Coping with unpredictable environments: mechanisms underlying settlement and predation in a long-distance migratory forest passerine

Inauguraldissertation
der Philosophisch-naturwissenschaftlichen Fakultät
der Universität Bern

vorgelegt von

Alexander Grendelmeier

von Dietikon (ZH)

Leiter der Arbeit

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PD Dr. Gilberto Pasinelli
Schweizerische Vogelwarte, Sempach

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Der Dekan
Prof. Dr. Gilberto Colangelo

Content

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Abstract

Abstract

Understanding the demography of a species is essential not only to increase our knowledge of this species but it is also pivotal if conservation measures have to be implemented to save the species. To understand the demography of a species it is important to study the ecosystem around a species. Ecosystems often underlie inter- and intra-annual fluctuations driven for example by intermittent resource-pulses, which can be observed all over the world and in various ecosystems. A prime example for resource pulses can be found in forest ecosystems where seed masting of beech (*Fagus* spp.), oak (*Quercus* spp.) or hornbeam (*Carpinus* spp.) may initiate cascading, direct and indirect effects up and/or down the food chain. Because of subsequent pulses, animals not directly linked to seed masts may be affected positively or negatively.

Through observational and experimental studies, the goal of this thesis was to examine several aspects of demography and life-history of a ground-nesting forest-interior passerine occupying a habitat driven by intermittent resource pulses, including rodents and various predators. The model species, the wood warbler (*Phylloscopus sibilatrix*), is a long distance migrant overwintering south of the Sahara desert and breeding in European beech and/or oak dominated deciduous and mixed forest communities between April and July. Through observational studies I addressed wood warbler settlement and reproductive performance in relation to: 1) the effect of various extrinsic factors on a territory scale, 2) rodent-mediated effects of predators on a forest stand scale and 4) resource pulse dynamics on a landscape scale. Experimentally I addressed the effect of social information on settlement and reproduction using wood warbler vocalization playbacks.

As a result of the conspecific attraction experiment (chapter one), wood warblers set up on average 1.2 territories on song plots compared to 0.4 territories on control plots, with settlement occurring more rapidly on song plots compared to control plots. Maximum song plot occupancy of 73% was reached after 5 weeks, whilst no more than 36% of control plots were occupied at any given time. Daily nest survival rate, average clutch size and number of fledglings per nest did not differ between song and control plots. We found increased brood reduction on song plots and extra-pair young on song and control plots.

Examining wood warbler reproduction in relation to various extrinsic and intrinsic factors (chapter two), we found that daily nest survival was positively related to the number of grass and sedge tussocks, nest concealment and nest age. Furthermore, clutch size and number of fledglings decreased, the later in the season a nest was initiated. We found that nest predation was the principal cause of wood warbler nest failure in Switzerland.

In chapter three I assessed the evidence of direct or indirect effects of rodents on wood warbler reproduction. I found that in rodent outbreak years, wood warbler daily nest survival rate was lower than in rodent crash years, but rodents were never important predators of wood warbler nests. In rodent outbreak years, abundance of rodent-hunting mammals and the proportion of wood warbler nests predated by rodent-hunting mammals were higher than in rodent crash years. Therefore I could show that rodent-hunting mammals exhibit a numerical response in relation to rodent abundances in our study forests and that rodent-hunting mammals were the main predator of wood warbler nests over the entire study period.

The patterns found in chapter three, fit well into a resource pulse system, which was further assessed in chapter four. We could show that seed masting is connected to various taxa and species. We found that rodent abundance was positively related to seed masting in the previous year and to number of snow days, and negatively related to frost days. Jay abundance was positively related to seed masting two years ago and negatively related to mean onset date of hazel (*Corylus avellana*) bloom in the previous year. Wood warbler (*Phylloscopus sibilatrix*) abundance was negatively related to rodent abundance and jay abundance, and positively related to cumulative rainfall in April and May, as well as to caterpillar abundance. Wood warbler abundance was thus indirectly and negatively related to seed masting via numerical responses of rodent populations (one year post-mast) and jay populations (two years post-mast). Jays, but much less rodents, are known to depredate wood warbler nests.

