1991) and Gil et al. (1999) might be due to the different treatments of the change-points in the studies they reviewed.

In songbirds, the singing activity of males often decreases immediately after pair formation, thus the switch in pairing status leads to a change-point in singing activity (Krebs et al. 1981, Hayes et al. 1986, Gibbs and Wenny 1993, Otter and Ratcliffe

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1993, Amrhein et al. 2002, Hennin et al. 2009). Ideally, studies on a behaviour like singing activity should be based on data from individuals for which the stages of the breeding cycle are known. However, investigating temporal patterns of singing with sudden changes of singing activity upon pair formation is challenging for at least two reasons. First, in many species, female breeding behaviour is elusive, and the dates of pair formation and of the stages of the breeding cycle may be unknown for part or most of the males. Second, sudden changes of singing activity lead to non-linear patterns that are difficult to describe with statistical methods assuming linearity, such as generalized linear models (GLM) or generalized linear mixed models (GLMM; Toms and Lesperance 2003).

Here, we suggest the use of change-point models in a Bayesian framework to overcome such difficulties. Change-point models are a class of models that were recently proposed for addressing ecological estimation problems when abrupt changes in states occur (Beckage et al. 2007). We define the pattern of the individually changing singing activity in the course of the day as the daily singing routine (Hutchinson et al. 1993). We provide a change-point model to analyse the nocturnal singing routines from dusk to dawn in individual male nightingales *Luscinia megarhynchos*, for which the exact date of female arrival and the individual stages of the breeding cycle were unknown. The nocturnal singing of nightingales conforms to one of two distinct types of singing routines (Amrhein et al. 2002, Thomas 2002), and the switches between the singing routines are related to switches in pairing status (Amrhein et al. 2002, Amrhein et al. 2004, Roth et al. 2009). The bachelor singing routine is characterized by high singing activity during most of the night; it is sung by males that remain unpaired throughout the breeding season (bachelors) and by paired males before arrival of the mate (Roth et al. 2009). Following pair formation, the males typically stop singing at night, which we call the paired male singing routine.

We developed a change-point singing activity model that accounts for the unknown male pairing success and the unknown date of female arrival. By including male pairing success as an unknown parameter into the model, we formalized the assignment of male pairing success. This is in contrast to earlier studies, where we usually assessed male pairing success from nocturnal singing activity of subjects by manually defining subjects as paired if they ceased regular nocturnal song after the beginning of the breeding season (e.g., Kunc et al. 2006, Schmidt et al. 2008). We show that purely observational

data on male nocturnal singing activity are sufficient to estimate meaningful dates of female arrival and of male pairing success, without the necessity to empirically collect data on females. Since similar switches in behavioural routines are likely to occur in many different fields of research, we argue that change-point models open up new opportunities for studies in ecology and evolution.

4.2 Methods

4.2.1 Study site and field protocol

Data collection took place from 10 April to 20 May 2008 at the Petite Camargue Alsacienne in the Upper Rhine Valley in France. The study site comprises a mosaic of forest patches, pastures, fields, reeds, ditches and artificial ponds of about one square kilometre. To survey the singing activity of males, we made standardized rounds of inspection throughout our study site and recorded for each territory whether a bird was singing (Amrhein et al. 2004, Amrhein et al. 2007). Singing activity of a male was defined as the probability that the male was heard singing during an inspection round. The nocturnal rounds lasted between 50 and 65 min and followed a fixed route of 8.5 km length; the direction of the rounds was fixed for a particular night, but the direction was changed from one night to the next. We made nine rounds of inspection per night (Roth et al. 2009). The first round started at sunset (dusk round), and the last round started 75 min before sunrise (dawn round). The seven remaining rounds (N1 to N7) were spaced out regularly between the dusk and the dawn round. Thus, the exact starting time of the rounds slightly changed from day to day due to the seasonal changes of sunset and sunrise. The mean starting times (\pm SD in minutes) were 20:44 \pm 20 (dusk round), 21:47 \pm 14 (N1), 22:50 \pm 9 (N2), 23:54 \pm 4 (N3), 0:57 \pm 2 (N4), 2:00 \pm 6 (N5), 3:03 \pm 12 (N6), 4:06 \pm 17 (N7) and 5:09 \pm 22 (dawn round). Territories with singing males were excluded from the analyses if males deserted their territories during the study period, or if male song posts were further than 100 m away from our route of inspection (perpendicular distance). We obtained suitable data on singing activity of 31 males. Based on our observations on ringed individuals from previous studies, we assumed that an individual singing in a territory was the same individual male throughout the study period. At the study site, the first male started to sing in its territory during the night from 11 to 12 April. Thus, the data cover 39

4. CHANGE-POINT ANALYSIS OF BEHAVIOURAL ROUTINES

nights, 9 rounds per night and 31 occupied territories, yielding 10,881 observations of male singing activity, which is whether or not a male was singing on a particular round of inspection.

As in our previous studies (Amrhein et al. 2002, Amrhein et al. 2004, Amrhein et al. 2007), the identity and pairing status of the studied males were ascertained by capturing and ringing the male and, if present, its mate. Pairing status of males was further controlled by examining the territories of males for female alarm calls (part of the data on singing activity and pairing status from this study were also published in Roth et al. 2009). Permission for ringing was granted by Henri Jenn and by the Centre de Recherches par le Bagueage des Populations d'Oiseaux, Paris. Mist-nets were usually opened before sunrise and stayed open for about 5 h. Mist nets were checked every 30 min, birds were ringed in their territory and were released within 30 min of capture. Since mist-netting sessions were distributed throughout the field season and were often not done exactly at the time of female arrival, the exact time of female arrival and pair formation was unknown in most cases. In this study, we therefore did not use information from mist-netting to estimate the parameters of the change-point singing activity model (see below), but the mist-netting data were used to test for the plausibility of the results obtained from the model.

4.2.2 Change-point singing activity model

Suppose that a population of $i = 1, \dots, N$ occupied territories are sampled during $t = 1, \dots, T$ days over the course of the breeding season. During each day t , the territories are surveyed at $r = 1, \dots, R$ rounds of inspection performed at different times of the day, yielding the observed singing state variable $X_{i,r,t}$. If a male in territory i was heard singing at day t during round of inspection r then $X_{i,r,t} = 1$, otherwise $X_{i,r,t} = 0$. Let the parameter $M_{i,r,t}$ be the probability a male is singing at day t during round of inspection r in territory i . From the day after a male was heard in territory i for the first time ($a_i + 1$), we assumed that the singing state variable $X_{i,r,t}$ is Bernoulli distributed with the singing probability $M_{i,r,t}$ as its parameter. Thus the singing state variable is given by the model

$$X_{i,r,t} \sim \text{Bernoulli}(M_{i,r,t}) \quad (4.1)$$

for $i = 1, \dots, N$, $r = 1, \dots, R$ and $t = (a_i + 1), \dots, T$.

A consistent pattern of the dusk-to-dawn singing for nightingales is that individual males sing according to one of two distinct types of singing routines (Amrhein et al. 2002, Thomas 2002). We define singing routine $k = 1$ for the bachelor singing routine and $k = 2$ for the paired male singing routine. We modelled the singing activity $M_{i,r,t}$ at the logit-scale and assumed a random male effect α_i , and for each round r and each singing routine k a different intercept $\mu_{r,k}$, as well as different linear $\beta_{1,r,k}$ and quadratic $\beta_{2,r,k}$ temporal trends of the singing activity in the course of the season:

$$\log\left(\frac{M_{i,r,t}}{1 - M_{i,r,t}}\right) = \alpha_i + \mu_{r,k} + \beta_{1,r,k}t + \beta_{2,r,k}t^2 \quad \text{with} \quad \alpha_i \sim N(0, \sigma_\alpha) \quad (4.2)$$

Eqn 4.1 and 4.2 is a formal description of the dusk-to-dawn singing in nightingales over the breeding season that allows for $k = 1, \dots, K$ distinct singing routines (in the case of Nightingales we assume $K = 2$). However, so far the singing routine k (or the individual stages of the breeding cycle that predict the singing routines) needs to be known for each of the males in their territories i and for all days t . As this is not the case in our data and will often not be the case in similar studies on song of territorial male birds, we assumed a random processes for the latent (i.e. not directly observable) pairing status and the latent day of female arrival. We assumed that the singing routine k is a deterministic function of the realizations of these two random processes. Denote the singing routine state variable $y_{i,t}$; if a male in territory i at day t sings the bachelor singing routine ($k = 1$) then $y_{i,t} = 1$, otherwise if the male in territory i at day t sings the paired male singing routine ($k = 2$) then $y_{i,t} = 2$. Denote the latent pairing state variable ps_i ; if a male in territory i remains unpaired throughout the breeding season (bachelor) then $ps_i = 0$. Otherwise if a female pairs to a male and settles in its territory i at some time during the season then $ps_i = 1$. We assumed the pairing state variable ps_i to be the outcome of a Bernoulli trial with the pairing probability π as its parameter

$$ps_i \sim \text{Bernoulli}(\pi) \quad (4.3)$$

In Nightingales, bachelors conform to the bachelor singing routine ($k = 1$) throughout the season (Amrhein et al. 2002). Thus we assumed $y_{i,t} = 1$ for all males with $ps_i = 0$ and for all days t . The dusk-to-dawn singing routine of paired nightingales, however, depends on the latent female arrival, and when a male pairs to a female it immediately switches from the bachelor to the paired male singing routine (Amrhein et al. 2002,

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Amrhein et al. 2004). Denote the latent female arrival time fa_i as the day t a female settles in territory i . We assumed the day of female arrival fa_i , (i.e. the change-point) to be normally distributed with average female arrival ϕ and standard deviation σ_ϕ , but the arrival of a female fa_i in territory i was restricted to the date the male arrived in that territory (a_i) and a latest possible date e of female arrival (see below):

$$fa_i \sim \text{Norm}(\phi, \sigma_\phi) \quad \text{with} \quad a_i \leq fa_i \leq e \quad (4.4)$$

A formal description of the singing routine state is then given as

$$y_{i,t} = \begin{cases} 1, & \text{for } ps_i = 0 \\ 1, & \text{for } ps_i = 1 \text{ and } t < fa_i \\ 0, & \text{for } ps_i = 1 \text{ and } t \geq fa_i \end{cases} \quad (4.5)$$

Thus, only paired males (i.e. $ps = 1$) from day t when the female arrived in their territory sing the paired male singing routine (i.e. $y_{i,t} = 2$). The entire change-point singing activity model (eqn 4.1 to 4.5) is thus specified with 58 parameters: the pairing probability π , the mean female arrival ϕ , the standard deviation of female arrival σ_ϕ , an intercept $\mu_{r,k}$, linear slopes $\beta_{1,r,k}$ and quadratic slopes $\beta_{2,r,k}$ for each of the nine inspection rounds and the two singing routines, and the standard deviation σ_α of the random male effect.

4.2.3 Bayesian analyses

We used a Bayesian analysis of our change-point singing activity model based on Markov chain Monte Carlo methods (MCMC; Link et al. 2002). We assessed convergence using the Gelman-Rubin diagnostic (Brooks and Gelman 1998). MCMC simulations were conducted using WinBUGS 1.4 (Gilks et al. 1994), executed in R using the R add-on library R2WinBUGS (Sturtz et al. 2005). Posteriors were based on three parallel chains with 15'000 iterations each, discarded the first 10'000 and thinned the remainder by five. The specification of the model was as follows: the study duration was from the day when the first male was heard singing in its territory ($t = 1$: night from 11 to 12 April) to the night from 19 to 20 May ($t = 39$). During these $T = 39$ days, each of the $N = 31$ occupied territories were visited daily during $R = 9$ rounds of inspection ($r = 1$: dusk round; $r = 2 \dots 8$: nocturnal rounds N1 to N7; $r = 9$: dawn round). We restricted the latest possible day of female arrival to 10 May ($e = 30$) because in earlier studies, we have never observed a female arriving after 10 May (unpublished

observations; Amrhein et al. 2007). We assumed diffuse prior distributions for the parameters, which were uniform $U(0, 1)$ for the pairing probability π , $U(1, 25)$ for the mean female arrival ϕ , $U(0, 10)$ for the standard deviation of female arrival σ_ϕ , $U(0, 1)$ for all of the intercepts on the probit scale $e^{\mu_{r,k}}/(1+e^{\mu_{r,k}})$, normal $N(0, 2)$ for linear slopes $\beta 1_{r,k}$ and for quadratic slopes $\beta 2_{r,k}$ and uniform $U(0, 2)$ for the standard deviation of the random male effect σ_α . In Appendix S.4.7, we provide the model description in the BUGS-language.

To compare the results obtained from the change-point singing activity model with the results from a traditional generalized linear mixed model (GLMM) on the singing activity that does not account for the stages of breeding cycle nor for different pairing status of the males, we used the LME4 package (Pinheiro et al. 2006) in the software R (v.2.12.1; R Development Core Team 2011). For each of the rounds, we fitted a separate GLMM with a logistic link function. We regressed a linear and quadratic temporal term on the binary singing activity (singing or not singing); to account for the repeated measures, we also included individual male as a random factor. For the GLMMs, as for the change-point singing activity model, we only used data from the day after the male was heard singing for the first time.

4.3 Results

4.3.1 Parameter estimates and performance of the model

We described a change-point model on singing activity in nightingales that does not incorporate prior information on pairing status and date of pair formation of the males, but allows for two distinct types of dusk-to-dawn singing routines. Using this model, we estimated the percentage of paired males in our population to be 76% (95%-credible interval CI: 60-89%). This estimate corresponded to our mist-netting data on the same subjects collected during the same year, from which we concluded that 25 out of the 31 studied males (81%) were paired (Roth et al. 2009). Note that the mist-netting data were not used in the current change-point singing activity model and that in the present study, the percentage of paired males was estimated using only the observational data on male singing activity. The estimated average female arrival was in the night from 27 to 28 April (CI: 25/26 April - 30 April/1 May), which corresponds to an earlier study

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at the same study site, in which we found a mean female arrival on 26 April (Amrhein et al. 2007).

Overall, the nocturnal and dawn singing activity was higher in bachelors than in paired males (Fig. 4.1). The largest differences in nocturnal and dawn singing activity were found at the end of the season, which was due to the distinct seasonal increase in nocturnal singing activity of bachelors (Table 4.1). Both for bachelors and paired males, the peak in singing activity was after the period when most females arrived to the study site (i.e. between 21 April and 3 May; Amrhein et al. 2007). Irrespectively of the time of the day, singing activity of paired males was highest in the first week of May, which is the period when females usually are laying eggs and start incubating (Amrhein et al. 2004), whereas the peak in singing activity of bachelors was in the second or third week of May. This corresponds to our earlier studies that reported highest diurnal singing activity of paired males during the laying period, whereas the diurnal singing activity of bachelors continuously increased until the end of the incubation period (Amrhein et al. 2002, 2004, 2007).

Round	Bachelors				Paired males							
	L-effect	L-trend	Q-effect	Q-trend	L-effect	L-trend	Q-effect	Q-trend				
Dusk	0.13	0.61	+	-0.47	0.01	0.59	1.85	+	-0.11	-0.03	∩	
N1	-0.39	2.17		-2.50	0.10	-1.46	3.12		-4.13	0.09		
N2	0.54	1.13	+	-0.27	0.29	-0.22	3.23		-2.92	-0.38	∩	
N3	0.73	1.23	+	-0.34	0.15	0.03	2.34	+	-2.47	-0.65	∩	
N4	0.80	1.31	+	-0.70	-0.21	∩	0.86	3.35	+	-4.05	-1.82	∩
N5	0.80	1.30	+	-0.72	-0.23	∩	0.69	3.12	+	-3.67	-1.69	∩
N6	0.83	1.34	+	-0.77	-0.28	∩	0.24	2.69	+	-3.33	-1.41	∩
N7	0.94	1.46	+	-0.69	-0.18	∩	0.32	1.63	+	-1.68	-0.77	∩
Dawn	0.79	1.40	+	-0.38	0.18	0.28	1.18	+	-0.83	-0.23	∩	

Table 4.1: Credible intervals of the linear (L) and quadratic (Q) temporal trends of nocturnal singing activity of male nightingales in the course of the season, for the bachelor singing routine and the paired male singing routine. A significant linear trend (+) or peak (∩) of singing activity is indicated by credible intervals that do not include zero.

The proportion of males singing the bachelor singing routine decreased from 100% at the start of the breeding season to about 20% at the end of the study period (Fig. 4.2), which corresponded to the 6 of the 31 males that remained unpaired throughout the breeding season (Roth et al. 2009).

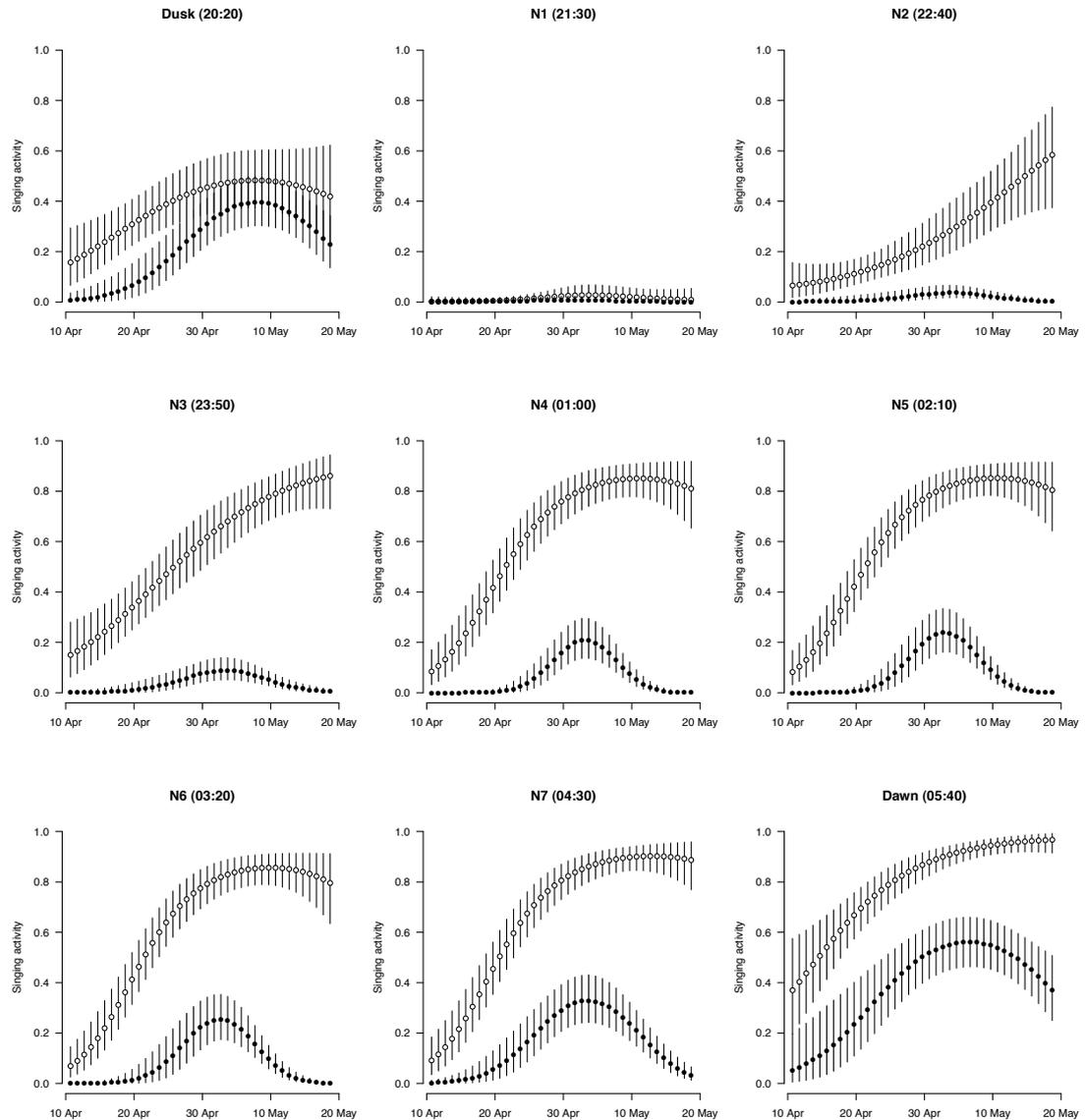


Figure 4.1: Seasonal singing activity - Seasonal development of nocturnal singing activity (i.e. the probability that a male was encountered singing) in nightingales, for nine daily rounds of inspection (dusk round, nocturnal rounds N1-N7, and dawn round). Given are mean and 95% credible intervals of the posterior distributions of the singing activities for bachelors (\circ) and paired males (\bullet ; pairing status of males was estimated from our model). The average starting times of each of the nine rounds are given in the headers of each panel.

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4.3.2 Traditional model

The traditional GLMMs that could not account for the pairing success of the males nor for the change-points of female arrival suggested different patterns of seasonal singing activity: the singing activity of the third nocturnal round (N3) linearly decreased over the season (quadratic term: $z=1.6$; $p=0.12$; linear term: $z=3.5$; $p<0.001$), while no temporal trend was detected for the first two nocturnal rounds (quadratic term: both $z<1.0$; both $p>0.30$; linear term: both $z<0.6$; both $p>0.52$). The seasonal singing activity at all other rounds peaked in the middle of the study period (quadratic term: all $z>3.3$; all $p<0.001$). This peak in singing activity was estimated to be around the period of female arrival at the end of April (see Fig. 4.3 for dusk round, fourth nocturnal round (N4) and dawn round). Therefore, the result of the GLMMs suggested an earlier peak in singing activity than the change-point singing activity model, which consistently with our earlier empirical data (Amrhein et al. 2002, 2004, 2007) suggested a peak in singing activity of bachelors and paired males after most females had arrived at the study site.

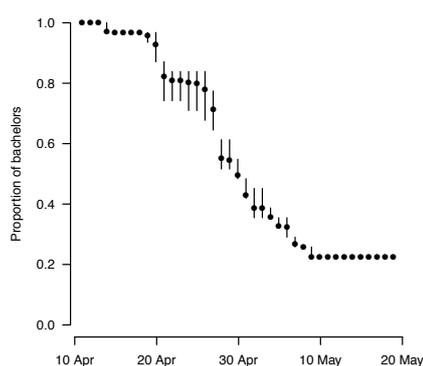


Figure 4.2: Proportion of male nightingales singing the bachelor singing routine
- The proportion is estimated for each day over the course of the season. Given are mean and 95% credible intervals of the posterior distributions.

4.4 Discussion

We described a change-point model of nightingale signalling routines that was based on observations of nocturnally singing males and did not use empirical data on the presence and behaviour of females, but incorporated general knowledge about nocturnal singing routines from previous studies (Amrhein et al. 2002, Amrhein et al. 2004, Amrhein et al. 2007, Roth et al. 2009). Compared to our earlier studies on nightingales from the same study population, our model provided realistic estimates of the pairing success of males and of the date when one of the most important change-points in the singing activity occurred, which is the event of female settlement in the territory of a male. Using the change-point model, we were also able to detect patterns of seasonal trends in singing activity that were obscured when using a traditional generalized linear mixed model that did not account for the two different singing routines nor for the change-points.

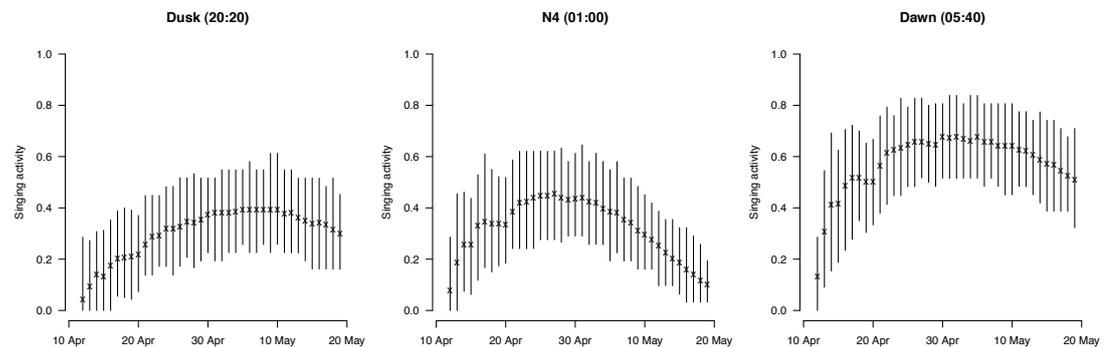


Figure 4.3: GLMM estimate of the seasonal singing activity - Seasonal development of nocturnal singing activity (i.e. the probability that a male was encountered singing) in nightingales, during the dusk round of inspection, during the round in the middle of the night (N4), and during the dawn round. Given are mean and 95% credible intervals of the posterior distributions of traditional generalized linear mixed models (GLMM). The GLMMs used the same data as in Fig. 1 but could not account for different singing routines in bachelors and paired males, nor for change points at the dates of female arrival. The average starting times of each of the nine rounds are given in the headers of each panel.

If in a population, different individuals follow a different daily signalling routine, then the proportion of singing individuals (i.e. the population-wide singing activity)

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is influenced by the proportion of individuals using the particular signalling routines. Thus, the population-wide signalling activity does not necessarily reflect patterns of individual behaviour. In the case of nightingales, at the beginning of the season, the males sang according to the bachelor singing routine. Because the individual singing activity of bachelors increased in the course of the season, the population-wide singing activity in our study population increased at the beginning of the breeding season before the females arrived. Thus, as estimated from the traditional generalized linear mixed model, the highest population-wide singing activity was at the period of female arrival, and from then the population-wide singing activity decreased. This decrease of population-wide singing activity after female arrival is mostly due to the decreasing number of males singing according to the bachelor singing routine and is in contrast to the increasing singing activity of bachelors revealed from the change-point singing activity model. Therefore, when analysing temporal patterns of singing activity, it is important to take male pairing status and different singing routines of paired and unpaired males into account.

After female arrival, paired males often resume nocturnal singing during a short period mainly during the first week of May, which is linked to the mate's egg laying period (Amrhein et al. 2002, Kunc et al. 2007). In an earlier study, 13 out of 15 paired males resumed nocturnal singing for about three nights once the females started egg laying (Amrhein et al. 2002). The functions of this second period of nocturnal song in paired nightingales are unclear, but likely are related to both intrasexual and intersexual behaviour (Amrhein et al. 2002, Naguib et al. 2011). A potential intersexual function could be to encourage the mate to increase the investment into the brood (Amrhein et al. 2002), whereas a potential intrasexual function is that increased singing during egg-laying serves to repel neighbouring males, to minimize the risk of cuckoldry (Møller 1991). In this study, we found that the nocturnal singing activity of paired males during the approximate time of egg laying was much lower than the nocturnal singing activity of bachelors during the same time period. Whereas the main function of nocturnal song in bachelors is most likely to attract females (Amrhein et al. 2002, Roth et al. 2009), the lower singing activity of paired males compared to bachelors suggests that the nocturnal singing of paired males during egg-laying is probably less likely to attract additional social mates (Amrhein et al. 2002).

In its current form, our change-point singing activity model estimates a single change-point in singing activity, which is the date of pair formation. However, analysing change-point models in a Bayesian framework has the advantage that the models can be adapted to different situations (Chen et al. 2011, Schutz and Holschneider 2011). For example, the beginning and end of nocturnal song in paired males during egg laying are additional change-points that could be included into the singing activity model. Further, one could also include covariates of the change-points into the model. If, for instance, data on territory quality are available, one could use our model to investigate whether the date of female settlement is correlated with characteristics of a male's territory such as food availability or scrub structure (Wilson et al. 2005). Here, we have shown that even a very simple change-point model can considerably improve inferences on signalling activity compared to the results of a traditionally used GLMM, and additionally can estimate important change points such as the date of pair formation.

In many fields of research, data do not have a linear functional relationship with time or space, but show abrupt changes in this relationship, as is the case with the nocturnal singing activity of nightingales that abruptly decreases once a male pairs to a female. For example, populations of animals can switch from stable to unstable states when the temperature increases (Ohlberger et al. 2011). In such cases, change-point models reliably identify the events of changes in the temporal dynamic of populations (Thomson et al. 2010). However, abrupt changes are also expected to occur in most behavioural contexts. Examples are likely to include: predator-prey interactions, where a predator may switch between different prey species depending on the abundance of the prey (Garrott et al. 2007), perhaps leading to changes in the vigilance of preferred and non-preferred prey; contest behaviour, where rivals switch between strategies to assess the fighting ability of the opponent (Hsu et al. 2008), which may lead to sudden changes in the intensity of a contest; or territory defence behaviour, where an activation of the immune system following the infection with a pathogen affects song production of the territorial male (Blumstein et al. 2010). We therefore argue that change-point models provide a flexible and reliable tool for analysing data with abrupt changes in functional relationships caused by an unobserved switch of state in the studied subjects.

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4.6 References

- Amrhein, V., P. Korner, and M. Naguib. 2002. Nocturnal and diurnal singing activity in the nightingale: correlations with mating status and breeding cycle. *Animal Behaviour* 64:939-944.
- Amrhein, V., H. P. Kunc, and M. Naguib. 2004. Seasonal patterns of singing activity vary with time of day in the nightingale (*Luscinia megarhynchos*). *Auk* 121:110-117.
- Amrhein, V., H. P. Kunc, R. Schmidt, and M. Naguib. 2007. Temporal patterns of territory settlement and detectability in mated and unmated Nightingales *Luscinia megarhynchos*. *Ibis* 149:237-244.
- Beckage, B., L. Joseph, P. Belisle, D. B. Wolfson, and W. J. Platt. 2007. Bayesian change-point analyses in ecology. *New Phytologist* 174:456-467.
- Blumstein, D. T., N. E. Munoz, and J. Foufopoulos. 2010. Immune system activation affects song and territorial defense. *Behavioral Ecology* 21:788-793.
- Brooks, S. P. and A. Gelman. 1998. General methods for monitoring convergence of iterative simulations. *Journal of Computational and Graphical Statistics* 7:434-455.
- Catchpole, C. K. and P. J. B. Slater. 2008. *Bird song*. Cambridge University Press, Cambridge.
- Chen, C. W. S., J. S. K. Chan, R. Gerlach, and W. Y. L. Hsieh. 2011. A comparison of estimators for regression models with change points. *Statistics and Computing* 21:395-414.

- Garrott, R. A., J. E. Bruggeman, M. S. Becker, S. T. Kalinowski, and P. J. White. 2007. Evaluating prey switching in wolf-ungulate systems. *Ecological Applications* 17:1588-1597.
- Gibbs, J. P. and D. G. Wenny. 1993. Song output as a population estimator - effect of male pairing status. *Journal of Field Ornithology* 64:316-322.
- Gil, D., J. A. Graves, and P. J. B. Slater. 1999. Seasonal patterns of singing in the willow warbler: evidence against the fertility announcement hypothesis. *Animal Behaviour* 58:995-1000.
- Gilks, W. R., A. Thomas, and D. J. Spiegelhalter. 1994. A language and program for complex Bayesian modelling. *Statistica* 43:169-178.
- Hayes, J. P., J. R. Probst, and D. Rakstad. 1986. Effect of mating status and time of day on Kirtland warblers song rate. *Condor* 88:386-388.
- Hennin, H. L., N. K. S. Barker, D. W. Bradley, and D. J. Mennill. 2009. Bachelor and paired male rufous-and-white wrens use different singing strategies. *Behavioral Ecology and Sociobiology* 64:151-159.
- Hsu, Y. Y., S. P. Lee, M. H. Chen, S. Y. Yang, and K. C. Cheng. 2008. Switching assessment strategy during a contest: fighting in killifish *Kryptolebias marmoratus*. *Animal Behaviour* 75:1641-1649.
- Hutchinson, J. M. C., J. M. McNamara, and I. C. Cuthill. 1993. Song, sexual selection, starvation and strategic handicaps. *Animal Behaviour* 45:1153-1177.
- Krebs, J. R., M. Avery, and R. J. Cowie. 1981. Effect of removal of mate on the singing behavior of Great tits. *Animal Behaviour* 29:635-637.
- Kunc, H. P., V. Amrhein, and M. Naguib. 2006. Vocal interactions in nightingales, *Luscinia megarhynchos*: more aggressive males have higher pairing success. *Animal Behaviour* 72:25-30.
- Kunc, H. P., V. Amrhein, and M. Naguib. 2007. Vocal interactions in common nightingales (*Luscinia megarhynchos*): males take it easy after pairing. *Behavioral Ecology and Sociobiology* 61:557-563.

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- Link, W. A., E. Cam, J. D. Nichols, and E. G. Cooch. 2002. Of BUGS and birds: Markov chain Monte Carlo for hierarchical modeling in wildlife research. *Journal of Wildlife Management* 66:277-291.
- Møller, A. P. 1991. Why mated songbirds sing so much - mate guarding and male announcement of mate fertility status. *American Naturalist* 138:994-1014.
- Naguib, M., H. P. Kunc, P. Sprau, T. Roth, and V. Amrhein. 2011. Communication Networks and Spatial Ecology in Nightingales. *Advances in the Study of Behavior*, Vol 43 43:239-271.
- Nemeth, E. 1996. Different singing styles in mated and unmated reed buntings *Emberiza schoeniclus*. *Ibis* 138:172-176.
- Ohlberger, J., E. Edeline, L. A. Vollestad, N. C. Stenseth, and D. Claessen. 2011. Temperature-Driven Regime Shifts in the Dynamics of Size-Structured Populations. *American Naturalist* 177:211-223.
- Otter, K. and L. Ratcliffe. 1993. Changes in singing behavior of male Black-capped chickadees (*Parus atricapillus*) following mate removal. *Behavioral Ecology and Sociobiology* 33:409-414.
- Pinheiro, J., D. Bates, S. DebRoy, and D. Sarkar. 2006. NLME: linear and nonlinear mixed effects models. R package, version 3.1-77. <http://cran.r-project.org>.
- R Development Core Team. 2011. R: A language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
- Roth, T., P. Sprau, R. Schmidt, M. Naguib, and V. Amrhein. 2009. Sex-specific timing of mate searching and territory prospecting in the nightingale: nocturnal life of females. *Proceedings of the Royal Society B-Biological Sciences* 276:2045-2050.
- Schmidt, R., H. P. Kunc, V. Amrhein, and M. Naguib. 2008. Aggressive responses to broadband trills are related to subsequent pairing success in nightingales. *Behavioral Ecology* 19:635-641.

- Schutz, N. and M. Holschneider. 2011. Detection of trend changes in time series using Bayesian inference. *Physical Review E* 84.
- Staicer, C. A. 1996. Honest advertisement of pairing status: Evidence from a tropical resident wood-warbler. *Animal Behaviour* 51:375-390.
- Sturtz, S., U. Ligges, and A. Gelman. 2005. R2WinBUGS: A Package for Running WinBUGS from R. *Journal of statistical Software* 12:1-16.
- Swift, T. L. and S. J. Hannon. 2010. Critical thresholds associated with habitat loss: a review of the concepts, evidence, and applications. *Biological Reviews* 85:35-53.
- Thomas, R. J. 2002. Seasonal changes in the nocturnal singing routines of Common Nightingales *Luscinia megarhynchos*. *Ibis* 144:E105-E112.
- Thomson, J. R., W. J. Kimmerer, L. R. Brown, K. B. Newman, R. Mac Nally, W. A. Bennett, F. Feyrer, and E. Fleishman. 2010. Bayesian change point analysis of abundance trends for pelagic fishes in the upper San Francisco Estuary. *Ecological Applications* 20:1431-1448.
- Toms, J. D. and M. L. Lesperance. 2003. Piecewise regression: A tool for identifying ecological thresholds. *Ecology* 84:2034-2041.
- Wilson, A. M., R. J. Fuller, C. Day, and G. Smith. 2005. Nightingales *Luscinia megarhynchos* in scrub habitats in the southern fens of East Anglia, England: associations with soil type and vegetation structure. *Ibis* 147:498-511.

S.4.7 The change-point singing activity model in the BUGS-language

```
# WINBUGS MODEL DESCRIPTION
model {
### Define Priors
### *****
pi    dunif(0,1) ### Pairing success
phi   dunif(1,25) ### Average female arrival
sigma.phi  dunif(0,10) ### SD of female arrival
tau.phi <- pow(sigma.phi, -2)
for(r in 1:R) {
for(k in 1:K) {
mu[r,k]    dunif(0,1) ### Intercept of singing probability of
round ### r and singing routine k
lmu[r,k] <- log(mu[r,k]/(1-mu[r,k]))

beta1[r,k]  dnorm(0,0.25)I(-5,5) ### Linear effect of time and singing routine
k
beta2[r,k]  dnorm(0,0.25)I(-5,5) ### Quadratic effect of time and singing
routine k
}
}
sigma.alpha  dunif(0,2) ### SD of random male effect
tau.alpha <- pow(sigma.alpha, -2)
for(i in 1:N) {
alpha[i]    dnorm(0,tau.alpha) ### Random male effect
}
### Model for singing activity MU[i,t,r]
### *****
for(i in 1:N) {
for(t in (a[i]+1):T) {
for(r in 1:R) {
```

S.4.7 The change-point singing activity model in the BUGS-language

```
logit(MU[i,t,r]) <- alpha[i] + lmu[r,y[i,t]] + beta1[r,y[i,t]]*((t-20)/10)
+ beta2[r,y[i,t]]*((t-20)/10)*((t-20)/10)
X[i,t,r] ~ dbern(MU[i,t,r])
}
}
}
### Model for the singing routine state (y[i,t])
### *****
for(i in 1:N) {
ps[i] ~ dbern(pi)
fa[i] ~ dnorm(phi, tau.phi)I(a[i],30)
for(t in 1:T) {
ty[i,t] <- ps[i] * step(t-fa[i])
y[i,t] <- ty[i,t] + 1
}
}
}
```

4. CHANGE-POINT ANALYSIS OF BEHAVIOURAL ROUTINES

Part II

Analyses of data from long-term surveys

5

**Sex-specific timing of mate
searching and territory
prospecting in the nightingale:
nocturnal life of females**

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5. SEX-SPECIFIC TIMING OF MATE SEARCHING AND TERRITORY PROSPECTING IN NIGHTINGALES

Abstract

Aim Formal models have shown that diel variation in female mate searching is likely to have profound influence on daily signalling routines of males. In studies on acoustic communication, the temporal patterns of the receivers' signal evaluation should thus be taken into account when investigating the functions of signalling.

Location Petite Camargue Alsacienne, France.

Methods In bird species in which diel patterns of signalling differ between males singing to defend a territory or singing to attract a mate, the diel patterns of mate and territory prospecting is suggested to depend on the sex of the prospector. We simulated newly arriving female nightingales (*Luscinia megarhynchos*) by translocating radio-tagged females to our study site.

Results The mate searching females prospected the area mostly at night, visiting several singing males. The timing of female prospecting corresponded to the period of the night when the singing activity of unpaired males was higher than that of paired males. In contrast to females, territory searching males have been shown to prospect territories almost exclusively during the dawn chorus. At dawn, both paired and unpaired males sang at high rates, suggesting that in contrast to nocturnal singing, dawn singing is important to announce territory occupancy to prospecting males.

Main conclusions In the nightingale, the sex-specific timing of prospecting corresponded to the differential signalling routines of paired and unpaired males. The temporal patterns in the behaviour of signallers and receivers thus appear to be mutually adapted.

Keywords: signalling routines, timing of prospecting, nocturnal song, dawn chorus

5.1 Introduction

Almost all animals show behavioural traits that vary depending on the time of day (McNamara et al. 1987). Studies investigating animal behaviour around the clock often reveal surprising temporal flexibility; for example, young reed warblers (*Acrocephalus scirpaceus*) regularly show nocturnal movements well before migration (Mukhin et al. 2005), and golden hamsters (*Mesocricetus auratus*) are nocturnal in captivity but diurnal in nature (Gattermann et al. 2008). Most behaviour is energy and time consuming, and the optimal daily routine is thought to be an adaptive compromise (Hutchinson et al. 1993). Behavioural routines have often been studied with an emphasis on external factors such as light, temperature, food availability or predation risk (e.g. Olsson et al. 2000; Thomas and Cuthill 2002; Macleod et al. 2005). However, behaviour frequently occurs in social contexts, and interactions with conspecifics may strongly shape behavioural routines (Davidson and Menaker 2003; Helm et al. 2006). In the context of social interactions, daily routines can be predicted using formal models without necessarily including environmental factors (McNamara et al. 1987).

Social interactions often involve information transfer from signalling individuals to receivers (Bradbury and Vehrencamp 1998). It has been shown that signalling individuals adjust the timing of their signals in order to avoid acoustic interference with other signalling individuals on short temporal scales (Todt and Naguib 2000; Gerhardt and Huber 2002; Brumm 2006). Individuals are also likely to time their signalling to the period when intended receivers are present and ready to collect information. On the receiver side, individuals often gather information by active prospecting an unfamiliar area or by visiting the territories of conspecifics (Reed et al. 1999). Receivers are expected to show prospecting activity at time periods when relevant information is available (Boulinier et al. 1996; Reed et al. 1999; Piper et al. 2006). Prospecting behaviour that would be independent of the behaviour of the signallers would be costly and inefficient and is therefore not likely to be adaptive (Kondoh and Ide 2003). Thus, patterns in the diel timing of signalling and in the diel timing of prospecting are expected to be correlated.

Using formal models, it has been demonstrated that diel variation in female prospecting behaviour is likely to have profound influence on the timing of daily routines in

5. SEX-SPECIFIC TIMING OF MATE SEARCHING AND TERRITORY PROSPECTING IN NIGHTINGALES

males (Hutchinson et al. 1993). However, few studies investigated female mate searching directly by tracking individuals during the period of primary mate choice (i.e., during the initial selection of a social partner; Bensch and Hasselquist 1992; Draud et al. 2008). Recently, Jacot et al. (2008) reported one of the first studies on daily routines of signalling and information gathering, investigating the diel signalling activity of male field crickets (*Gryllus campestris*). Most females were captured near the males in the late afternoon, when singing activity of the males was highest and best reflected male nutritional condition. However, such a temporal pattern of capturing success could arise even if female prospecting activity would show no clear diel pattern: males signalling at particularly high rates could simply have attracted more females because the signalling males were more easily detected by the females. It thus remains to be shown whether, during the period of social mate choice, the timing of female prospecting activity correlates with male signalling patterns.

Among the several signal modalities, acoustic communication is particularly suitable to investigate diel variation in the timing of signalling and prospecting, because acoustic signals can be modulated within a short time period, and often follow diel rhythms. A well studied acoustic communication system is bird song, which is mostly used by territorial males, to repel competitors and to attract potential mates (Catchpole and Slater 2008). In some bird species, resource holding males signal their quality to females mainly at dawn (Otter et al. 1997; Double and Cockburn 2000; Dalziel and Cockburn 2008; Murphy et al. 2008). In other species, dawn singing seems to be relatively unimportant in mate attraction, but males may address potential mates during other times of the day (Staicer 1996; Staicer et al. 1996).

Here, we investigated the association between the timing of male signalling and the timing of sex-specific prospecting in nightingales (*Luscinia megarhynchos*). Territorial male nightingales sing intensely at dawn, and mostly unpaired males sing also at night but stop nocturnal song after pair formation (Amrhein et al. 2004a). Nocturnal song was thus suggested to serve attracting females (Amrhein et al. 2002), and dawn singing seems to serve mainly to defend a territory (Amrhein et al. 2004b; Kunc et al. 2005). In an earlier study, it has been shown that non-territorial male nightingales prospect territories during the dawn chorus (Amrhein et al. 2004b). If nocturnal song of unpaired males serves to attract females, we predicted that female nightingales prospect for mates at night. In this study, we thus simulated unpaired females that prospect an

unfamiliar area by translocating female nightingales to our study site. We used radio telemetry to observe their mate searching behaviour during the first two days and nights after translocation. We then compared the diel prospecting patterns of females with the results obtained on males (Amrhein et al. 2004b). We found that the timing of prospecting is sex-specific in the nightingale and is related to the timing of signalling in paired males and unpaired males.