My findings connecting seed masting, rodent outbreaks and numerical responses of rodent-hunting mammals, as well as Eurasian jays fit general patterns found for resource pulse systems elsewhere, where consumer response magnitude is related to resource pulse magnitude and resource trophic level, and consumer response lag and duration are related to consumer body mass.

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General Introduction

Topic overview

Understanding the demography of a species is essential not only to increase our knowledge of this species but is also pivotal if conservation measures have to be implemented to save the species. Questions most frequently asked by ecologists include the factors influencing settlement behavior, habitat selection and demographic aspects such as reproductive performance. Generally speaking, such factors can be divided into density-dependent and density-independent mechanisms. Density-dependence constitutes biotic factors which act varyingly with decreasing or increasing population density. The most common density-dependent factors include inter- and intraspecific competition for recourses, such as food, habitat and mating partners, but also predation and parasitism. In contrast, density-independence constitutes abiotic factors which act independently of population density, such as weather, catastrophes or stochasticity. Both of density-dependent and density-independent mechanisms together shape population dynamics and demography (Jonsson et al. 1998).

The sum of all species-specific combinations of density-dependent and independent factors result in the processes making up ecosystems, which often underlie great inter- and intra-annual fluctuations. Examples of such fluctuations are known as resource-pulses, which are associated with strong growth and decline of populations and are observed all over the world (King 1983, Jaksic et al. 1997, Schmidt and Ostfeld 2008). One such ecosystem with especially distinct resource-pulses is mixed deciduous forest, where masts of beech (*Fagus* spp.), oak (*Quercus* spp.) or hornbeam (*Carpinus* spp.) represent the primary pulse during the fall of “year t”, initiating cascading, direct and indirect effects up and/or down food chains (King 1983, Jędrzejewski et al. 1994a, Schmidt and Ostfeld 2003, Schmidt and Ostfeld 2008). Seed masts may trigger secondary resource pulses of seed-consuming animals such as rodents (*Apodemus* spp. and *Myodes glareolus*) or Eurasian jays (*Garrulus glandarius*) (jays hereafter), which may be in, but not limited to “year t+1”. Various subsequent resource pulses may then occur. A prominent example includes numerical responses of rodent-hunting predators, which may also be in, but not limited to “year t+1”. Alternatively, rodent-hunting predators may exhibit a behavioral response, i.e. prey switching (Ostfeld et al. 1996, McShea 2000, Blomqvist et al. 2002). To accurately describe the system, it is important to identify the type of involvement a predator has during an ongoing resource-pulse and thereafter.

Furthermore, a resource-pulse may not only include one prey species (i.e. rodents). Due to predatory behavior of the secondary- and tertiary-pulse species, animals not directly linked to seed masts may be affected as incidental or alternative prey. One could however assume that alternative prey species have evolved strategies to avoid areas with temporarily high abundances of predators.

Plasticity in settlement behavior may allow individuals to avoid temporarily high risk areas. The question, why individuals choose to settle in a given habitat has kept researchers busy for centuries. While much of the early work has focused on factors related to habitat availability and quality (Cody 1981), recent studies additionally suggest a social component to settling (Muller et al. 1997, Arlt and Pärt 2008, Ahlering et al. 2010), which may even trump habitat cues (Betts et al. 2008). By observing conspecifics or even heterospecifics an individual can obtain information regarding resource availability and quality through two processes. Information can either be derived from reproductive performance of others or simply from the presence or absence of others (review in Valone 2007, Ahlering et al. 2010). Instead of having to survey a habitat at length, obtaining information quicker through the presence or performance of others may be especially important for species not occurring in a habitat year round, as is the case with migratory species. In fact, most of the current knowledge on social information stems from migratory songbirds, specifically conspecific attraction during the breeding season (Ahlering et al. 2010). It seems reasonable to assume that both habitat and social cues act together in the process of habitat selection. However, knowledge concerning social information is still limited and has rarely been applied to conservation.

If only settlement of a species is investigated, wrong conclusions could be drawn as to how well a species is doing in an area. It is therefore necessary to keep studies running past settlement and incorporate reproductive performance (Lack 1954), which can be measured based on several components of reproduction such as nest success and survival, clutch size or number of fledglings.