5.2 Material and methods

The study took place in two years (2007 and 2008) at the Petite Camargue Alsacienne in the Upper Rhine Valley in France, where we had surveyed about 50 nightingale territories per year since 1994 (Amrhein et al. 2002). The identity of males and females were controlled by regular mist-netting, and the birds were individually marked with a metal ring and a unique combination of three colour rings. Pairing status of males was further controlled by examining the territories of males for female alarm calls. The first males started singing in their territories on 10 April in 2007 and on 11 April in 2008, and the first female was captured on 21 April in 2007 and 20 April in 2008.

5.2.1 Translocation

We captured female nightingales 70 km north of our study site. At the capture site, we monitored singing activity of males by surveying singing males at midnight and in the early morning. When a resident male stopped singing at night, indicating the arrival of a female (Amrhein et al. 2002, 2004a), we placed mist nets in its territory and captured the female within three days after the male had stopped nocturnal song. From 21 April to 4 May 2007, we translocated 10 females from the capture site to our study site. We released the females with a transmitter glued to their back feathers at about 12.00, within 5 hours of capture. All translocated females were tracked continuously during the first 42 hours at the release site. We used the total stretch of way a female covered per hour as our measure of prospecting activity. In cases in which the location of the females could not always be identified precisely because of particularly rapid and lengthy movements, the distance measurements taken during the corresponding hours were omitted from the analyses. The resulting sample sizes for each hour are given in Fig 5.1. Translocated females that eventually settled within the study area

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were checked at least once within three days until the transmitters fell off or stopped signalling after ca. 3-4 weeks. We used telemetry equipment by Titley Electronics, Australia: three element Yagi antennae, Regal 2000 receivers and LT1 transmitters (equipment mass of 1.0 g = 4.6% of the average mass of our subjects). We stopped translocating females as soon as we captured the first female carrying an egg at the capture site. The study plots and the methods used in the present study were the same as in an earlier translocation study on male nightingales (Amrhein et al. 2004b).

5.2.2 Singing activity

Singing activity of males was surveyed in a preliminary study from 2 May to 6 May 2007, and during a more extended period from 11 April to 4 May 2008, one year after the female translocation experiment. We made nine rounds of inspection per night at our study site. The first round started at sunset (dusk round), and the last round started 75 min before sunrise (dawn round); the seven remaining rounds (N1 to N7) were spaced out regularly between the dusk and the dawn round. The exact starting time of the rounds slightly changed from day to day due to the seasonal changes of sunset and sunrise; mean starting times for the rounds are given in Fig 5.3. Rounds lasted between 50 and 65 min and followed a fixed route of 8.5 km length; the direction of the rounds was fixed for a particular night, but the direction was changed from one night to the next. Territories with singing males were excluded from the analyses if males deserted their territories during the study period, or if male song posts were further than 100 m (perpendicular distance) away from our route. We used the date at which we captured the first female at our study site to subdivide the study period into a period prior to female arrival, when all males were unpaired (11 April to 20 April) and a period during female arrival when males started to get paired (21 April to 4 May). For each period (before female arrival and during female arrival) and for each round (dusk-round, N1 to N7 and dawn-round), we plotted singing activity in the figures as the proportion of rounds a male was recorded to sing. We also subdivided the males into paired males and unpaired males (bachelors), depending on whether a male was paired at the end of the study period. Because we used the arrival date of the first female at the study site to define the period of female arrival for all males, some subsequently paired males were still unpaired in the beginning of the period of female arrival.

5.2.3 Statistical analyses

All statistical analyses were performed using the software R (v. 2.6.1; R Development Core Team 2007). All sample sizes refer to the number of individuals. Descriptive statistics in the text are given as mean \pm sd. To account for the repeated sampling of the same individuals and, thus, the non-independence of data points, we used linear mixed-effect models (LMM) with individual subject fitted as random factor, including individual-specific intercepts and slopes (Gelman and Hill 2007). To investigate temporally changing prospecting activities of females, we fitted the distance covered per hour as response variable, the individual females as random factor, and the date of translocation and the hour (time of day) as covariates; to account for the daily cycles of prospecting activity, we modelled the hour as a sine-cosine function (Crawley 2007). We started with the full models including all variables, and then removed non-significant terms (Crawley 2007). To investigate the effect of pairing status on daily singing patterns, we used generalized linear mixed models (GLMM) with a logistic link function (LME4 package; Bates and Sarkar 2006), because the response variable was binary (singing or not singing). We fitted the singing activity as response variable, the rounds (numbered from 1 to 9; 1=dusk-round, 9=dawn-round) as covariate, the pairing status (paired male or bachelor) and the seasonal period (before and during female arrival) as fixed factors, and the individual males as random factor. To test for a possible curvilinear pattern in the nocturnally changing singing activity, we additionally fitted the quadratic term of the covariate round2 to the model. In the figures, we give the mean values of prospecting activity and singing activity with bootstrapped 95% confidence intervals (10'000 iterations; Crawley 2007).

5.3 Results

5.3.1 Translocation

The prospecting activity of females, as indicated by the total distance covered per hour, showed a distinct diel pattern (LMM, hour: $df=2$, $p<0.001$): the females covered short distances during the day, they were stationary in the hour between 22.00 and 23.00, but covered long distances during the second half of the night from about 01.00 to about 04.00 (Fig. 5.1). At dawn, the distances covered per hour dropped to low levels.

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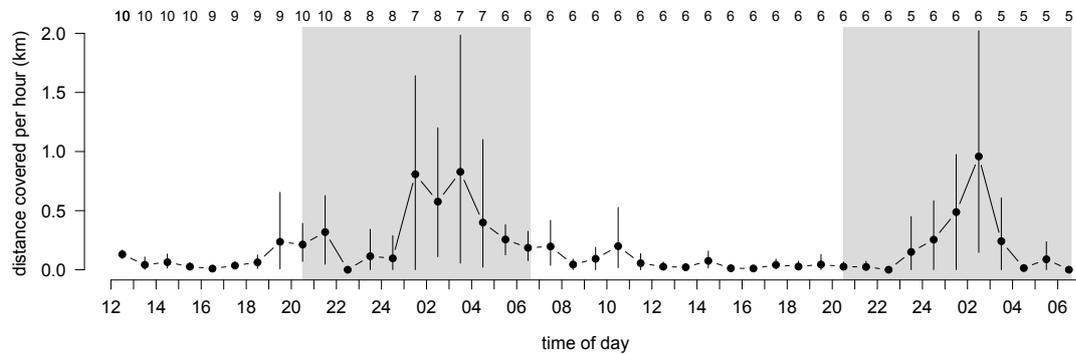


Figure 5.1: Prospecting activity of female nightingales - Total distances covered per hour (mean and bootstrapped 95% confidence interval) are given for the 42 hours after translocation of females to the study site. Sample sizes are given at the top of the figures; grey shaded areas indicate nocturnal periods from sunset to sunrise.

The length of the distances covered per hour did not change as the season progressed (LMM, date of translocation: $df=1$, $p=0.84$). The eight females for which we could determine the exact starting times started nocturnal movements between 23.50 and 3.38, and average starting times were $02.29 (\pm 1.77 \text{ h}; n=7)$ in the first night and $00.38 (\pm 1.32 \text{ h}; n=5)$ in the second night. The prospecting trips lasted from 13 min to 235 min ($103.23 \pm 76.14 \text{ min}; n=7$). In total, the females covered 0 to 4.71 km ($1.12 \pm 1.67 \text{ km}; n=7$) during the first night and 0 to 6.17 km ($1.49 \pm 2.67 \text{ km}; n=5$) during the second night. Note that the average distances covered are likely to be underestimated, because hours during which we lost track of the females were omitted from the analyses. Fig. 5.2 shows the prospecting path of a female performed during the second night after translocation, visiting at least six males singing. Each female performed a prospecting trip at least during one night. Five of the 10 females finally settled in a territory of a male within our study area, three females returned to the capture site, and the remaining two females left our study site but were not recorded back at the capture site. From the five females that left our study site, four left during the first night (after having visited several males within our study area) and one during the second night. Of the five females that settled and paired to a male within the study area, three settled in a territory of a male during the first night, one during the second night, and one during the third night. After settlement in a male's territory, none of the females were located outside the territory again during our occasional checks. In 2008, at least one

translocated female returned to the same territory in our study area in which it settled in 2007.

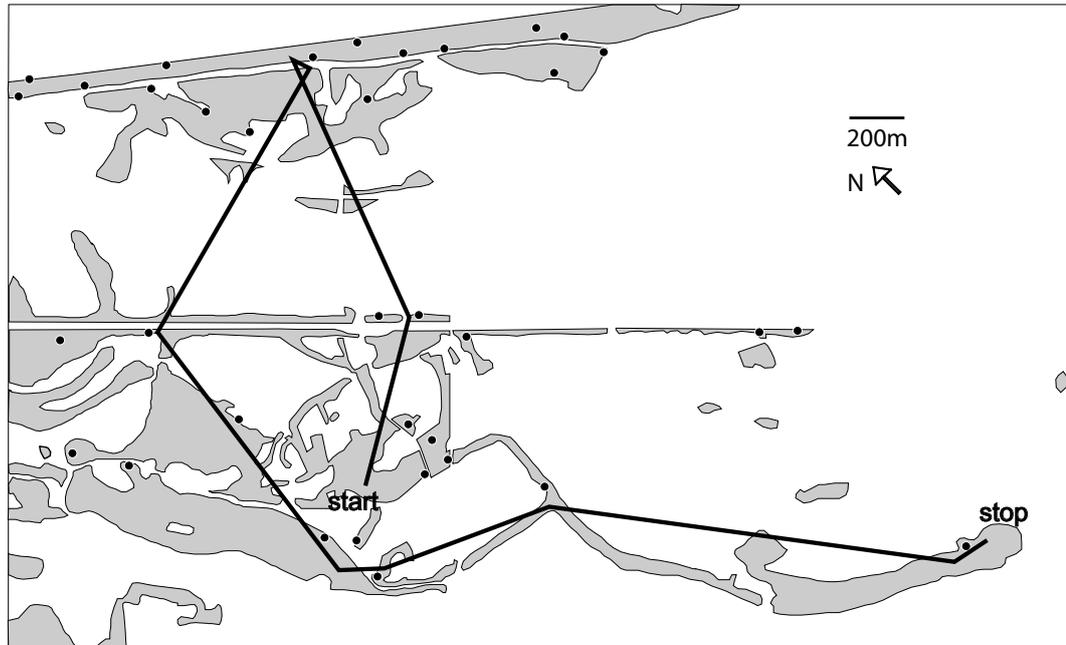


Figure 5.2: Path of prospecting females - The prospecting path of a single radio-tracked female in the second night after translocation. Between 23.50 and 3.30, it covered 5.8 km and visited at least six of the territorial males singing that night (black dots), spending between 5 and 35 minutes in the territories of the males. The female finally settled and paired to the male in the last territory visited that night (stop).

5.3.2 Singing activity of paired males and bachelors

To test for an effect of study year on singing activity, we fitted a first generalized linear mixed model (GLMM) using the data on singing activity of 34 males surveyed during a limited period in 2007 and of 31 males from the corresponding period in 2008. The changes of singing activity across our nocturnal rounds seemed not to differ between the two years (GLMM, interaction round \times year: $df=1$, $p=0.634$; interaction round² \times year: $df=1$, $p=0.723$), and the measures of average singing activity across nocturnal rounds were strongly correlated between years (Pearson correlation, mated males: $r=0.875$, $t=4.773$, $df=7$, $p=0.002$; bachelors: $r=0.950$, $t=8.087$, $df=7$, $p<0.001$). Therefore, in all further analyses we used the data of 2008 only, when singing activity

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was surveyed continuously during the entire study period. In 2008, we monitored the singing activity of 31 males that arrived at the study site on average on 16 April (± 4.2 days). Later during the breeding season, 25 of those males were paired and 6 were bachelors. Male singing activity followed a distinct temporal pattern between dusk and dawn: singing activity dropped to zero in the first round after dusk, and thereafter increased continuously until dawn (Fig. 5.3). This general development of singing activity over the night was not found to differ between the period before and during female arrival (GLMM, interaction round?period: $df=1$, $p=0.132$). However, singing activity differed between paired males and bachelors depending on the period before or during female arrival (GLMM, interaction period?status: $df=1$, $p<0.001$) and on the time of the night (GLMM, interaction round?status: $df=1$, $p<0.001$). Before female arrival, paired males sang more than bachelors during the second and third nocturnal rounds (N2 and N3, as indicated by non overlapping 95% CI in Fig. 5.3.a). During the period of female arrival, during the rounds from about midnight (N3) until the last nocturnal round (N7; Fig. ??b), bachelors sang more than paired males (note that some subsequently paired males were still unpaired in the beginning of the period of female arrival, which explains why there was nocturnal singing activity of paired males during that period). No difference in singing activity among paired males and bachelors could be detected for the dusk or dawn rounds (Fig. 5.3).

5.4 Discussion

Translocated female nightingales covered the longest distances between 01.00 and 04.00 at night. This is in contrast to the temporal pattern of territory prospecting in non-territorial male nightingales that made significant movements only during the dawn chorus in the one or two hours before sunrise, as shown in an earlier study using the same methods and the same study populations (Amrhein et al. 2004b). This sex-specific timing of prospecting corresponded to the singing activity of territorial males: females searching for mates showed prospecting activity mostly at night when mainly bachelors were singing, while territory searching males showed prospecting activity only at dawn when all territorial males were singing intensely, and vacant territories should become apparent (Amrhein et al. 2004b). Thus, in the nightingale, the sex-specific

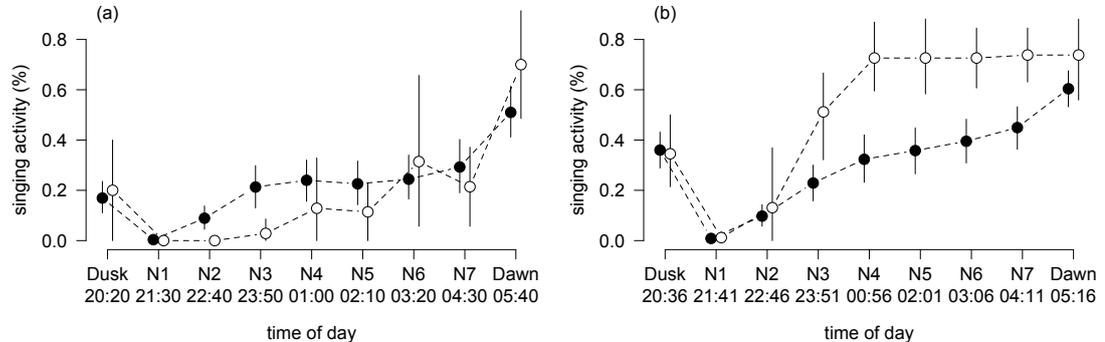


Figure 5.3: Male singing activity - Singing activity of 31 males as censused during nine rounds per night, starting at sunset and ending at sunrise, (a) prior to female arrival (11 April until 20 April) and (b) during the time of female arrival (21 April until 4 May). Singing activity of a male is expressed as the proportion of rounds it was heard singing (mean and bootstrapped 95% confidence interval). Closed circles indicate males that are paired or will be paired (N=25), open circles indicate bachelors (N=6). Dusk and dawn rounds started at sunset and 75 minutes before sunrise, respectively; the remaining rounds (N1 to N7) were spaced out regularly between the dusk and dawn round. Starting times of the rounds are given as averages for the respective periods of the breeding season.

patterns in the diel timing of prospecting and the patterns in the diel timing of male signalling were correlated.

State dependent models of daily singing routines have been used to simulate diel fluctuations in the birds' energy reserves (McNamara et al. 2001). These models accurately predicted the typical temperate zone passerine singing routines. However, male singing routines have also been suggested to depend on female behaviour if the male pairing propensity (i.e. the probability that a singing male pairs in a particular time interval) varies with time of day (Hutchinson et al. 1993). Therefore, the optimal singing routine of males may strongly be influenced by the temporally changing availability of females. In nightingales, unpaired males that are singing at night when females are prospecting for mates most likely have a higher pairing probability than unpaired males that would be singing exclusively at dawn. As predicted by the formal models (Hutchinson et al. 1993), this should shape the optimal singing routine of signalling males and may explain the occurrence of nocturnal song in the nightingale.

Nocturnal song of otherwise diurnal species is comparatively rare in western Palaearctic songbirds (Amrhein et al. 2002); in those species, nocturnal prospecting of mate

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searching females could potentially explain nocturnal singing of the males. However, nocturnal prospecting by females seems to be adaptive only if there is nocturnal song by males. It still remains unclear whether nocturnal singing is a cause for or an effect of nocturnal prospecting by females, and how nocturnal song evolved in the first place. A possible scenario is that in nocturnally migrating species like the nightingale, males that happened to sing at night had a higher pairing success because they more readily attracted females arriving from migration. This could have led to the evolution of nocturnal song in males, and of nocturnal prospecting in females. Because of the mutual dependence of the timing of signalling and of the timing of signal evaluation by receivers, formal models of daily routines in both behaviours would need to include game theoretic approaches (McNamara et al. 2001).

Females usually base their choice of mate on reliable signals indicating male quality (Andersson 1994). Particularly in monogamous species, females are likely to evaluate males also with regard to their pairing status (Staicer 1996), and females are expected to trade between male quality and pairing status (Slagsvold and Drevon 1999). By prospecting at night, female nightingales may be able to infer both the pairing status and the quality of singing males. Clearly, nocturnal song is a good indicator of male pairing status, since it is mainly bachelors that sing at night (Amrhein et al. 2002, 2004a). However, if nocturnal song is costly in the nightingale (Thomas 2002), nocturnal singing may also serve as an honest signal of male quality. In this study, at the beginning of the season before the arrival of females, the singing activity of males that later in the breeding season successfully attracted a female was higher around midnight (rounds N2 and N3), as compared to the singing activity of males that later could not attract a female. An early start of nocturnal singing in the first hours of the night could thus indicate male quality. In contrast to the first hours of the night, the singing activity at dawn or dusk did not predict future pairing status of males. Thus, females may not base their choice of mate on dawn or dusk singing in the nightingale. This is in line with an increasing number of studies providing evidence that a main function of dawn singing is territory defence in several songbirds (Slagsvold et al. 1994; Liu 2004; Kunc et al. 2005; Amrhein and Erne 2006).

Our study showed that sex-specific timing of prospecting for territories or mates corresponded to the differential singing activity of paired and unpaired males in the

nightingale. The temporal patterns in the behaviour of signallers and receivers thus appear to be mutually adapted.

5.5 Acknowledgements

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5.6 References

- Amrhein, V. and Erne, N. 2006 Dawn singing reflects past territorial challenges in the winter wren. *Anim. Behav.* 71, 1075-1080. (doi:10.1016/j.anbehav.2005.07.023)
- Amrhein, V., Korner, P. and Naguib, M. 2002 Nocturnal and diurnal singing activity in the nightingale: correlations with mating status and breeding cycle. *Anim. Behav.* 64, 939-944.
- Amrhein, V., Kunc, H. P. and Naguib, M. 2004a Seasonal patterns of singing activity vary with time of day in the nightingale (*Luscinia megarhynchos*). *Auk* 121, 110-117.
- Amrhein, V., Kunc, H. P. and Naguib, M. 2004b Non-territorial nightingales prospect territories during the dawn chorus. *Proc. R. Soc. B* 271, S167-S169.
- Andersson, M. 1994 Sexual selection. *Monographs in Behaviour and Ecology*. Princeton: Princeton University Press.
- Bates, D. and Sarkar, D. 2006 LME4: linear mixed-effects models using S4 classes. R package, version 0.9975-10. See <http://cran.r-project.org>.
- Bensch, S. and Hasselquist, D. 1992 Evidence for active female choice in a polygynous warbler. *Anim. Behav.* 44, 301-311.

5. SEX-SPECIFIC TIMING OF MATE SEARCHING AND TERRITORY PROSPECTING IN NIGHTINGALES

- Boulinier, T., Danchin, E., Monnat, J. Y., Doutrelant, C. and Cadiou, B. 1996 Timing of prospecting and the value of information in a colonial breeding bird. *J. Avian Biol.* 27, 252-256.
- Bradbury, J. W. and Vehrencamp, S. L. 1998 Principles of animal communication. Sunderland, Massachusetts: Sinauer.
- Brumm, H. 2006 Signalling through acoustic windows: nightingales avoid interspecific competition by short-term adjustment of song timing. *J. Comp. Physiol. A* 192, 1279-1285.
- Catchpole, C. K. and Slater, P. J. B. 2008 Bird song. Cambridge: Cambridge University Press.
- Crawley, M. 2007 The R book. London, UK: Wiley.
- Dalziell, A. H. and Cockburn, A. 2008 Dawn song in superb fairy-wrens: a bird that seeks extrapair copulations during the dawn chorus. *Anim. Behav.* 75, 489-500.
- Davidson, A. J. and Menaker, M. 2003 Birds of a feather clock together - sometimes: social synchronization of circadian rhythms. *Curr. Op. Neurobiol.* 13, 765-769.
- Double, M. and Cockburn, A. 2000 Pre-dawn infidelity: females control extra-pair mating in superb fairy-wrens. *Proc. R. Soc. B* 267, 465-470.
- Draud, M. J., Verga, J. N., Haley, M. P. and Itzkowitz, M. 2008 Mate inspection patterns in the female beaugregory damselfish (*Stegastes leucostictus*). *Acta Ethol.* 11, 6-15.
- Gattermann, R., Johnston, R. E., Yigit, N., Fritzsche, P., Larimer, S., Ozkurt, S., Neumann, K., Song, Z., Colak, E., Johnston, J. and McPhee, M. E. 2008 Golden hamsters are nocturnal in captivity but diurnal in nature. *Biol. Lett.* 4, 253-255.
- Gelman, A. and Hill, J. 2007 Data analysis using regression and multilevel/hierarchical models. Analytical methods for social research. Cambridge: Cambridge University Press.
- Gerhardt, H.C. and Huber, F. 2002 Acoustic communication in insects and anurans: common problems and diverse solutions. Chicago: University of Chicago Press.

- Helm, B., Piersma, T. and Van der Jeugd, H. 2006 Sociable schedules: interplay between avian seasonal and social behaviour. *Anim. Behav.* 72, 245-262.
- Hutchinson, J. M. C., McNamara, J. M. and Cuthill, I. C. 1993 Song, sexual selection, starvation and strategic handicaps. *Anim. Behav.* 45, 1153-1177.
- Jacot, A., Scheuber, H., Holzer, B., Otti, O. and Brinkhof, M. W. G. 2008 Diel variation in a dynamic sexual display and its association with female mate-searching behaviour. *Proc. R. Soc. B* 275, 579-585.
- Kondoh, M. and Ide, J. Y. 2003 Evolution of periodicity in insect mate-seeking behaviour: a male-female coevolutionary game model. *Anim. Behav.* 65, 1013-1020.
- Kunc, H. P., Amrhein, V. and Naguib, M. 2005 Seasonal variation in dawn song characteristics in the common nightingale. *Anim. Behav.* 70, 1265-1271.
- Liu, W. C. 2004 The effect of neighbours and females on dawn and daytime singing behaviours by male chipping sparrows. *Anim. Behav.* 68, 39-44.
- Macleod, R., Gosler, A. G. and Cresswell, W. 2005 Diurnal mass gain strategies and perceived predation risk in the great tit *Parus major*. *J. Anim. Ecol.* 74, 956-964.
- McNamara, J. M., Mace, R. H. and Houston, A. I. 1987 Optimal daily routines of singing and foraging in a bird singing to attract a mate. *Behav. Ecol. Sociobiol.* 20, 399-405.
- McNamara, J. M., Houston, A. I. and Collins, E. J. 2001 Optimality models in behavioral biology. *Siam Review* 43, 413-466.
- Mukhin, A., Kosarev, V. and Ktitorov, P. 2005 Nocturnal life of young songbirds well before migration. *Proc. R. Soc. B* 272, 1535-1539.
- Murphy, M. T., Sexton, K., Dolan, A. C. and Redmond, L. J. 2008 Dawn song of the eastern kingbird: an honest signal of male quality? *Anim. Behav.* 75, 1075-1084.
- Olsson, O., Wiktander, U. and Nilsson, S. G. 2000 Daily foraging routines and feeding effort of a small bird feeding on a predictable resource. *Proc. R. Soc. B* 267, 1457-1461.

5. SEX-SPECIFIC TIMING OF MATE SEARCHING AND TERRITORY PROSPECTING IN NIGHTINGALES

- Otter, K., Chruszcz, B. and Ratcliffe, L. 1997 Honest advertisement and song output during the dawn chorus of black-capped chickadees. *Behav. Ecol.* 8, 167-173.
- Piper, W. H., Walcott, C., Mager, J. N., Perala, M., Tischler, K. B., Harrington, E., Turcotte, A. J., Schwabenlander, M. and Banfield, N. 2006 Prospecting in a solitary breeder: chick production elicits territorial intrusions in common loons. *Behav. Ecol.* 17, 881-888.
- R Development Core Team. 2007 R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing.
- Reed, J., Boulinier, R., Danchin, E. and Oring, L. 1999 Informed dispersal: prospecting by birds for breeding sites. *Curr. Ornithol.* 15, 189-259.
- Slagsvold, T. and Drevon, T. 1999 Female pied flycatchers trade between male quality and mating status in mate choice. *Proc. R. Soc. B* 266, 917-921.
- Slagsvold, T., Dale, S. and Saetre, G. P. 1994 Dawn singing in the great tit (*Parus major*) - mate attraction, mate guarding or territorial defense. *Behaviour* 131, 115-138.
- Staicer, C. A. 1996 Honest advertisement of pairing status: evidence from a tropical resident wood-warbler. *Anim. Behav.* 51, 375-390.
- Staicer, C. A., Spector, D. A. and Horn, A. g. 1996 The dawn chorus and other diel patterns in acoustic signalling. In *Ecology and Evolution of Acoustic Communication in Birds* (ed. D. E. Kroodsma and E. H. Miller), pp. 426-453. Ithaca, NY: Comstock Publishing Associates.
- Thomas, R. J. 2002 The costs of singing in nightingales. *Anim. Behav.* 63, 959-966.
- Thomas, R. J. and Cuthill, I. C. 2002 Body mass regulation and the daily singing routines of European robins. *Anim. Behav.* 63, 285-292.
- Todt, D. and Naguib, M. 2000 Vocal interactions in birds: the use of song as a model in communication. In *Advances in the Study of Behavior*, vol. 29, pp. 247-296. San Diego: Academic Press.

6

A Swiss agri-environment scheme effectively enhances species richness for some taxa over time

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6. A SWISS AGRI-ENVIRONMENT SCHEME ENHANCES SPECIES RICHNESS OVER TIME

Abstract

Aim *The effectiveness of agri-environment schemes (AESs) in promoting biodiversity was recently debated. One reason for limited effectiveness of AESs may be their application to small and scattered patches of land. This study presents the evaluation of a scheme adopted by the canton of Aargau, Switzerland, which seems to be unique in its consequent focus on entire farms, aiming at increasing quality and quantity of ecological compensated areas (ECAs).*

Location *Canton of Aargau, Switzerland.*

Methods *The temporal changes of species richness of plots with ECA were compared with the temporal changes of species richness of plots without ECA.*

Results *In vascular plants and snails, the species richness increased during a period of five years on plots with AES, but not on control plots without AES. In butterflies and birds, no significant differences were found between AES plots and control plots in the change of species richness over time. While butterfly species numbers generally decreased, bird species numbers increased on both AES plots and control plots.*

Main conclusions *It appears that agri-environment schemes can be effective in protecting and promoting biodiversity, but the effect may depend on the group of organisms.*

Keywords: agri-environment scheme, policy evaluation, species diversity, ecological compensated area, Aargau, Switzerland

6.1 Introduction

Most European countries have launched agri-environment schemes (AESs) more than one decade ago (Kleijn and Sutherland 2003), and schemes currently cover more than 25% of all farmland in the EU15 countries (EU 2005). The total average annual expenditure on agri-environment payments is estimated at €3.7 billions for 2003 in the European Union (EEA 2002). In the United States, for the period between 2000 and 2003, the expenditures averaged US\$ 2.0 billions annually (Herzog 2005). In the OECD (Organisation for Economic Cooperation and Development) countries, the expenses for AES sum up to about 8% of the total budget for agriculture (OECD 2003). Kleijn and Sutherland (2003) reviewed 62 studies evaluating European AES and pointed out that the majority of studies were inadequate to assess reliably the effectiveness of the AES because no baseline data were collected to examine trends in biodiversity over time (Kleijn and Sutherland 2003, Herzog 2005). The few studies that compared the change of species richness in AES fields and control plots included only few species groups (mainly plants and birds) or were located within or in the direct vicinity of nature reserves that were protected for a long time (Peter and Walter 2001, Brereton et al. 2002). A particularly comprehensive study of several species groups in five European countries compared current species richness in AES plots with control plots, but did not include trends over time (Kleijn et al. 2006).

AES are often applied to small patches of land, which are referred to as ecological compensated areas (ECAs). Frequently, ECAs are scattered and unconnected, with negative influence on the effectiveness of AES in promoting biodiversity (Whittingham 2007). In 1994, the canton of Aargau, Switzerland, started to establish an AES that was aimed to take this shortcoming of AES into account. The scheme was based on special contracts with farmers (Kanton Aargau 2005). In addition to high standards concerning the quality of the ECA, the quantity and distribution of the ECA within the farm were evaluated and improved before a farmer could get a contract and additional payments. New ECAs were placed in a way to supplement and link existing ECAs or nature reserves in the area. If a farmer implemented a minimum proportion (currently 12%) of his farmland, he received an additional bonus.

Generally, ECA categories may differ in the way they affect species richness spatially or temporally, which often renders evaluating the success of the entire AES difficult.

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So far, AES evaluations mainly investigated the effect of single categories of ECA on species richness (Kleijn and Sutherland 2003, Kleijn et al. 2006). However, it is often the general aim of an AES that all ECA categories taken together successfully increase species richness in the entire agricultural landscape.

Here, we present a long-term study evaluating the effects of the Aargau AES on the biodiversity of several trophic levels (primary producers: vascular plants; pollinators: butterflies; first level consumers: snails; top level consumers: birds). Sampling plots based on a regular grid were selected from the entire surface of the Aargau agricultural landscape, and species richness per study plot at an initial phase of the AES was compared with the species richness five years later. The effects of the AES were then tested against the change of species richness in conventionally used agricultural areas.

6.2 Material and methods

The canton of Aargau is a 1403 km² sized county in the north of Switzerland with relatively large areas of intense farming. More than half of the farmlands are meadows or pastures (53%), and most of the rest is arable land (44%; mainly maize, wheat, barley, potatoes, sugar beets, and rape). Farmland size of an average farm in the canton of Aargau is 20.8 ha (all figures from Swiss Statistics, *www.bfs.admin.ch*). The focus of the Aargau AES was on entire farms, aiming at increasing the quality and quantity of ECA (Schmid et al. 1990, Kanton Aargau 2005). To implement an efficient strategy, farmers that joined the AES in Aargau were advised by persons with ecological and agricultural education. The ecological potential of the entire land of a farm was assessed with a particularly close look at the grassland, on which a plant inventory was taken. Farmer and adviser collaborated in devising how to realise an environmentally and biodiversity friendly farming practice and a target-oriented management of the ECA. On each farm, ECAs were established on the most promising areas (in terms of maximum biodiversity gain and not in terms of the economic perspective of the farmer). Care was taken that ECAs were grouped close together and that the surrounding farmland of the farm under contract was less intensively farmed (mainly by reducing the use of fertilizers). Making a contract secured additional payments, and farmers committed themselves to strict ecological measures for at least six years. General payments were made for the entire surface of a farm to compensate for the generally environmental friendly farming

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practice, and additional payments were made for each ECA depending on the category of the ECA. The average year (\pm SD) of contract starts of the ECA situated within our study plots (see below) was in July 1995 (\pm 3.2 years). At the end of 2006, more than 530 farmers had agreed on such a contract, and the surface of those farms was about 20% of the Aargau agricultural landscape. The average area of ECA of the farms under contract amounted to 23% of their land and to 2'565 ha in total.

species group	number of treatment plots	number of control plots	number of species A	number of species B	p-value state	p-value change
vascular plants	33	211	15.3 (\pm 8.7)	16.2 (\pm 9.8)	0.007**	0.005**
snails	33	209	4.1 (\pm 4.3)	3.9 (\pm 4.9)	0.097	0.012*
butterflies	52	35	6.7 (\pm 3.7)	5.6 (\pm 3.4)	0.014*	0.607
birds	120	61	9.0 (\pm 4.3)	11.5 (\pm 4.4)	0.004**	0.420

*p<0.05; **p<0.01; ***p<0.001

Table 6.1: Sample sizes and mean species numbers (\pm SD) of all study plots at the initial survey (number of species A) and at the second survey 5 years later (number of species B).

In 1996, a long-term research project was started to monitor biodiversity in the whole canton of Aargau (Stapfer 1999). We used the data from this biodiversity monitoring program to investigate the impact of the Aargau AES on biodiversity. The sampling scheme was based on a regular grid that covered the entire canton. Based on the national coordinate system, 516 grid points were selected by taking every second grid point of a grid with 1 km grid length. On each study plot at such a grid point, vascular plant, snail, butterfly and bird species were counted twice, the first time between 1996 and 2000 (1998 and 2000 for butterflies) and the second time between 2001 and 2005 (2003 and 2005 for butterflies). For each study plot, there were exactly five years between the first and the second census period. The sampling protocol was adapted to the different species groups, and sampling was done at two different spatial scales: On the small scale, vascular plants and snails were surveyed. Plants species were counted in a circle of 10 m², and on the outer line of the circle in which plant species were counted, eight soil samples were taken during the plant surveys and the number of snail species was estimated from these soil samples. On the larger scale, bird species were estimated from five surveys in a circle with 100 m radius, and for butterflies, 11 surveys were made along a transect of 250 m length (butterflies were recorded within 5 m to each side of the transect line). If possible, all individuals within the study plots of the four species groups were identified to the species level. The few individuals not

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identified to the species level were excluded from the data. Land use information for each study plot was collected during the first visit. For the present study, only plots with at least 75% agricultural land use were included into the analyses. A few surveys not fulfilling the criteria of the sampling protocol were excluded from the analyses (see Table 6.1 for the sizes of each data set).

For the analysis, the study plots were divided into two groups: if there was ECA within a plot, independently of the category and the size of ECA, the plot was included into the treatment group (AES plot). If there was no ECA within the plot, the plot was included into the control group. Because the plot size depended on the study group, the study plots were divided into treatment and control groups for each species group separately: The study plots of plants and snails were included into the treatment group if there was ECA within the study circle of 10 m². Similarly, the study plots of birds were included into the treatment group if there was ECA within the 100 m circle. For the butterflies, a study plot was included into the treatment group if there was ECA within 50 m of the transect. This approach using two spatial scales implies that the proportion of study plots that were included into the treatment groups differed among taxa: for plants and snails, 14% of the study plots were included into the treatment group, while for birds and butterflies, 60 and 66%, respectively, were included into the treatment group (Table 6.1). Furthermore, the mean proportion of a study plot area covered by ECA differed among species groups. For vascular plants and snails, the mean (\pm SD) proportional area of ECA within a study plot was 89.9% (\pm 26.4), for butterflies 13.3% (\pm 15.6), and for birds 16.7% (\pm 8.5) (reference date: 31.12.2005). Differences in species numbers per plot between the two groups (treatment and control) were tested using Wilcoxon rank sum tests.

Within or in the surroundings of the study plots, defined as a circle of 500 m radius around the centre of the sample plot, ECA had been established in 129 (53%) of the 244 study plots (reference date: 31.12.2005) and the overall surface of the ECA per circle ranged from 0.07 to 29.9 ha. The total area of the ECA within the 500 m circles was 592.0 ha, of which 308.8 ha (52.2%) were low intensity hay or litter meadows, 186.8 ha (31.6%) hedges, traditional orchards or trees, 43.6 ha (7.3%) pastures, and the remaining 52.8 ha (8.9%) of other categories such as wild flower strips, arable fallows or ruderal areas.

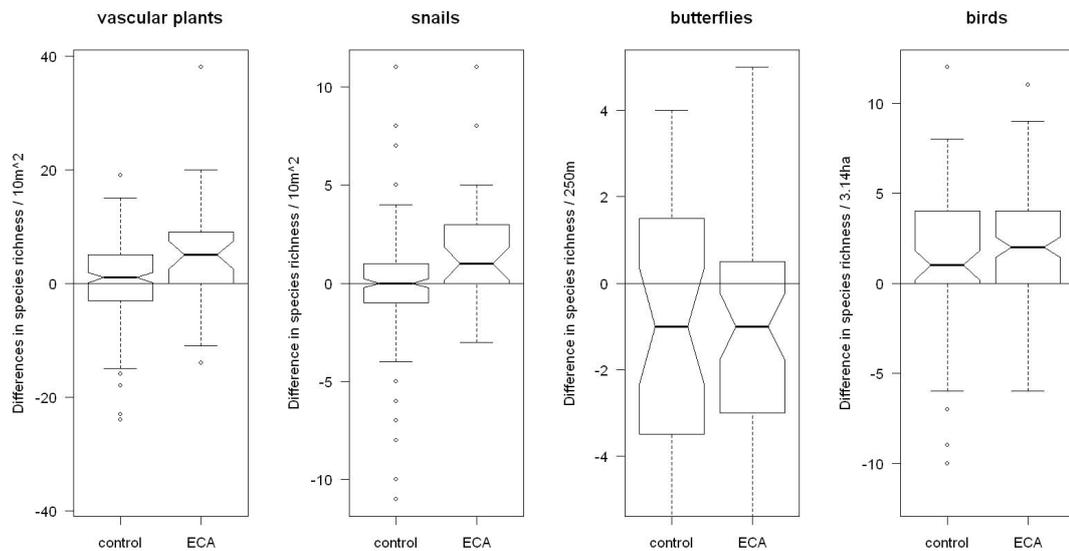


Figure 6.1: Change of species richness over time - Notched box-plots show the differences of species richness per study plot between the two study periods (initial survey 1996–2000 and repeated survey 2001–2005 for vascular plants, snails and birds; 1998–2000 and 2003–2005 for butterflies). For each study plot, there were exactly five years between the first and the second census period. ECAs are study plots with ecological compensated area, and controls are study plots without ecological compensated area. For sample sizes, see Table 6.1. Boxes are median and 25% and 75% percentiles, whiskers are non-outlier ranges, dots are outliers, and non-overlapping notches indicate significant differences in central tendency (Wilcoxon rank sum tests: vascular plants: $p = 0.005$; snails: $p = 0.012$; butterflies: 0.607; birds: 0.429).

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To examine the change of single species, the number of study plots in which a particular species was not observed during the first study period but was observed during the second study period (increase) were compared with the number of study plots in which the species was observed during the first but not during the second study period (decrease). This was done for all observed species, and numbers of increase and decrease were evaluated using McNemar tests (Zar 1999). All analyses for this study were done using the software R 2.4.0 (R Development Core Team 2006).

6.3 Results

During the first study period, three of the four species groups (plants, butterflies and birds) showed significantly higher species richness in study plots with ECA compared to control plots (all numbers mean \pm SD, p-values from Wilcoxon rank sum tests; vascular plants: ECA = 19.2 (\pm 9.9), control = 14.6 (\pm 7.9), p = 0.007; snails: ECA = 5.0 (\pm 4.3), control = 4.0 (\pm 4.3), p = 0.097; butterflies: ECA = 7.3 (\pm 3.8), control = 5.6 (\pm 3.1), p = 0.014; birds: ECA = 9.7 (\pm 4.0), control = 7.7 (\pm 4.4), p = 0.004). Between the first and the second study period, the species richness of vascular plants and snails increased on plots with ECA, but not on control plots without ECA (Fig. 6.1). In study plots with ECA, the increase in species numbers of plants and snails per study plot was on average 5.1 species (relative increase: 26.9%) and 1.4 species (27.2%), respectively. The number of bird species per study plot increased significantly in the agricultural landscape of Aargau (mean increase of all study plots between 1996–2000 and 2001–2005: 2.05 species, n = 181, Wilcoxon signed rank test: p < 0.001). However, the increase in bird species numbers in plots with ECA was not different from control plots (Fig. 6.1). The number of butterfly species generally decreased in the agricultural landscape of Aargau, irrespective of whether the study plots included ECA or not (mean decrease of all study plots between 1998–2000 and 2003–2005: -1.13 species, n = 87, Wilcoxon signed rank test: p < 0.001). The decrease in butterfly species numbers in plots with ECA was not different from control plots (Fig. 6.1). In the agricultural landscape of Aargau, 16 species increased significantly (5 plant species, 3 butterfly species, 8 bird species), while 18 species decreased significantly (12 plant species, 1 snail species, 5 butterfly species; for tests and details, see Table 6.2).

6.4 Discussion

During the first study period, which corresponded to an early state of the AES, three of the four species groups (plants, butterflies and birds) showed significantly higher species richness in study plots with ECA compared to control plots. Thus, the study plots with ECA could have profited from the AES already at this early stage of the contracts. Alternatively, the higher initial species richness could reflect the fact that ECAs were established mainly in ecologically more valuable agricultural areas. In the present study, the initial dissimilarity among plots was controlled for by comparing the temporal change of species richness on both the AES and control plots (Kleijn and Sutherland 2003). Between the first and the second study period, the species richness of vascular plants and snails increased on plots with ECA, but not on control plots. Therefore, this study suggests that the AES in the canton of Aargau effectively enhanced species diversity for vascular plants and snails. Studies testing for an effect of AES on biodiversity have regularly investigated plant species numbers and often found that it is difficult to enhance plant species diversity in intensively used agricultural landscape (Kleijn and Sutherland 2003). This conclusion is in contrast to our results and to the results from another study in Switzerland that confirmed higher species richness of vascular plants on ECA compared to conventionally managed fields (Knop et al. 2006).

Herzog et al. (2005) found almost no general benefits of ECA for grassland birds and orchard birds in the agricultural landscape of the entire Switzerland. In contrast, we found that in the agricultural landscape of the canton of Aargau, the bird species richness per study plot increased, and the negative trend in the number of bird species found on a larger scale may have been reversed (Zbinden et al. 2005, Donald et al. 2006). Three of the eight bird species for which a positive trend could be identified were proposed as indicator species for agriculture landscapes [*Columba palumbus*, *Passer montanus* and *Emberiza citrinella*; Gregory et al. (2005)]. The farms under contract covered around 20% of the Aargau agricultural landscape and provided resources that are most valuable for farmland birds [e.g. fallows, non-cropped habitats, or extensively managed grassland; Vickery et al. (2004)].