Aim of this thesis

Through observational and experimental studies, the main goal of this thesis was to examine several of the above introduced aspects associated with demography and life-history of a ground-nesting forest-interior passerine occupying a habitat driven by intermittent resource pulses, rodents and various predators (Fig. 1). The model species, the wood warbler (*Phylloscopus sibilatrix*), inhabits an ecosystem experiencing intermittent resource pulses including rodent outbreaks as introduced above. Occurrence of wood warblers and rodents seem to be inversely related (Wesołowski et al. 2009), and wood warbler territories are set up in areas with decreased rodent abundance compared to non-occupied forest areas (Pasinelli et al. accepted, BMC Ecology).

In a large field experiment, I addressed the effect of social information on wood warbler settlement and reproduction through vocalization playbacks on a forest patch scale (chapter one). In relation to wood warbler reproductive performance, I addressed the effect of biotic and abiotic factors on a territory scale (chapter two) and rodent-mediated effects of predators on a forest patch scale (chapter three). In relation to wood warbler abundance, I addressed the effect of resource pulses on a landscape scale (chapter four).

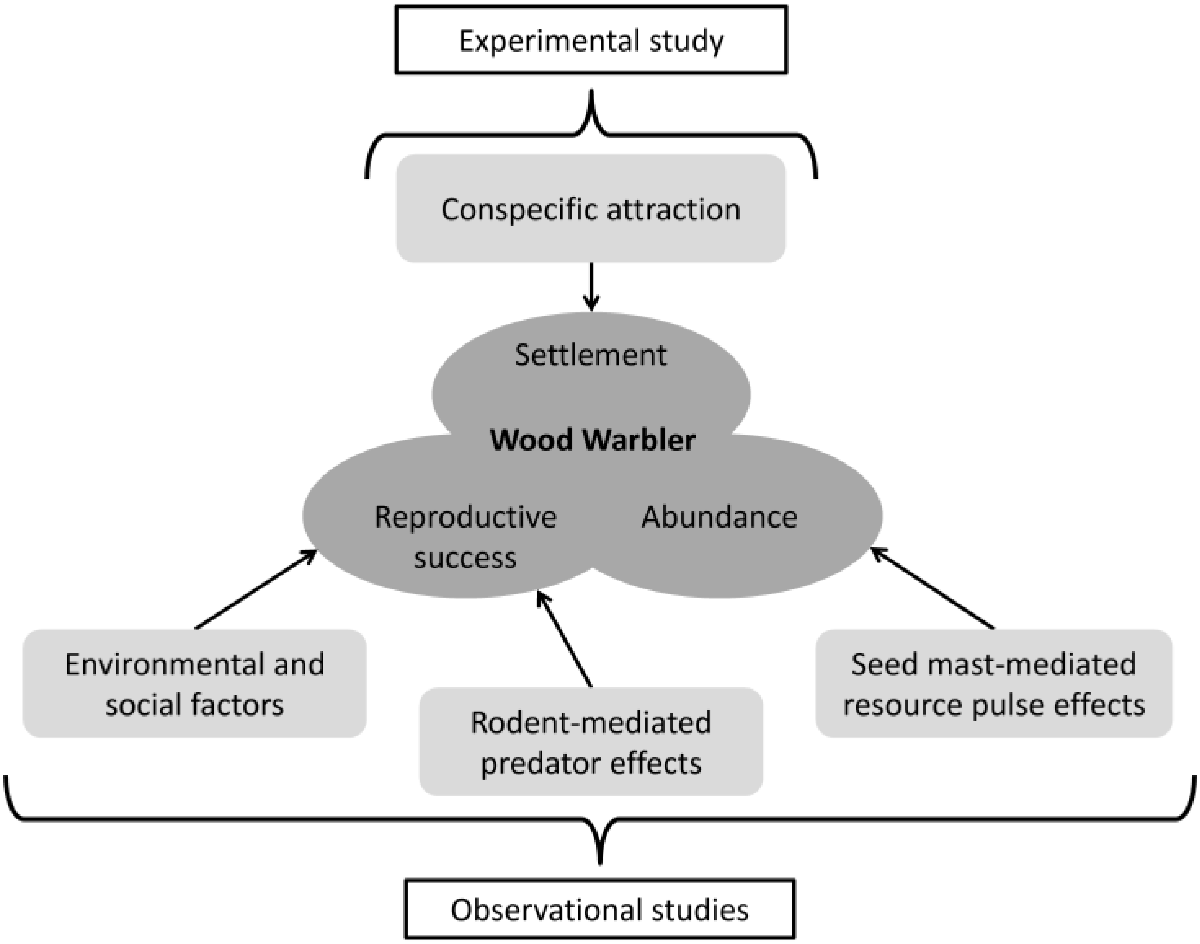

Fig. 1. Study design scheme depicting all aspects to be investigated in relation to settlement, reproductive performance and abundance of the wood warbler

Model species

The wood warbler (Fig. 2) has suffered long-term declines in many EU countries (http://bd.eionet.europa.eu/article12/summary?period=1&subject=A314, accessed February 28, 2016). Population declines appear to have been stronger in western Europe compared to eastern Europe, where long-term population trends are more stable (Glutz von Blotzheim et al. 1991, Flade and Schwarz 2004, Škorpilová et al. 2007, Wesołowski and Maziarz 2009). Throughout its distribution range, local wood warbler populations are known to underlie great annual fluctuations. Reasons for these fluctuations have been hypothesized to be linked to climatic factors during migration and settlement, varying food availability on the breeding grounds and even varying abundance of rodents following mast years in the breeding area. In Switzerland, the wood warbler has recently been classified as vulnerable (VU) on Switzerland's red list (Keller et al. 2010a) and is considered a priority species for the Swiss species recovery program for birds (Keller et al. 2010b). The wood warbler is a long distance migrant that overwinters south of the Sahara desert (Hobson et al. 2014). Spring migration starts following a complete molt in the late winter months