However, the similarly mobile butterfly species decreased in the canton of Aargau irrespective of the AES. This is an alarming result, as butterfly diversity is at a very low

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Species	change	increase	decrease	χ^2	p-value
Plants:					
<i>Bromus hordeaceus</i>	+	22	8	5.63	0.018
<i>Phleum pratense</i>	+	28	10	7.61	0.006
<i>Poa trivialis</i>	+	75	35	13.83	<0.001
<i>Veronica arvensis</i>	+	36	1	31.24	<0.001
<i>Veronica chamaedrys</i>	+	27	8	9.26	0.002
<i>Achillea millefolium</i>	-	0	7	5.14	0.023
<i>Cardamine pratensis</i>	-	12	34	9.59	0.002
<i>Galinsoga ciliata</i>	-	0	7	5.14	0.023
<i>Helictotrichon pubescens</i>	-	6	18	5.04	0.025
<i>Lolium multiflorum</i>	-	34	59	6.19	0.013
<i>Matricaria recutita</i>	-	4	16	6.05	0.014
<i>Poa annua</i>	-	31	55	6.15	0.013
<i>Poa pratensis</i>	-	7	54	34.69	<0.001
<i>Polygonum persicaria</i>	-	11	27	5.92	0.015
<i>Rumex obtusifolius</i>	-	15	31	4.89	0.027
<i>Taraxacum officinale</i>	-	30	62	10.45	0.001
<i>Veronica persica</i>	-	12	91	59.07	<0.001
Snails:					
<i>Carychium tridentatum</i>	-	16	35	6.35	0.012
Butterflies:					
<i>Cynthia cardui</i>	+	19	7	4.65	0.031
<i>Gonepteryx rhamni</i>	+	6	0	4.17	0.041
<i>Lasiommata megera</i>	+	9	0	7.11	0.008
<i>Aphantopus hyperantus</i>	-	4	21	10.24	0.001
<i>Colias hyale/alfacariensis</i>	-	5	20	7.84	0.005
<i>Inachis io</i>	-	4	22	11.12	0.001
<i>Melicta parthenoides</i>	-	0	10	8.1	0.004
<i>Pararge aegeria</i>	-	1	27	22.32	<0.001
Birds:					
<i>Dendrocopos major</i>	+	24	11	4.11	0.043
<i>Passer montanus</i>	+	30	13	5.95	0.015
<i>Emberiza citrinella</i>	+	27	11	5.92	0.015
<i>Turdus viscivorus</i>	+	28	12	5.63	0.018
<i>Sylvia atricapilla</i>	+	29	8	10.81	0.001
<i>Columba palumbus</i>	+	47	11	21.12	<0.001
<i>Erithacus rubecula</i>	+	21	8	4.97	0.026
<i>Parus palustris</i>	+	27	13	4.23	0.04

Table 6.2: Species for which a significant trend between the first study period and the second study period 5 years later could be detected (change) in the agricultural landscape of the canton of Aargau. Number of study plots in which a particular species was not observed during the first study period but was observed during the second study period (increase) were compared with the number of study plots in which the species was observed during the first but not during the second study period (decrease). The significance of the trends was tested using McNemar tests.

level and generally decreases in the Central Plateau of Switzerland (Koordinationsstelle Biodiversitätsmonitoring Schweiz 2006), and the AES was apparently not able to stop this decrease so far. Note, however, that the differences of the responses to the Aargau AES in the four species groups may be partly explained by differences in the plot sizes. ECA covered most of the area of the small sized study plots for plants and snails, but only a smaller fraction of the larger study plots for birds and butterflies. Therefore, the larger proportion of conventional land use within the study plots for birds and butterflies may have blurred the effect of AES.

In the majority of cases, the general goal of AES is to protect and increase overall species diversity (Kleijn and Sutherland 2003) and not to protect a single species group (e.g. Ottvall and Smith 2006) or a particular species (Peach et al. 1998, Aebischer et al. 2000). However, our study showed that the effect of AES on biodiversity may vary depending on the group of organisms. This was also found in other studies including more than one species group to investigate the effect of AES on biodiversity (Kleijn and Sutherland 2003, Kleijn et al. 2006, Knop et al. 2006). Therefore, if the goal of AES is to protect general biodiversity, then the effectiveness of an AES can only be assessed adequately if several indicator species groups are included into the study.

Less mobile species groups are likely to benefit from an AES only if ECA plots are close to each other (Ockinger and Smith 2007). In the canton of Aargau, the species richness per study plot increased among the less mobile species (plants and snails), which suggests that the aims of the Aargau AES to connect ECA were achieved. The effect of the Aargau AES was not tested against the effect of other conventional AES, and the average farm in the canton of Aargau is small compared to farm sizes in other parts of Europe. However, the Aargau AES with its contracts focussing on entire farms instead of single fields and its effort to connect ECA seem to have had positive effects at least on parts of biodiversity measures and may be regarded as a model for other regions and countries.

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6.6 References

- Aebischer, N. J., R. E. Green, and A. D. Evans. 2000. From science to recovery: four case studies of how research has been translated into conservation action in the UK. *Ecology and Conservation of Lowland Farmland Birds*:43-54.
- Brereton, T., K. S. Stewart, and M. S. Warren. 2002. Developing a System for Assessing the Effect of Agri-Environment Schemes on Butterfly Populations. UK Department for Environment, Food and Rural Affairs, London.
- Donald, P. F., F. J. Sanderson, I. J. Burfield, and F. P. J. van Bommel. 2006. Further evidence of continent-wide impacts of agricultural intensification on European farmland birds, 1990-2000. *Agriculture Ecosystems & Environment* 116:189-196.
- EEA. 2002. Environmental Signals 2002–Benchmarking the Millennium. European Environmental Agency, Copenhagen.
- EU. 2005. Agri-environment Measures–Overview on General Principles, Types of Measures, and Application. European Commission-Directorate., General for Agriculture and Rural Development.
- Gregory, R. D., A. van Strien, P. Vorisek, A. W. G. Meyling, D. G. Noble, R. P. B. Foppen, and D. W. Gibbons. 2005. Developing indicators for European birds. *Philosophical Transactions of the Royal Society B-Biological Sciences* 360:269-288.
- Herzog, F. 2005. Agri-environment schemes as landscape experiments - Preface. *Agriculture Ecosystems & Environment* 108:175-177.
- Herzog, F., S. Dreier, G. Hofer, C. Marfurt, B. Schupbach, M. Spiess, and T. Walter. 2005. Effect of ecological compensation areas on floristic and breeding bird di-

- iversity in Swiss agricultural landscapes. *Agriculture Ecosystems & Environment* 108:189-204.
- Kanton Aargau. 2005. Projekt Bewirtschaftungsverträge Naturnahe Landwirtschaft. Beitragssystem und Bewirtschaftungsrichtlinien. Baudepartement, Abteilung Landschaft und Gewässer, Aarau.
- Kleijn, D., R. A. Baquero, Y. Clough, M. Diaz, J. De Esteban, F. Fernandez, D. Gabriel, F. Herzog, A. Holzschuh, R. Johl, E. Knop, A. Kruess, E. J. P. Marshall, I. Steffan-Dewenter, T. Tscharntke, J. Verhulst, T. M. West, and J. L. Yela. 2006. Mixed biodiversity benefits of agri-environment schemes in five European countries. *Ecology Letters* 9:243-254.
- Kleijn, D. and W. J. Sutherland. 2003. How effective are European agri-environment schemes in conserving and promoting biodiversity? *Journal of Applied Ecology* 40:947-969.
- Knop, E., D. Kleijn, F. Herzog, and B. Schmid. 2006. Effectiveness of the Swiss agri-environment scheme in promoting biodiversity. *Journal of Applied Ecology* 43:120-127.
- Koordinationsstelle Biodiversitätsmonitoring Schweiz. 2006. Zustand der Biodiversität in der Schweiz. Bundesamt für Umwelt, Bern.
- Ockinger, E. and H. G. Smith. 2007. Semi-natural grasslands as population sources for pollinating insects in agricultural landscapes. *Journal of Applied Ecology* 44:50-59.
- OECD. 2003. *Agricultural Policies in OECD Countries: Monitoring and Evaluation*. Organisation for Economic Co-operation and Development, Paris.
- Ottvall, R. and H. G. Smith. 2006. Effects of an agri-environment scheme on wader populations of coastal meadows of southern Sweden. *Agriculture Ecosystems & Environment* 113:264-271.
- Peach, W. J., S. R. Baillie, and D. E. Balmer. 1998. Long-term changes in the abundance of passerines in Britain and Ireland as measured by constant effort mist-netting. *Bird Study* 45:257-275.

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- Peter, B. and T. Walter. 2001. Heuschrecken brauchen kologische Ausgleichsflächen. *Agrarforschung* 8:452-457.
- R Development Core Team. 2006. R: A language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
- Schmid, W., A. Georg, M. Lüthy, J. Schmidlin, and M. Staub. 1990. Betriebsmodelle naturgemässe Landwirtschaft. . Baudepartement Aar- gau und Finanzdepartement Aargau, Aarau.
- Stapfer, A. 1999. Volkszählung in der Aargauischen Natur? *Umwelt Aargau* 6:5-60.
- Vickery, J. A., R. B. Bradbury, I. G. Henderson, M. A. Eaton, and P. V. Grice. 2004. The role of agri-environment schemes and farm management practices in reversing the decline of farmland birds in England. *Biological Conservation* 119:19-39.
- Whittingham, M. J. 2007. Will agri-environment schemes deliver substantial biodiversity gain, and if not why not? *Journal of Applied Ecology* 44:1-5.
- Zar, H. J. 1999. *Biostatistical Analysis*. Prentice Hall, New Jersey.
- Zbinden, N., H. Schmid, M. Kéry, and V. Keller. 2005. Swiss bird index SBI registered trademark—Kombinierte Indices für die Bestandsentwicklung von Artengruppen regelmässig brütender Vogelarten der Schweiz 1990–2004. *Der Ornithologische Beobachter* 102:283-291.

7

Spread of common species results in local-scale floristic homogenization in grassland of switzerland

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TR did the analyses; both authors wrote the manuscript.

7. FLORISTIC HOMOGENIZATION OF SWISS GRASSLAND

Abstract

Aim We assess changes of plant species richness and changes in species dissimilarity at local scale in Swiss grassland between the time periods 2001–2004 and 2006–2009. Further, we provide an ecological interpretation of the observed taxonomic homogenization of vascular plants.

Location Switzerland.

Methods Changes in species richness and changes in Simpson dissimilarity index of vascular plants in grassland (meadows and pastures) were examined. The analyses were based on species lists recorded on 339 10 m² sample plots from a systematic sample covering the entire Switzerland. Each sample plot had been surveyed once in 2001–2004 and once in 2006–2009 with 5 years between the first and the second survey. Changes in species dissimilarity were interpreted by comparing the relative contribution of several indicator species groups.

Results Mean species richness of vascular plants in grassland increased during the study period. In contrast, species dissimilarity of plants decreased, suggesting local scale floristic homogenization of grassland in Switzerland. It was mostly due to the spread of common species, namely the species that are tolerant to high nutrient levels, the species of low conservation value and the species adapted to moderate temperature levels that led to taxonomic homogenization. Target species for conservation did only marginally affect taxonomic homogenization. In contrast to the predictions from studies of taxonomic homogenization on larger scales, the taxonomic homogenization of grassland at local scale was not explained by the spread of neophytic species.

Main conclusions The biotic diversity of grassland in Switzerland changed considerably between 2001–2004 and 2006–2009. The observed taxonomic homogenization was merely due to the spread of common species. Local-scale changes in land use regimes implemented by agri-environmental schemes and other conservation efforts on parts of the entire grassland area were, apparently, not enough to prevent the total grassland from recent taxonomic homogenization.

Keywords: Beta diversity, biodiversity monitoring, biotic homogenization, grassland, meadows, Simpson index

7.1 Introduction

Taxonomic homogenization is the decrease in species dissimilarity between sample units over time (Olden and Rooney 2006). It is a simple prediction that follows from human-induced changes of environments that favour few winning species and negatively affect many others (Smart et al. 2006, Rooney et al. 2007). So far, studies on taxonomic homogenization have been mainly conducted by comparing extant and historic species lists among large grid cells, counties, countries or even continents, i.e. on large spatial scales (e.g. Kühn and Klotz 2006, Schwartz et al. 2006, Melo et al. 2009). In such studies on large spatial scales, taxonomic homogenization has been shown to take place in various species groups, and has often been attributed to the invasion of alien species or the replacement of specialist species by generalist species (Wiegmann and Waller 2006, Kerbiriou et al. 2009, Qian and Guo 2010).

In contrast to many studies on a large spatial scale, only few studies on taxonomic homogenization have been conducted on a local scale, i.e. by comparing study plots of about one hectare (Smart et al. 2006, Lambdon et al. 2008, Arevalo et al. 2010, Naaf and Wulf 2010). However, to understand the effect of human-induced environmental changes on biodiversity, studies on local scale are equally important as studies on large spatial scale. Firstly, this is because changes in land use regimes or changes in conservation planning are often implemented at a local scale (Margules and Pressey 2000, Naaf and Wulf 2010). Furthermore, it is at the local scale that interactions between species and their physical environment are strongest and thus local scale studies provide insights into ecological mechanisms and allow predictions of how human activities will affect biodiversity (Huston 1999). Secondly, local scale studies on taxonomic homogenization are needed because it could be challenging or even misleading to predict effects of human activity on biodiversity at the local scale from studies of taxonomic homogenization on large spatial scales. A variety of different processes affect biotic diversity only some of which may operate equally at all spatial scales. For example, species richness generally decreases at the global scale but often increases at the local scale (Sax and Gaines 2003). Similarly, opposing trends of taxonomic homogenization at different spatial scales may become apparent, as soon as more studies on taxonomic homogenization at the local scale are available. For example, the invasion of alien species that is one of the major causes for taxonomic homogenization at large spatial

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scale, seems unlikely to be a major driver for taxonomic homogenization at local scale (Smart et al. 2006, Lambdon et al. 2008).

Meadows and pastures (that we refer to as grassland) are probably among the habitat types that are most severely affected by land use regimes and have high priority in conservation planning (Jacquemyn et al. 2003). Grassland with high biological diversity used to be common in Central Europe, but intensification of land use have severely reduced the biotic diversity of most grassland areas in the last century (Marini et al. 2008). In the last few decades considerable conservation efforts, for example in the form of agri-environmental schemes and the legal protection of habitats, are targeting grassland with the aim of increasing their biotic diversity (Kleijn and Sutherland 2003, Oster et al. 2009, FOEN 2010). The central instruments of the implementation of measures to conserve grassland are contracts between farmers and authorities or conservation bodies. These contracts contain agreements on land management, conservation, maintenance measures and the financial compensation for all efforts (FOEN 2010). However, it is an open question if the local-scale changes in land use regimes induced by agri-environmental schemes and other conservation efforts on parts of the entire grassland area were enough to prevent the total grassland area from further decline in species richness and from taxonomic homogenization. Alternatively, factors known to have a strong and usually negative effect on biodiversity at large spatial scales, such as climate change or the introduction of neophytic (i.e. alien plant) species may have led to taxonomic homogenization of grassland also at a local scale.

In Switzerland, meadows and pastures are habitat types of high priority for conservation, and more than 93,000 hectares of grassland have been registered as ecological compensation areas and are under contract with farmers (FOEN 2010). Several studies in different regions of Switzerland have reported a positive effect of ecological compensation areas on plant species richness (Herzog et al. 2005, Knop et al. 2006, Roth et al. 2008). Our first goal in this study was to assess recent changes in biotic diversity of Swiss grassland across the entire range of land use regimes. Our second and main goal was then to identify potential mechanism that may explain the observed temporal changes in species dissimilarity. We investigated the temporal change in species richness and species dissimilarity of vascular plants at the vegetation plot level between the two time periods 2001-2004 and 2006-2009, using the data from the Swiss biodiversity monitoring program (BDM, Weber et al. 2004). Since conservation is targeting species

that became rare, we expected that due to conservation efforts in the last decade, an increase in distribution of the group of rare species should have led to both an increase in plant species richness and an increase in plant species dissimilarity. Specifically, we asked (1) whether or not taxonomic homogenization (i.e. a decrease in species dissimilarity) occurred in the grassland of Switzerland over the last decade, (2) whether the change of species dissimilarity in grassland depended on the altitudinal levels, on the species richness of the sample plots or on the relevance of the sample plots for conservation (i.e. grassland habitat of high conservation relevance vs. grassland habitats of low conservation relevance), (3) whether the change in species dissimilarity was differentially driven by groups of species assumed to reflect processes that act locally (i.e. species groups indicating different nutrient levels and species groups reflecting different levels of conservation value) and (4) whether the change in species dissimilarity was differentially driven by groups of species assumed to reflect processes that act globally (i.e. species groups indicating different temperature levels or neophytic species vs. indigenous species).

7.2 Methods

7.2.1 Study site and field protocol

The study took place between 2001 and 2009 in Switzerland. The country covers approx. 41000 km² in central Europe and altitudes from 193 to 4634 m a.s.l. About 70% of Switzerland is mountainous (60% Alps and 10% Jura Mountains). We used the data from the Biodiversity Monitoring of Switzerland (BDM, www.biodiversitymonitoring.ch) that was launched in 2001 to monitor Switzerland's biodiversity and to meet the Convention on Biological Diversity of Rio de Janeiro (Hintermann et al. 2000). In the BDM scheme, vascular plants are one of three species groups investigated on a systematic grid with random origin, covering 1650 circular 10 m² plots. Every year, one fifth of these sample plots are surveyed and each plot is surveyed every five years. Thus, between 2001 and 2009 four fifth of the 1650 plots were surveyed twice.

Fieldwork was highly standardised and was carried out by qualified botanists that recorded all plants on a surveyed plot. Each surveyed plot was visited two times per field season, except for plots at high altitudes with short vegetation period where only one inspection per field season was conducted. For each sample plot, the botanists identified

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the type of habitat according to the definition developed for Switzerland (Delarze and Gonseth 2008). Further the land use category was identified using a system of 32 pre-defined land use categories similar to the CORINE Land Cover system (Büttner et al. 2004). For annual reporting of the BDM results, the 32 land use categories were then aggregated to six main types of land use, i.e. forests, meadows and pastures, arable land, settlements, alpine pastures and mountains.

For the present study, we analysed a subset of the 1650 BDM sample plots that were surveyed once between 2001-2004 (i.e. the first survey) and a second time between 2006-2009 (i.e. the second survey), and of which the land use category was either meadows and pastures or alpine pastures in both surveys. It should be noted that the definition of grassland applied for this study is, thus, defined by the management regime and independent of the species association found on the plots. The sample size was 339 grassland plots in total 7.1.

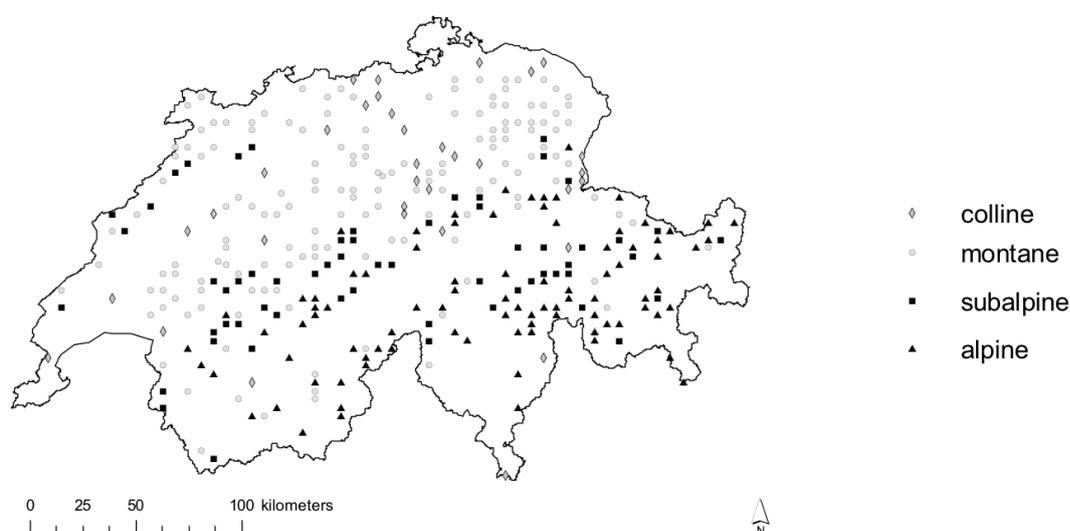


Figure 7.1: Distribution of study plots - The figure gives the distribution of the 339 grassland sample plots from the Swiss Biodiversity Monitoring programme used in this study.

For the analyses, individual plants too small for reliable identification on species level were omitted. The proportion of the individual plants not identified on species level compared to the total number of recorded species per sample plot was small (mean \pm SD of all sample plots: $5.6 \pm 5.4\%$ unidentified plants). However the proportion of

unidentified plants slightly decreased from the first survey to the second survey (mean \pm SD difference: $-1.4 \pm 7.3\%$ unidentified plants). Since the proportion of unidentified plants was small and the temporal decrease of the proportion of unidentified plants did not depend on the classes of sample plots we analysed, i.e. altitude (ANOVA: $F=0.8$, $df=3$, $p=0.50$), species richness of the plots (Welch t-test: $t=0.13$, $df=295.3$, $p=0.89$) or relevance for conservation (Welch t-test: $t=0.10$, $df=308.5$, $p=0.92$), we were confident that the omission of unidentified plants did not bias our results on species richness or species dissimilarity.

7.2.2 Classes of sample plots and classes of species groups

Prior to analyses, we defined different classes of sample plots and classes of species groups that we assumed to behave differently in terms of temporal change in species richness or species dissimilarity. We assorted the 339 plots in three different ways. First, plots were classed according to four altitudinal levels based on the temperature zonation of Switzerland (Schreiber et al. 1997), i.e. colline, montane, subalpine and alpine. Second, plots were classed according to their species richness as either species-poor (<35 species, i.e. below the average species richness of the second survey) or species-rich (≥ 35 species). And third, plots were classed according to their relevance for conservation into plots of low relevance for conservation and plots of high relevance for conservation. Plots containing the habitat types ‘nutrient-rich meadows’ or ‘nutrient-rich pastures’ following Delarze and Gonseth (2008) were considered as being of low relevance for conservation. The remaining plots, i.e. the plots with high relevance for conservation, contained different habitat types of dry or wet nutrient poor sites that corresponded to the protected biotope types adopted by Swiss law since 2000 (Swiss Federal Council 1991).

We also assorted the species in four different ways (Table 7.1). We classed the species into species groups indicating different nutrient level, i.e. eutrophic, mesotrophic and oligotrophic species and into groups indicating species of different conservation value, i.e. very low, low and high conservation value. The rationale was that if local scale factors such as changes in land use regimes or changes in conservation efforts had strong effects on species richness and species dissimilarity, we assumed that the temporal changes in species richness and species dissimilarity would differ between the species groups of different nutrient-level and the species groups of different conservation

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value. We further classed the species into groups with different altitudinal centres of distribution, i.e. species of warm, moderate and cold temperature levels and into neophytes, archaephytes and indigenous species. Here, the rationale was that if global scale factors such as climate change or the introduction of neophytic species had strong effect on the observed species richness and species dissimilarity, we assumed that the temporal change in species richness and species dissimilarity would differ between the species of different temperature levels and between indigenous species and neophytes.