Fig. 2. Female wood warbler with nest material © Michael Gerber

(Stresemann 1955). The wood warbler's breeding distribution range largely coincides with the distribution range of European beech (*Fagus sylvatica*) and English oak (*Quercus robur*) and is limited to Europe with a range offshoot into the South Ural region. It settles in the interior of beech and/or oak dominated deciduous and mixed forest communities characterized by closed canopy (80-90%), little to no shrub layer, open lower stem space and some ground vegetation layer, with grass being very important (Marti 2007, Grendelmeier et al. 2015; Pasinelli et al. accepted, BMC Ecology; Fig. 3). Wood warblers occur in Europe between approximately April and August, with the main breeding time being late April to late July (Wesołowski 1985, Glutz von Blotzheim et al. 1991, Grendelmeier et al. 2015). During this time, one brood is the rule, while true second broods constitute the exception. On the other hand, replacement broods following loss of the first nest are common. Predation is the primary cause of failure of wood warbler nests. (Glutz von Blotzheim et al. 1991, Wesołowski et al. 2009). It has been stated that broods are easily abandoned due to disturbance of the nest area (Mildenberger 1940). However, this could depend on the geographic region and on the frequency and degree of disturbance. Of 250

Fig. 3. Typical wood warbler habitat in northern Switzerland © Alex Grendelmeier

monitored nests during six years, only 8.8% (n = 22) of the nests failed due to unknown reasons. However, how many of these 22 nests have truly been abandoned due to disturbance remains unknown, and I generally worked with the assumption that these cases occurred due to predation of one or both parent birds. When nests that failed due to predation are omitted, hatching rate (proportion of hatched eggs) was 93% (n = 1114 eggs in 201 nests), nestling survival (proportion of surviving hatchlings) was 95% and fledging rate (proportion of eggs to produce fledglings) was 88% (n = 604 nestlings in 125 nests; Grendelmeier, unpublished data). Reproductive performance however can vary greatly locally and annually (Glutz von Blotzheim et al. 1991, Hillig 2009, Wesołowski and Maziarz 2009, Mallord et al. 2012b, Grendelmeier et al. 2015).

Nests are usually well hidden and are best found during construction (n = 83) and incubation (n = 124) by following the female, which approaches the nest using several branches while calling frequently. Vocalization is the only possibility in the field for sex differentiation, as plumage coloration and even morphological characteristics, such as wing length, do not differ between the sexes. Wood warblers have four vocalization types (Cramp and Brooks 1992): the trill song, used primarily for territory defense and mate attraction; the short song, used primarily in the primary territory when paired; the piping song, intermixed with the trill song; and the call, used to communicate and warn. Both male and female use the same call and generally, only males us the three song types, although females have been observed using very short versions of all three songs as well (Glutz von Blotzheim et al. 1991, Trees 1996; personal observation).

Males strongly react to playback vocalization and can be caught using mist nets for subsequent ringing. There seems to be a correlation between diminishing vocalization of the male once it is paired (Trees 1996) and territoriality towards other males, as it becomes more difficult to catch males with the playback method as nesting progresses. Females can be caught directly off the nest with a dip net. Although not quantified, stress to caught birds seems minimal, as females return to their nest within minutes and males start singing and calling within minutes, sometimes seconds.

Frequent vocalization is also used during foraging. Wood warbler primarily forage in the lower forest canopy, with caterpillars constituting one of the most important food components fed to nestlings, even when caterpillars decrease in abundance with progressing season (Maziarz and Wesołowski 2010). However, the diet also includes adult Lepidoptera as well as members of the orders Diptera, Mecoptera, Neuroptera, Ephemeroptera, Dermeptera, Hymenoptera, Hemiptera, Arachnida, Gastropoda and very seldom vegetal matter (Glutz von Blotzheim et al. 1991). Wesołowski et al. (2009) found a correlation between wood warbler numbers and caterpillar abundance, but there was no relationship in the ratio of annual change. Herremans (1993) did not find an overlap of wood warbler territories with areas of high caterpillar abundance. The often proposed mismatch between peak caterpillar abundance and wood warbler reproductive success could not be found in Switzerland, but here as well local wood warbler populations were higher in years with increased caterpillar abundance (Kühn 2015).

Overview of this thesis

From preliminary studies, relationships between wood warbler settlement and environmental factors (slope, herb layer cover, number of grass tussocks, number of trees and number of rodents) were known (Pasinelli et al. accepted, BMC Ecology). In chapter one, I examine the importance of a social factor, conspecific song, for wood warbler settlement. Using public information in form of conspecific cues may be advantageous to a migrant species that has very limited time to make a settlement decision after arriving on the breeding grounds. With a two-year field experiment using song playback of wood warblers, I tested the conspecific attraction hypothesis. Furthermore, I evaluated reproductive performance, a vital, but often neglected aspect during attraction experiments, which is however crucial to assess for deciding whether attraction methods are suitable for conservation. I also evaluated the importance of extra-pair paternity in this species and whether it may explain the often observed clustering of territories (Herremans 1993).

Once settlement has taken place, reproduction is the next important aspect in a species' life-history. In chapter two, I evaluate thematically grouped hypotheses regarding the relationship between three components of wood warbler reproductive performance (clutch size, number of fledglings and nest survival) and various environmental and social factors, which may provide important information on the wood warbler's life-history.

In chapter three, I take a closer look at the relationships between wood warbler reproduction, rodents and rodent-mediated responses of rodent-hunting predators.

Wood warblers as alternative prey species may face decreased or increased predation pressure of rodent-hunting predators, depending on rodent abundance and the type of response (numerical or behavioral) that a predator species exhibits in relation to rodent abundance. Assessing how predation influences wood warbler reproduction is crucial, as predation is a major driver of avian life-history (Martin 1995).

Environmental and social conditions during settlement and reproduction in one year may determine abundance of a species in the next year. In chapter four, I examine the time-lagged influence of resource pulses on wood warbler abundance. Resource pulses in the form of seed masting can trigger multiple secondary and tertiary pulses of various taxa, including seed-consumers and predators of seed-consumers, sometimes over multiple years. Via numerical or behavioral responses of these secondary and tertiary pulse taxa, animals that are normally not influenced directly by seed masting may face increased predation pressure. The wood warbler may be one of these alternative prey species.