Indicator	Classes	Source
Nutrient level	eutrophic = typically on nutrient rich sites (171 species) mesotrophic = no clear preference (251 species) oligotrophic = typically on nutrient poor sites (397 species) not assigned = no indicator value available (6 species)	Landolt (2010)
Conservation value	very low = ubiquitous, often dominant on intensely managed sites (27 species) low = ubiquitous, "standard" or commonplace grassland species (37 species) high = target- or indicator species for grassland according to conservation objectives of the Swiss authorities (235 species) rest = remaining species not typically grassland species: no conservation value assigned (526 species)	BAFU and BLW (2008); Landolt (2010)
Temperature level	warm = centre of distribution at colline and lower montane levels (281 species) moderate = centre of distribution at montane level (160 species) cold = centre of distribution at higher montane level or above (350 species) not assigned = no indicator value available (34 species)	Landolt (2010)
Alien species	neophytes = species introduced by humans after 1500 AD (14 species) archaephytes = species introduced by humans before 1500 AD (37 species) indigenous = species that appeared without assistance by humans (681 species) not assigned = no indicator value available (93 species)	Landolt, 2010

Table 7.1: Description of the classes used for the grouping of the 825 recorded species into species groups.

The analyses of the four species groups (Table 7.1) suggested that the observed taxonomic homogenization is mainly due to the spread of common species (see results). We therefore used the BDM data of all 1650 study plots to class the species into different

categories of abundance and analysed the following groups of species separately: species recorded on less than 5%; on 5-25%, on >25-50%, on >50%-75% and on >75% of the 1650 sample plots.

7.2.3 Statistical analysis

For all classes of sample plots and all classes of species groups (see previous chapter), we calculated the mean changes in species richness between the first and second survey. Further, we computed a measure of temporal change in species dissimilarity (i.e. the ‘differentiation diversity’, sensu Jurasinski et al. 2009). Among the many indices that measure species dissimilarity (or similarity), the Simpson dissimilarity index was among the ones with the best properties (Koleff et al. 2003, but see Tuomisto 2010). The Simpson dissimilarity index is especially useful when the species dissimilarity between sample plots should be expressed independently of the species richness of the sample plots (Lennon et al. 2001, Kühn and Klotz 2006). In this study, we aimed to analyse the change in species richness and the change in species dissimilarity independently from each other. Thus, we preferred to use the Simpson index instead of another commonly used index, the Jaccard dissimilarity index. However, as a basis for comparison, we also presented the results for the Jaccard index in the figures, but discussed mainly the results of the Simpson index. The Jaccard dissimilarity index between two sampling plots was calculated as

$$\beta_J = 1 - \frac{a}{a + b + c} \quad (7.1)$$

where a is the number of species shared between two sample plots, and b and c are the numbers of species only found in one or only in the other sampling plot. The Simpson dissimilarity index between two sampling plots was computed as

$$\beta_S = \frac{\min(b, c)}{\min(b, c) + a} \quad (7.2)$$

Thus, both the Simpson dissimilarity index and the Jaccard index range from 0, i.e. all species in common, to 1, i.e. no species in common.

Our measure of the temporal change in species dissimilarity of several sampling plots (Δ_{Sim}) was then the average difference of the Simpson dissimilarity index of the second survey (β_k^2) minus the Simpson dissimilarity index of the first survey (β_k^1) for

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all $k = 1, \dots, K$ possible combinations of two sample plots from the totally N sample plots.

$$\Delta_{Sim} = 100 \frac{\sum_k^K (\beta_k^2 - \beta_k^1)}{K} \quad \text{with} \quad K = \binom{N}{2} \quad (7.3)$$

A positive value of Δ_{Sim} would indicate that the species composition between the two plots became less similar from the first to the second survey, i.e. taxonomic differentiation; a negative value of Δ_{Sim} would indicate that the species composition became more similar, i.e. taxonomic homogenization.

To get an estimate of the precision of the change in species dissimilarity Δ_{Sim} , we adopted a Jackknife approach (Jones 1974): we removed one sample plot from the analysis and again calculated Δ_{Sim} as described above. We repeated that procedure until every sample plot was once removed from the calculation of Δ_{Sim} . The 2.5% and 97.5% percentiles of all the calculated Δ_{Sim} each with one sample plot removed were taken as an estimation of a 95% confidence interval. The approach to estimate the change in species dissimilarity Δ_{Sim} and its precision as described here, is the same as the one used to calculate the indicator Diversity of Species Communities' of the BDM (see indicator 'Z12', www.biodiversitymonitoring.ch).

Testing for group differences of the change in species dissimilarity using traditional tests such as t-test or ANOVA would lead to an inflation of sample size. This is because there are $N(N - 1)/2$ elements in a dissimilarity matrix calculated from N sample plots (Naaf and Wulf 2010). To avoid an inflation of sample size, we instead used a permutation test with 1000 permutations of the group identities of the sample plots (Manly 2007). As a test statistic for the permutation test we used the averaged residuals.

For each subset of species (i.e. the analyses of the species groups), we calculated the change in Δ_{Sim} as follows. The Simpson dissimilarity index for the first survey for a given pair of sampling plots (β_k^1) was calculated exactly as above, including the records of all species. For the Simpson dissimilarity index of the second survey (β_k^2), however, we allowed to change only the species of the analysed species group, the records of all the other species were held constant (i.e. as recorded during the first survey). The resulting Δ_{Sim} was then taken as a measure of the net effect on the change in species dissimilarity of the analysed species group only.

Sample sizes for the different groupings of sample plots, mean species richness of the first and second survey and the mean Simpson index of the first and second survey are given in Table 7.2. All analyses were done with the statistical software R (R Development Core Team 2011).

Stratum	N	Simpson index		Species richness	
		first	second	first	second
All types	339	0.723	0.715	33.6	35.0
Colline	34	0.534	0.536	25.2	25.1
Montane	156	0.506	0.494	29.9	31.5
Subalpine	60	0.685	0.674	41.3	42.7
Alpine	89	0.705	0.697	38.1	39.9
Species-rich	163	0.756	0.742	45.2	46.0
Species-poor	176	0.656	0.641	22.8	24.9
High-value	126	0.776	0.771	38.9	40.5
Low-value	213	0.542	0.530	30.5	31.8

Table 7.2: Given are the sample sizes (N), mean species dissimilarities of the first and second survey (Simpson index) and mean species richness of the first and second surveys of the different classes of sample plots that were analysed.

7.3 Results

Over all plots, the species dissimilarity (Δ_{Sim}) of Swiss grassland decreased between the first and the second survey, suggesting recent and short-term taxonomic homogenization of grassland in Switzerland (permutation test: $p < 0.001$, 7.2). In contrast, the mean species richness of the same plots increased from the first to the second survey by 4.2% (mean increase of 1.4 species, paired t-Test: $t = 4.3$, $df = 338$, $p < 0.001$). Note, however, that the proportion of unidentified species slightly decreased from the first to the second survey, which could partly explain the increase in species richness between the first and the second survey.

7.3.1 Taxonomic homogenization of different groups of sampling plots

The temporal change in species dissimilarity depended on the altitudinal level (permutation test: $p < 0.001$), with highest taxonomic homogenization (i.e. the lowest values

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of Δ_{Sim}) found in montane and subalpine grassland whereas no biotic homogenization was found at the colline level (7.2a). Temporal change in species dissimilarity was not found to differ between species rich and species poor plots (permutation test: $p=0.998$; 7.2b). However, this finding depended on the type of index used for the analysis. Using the Jaccard index instead of the Simpson index resulted in a higher degree of homogenization for species poor plots compared to species rich plots. Furthermore, the temporal change in species dissimilarity depended on the conservation value of the plots (permutation test: $p<0.001$): strong taxonomic homogenization was found in plots of low conservation while taxonomic homogenization was relatively weak in plots of high conservation value (7.2c).

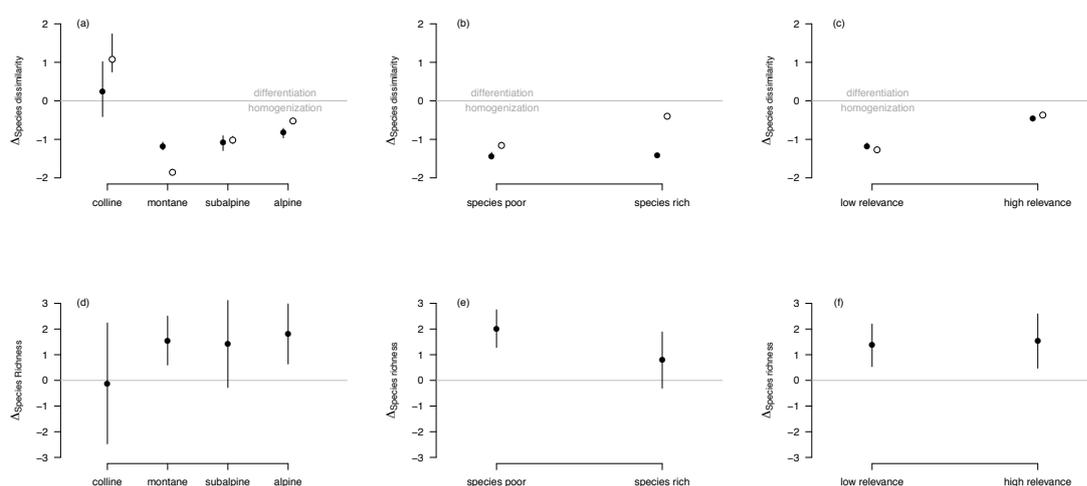


Figure 7.2: Temporal change in species dissimilarity and species richness between first and second survey in Swiss grassland - The sample plots are classed according to the altitudinal levels (a/d), according to the species richness of the second survey (species poor: below average species richness; species rich: above average species richness, b/e) and according to the conservation relevance of the meadow type (c/f). Shown are the mean $\pm 95\%$ confidence intervals of the temporal changes in species dissimilarity based on the Simpson index (solid circles of a-c), based on the Jaccard coefficient (open circles of a-c) and of the temporal change in species richness (solid circles of d-f).

The increase in species richness was not found to differ between groups of different altitudinal levels (ANOVA: $F=0.9$, $df=3$, $p=0.46$, 7.2d) nor between groups of different relevance for conservation (Welch t-test: $t=0.2$, $df=267.4$, $p=0.81$, Fig 2f). However, the species richness of plots of low species richness tended to increase more than of

plots with high species richness (Welch t-test: $t=1.8$, $df=286.5$, $p=0.07$, 7.2e).

7.3.2 Taxonomic homogenization of different groups of species

The analyses of the species groups that we assumed to indicate local land use regimes and local conservation efforts, i.e. the species groups reflecting nutrient-level and conservation value, suggested that it were mainly the eutrophic and mesotrophic species, and thus, the species of low conservation value that were responsible for the taxonomic homogenization in the grassland of Switzerland. In contrast, the changes of species dissimilarity induced by oligotrophic species or by species of high conservation value were only marginal (7.3a and b). In terms of the change in species richness, however, all the different sets of species contributed to the overall increase in species richness (7.3c and d).

The effect on change in species dissimilarity of the species groups we assumed to indicate climate change, i.e. the species groups of different temperature levels, seemed to vary strongly between the different species groups. Species that prefer warm temperatures (i.e. species with a distribution mainly at colline and lower montane levels) increased species dissimilarity, while species of moderate temperature level (i.e. species with distribution mainly at montane level) led to taxonomic homogenization (7.4a). The large differences of the temporal change in species dissimilarity found between the species of different temperature levels was not apparent when analysing the change in species richness: independent of the temperature level of the species, the species richness tended to increase (7.4c).

The effect of neophytic species on the temporal change in species dissimilarity was only marginal and, contrary to expectation, it tended to increase species dissimilarity weakly (7.4b). Overall, only few neophytic species were recorded in our data set and no change in species richness was recorded for neophytes between first and second survey (7.4d).

The results for taxonomic homogenization of different species groups suggested that taxonomic homogenization was mainly due to the increase in common species, namely the species that are tolerant to high nutrient levels, the species of low conservation value and the species adapted to moderate temperature levels. We therefore directly analysed the effect of species groups that differ in their abundance. We found that the contribution to taxonomic homogenization strongly varied between species groups

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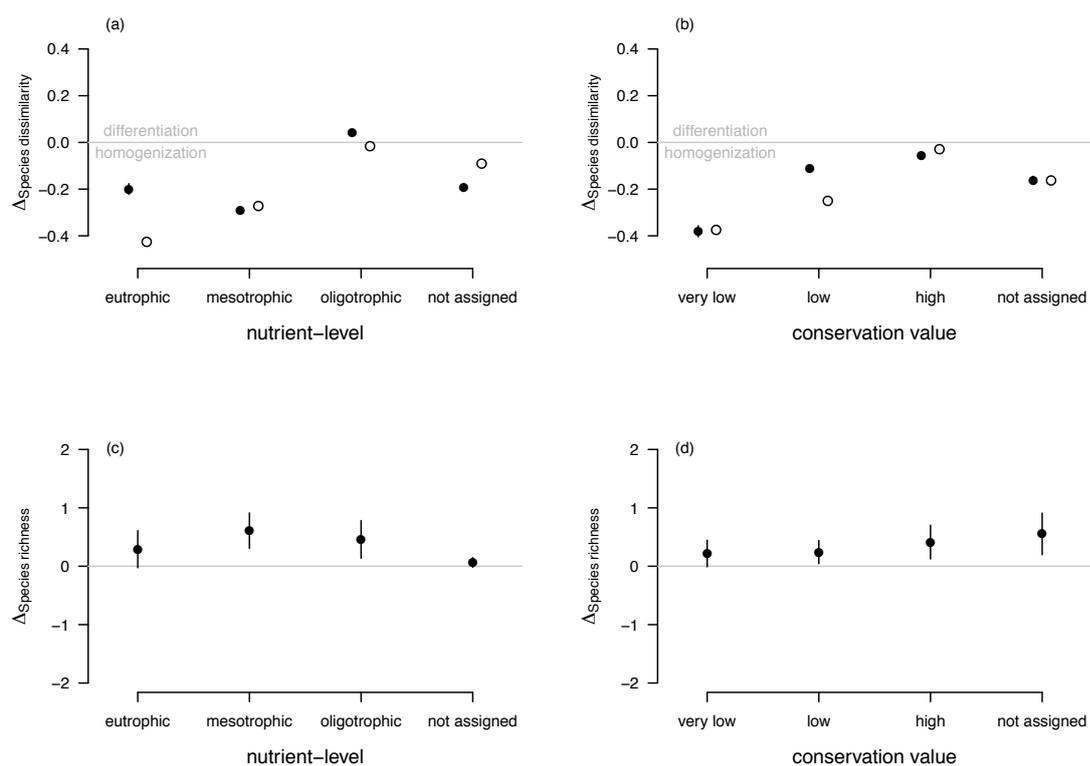


Figure 7.3: Effect of species groups - Temporal change of species dissimilarity and species richness between first and second survey for species groups that are assumed to reflect land use regime (i.e. nutrient level a/c) and conservation effort (i.e. species of different conservation value, b/c). Shown are the mean \pm 95% confidence intervals of the temporal changes in species dissimilarity based on the Simpson index (solid circles of a-b), based on the Jaccard coefficient (open circles of a-b) and of the temporal change in species richness (solid circles of c-d).

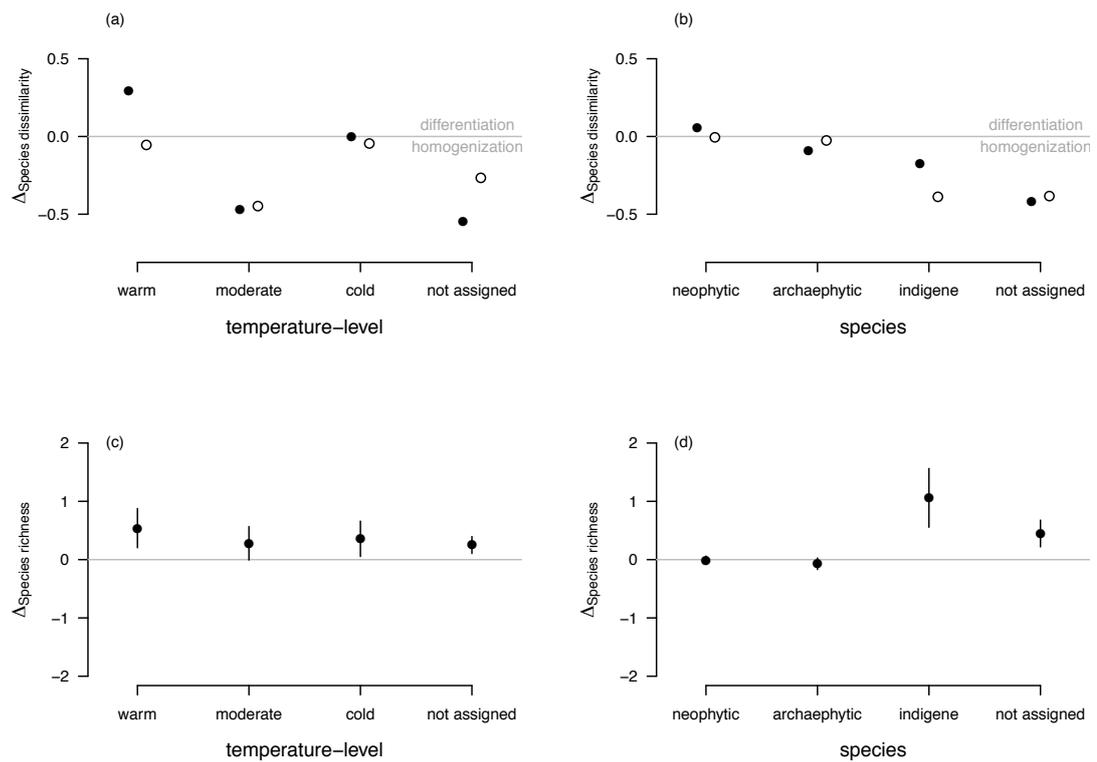


Figure 7.4: Effect of species with different temperature level and differences between neophytic, archaeophytic and indigenous species - Temporal change of species dissimilarity and species richness between first and second survey for species groups that are assumed to reflect climate change (i.e. species groups indicating temperature level a/c) and the species group of neophytic, archaeophytic and indigenous species (b/c). Shown are the mean \pm 95% confidence intervals of the temporal changes in species dissimilarity based on the Simpson index (solid circles of a-b), based on the Jaccard coefficient (open circles of a-b) and of the temporal change in species richness (solid circles of c-d).

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that differ in abundance (7.5a). Although species of intermediate abundance and very abundant species equally increased in species richness (7.5b), the increase of species of intermediate abundance resulted in higher species dissimilarity while the very common species resulted in strong taxonomic homogenization.

7.4 Discussion

In Switzerland, the mean plant species richness of grassland at local scale increased from 2001-2005 to 2006-2010, while during the same period the species dissimilarity decreased suggesting local scale and short-term taxonomic homogenization of the grassland in Switzerland. Apparently, recent conservation efforts targeting Swiss grassland – for example in the form of agri-environmental schemes – were not able to counteract local scale floristic homogenization. To our knowledge, this is the first study to demonstrate recent floristic homogenization of grassland for an entire country in spite of the sustained conservation efforts aiming at increasing biotic diversity of grassland.

The analyses of the different species groups suggested that the taxonomic homogenization was mainly due to an increase of already common and generalist species, namely the species that are tolerant to high nutrient levels, the species of low conservation value and the species of moderate temperature level. It is important to note that sample plots with change in land use between the first and the second survey had been excluded from the analyses. Therefore, the observed taxonomic homogenization took place in sites continuously managed as grassland. Unlike habitat destruction, taxonomic homogenization within a habitat is evidence for a rather inconspicuous change in biotic diversity that took place in a short time period. From a conservation perspective, several of our findings are important. On the one hand, overall species diversity of grassland has increased including sites of high conservation value. Furthermore, part of the increase in species richness was due to an increase of target species for conservation. These results on its own may be considered as a success of conservation efforts. On the other hand, the spread of a limited number of ubiquitous generalist species has led to more uniform species assemblages, i.e. taxonomic homogenization. To some extent, taxonomic homogenization counteracts conservation objectives aiming to preserve locally typical species assemblages.

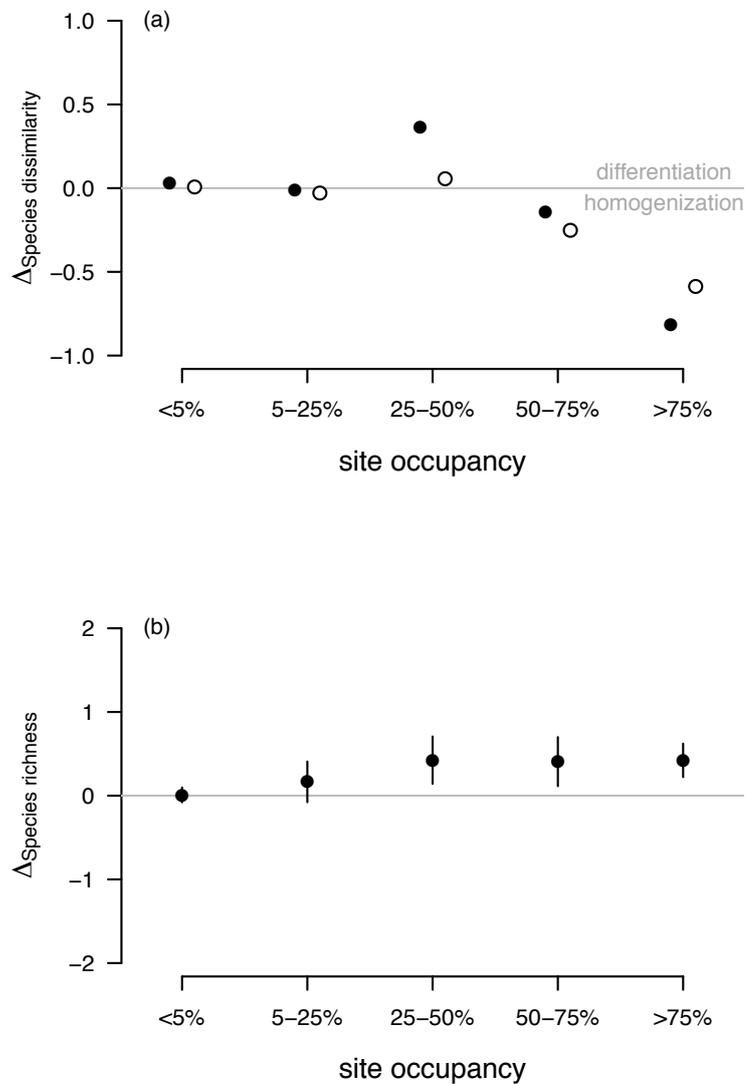


Figure 7.5: Differences between abundant and rare species - Temporal change of species dissimilarity and species richness between first and second survey for species that differ in total abundance over all habitats in Switzerland. Species are grouped according to proportion of the ca.1650 sample sites of the Biodiversity Monitoring Switzerland that are occupied by the species. Shown are the mean \pm 95% confidence intervals of the temporal changes in species dissimilarity based on the Simpson index (solid circles of a), based on the Jaccard coefficient (open circles of a) and of the temporal change in species richness (solid circles of b).