The thesis ends with a general discussion that will shortly summarize and synthesize the outcomes of each chapter, provide some recommendations for management and outline perspectives for further research.

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Experimentally manipulated conspecific acoustic cues boost bird territory settlement but not overall breeding performance

Experimentally manipulated conspecific acoustic cues boost bird territory settlement but not overall breeding performance

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ABSTRACT

Decision-making during different life history stages requires information, which is obtained through own or others' experience and interaction with the physical environment. In birds, song is important for territory selection and defense, and while this trait has evolved to purposely convey information it can be inadvertently exploited by conspecifics. Experiments attempting to attract focal species by playing back song are numerous, yet the consequences for reproductive performance remain little understood. In 2013 and 2014, settlement, reproduction and extra-pair paternity of *Phylloscopus sibilatrix* were assessed in a randomized and fully crossed experiment. We hypothesized that territory numbers, reproductive performance and extra-pair paternity would be higher on song plots (song playbacks during pre-breeding periods) than control plots (no playback). On song plots, three times more territories were established, settlement occurred faster and maximum plot occupancy was higher compared to control plots. Daily nest survival rate, clutch size and number of fledglings did not differ, but brood reduction (lower hatching and fledging rates) was higher on song plots compared to control plots. One of seven and one of three nests on song and control plots, respectively, had extra-pair young. Our results demonstrate that the presence of conspecifics is a major cue for territory settlement decision in wood warblers. Yet, even though territory density could be tripled experimentally, individual reproductive performance was not enhanced on song plots. In contrast, increased brood reduction on song plots suggests density-dependent regulation and gives reason to further evaluate whether acoustic attraction represents a suitable method for songbird conservation.

Key words: field experiment, passerine, conspecific acoustic cues, song playback, territory density, reproductive performance, brood reduction, extra-pair parentage, wood warbler

INTRODUCTION

In several animal taxa, decision-making is key in, e.g. habitat selection, mating, foraging, and predation avoidance (Danchin et al. 2004). Decision-making relies on information, which can be personal or public. Personal information can be obtained from direct interactions with one's physical environment: hermit crabs (*Pagurus bernhardus*), for instance, rely on knowledge of their own shell conditions – an information unavailable to rivals – to adjust their pre-fight displaying behavior, which ultimately increases their chance of swapping to better shells (Arnott and Elwood 2007). Personal information can also arise from own previous reproductive performance: in mountain bluebirds (*Sialia currucoides*), for example, dispersal propensity is directly related to reproductive performance in previous years (Citta and Lindberg 2007). Alternatively, information can be obtained by observing con- and heterospecifics, which is referred to as social or public information (Danchin et al. 2004). Social information can stem from purposely conveyed signals specifically evolved, such as song in birds. An individual can also obtain inadvertently conveyed social information, which may be derived from the performance of other individuals (public information or PI, Valone 2007) and/or from the presence or abundance of individuals (conspecific and/or heterospecific attraction via location cues, Ahlering et al. 2010).

The use of inadvertent social information appears to be widespread across plant and animal taxa. Examples include tobacco plants (*Nicotiana attenuata*) increasing chemical defense when growing near artificially clipped sagebrush (*Artemisia tridentate*) (Karban and Maron 2002), American toads (*Bulb americanus*) and cope's gray tree frog (*Hyla chrysoscellis*) using chorus sounds to join breeding aggregations (Swanson et al. 2007), nine-spined sticklebacks (*Pungitius pungitius*) using foraging activity and success of conspecifics to evaluate foraging patch quality (Coolen et al. 2003, van Bergen et al. 2004), and female mice (*Mus musculus*) choosing mates diffusing odor of other estrous females (Kavaliers et al. 2014). Inadvertent social information is especially well documented in birds in regard to foraging site location, mate and territory selection and often results in individuals settling near conspecifics (conspecific attraction hypothesis; reviewed in Danchin et al. 2004). With respect to territory selection, the conspecific attraction hypothesis predicts that individuals are attracted to and settle near conspecifics based on information gathered from conspecifics either in previous years or right before settlement. In birds, territory defense and mate attraction are often achieved via singing, an acoustic cue. Some species rely on song cues to monitor the presence of conspecifics principally during the pre-breeding, territory settlement period, either to assess territory quality (the best territories available being colonized first; e.g. Tschumi et al. 2014) or to identify sites with increased opportunities for promiscuity (see the social mate choice hypothesis by Allee 1958). Acoustic cues are also used for the assessment of territory quality after the breeding season: post-breeding song may provide information not only about habitat quality but also about reproductive success (Betts et al. 2008). However, the use of post-breeding song as a proxy of future habitat quality holds only if site quality is correlated across years.