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Taxonomic homogenization, however, is not always a negative indication of decreasing biodiversity (Rooney et al. 2007). For the grassland in Switzerland, the taxonomic homogenization seemed to be caused mainly by an increase of common and generalist species. This finding is in accordance with results from other studies that found an increase of native ubiquitous, meso- or eutrophic species into species-rich grassland (Bennie et al. 2006, Bergamini et al. 2009) or temperate forest plant-communities (Rooney et al. 2004, Naaf and Wulf 2010). But, since we found no indication that the increase of common species negatively affected species of conservation value in the last decade, the taxonomic homogenization of Swiss grassland presumably is not an indication of decreasing biodiversity. However, such an interpretation needs to be treated with caution, since a study period of only a decade might not be enough to demonstrate a decline of uncommon specialists caused by the spread of common generalists. For example in forest understory plant communities, the increase of species with a broad habitat range was accompanied by biotic impoverishment to a lower degree after two decades than after 50 years (Rooney et al. 2004, Naaf and Wulf 2010).

Taxonomic homogenization at large spatial scales has usually been attributed to the invasion of alien species or the replacement of specialist species by generalist species (Wiegmann and Waller 2006, Kerbiriou et al. 2009, Qian and Guo 2010). However, in Switzerland the taxonomic homogenization of grassland at a local scale could not be explained by the spread of neophytic (i.e. alien) species. This is in accordance with other local-scale studies that also did not find an effect of alien species on taxonomic homogenization (Smart et al. 2006, Lambdon et al. 2008, Naaf and Wulf 2010). Furthermore, in our case the increase in common and generalist species within the last decade seemed not to have negatively affected specialist species of high conservation value. These results suggest that floristic homogenization in Swiss grassland was neither attributed to the invasion of neophytic species nor to the replacement of specialist species by generalist species. Therefore, our study adds also to the evidence that it is difficult to predict changes in taxonomic homogenization at the local scale from studies on large spatial scales.

Biotic homogenization is often linked to an increase in species richness (Rahel 2002, Olden 2006, Smart et al. 2006, Kerbiriou et al. 2009, Naaf and Wulf 2010). Similarly, in our study, the overall trend in the Swiss grassland was towards an increase in species richness but towards a decrease in species dissimilarity. In spite of the prevalence of

studies that reported a negative correlation in the development of species richness and temporal change in species dissimilarity, the temporal trend of species dissimilarity has to be viewed as a process on its own and needs to be evaluated independently of species richness but in the context of other environmental factors (Smart et al. 2006, Devictor and Robert 2009, Filippi-Codaccioni et al. 2010). In our study, the species richness of the group of species typical for warm temperatures and for low altitudes increased. This increase in species richness was positively linked to a moderate increase in species dissimilarity and indicates that both the species richness and the species dissimilarity diversity may increase.

We conclude that between the two surveys of 2001-2005 and 2006-2009 the species dissimilarity of Swiss grassland considerably declined suggesting local scale taxonomic homogenisation. The observed taxonomic homogenization was mainly due to the spread of common species. Local-scale changes in land use regimes implemented by agri-environmental schemes and other conservation efforts on parts of the entire grassland area were apparently not enough to prevent the total grassland from recent taxonomic homogenization.

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7.6 References

- Arevalo, J. R., R. Otto, C. Escudero, S. Fernandez-Lugo, M. Arteaga, J. D. Delgado, and J. M. Fernandez-Palacios. 2010. Do anthropogenic corridors homogenize

7. FLORISTIC HOMOGENIZATION OF SWISS GRASSLAND

- plant communities at a local scale? A case studied in Tenerife (Canary Islands). *Plant Ecology* 209:23-35.
- Bennie, J., M. O. Hill, R. Baxter, and B. Huntley. 2006. Influence of slope and aspect on long-term vegetation change in British chalk grasslands. *Journal of Ecology* 94:355-368.
- Bergamini, A., M. Peintinger, S. Fakheran, H. Moradi, B. Schmid, and J. Joshi. 2009. Loss of habitat specialists despite conservation management in fen remnants 1995-2006. *Perspectives in Plant Ecology Evolution and Systematics* 11:65-79.
- Büttner, G., J. Feranec, G. Jaffrain, L. Mari, G. Maucha, and T. Soukup. 2004. The CORINE land cover 2000 project. Pages 331346 in EARSel. EARSel, Paris.
- Delarze, R. and R. Gonseth. 2008. *Lebensräume der Schweiz*. 2nd edition edition. Hep Verlag AG, Bern.
- Devictor, V. and A. Robert. 2009. Measuring community responses to large-scale disturbance in conservation biogeography. *Diversity and Distributions* 15:122-130.
- Filippi-Codaccioni, O., V. Devictor, Y. Bas, and R. Julliard. 2010. Toward more concern for specialisation and less for species diversity in conserving farmland biodiversity. *Biological Conservation* 143:1493-1500.
- FOEN. 2010. *Switzerlands Fourth National Report under the Convention on Biological Diversity*. Bern.
- Guest Editorial. 2001. Evolutionary biogeography and speciation: essay on a synthesis. *Journal of Biogeography* 28:13-27.
- Herzog, F., S. Dreier, G. Hofer, C. Marfurt, B. Schupbach, M. Spiess, and T. Walter. 2005. Effect of ecological compensation areas on floristic and breeding bird diversity in Swiss agricultural landscapes. *Agriculture Ecosystems & Environment* 108:189-204.
- Hintermann, U., D. Weber, and A. Zangger. 2000. Biodiversity monitoring in Switzerland. *Schriftenreihe Landschaftspflege Naturschutz* 62:47-58.

- Huston, M. A. 1999. Local processes and regional patterns: appropriate scales for understanding variation in the diversity of plants and animals. *Oikos* 86:393-401.
- Jacquemyn, H., R. Brys, and M. Hermy. 2003. Short-term effects of different management regimes on the response of calcareous grassland vegetation to increased nitrogen. *Biological Conservation* 111:137-147.
- Jones, H. L. 1974. Jackknife estimation of functions of stratum means. *Biometrika* 61:343-348.
- Jurasinski, G., V. Retzer, and C. Beierkuhnlein. 2009. Inventory, differentiation, and proportional diversity: a consistent terminology for quantifying species diversity. *Oecologia* 159:15-26.
- Kerbiriou, C., I. Le Viol, F. Jiguet, and V. Devictor. 2009. More species, fewer specialists: 100 years of changes in community composition in an island biogeographical study. *Diversity and Distributions* 15:641-648.
- Kleijn, D. and W. J. Sutherland. 2003. How effective are European agri-environment schemes in conserving and promoting biodiversity? *Journal of Applied Ecology* 40:947-969.
- Knop, E., D. Kleijn, F. Herzog, and B. Schmid. 2006. Effectiveness of the Swiss agri-environment scheme in promoting biodiversity. *Journal of Applied Ecology* 43:120-127.
- Koleff, P., K. J. Gaston, and J. J. Lennon. 2003. Measuring beta diversity for presence-absence data. *Journal of Animal Ecology* 72:367-382.
- Kühn, I. and S. Klotz. 2006. Urbanization and homogenization – Comparing the floras of urban and rural areas in Germany. *Biological Conservation* 127:292-300.
- Lambdon, P. W., F. Lloret, and P. E. Hulme. 2008. Do non-native species invasions lead to biotic homogenization at small scales? The similarity and functional diversity of habitats compared for alien and native components of Mediterranean floras. *Diversity and Distributions* 14:774-785.

7. FLORISTIC HOMOGENIZATION OF SWISS GRASSLAND

- Landolt, E. 2010. Flora indicativa. Ökologische Zeigerwerte und biologische Kennzeichen zur Flora der Schweiz und der Alpen. Haupt Verlag.
- Lennon, J. J., P. Koleff, J. J. D. Greenwood, and K. J. Gaston. 2001. The geographical structure of British bird distributions: diversity, spatial turnover and scale. *Journal of Animal Ecology* 70:966-979.
- Manly, B. F. J. 2007. Randomization, Bootstrap and Monte Carlo Methods in Biology. Third edition. Chapman & Hall/CRC, Boca Raton.
- Margules, C. R. and R. L. Pressey. 2000. Systematic conservation planning. *Nature* 405:243-253.
- Marini, L., M. Scotton, S. Klimek, and A. Pecile. 2008. Patterns of plant species richness in Alpine hay meadows: Local vs. landscape controls. *Basic and Applied Ecology* 9:365-372.
- Melo, A. S., T. Rangel, and J. A. F. Diniz. 2009. Environmental drivers of beta-diversity patterns in New-World birds and mammals. *Ecography* 32:226-236.
- Naaf, T. and M. Wulf. 2010. Habitat specialists and generalists drive homogenization and differentiation of temperate forest plant communities at the regional scale. *Biological Conservation* 143:848-855.
- Olden, J. D. 2006. Biotic homogenization: a new research agenda for conservation biogeography. *Journal of Biogeography* 33:2027-2039.
- Olden, J. D. and T. P. Rooney. 2006. On defining and quantifying biotic homogenization. *Global Ecology and Biogeography* 15:113-120.
- Oster, M., K. Ask, S. A. O. Cousins, and O. Eriksson. 2009. Dispersal and establishment limitation reduces the potential for successful restoration of semi-natural grassland communities on former arable fields. *Journal of Applied Ecology* 46:1266-1274.
- Qian, H. and Q. F. Guo. 2010. Linking biotic homogenization to habitat type, invasiveness and growth form of naturalized alien plants in North America. *Diversity and Distributions* 16:119-125.

- R Development Core Team. 2011. R: A language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
- Rahel, F. J. 2002. Homogenization of freshwater faunas. *Annual Review of Ecology and Systematics* 33:291-315.
- Rooney, T. P., J. D. Olden, M. K. Leach, and D. A. Rogers. 2007. Biotic homogenization and conservation prioritization. *Biological Conservation* 134:447-450.
- Rooney, T. P., S. M. Wiegmann, D. A. Rogers, and D. M. Waller. 2004. Biotic impoverishment and homogenization in unfragmented forest understory communities. *Conservation Biology* 18:787-798.
- Roth, T., V. Amrhein, B. Peter, and D. Weber. 2008. A Swiss agri-environment scheme effectively enhances species richness for some taxa over time. *Agriculture Ecosystems & Environment* 125:167-172.
- Sax, D. F. and S. D. Gaines. 2003. Species diversity: from global decreases to local increases. *Trends in Ecology & Evolution* 18:561-566.
- Schreiber, K. F., N. Kuhn, C. Hug, and R. Häberli. 1997. *Wärmegegliederung der Schweiz.*, Eidg. Justiz- und Polizeidepartement, Bern.
- Schwartz, M. W., J. H. Thorne, and J. H. Viers. 2006. Biotic homogenization of the California flora in urban and urbanizing regions. *Biological Conservation* 127:282-291.
- Smart, S. M., K. Thompson, R. H. Marrs, M. G. Le Duc, L. C. Maskell, and L. G. Firbank. 2006. Biotic homogenization and changes in species diversity across human-modified ecosystems. *Proceedings of the Royal Society B-Biological Sciences* 273:2659-2665.
- Swiss Federal Council. 1991. Ordinance on the Protection of Nature and Cultural Heritage (NCHO). SR 451.1.
- Tuomisto, H. 2010. A diversity of beta diversities: straightening up a concept gone awry. Part 2. Quantifying beta diversity and related phenomena. *Ecography* 33:23-45.

7. FLORISTIC HOMOGENIZATION OF SWISS GRASSLAND

Weber, D., U. Hintermann, and A. Zangger. 2004. Scale and trends in species richness: considerations for monitoring biological diversity for political purposes. *Global Ecology and Biogeography* 13:97-104.

Wiegmann, S. M. and D. M. Waller. 2006. Fifty years of change in northern upland forest understories: Identity and traits of 'winner' and 'loser' plant species. *Biological Conservation* 129:109-123.

8

Top predators as indicators for species richness? Prey species are just as useful

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8. TOP PREDATORS AS BIODIVERSITY INDICATORS

Abstract

Aim *The use of surrogates to identify protected areas is a common practice in conservation biology. The use of top predators as surrogates has been criticized but recently a strong positive relationship was found between the presence of top predators and species diversity of several taxa. As mentioned by the authors, these striking results need to be assessed on a larger scale.*

Location *Switzerland.*

Methods *We used data from the Swiss Biodiversity Monitoring Programme and the Swiss breeding bird survey to analyse the use of raptor species as a surrogate for plant, butterfly and bird species richness. For each raptor species, we compared species richness in sites where a raptor species was recorded and compared these sites with the remaining sites in which the raptor species was not recorded. For comparison we conducted the same analyses using tits *Parus* spp. Tits are common prey species of some raptor species and were the most species-rich generalist genus in our data.*

Results *We found little justification for a focus on top predators when identifying conservation areas. For bird and plant species richness, raptors were reasonable surrogates for high species richness but no raptor species predicted sites with above-average butterfly species richness. The presence of tit species performed equally as well as the presence of raptor species to predict sites with high species richness of birds and plants, and performed even better for predicting high butterfly species richness.*

Main conclusions *Conservation planners using indicator species should be aware that relationships among higher taxa are complex and depend on the species group and the scale of analysis. As shown with the case of raptors, the usefulness of a biodiversity indicator can vary between adjacent areas even if the same species groups are analysed. We recommend the use of more than one indicator species from different taxonomic groups when identifying areas of high biodiversity.*

Keywords: biodiversity, indicator species, *Parus*, predictor, raptor, surrogate, Switzerland, tit

8.1 Introduction

A key interest in applied ecology is the identification of areas with high native species richness, partly because it has been argued that these areas have high conservation importance. In fact, few conservation practitioners select areas based on species richness alone (Pressey 1994, Margules and Pressey 2000, Jackson et al. 2004). In particular, some impoverished places, such as semi-arid areas and mountain tops, host a specific fauna and/or flora not found elsewhere. In these cases, complementarity and not species richness might be the goal for conservation (Cabeza and Moilanen 2001, Williams et al. 2006). Nevertheless, there is continued interest in whether a single or few species groups should be used as indicators of high species richness (Noss 1990, Simberloff 1998, Thomson et al. 2007).

Top predators have considerable publicity value but their use as indicator species in conservation is controversial (Kerr 1997, Andelman and Fagan 2000, Roberge and Angelstam 2004, Ozaki et al. 2006). Recently, Sergio and colleagues (Sergio et al. 2005, Sergio et al. 2006) emphasized the benefits to biodiversity conservation of the preservation of top predators. In the Italian Trentino region, Sergio, Newton and Marchesi (2005) and Sergio et al. (2006) recorded more bird, tree and butterfly species in 1-km squares inhabited by raptor species compared with paired controls. They concluded that there is a tight association between the occurrence of top predators and high biodiversity value, at least in the Trentino region, and suggested that the generality of these findings should be assessed further. We have performed one such assessment.

In a comprehensive national biodiversity monitoring programme (Biodiversity Monitoring Switzerland, www.biodiversitymonitoring.ch), bird, butterfly and plant species richness were estimated based on repeated visits to about 500 grid cells of 1 km width (Hintermann et al. 2000, Weber et al. 2004). We tested whether grid cells where a raptor species was observed had higher species counts of birds, butterflies and plants than grid cells where the same raptor species had not been observed. This approach is similar to the one used by Sergio, Newton and Marchesi (2005) and Sergio et al. (2006) but we aimed to assess the generality of their findings at a larger spatial scale. Sergio, Newton and Marchesi (2005) and Sergio et al. (2006) suggested that predators are more useful as an indicator than species from a lower trophic level. We tested that

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assertion by performing the same analyses on both raptors and the most species-rich generalist genus, selected a priori, the tits *Parus spp.*

8.2 Methods

Switzerland is a small country (41'285 km²) in western Europe. A country-wide biodiversity monitoring programme was begun in 2001 (Hintermann et al. 2000). We selected 509 out of the 41'285 possible 1 km grid cells (hereafter called cells) by taking a systematic sampling grid fixed to a randomly selected reference cell. This sampling scheme was designed to produce factual information on the dynamics of biodiversity within the country for government agencies, politicians and the general public (Weber et al. 2004). Eight cells were covered entirely by lakes or glaciers and 26 others were too dangerous to survey. Those cells were excluded, hence the data set represents Switzerland excluding the area of lake surfaces, glaciers and steep cliffs. The altitudes of the cells excluded because of steep cliffs were too high to provide potential breeding habitat for raptors or tits (Schmid et al. 1998) and we did not expect the exclusion of these cells to bias our analyses systematically. Average forest cover (\pm SD) was 31.5% (\pm 27.8) and 18% of cells were attributed to the Jura mountains, 23% to the Swiss plateau and the remaining 59% to the Alps.

Fieldwork lasted from 2001 (2003 for butterflies) to 2005, with one-fifth of the cells surveyed each year. The subsample of cells surveyed each year was regularly spaced over the whole of Switzerland. Therefore the shorter monitoring period for butterflies resulted in a smaller sample size but not in a systematic bias in the results. Species richness of birds, butterflies and plants was estimated based on repeated visits by specialists to each cell. Each cell was visited twice for plants, up to three times for birds [three visits in cells \leq 2000 meters above sea level (m a.s.l.) and two in cells $>$ 2000 m a.s.l.] and up to seven times for butterflies (seven visits in colline and montane cells, six in subalpine cells and four in alpine cells). Plants and butterflies were counted along the same 2.5-km long transect within cells. The transect was selected using fixed rules that aimed to cover as much as possible of the cell area. Bird data originated from the Swiss breeding bird survey Monitoring Häufige Brutvögel (Schmid et al. 2004, Kéry and Schmid 2006). A few surveys of cells not fulfilling the strict sampling protocol (e.g. restrictions on date, time or weather conditions) were excluded

from the analyses. Studies of biodiversity patterns are sometimes criticized because of detectability problems (Boulinier et al. 1998) but we were confident that species detectability in this study was high for the following reasons: (i) species detectability of birds has been assessed and has been proven to be high and vary little with sources of variation such as species observer and sites (Kéry and Schmid 2006); (ii) species detectability of plants and butterflies was enhanced by repeated visits. For more details about data collection see Pearman and Weber (2007) and Schmid, Zbinden and Keller (2004).

	Switzerland	Tessin	Trentino
Total area (km ²)	41'285	2'812	6'206
Number of 1 km grid cells	402*	47*	64*†
Minimum elevation (m a.s.l.)	192	192	67
Maximum elevation (m a.s.l.)	4634	3400	3769
Number of regular breeding raptors	15-17‡	7-8‡	8-9‡
Number of regular breeding bird species	174§	148§	145¶

*Mean number of grid cells among the three species groups.

*Mean number of sample sites (raptor territories and controls).

†Sergio et al. 2006; ‡Hagemeijer and Blair (1997); §Schmid et al. (1998);

¶Pedrini, Caldonazzi and Zanghellini (2005)

Table 8.1: Features of the study sites, throughout Switzerland (this study), the canton Tessin (this study) and the Trentino mountains [study site of Sergio, Newton and Marchesi (2005) and Sergio et al. (2006)].

For the main analyses we used the entire data set, which contained the species lists of 464 (for birds), 283 (for butterflies) and 459 (for plants) 1-km grid cells. The canton of Tessin in the southern part of Switzerland and the Trentino mountains (the study area of Sergio, Newton and Marchesi 2005 and Sergio et al. 2006) are adjacent areas with, presumably, much the same species pool (Table 8.1). To compare better our results with those reported by Sergio, Newton and Marchesi et al. (2005) and Sergio et al. (2006) we also analysed a subset of the data that included the cells from the canton of Tessin only. For each analysis, the 1-km cells from the Swiss Biodiversity Monitoring Programme were divided into two groups: one group of cells where a raptor species was recorded (raptor cells) and a second group with all the remaining cells (control cells). All raptor species recorded in at least 20 cells were analysed: Red Kite *Milvus milvus L.*

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(103 cells), Black Kite *Milvus migrans* Bodd. (117), Goshawk *Accipiter gentilis* L. (26), Sparrowhawk *Accipiter nisus* L. (47), Common Buzzard *Buteo buteo* L. (260), Common Kestrel *Falco tinnunculus* L. (138) and Tawny Owl *Strix aluco* L. (38). We assessed the differences in species richness of birds (excluding the raptor species analysed), butterflies and plants between raptor and control cells. As count data often deviate from a normal distribution, we used the non-parametric MannWhitney U-test to assess differences among raptor and control cells.

	Bird			Butterflies			Vascular plants		
	<i>w</i>	<i>n</i>	p-value	<i>w</i>	<i>n</i>	p-value	<i>w</i>	<i>n</i>	p-value
Raptors:									
<i>Milvus milvus</i>	5885	103	<0.001 ***	10418	67	<0.001 ***	18104	102	0.931
<i>Milvus migrans</i>	7440	117	<0.001 ***	11770	78	<0.001 ***	18947	116	0.443
<i>Accipiter gentilis</i>	2661	26	<0.001 ***	2485	17	0.392	3996	26	0.013 *
<i>Accipiter nisus</i>	6451	47	<0.001 ***	3275	27	0.800	7420	47	0.009 **
<i>Buteo buteo</i>	7438	260	<0.001 ***	10781	161	0.028 *	16551	257	<0.001 ***
<i>Falco tinnunculus</i>	18695	138	0.004 **	7784	87	0.437	20764	136	0.355
<i>Strix aluco</i>	4417	33	<0.001 ***	2789	21	0.779	5089	32	0.016 *
Tits:									
<i>Parus ater</i>	3418	368	<0.001 ***	2936	226	<0.001 ***	4952	363	<0.001 ***
<i>Parus caeruleus</i>	8285	257	<0.001 ***	13070	157	<0.001 ***	17372	252	<0.001 ***
<i>Parus cristatus</i>	14549	264	<0.001 ***	5911	161	<0.001 ***	14323	262	<0.001 ***
<i>Parus major</i>	2584	330	<0.001 ***	8900	202	0.025 *	9059	325	<0.001 ***
<i>Parus montanus</i>	24243	145	0.405	2878	91	<0.001 ***	16027	144	<0.001 ***
<i>Parus palustris</i>	7708	236	<0.001 ***	11695	143	0.002 **	16012	231	<0.001 ***

* P<0.05, ** P<0.01, ***P<0.001.