We conducted a two-year field experiment that aimed at testing the conspecific attraction hypothesis in the wood warbler (*Phylloscopus siblatrix*), a migratory forest bird that appears to breed in social clusters (e.g. Herremans 1993). We focused on pre-breeding singing activity for two reasons. First, song activity of the wood warbler sharply drops after pairing, never returning to pre-breeding levels later on (Trees 1996). Second, habitat quality of breeding grounds is likely to vary a lot between years due to intermittent resource pulses triggered by seed masts in the mixed-deciduous forests inhabited by the wood warbler: autumn seed masts initiate a cascade of responses, including outbreaks of ground-dwelling rodents (*Apodemus* and *Myodes* spp.), that alter the habitat selection pattern by the wood warbler in the following year (Wesołowski et al. 2009; Pasinelli et al. accepted, BMC Ecology). As a result, post-breeding acoustic cues to assess future territory quality cannot apply in this case. Conspecific attraction has been found in many bird species, with early territories usually being established on or around artificial attraction plots and not on control plots without artificial attractants (Ahlering et al. 2010). Social cues can be so strong that birds even settle in seemingly unsuitable habitat (Betts et al. 2008). In this study we evaluated whether wood warblers settle in response to the simulated presence of conspecifics. More specifically, we compared the settling behavior of the study species on plots with experimental playback of wood warbler song (song plots) to control plots without song. We expected more males setting up territories on song plots compared to control plots.

Furthermore we evaluated reproductive performance in terms of clutch size, number of fledglings and daily nest survival rate on song plots compared to control plots. There is a steadily growing number of studies on conspecific attraction, but fitness consequences are often not investigated. This gap in knowledge hinders assessing whether artificial conspecific attraction with acoustic methods may provide a suitable tool for species conservation (Ahlering et al. 2010). Based on studies having addressed fitness consequences (reviewed in Ahlering et al. 2010), artificial attraction methods have generally boosted in some way measures of reproductive performance. We thus predicted an overall higher breeding output on song plots compared to control plots. Specifically we expected that mean and total number of fledglings, respectively, was higher on song plots compared to control plots.

Preliminary results after the first year of the experiment provided evidence for territory clustering on song plots. We propose two *a posteriori* hypotheses to explain clustering of territories in this species. 1) The social mate choice hypothesis predicts that clustered settlement may, at least in some breeding systems, offer an increased chance of successfully finding mates (Tarof et al. 2004). We therefore expected that pairing rates on song plots were higher than on control plots. 2) The hidden lek hypothesis predicts that females seek out aggregations to increase the chance for extra pair copulations (Wagner 1998). Hidden leks share in fact the most important resource typically encountered in the normal leks of promiscuous species: mating partners. Extra-pair copulations regularly occur even in socially monogamous species (Segelbacher et al. 2005), because males and females can gain various direct and indirect benefits (reviewed inGriffith et al. 2002). Thus, if territory clustering is driven by opportunities for extra-pair copulations, we expected a) a higher number of nests with extra-pair young and b) a higher share of extra-pair young on song plots than on control plots.