Table 8.2: Results of the Mann-Whitney *U*-test. The Bonferroni critical value for 36 tests is 0.0014; *w*: test statistic, *n*: number of grid cells with presence of the raptor species or *Parus* species.

The genus *Parus* (tits) represents species that are more generalist in their diets and have smaller per-pair area requirements than raptors. They were the most species-rich generalist genus recorded. All *Parus* species recorded in at least 20 cells were analysed in the same way as the raptors. The following *Parus* species were included in the analysis: Coal Tit *Parus ater* L. (368 cells), Blue Tit *Parus caeruleus* L. (257), Crested Tit *Parus cristatus* L. (264), Great Tit *Parus major* L. (330), Willow Tit *Parus montanus* Conrad (145) and Marsh Tit *Parus palustris* L. (236). All calculations and graphs were carried out using the software R (R Development Core Team 2006).

8.3 Results

The mean \pm SD number of observed species for all cells in the Swiss Biodiversity Monitoring Programme was 32.1 ± 12.6 bird species, 34.0 ± 17.3 butterfly species and 230.1 ± 64.9 plant species. The mean number of cells only from the canton of Tessin was 23.8 ± 9.7 bird species, 42.7 ± 14.3 butterfly species and 230.5 ± 91.0 plant species.

For each of the seven raptor species, bird species richness per cell was higher in cells where the raptor was observed than in cells where it was not observed (Table 8.2 and Fig. 8.1). Four raptor species indicated cells with high plant species richness but none of the raptor species indicated high butterfly species richness. In contrast, the mean number of butterfly species in cells with records of Black Kite, Red Kite and Common Buzzard was significantly lower compared with control cells.

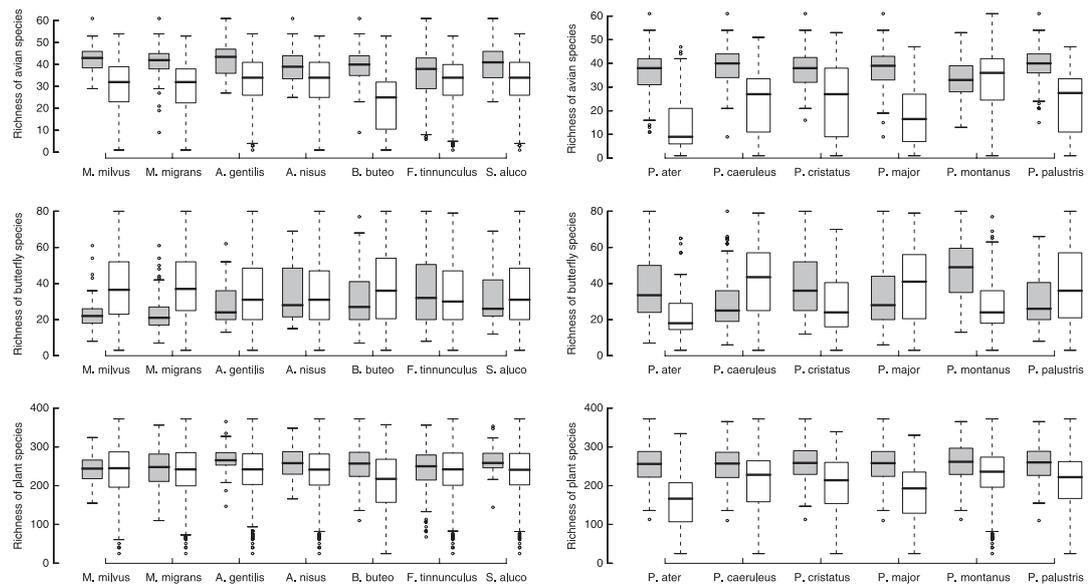


Figure 8.1: Raptor species and *Parus* species as biodiversity indicators - Performance of raptor species (graphs to the left) and *Parus* species (graphs to the right) as species richness indicators. The box plots show species richness per 1 km grid cells occupied by a raptor or *Parus* species (dark boxes) and grid cells not occupied by the species (light boxes). Boxes represent median and 25% and 75% percentiles, whiskers are non-outlier ranges and dots are outliers of avian (first row), butterfly (second row) and plant (third row) species richness.

Five out of six tit species indicated high bird species richness, and all tit species indicated high plant species richness per cell (Table 2 and Fig. 1). The occurrence

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of coal tit, crested tit and willow tit also indicated cells with high butterfly species richness, but the mean of butterfly species richness of cells with blue tit, great tit and marsh tit was significantly lower compared with control cells.

All analyses were repeated using the grid cells from the canton of Tessin only. The results of these analyses were comparable with the above results (Table 8.3).

8.4 Discussion

We used data from the national Swiss Biodiversity Monitoring Programme to show that the observed presence of a raptor species indicated cells with high species richness of birds and plants. We did not find that the presence of a raptor indicated high butterfly species richness. Moreover, *Parus* species performed equally well compared with raptor species as predictors for cells with high bird and plant species richness, and even better as predictors for cells with high butterfly species richness.

Sergio, Newton and Marchesi (2005) and Sergio et al. (2006) provided evidence of the usefulness of raptor species as an indicator of high species richness. The authors also claimed that bird species of lower trophic level, such as insectivorous and herbivorous species, are not good predictors of high species diversity. However, our results suggest that the performance of raptor species as indicators of high species richness largely depends on the species group analysed; raptors predicted cells with high bird species richness, to a lesser extent cells with high plant species richness, but not cells with high butterfly species richness. Furthermore, the species of tit, representing a lower trophic level, performed equally well in indicating cells with high species richness. Our results support other studies that show indicator relationships among higher taxa to be complex and to depend on the species group (Vessby et al. 2002, Thomson et al. 2007).

In this study we assessed the value of top predators as indicators of high species richness at a larger scale than the study of Sergio, Newton and Marchesi (2005) and Sergio et al. (2006). In biodiversity indicator studies, variation in scale may lead to different results because of the inclusion of more or fewer biogeographical regions or habitat types (Bohning-Gaese 1997, Favreau et al. 2006). For example *Parus* species that are more common in the Alps than in other parts of Switzerland, such as the Coal Tit, Crested Tit and Willow Tit (Schmid et al. 1998), were good predictors of high

butterfly species richness in this study. These results may simply reflect the fact that the numbers of butterfly species are higher in the Alps than in other parts of Switzerland (Koordinationsstelle Biodiversitätsmonitoring Schweiz 2006). These particular *Parus* species might be of less value in predicting species richness in a study on a smaller scale that only included the Alps. However, we also analysed data from the canton of Tessin, adjacent to the study area of Sergio, Newton and Marchesi (2005) and Sergio et al. (2006) and at a comparable scale. Our conclusions remained the same as from our analyses of data from the whole of Switzerland: *Parus* species predict species richness at least equally as well as raptor species.

	Bird			Butterflies			Vascular plants		
	<i>w</i>	<i>n</i>	p-value	<i>w</i>	<i>n</i>	p-value	<i>w</i>	<i>n</i>	p-value
<i>Milvus milvus</i>		0			0			0	
<i>Milvus migrans</i>	52	3	0.344		1		65	3	0.630
<i>Accipiter gentilis</i>		1			1			1	
<i>Accipiter nisus</i>	51	5	0.030 *	27	2	0.815	60	5	0.059
<i>Buteo buteo</i>	166	11	0.109	59.5	5	0.697	158	11	0.077
<i>Falco tinnunculus</i>	324	16	0.838	116	9	0.615	378	16	0.225
<i>Strix aluco</i>	78	6	0.064	42	4	0.441	112	6	0.345
<i>Parus ater</i>	153	38	0.002 **	62	23	0.082	172	38	0.006 **
<i>Parus caeruleus</i>	174	25	0.001 **	119	12	0.984 ***	105	25	0.001 ***
<i>Parus cristatus</i>	199	17	0.025 *	82	9	0.367	252	17	0.199
<i>Parus major</i>	138	30	0.001 ***	127	16	0.985	115	30	0.001 ***
<i>Parus montanus</i>	313	28	0.277	59	19	0.014 *	329	28	0.414
<i>Parus palustris</i>	157	24	0.001 ***	88	12	0.220	91	24	0.001 ***

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Table 8.3: Results of the Mann-Whitney U -test using grid cells from Tessin only. For empty table cells, too few data were available to perform the test. w : test statistic, n : number of grid cells with presence of the raptor species or *Parus* species.

Sergio, Newton and Marchesi (2005) and Sergio et al. (2006) stated that each of their bird species assessments reflected the biodiversity of an area of approximately 1 km² (Sergio et al. 2006). However, these authors detected only around 6.5 avian species on average, which is about four times less than the number of species detected per 1 km cell in this study. The canton of Tessin in the southern part of Switzerland and the Trentino mountains are adjacent areas with, presumably, much the same species pool. If we considered cells from the canton of Tessin only, the average avian species richness of the Sergio, Newton and Marchesi (2005) and Sergio et al. (2006) study was 3.5 times lower than ours. The species detectability of birds in the Swiss Biodiversity Monitoring

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Programme used for this study was estimated to be 89% (Kéry and Schmid 2006). In contrast, we assume that a large number of birds remained undetected in Sergio, Newton and Marchesi (2005) and Sergio et al. (2006) study. Imperfect detection of species is a fundamental problem in ecological studies (Boulinier et al. 1998): measures of species richness may be confounded by the detectability of species and the problem is pronounced for very low species detection probabilities.

Sergio, Newton and Marchesi (2005) and Sergio et al. (2006) concentrated on regions where the target raptor species occurred. For each raptor species the regions differed in size and location. Therefore the results may be biased towards the representation of these species and interpretation of the results may be difficult. More importantly, conservation priorities are usually drawn up within administrative regions or biogeographically meaningful regions: a method based on the presence of a raptor species as a surrogate for species richness cannot judge if some of the most important places for conservation are outside the range of the raptor species. Our study used sites throughout Switzerland, therefore our assessment was based on a given region, which is a rational unit within which conservation priority decisions can be made. We also noted that, while some studies have suggested that species with few occurrences are better indicators of species richness (Lawler et al. 2003) and others have found the opposite pattern (particularly for Switzerland; (Pearman and Weber 2007)), the spatial pattern of species richness of widely distributed species is correlated to a greater degree with overall richness than the spatial pattern of species with few occurrences. Our study provides no evidence that single species with few occurrences (e.g. Goshawk and Sparrowhawk in this study) differed in their potential to indicate cells with high species richness from widely distributed species (e.g. *Parus spp.* and Common Buzzard).

Sergio, Newton and Marchesi (2005) and Sergio et al. (2006) reframed an old debate in conservation biology by suggesting that top predators are valuable as biodiversity surrogates. However, from an ecological perspective, based on the data-base of the Swiss Biodiversity Monitoring Programme and the Swiss breeding bird survey, we have found little evidence to justify conservation focusing on top predators. Raptor presence indicated areas with high species richness reasonably well, at least for avian and plant species richness. However, other species groups, such as tit species, are of equal value in identifying areas of high species richness. We conclude that the usefulness of a biodiversity indicator can vary between adjacent areas even if the same species groups

are analysed. This should be considered when using surrogate species for conservation planning. We recommend the use of complementary indicator species from different trophic groups to assess biodiversity.

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8.6 References

- Andelman, S. J. and W. F. Fagan. 2000. Umbrellas and flagships: Efficient conservation surrogates or expensive mistakes? *Proceedings of the National Academy of Sciences of the United States of America* 97:5954-5959.
- Bohning-Gaese, K. 1997. Determinants of avian species richness at different spatial scales. *Journal of Biogeography* 24:49.
- Boulinier, T., J. D. Nichols, J. R. Sauer, J. E. Hines, and K. H. Pollock. 1998. Estimating species richness: The importance of heterogeneity in species detectability. *Ecology* 79:1018-1028.
- Cabeza, M. and A. Moilanen. 2001. Design of reserve networks and the persistence of biodiversity. *Trends in Ecology & Evolution* 16:242-248.
- Favreau, J. M., C. A. Drew, G. R. Hess, M. J. Rubino, F. H. Koch, and K. A. Eschelbach. 2006. Recommendations for assessing the effectiveness of surrogate species approaches. *Biodiversity and Conservation* 15:3949-3969.
- Hagemeijer, W. J. M. and M. J. Blair. 1997. *The EBCC atlas of European breeding birds: their distribution and abundance*. Poyser, London.
- Hintermann, U., D. Weber, and A. Zangger. 2000. Biodiversity monitoring in Switzerland. *Schriftenreihe Landschaftspflege Naturschutz* 62:47-58.

8. TOP PREDATORS AS BIODIVERSITY INDICATORS

- Jackson, S. F., M. Kershaw, and K. J. Gaston. 2004. The performance of procedures for selecting conservation areas: waterbirds in the UK. *Biological Conservation* 118:261-270.
- Kerr, J. T. 1997. Species richness, endemism, and the choice of areas for conservation. *Conservation Biology* 11:1094-1100.
- Kéry, M. and H. Schmid. 2006. Estimating species richness: calibrating a large avian monitoring programme. *Journal of Applied Ecology* 43:101-110.
- Koordinationsstelle Biodiversitätsmonitoring Schweiz. 2006. Zustand der Biodiversität in der Schweiz. Bundesamt für Umwelt, Bern.
- Lawler, J. J., D. White, J. C. Sifneos, and L. L. Master. 2003. Rare species and the use of indicator groups for conservation planning. *Conservation Biology* 17:875-882.
- Margules, C. R. and R. L. Pressey. 2000. Systematic conservation planning. *Nature* 405:243-253.
- Noss, R. F. 1990. Indicators for Monitoring Biodiversity - a Hierarchical Approach. *Conservation Biology* 4:355-364.
- Ozaki, K., M. Isono, T. Kawahara, S. Iida, T. Kudo, and K. Fukuyama. 2006. A mechanistic approach to evaluation of umbrella species as conservation surrogates. *Conservation Biology* 20:1507-1515.
- Pearman, P. and D. Weber. 2007. Common Species Determine Richness Patterns in Biodiversity Indicator Taxa. *Biological Conservation* 138:109-119.
- Pedrini, P., M. Caldonazzi, and S. Zanghellini. 2005. Atlante degli Uccelli nidificanti e svernanti in provincia di Trento. Museo Tridentino di Scienza Naturali, Trento. Studi Trentini di Scienze Naturali. *Acta Biologica* 80:1662.
- Pressey, R. L. 1994. Ad Hoc Reservations - Forward or Backward Steps in Developing Representative Reserve Systems. *Conservation Biology* 8:662-668.
- R Development Core Team. 2006. R: A language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

- Roberge, J. M. and P. Angelstam. 2004. Usefulness of the umbrella species concept as a conservation tool. *Conservation Biology* 18:76-85.
- Schmid, H., R. Luder, B. Naef-Daenzer, R. Graf, and N. Zbinden. 1998. Schweizer Brutvogelatlas. Verbreitung der Brutvögel in der Schweiz und im Fürstentum Liechtenstein 1993-1996. Schweizerische Vogelwarte, Sempach, Switzerland.
- Schmid, H., N. Zbinden, and V. Keller. 2004. Überwachung der Bestandsentwicklung häufiger Bruvögel in der Schweiz. Schweizerische Vogelwarte, Sempach, Switzerland.
- Sergio, F., I. Newton, and L. Marchesi. 2005. Top predators and biodiversity. *Nature* 436:192-192.
- Sergio, F., I. Newton, L. Marchesi, and P. Pedrini. 2006. Ecologically justified charisma: preservation of top predators delivers biodiversity conservation. *Journal of Applied Ecology* 43:1049-1055.
- Simberloff, D. 1998. Flagships, umbrellas, and keystones: is single-species management passé in the landscape era? *Biological Conservation* 83:247-257.
- Thomson, J. R., E. Fleishman, R. Mac Nally, and D. S. Dobkin. 2007. Comparison of predictor sets for species richness and the number of rare species of butterflies and birds. *Journal of Biogeography* 34:90-101.
- Vessby, K., B. Soderstrom, A. Glimskar, and B. Svensson. 2002. Species-richness correlations of six different taxa in Swedish seminatural grasslands. *Conservation Biology* 16:430-439.
- Weber, D., U. Hintermann, and A. Zangger. 2004. Scale and trends in species richness: considerations for monitoring biological diversity for political purposes. *Global Ecology and Biogeography* 13:97-104.
- Williams, P., D. Faith, L. Manne, W. Sechrest, and C. Preston. 2006. Complementarity analysis: Mapping the performance of surrogates for biodiversity. *Biological Conservation* 128:253-264.

8. TOP PREDATORS AS BIODIVERSITY INDICATORS

Appendix A

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Appendix B

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Books

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Journal publications

- Bühler, C. and Roth, T. 2011. Spread of common species results in local-scale floristic homogenization in grassland of Switzerland. *Diversity and Distributions* 17:1089-1098.
- Naguib, M., Kunc, H. P., Sprau, P., Roth, T. and Amrhein, V. 2011. Communication networks and spatial ecology in Nightingales. *Advances in the Study of Behavior* 43: 239-271.
- Roth, T. and Amrhein, V. 2010. Estimating individual survival using territory occupancy data on unmarked animals. *Journal of Applied Ecology* 47: 386-392.
- Sprau, P., Roth, T., Schmidt, R., Amrhein, V. and Naguib, M. 2010. Communication across territory boundaries: distance dependent responses in nightingales. *Behavioral Ecology*, 21: 1011-1017.
- Sprau, P., Schmidt, R., Roth, T., Amrhein, V. and Naguib, M. 2010. Effects of rapid broadband trills on responses to song overlapping in nightingales. *Ethology* 116: 300-308.
- Roth, T., Sprau, P., Schmidt, R., Naguib, M. and Amrhein, V. 2009. Sex-specific timing of mate searching and territory prospecting in the nightingale: nocturnal life of females. *Proceedings of the Royal Society, Series B*, 276, 2045-2050.
- Naguib, M., Schmidt, R., Sprau, P., Roth, T., Flörcke, C. and Amrhein, V. 2008. The ecology of vocal signaling: male spacing and communication distance of different song traits in nightingales. *Behavioral Ecology*, 19, 1034-1040.
- Roth, T. 2008. Outward (autumn) bird migration at the southeastern peninsula and cape greco, Cyprus: the phenologies of regular migrants. *Sandgrouse*, 30, 77-89.
- Roth, T., Amrhein, V., Peter, B. and Weber, D. 2008. A Swiss agri-environment scheme effectively enhances species richness for some taxa over time. *Agriculture, Ecosystems and Environment*, 125, 167-172.
- Roth, T. and Weber, D. 2008. Top predators as indicators for species richness? Prey species are just as useful. *Journal of Applied Ecology*, 45, 987-991.

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- Roth, T. and Corso, A. 2007. Cyprus the autumn 2005 raptor migration at the southeast peninsula (terminating at Cape Greco). *Sandgrouse*, 29, 79-90.
- Roth, T., Aye, R., Burri, R. and Schweizer, M. 2005. Bird observations from Iran in February-March 2001, including a new species for the Middle East. *Sandgrouse*, 27, 63-68.
- Thiel, D., Ehrenbold, S. and Roth, T. 2005. Grosse Wintergruppen und Winterbalz beim Auerhuhn *Tetrao urogallus*. [Large winter groups and early displaying behaviour of capercaillie *Tetrao urogallus*]. *Der Ornithologische Beobachter*, 102, 44-46.
- Roth, T. and Jalilova, G. 2004. First confirmed breeding record of Palla's Grasshopper Warbler in Kyrgyzstan. *Sandgrouse*, 26, 141-145.
- Aye, R. and Roth, T. 2002. Aussergewöhnliche Winterflucht von Mäusebussarden *Buteo buteo* im November 1999. [Strong hard-weather movements of common buzzard *Buteo buteo*]. *Der Ornithologische Beobachter*, 99, 117-121.
- Aye, R. and Roth, T. 2001. Observation d'un Pluvier fauve *Pluvialis pacificus* dans le Golfe de Gabs. [Pacific Golden Plover in Tunisia]. *Alauda*, 69, 203-204.
- Aye, R. and Roth, T. 2000. Chevalier Bargette (*Tringa cinerea*) hivernant dans le golfe de gabes. *Alauda*, 68, 235.

Invited talks

- Roth, T. and Plattner, M. 2011. Temporal trends in community temperature indices: altitude matters.. Workshop "Beyond the climate envelope", Lund University.

Contributed talks and posters

- Roth, T. and Plattner, M. 2011. Können Monitoringdaten die Klimaerwärmung abbilden? Ein Vergleich zwischen Tagfaltern, Pflanzen und Voögeln. 3. UFZWorkshop zur Populationsbiologie von Tagfaltern & Widderchen, Leipzig, Germany.
- Roth, T. and Amrhein, V. 2009. Piecewise regression models: estimating stages of the breeding cycle from nocturnal song of nightingales. International Statistical Ecology Conference 2010. Kent, Great Britain.

Roth, T. and Amrhein, V. 2009. Hierarchical Bayes Estimation of Apparent Survival in Observed Territory Occupancy Surveys. 7th European Ornithologists Union Conference, Zurich, Switzerland.

Roth, T., Kunc, H., Naguib, M. and Amrhein, V. 2008. Signalling patterns match receivers sampling behaviour in the nightingale. 12th Biennial Congress of the International Behavioral Ecology Society, Ithaca, USA.

Roth, T., Schmidt, R., Sprau, P., Kunc, H., Naguib, M. and Amrhein, V. 2007. Territory settlement of the Nightingale *Luscinia megarhynchos*. 6th European Ornithologists Union Conference, Vienna, Austria.

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