METHODS

Study area and species

The study took place in the Jura mountains (N Switzerland). The two study areas Blauen and Erschwil were located on slopes exposed to the and south-west, respectively, and consisted of mixed deciduous forest stands dominated by european beech (*Fagus sylvatica*), with other deciduous and coniferous tree species interspersed. Stands predominantly consisted of old polewood and young timber with a relatively closed canopy and a sparse shrub layer, if at all present. As part of our ongoing studies on the wood warblers, we also worked in four additional study areas that were not involved in the experiment, but were used in this study for breeding condition comparison among years (Lauwil, Montsevelier, Kleinlützel and Scheltenpass (see Grendelmeier et al. 2015 for location details). The wood warbler has suffered long-term declines in many EU countries (http://bd.eionet.europa.eu/article12/summary?period=1&subject=A314, accessed 3 December 2015). It has recently been classified as vulnerable (VU) on Switzerland's red list (Keller et al. 2010a) and is considered a priority species for the Swiss recovery program for breeding birds (Keller et al. 2010b). This insectivorous forest-interior passerine exhibits very little breeding site fidelity (ring return percentages reviewed in Wesołowski et al. 2009), resulting in high inter-annual turnover of individuals and in strong annual fluctuations of local population size. The wood warbler is a long distance migrant that overwinters south of the Sahara (Hobson et al. 2014). Breeding sites are typically occupied between the end of April and July.

Experimental plots

In early April, before the arrival of males, 29 experimental plots (22 in Blauen, 7 in Erschwil) were set up in areas known to have had wood warbler territories in 2010, 2011 and 2012. This allowed wood warblers to settle in habitats suitable in terms of structure and to some degree rodent abundance, which both influence territory choice (Pasinelli et al. accepted, BMC Ecology). In each study area, song and control treatments were randomly assigned to experimental plots, and the assignment was switched between the two years of the experiment. Switching the assignment of song and control plots between 2013 and 2014 ensured that experimental results arose from the treatment and not from some confounding effect (e.g. habitat). In total, 15 plots served as song plots and 14 others as controls. Size of each experimental plot was 5 ha which is roughly equivalent to a circle with radius of 125 m and which would allow wood warblers to settle within the experimental plot (territory size spans 0.12 – 3 ha or circles of 20 – 100 m radius, Glutz von Blotzheim et al. 1991). The centers of each experimental plot were not farther away than 50 m from a nest or the recorded location of singing males in the previous years.

Treatments, vocalizations and playback schedules

To avoid pseudo-replication, we broadcasted on each of the 15 song plots a unique song of a different wood warbler recorded in different locations in northern Switzerland during settlement in the 3 years preceding the experiment. Song bouts mimicking the natural song frequency were broadcasted from the beginning of the third week of April until the end of the second week of June. This 8-week interval corresponds to the settlement period of the wood warbler in our study areas. At each song plot, two playback stations broadcasting vertically up were set up 50 m from the plot center, i.e. 100 m apart from each other on an east-west alignment. To simulate movement of a singing male, song playback alternated between the two stations. While station one played back a 6 minutes file where the first 3 minutes contained song and the remaining 3 minutes complete silence, station 2 played back a 6 minutes file with 3 minutes of silence first and then 3 minutes of song. Playback equipment (.wav format mp3-player, loudspeaker, timer, lead-acid battery) was placed in small plastic boxes (casing) to protect from the elements. Songs of the 15 males had been recorded with Sennheiser ME-66 microphones and Olympus LS-10 and Marantz PMD670 digital recorders (.wav format, sampling frequency: 44.1 kHz, resolution: 16 bit), edited and brought to standardized amplitude with sound-editing software (Audacity).

Intentionally broadcasted sound itself and/or unintentional background or loudspeaker noise may attract or deter birds from the experimental plots. To test for this possible loudspeaker effect, we divided the 14 control plots into 7 silent controls with loudspeaker dummies and 7 noise controls playing back song of the common wood pigeon (*Columba palumbus*), a species commonly occurring in our study forests. We used the exact same set up and equipment on noise control plots as on song plots, but only the casing and loudspeaker dummies on silent control plots. Equipment on song and control plots was checked twice a week.

Field methods

Each study area was visited twice a week to map singing males, pairs and nests. Upon finding a nest, one trail camera (Reconyx PC900 HyperFire Professional High Output Covert; Reconyx, Inc., Holmen, Wisconsin, USA) was installed, pointing directly at the nest entrance at a distance of 1-2 m. Trail cameras allowed to simultaneously monitor many nests, while keeping researcher disturbance at a minimum (Ibanez-Alamo et al. 2012), to survey activity of adults and (old) nestlings, to identify nest predators and to determine the exact date of nest predation and/or fledging of nestlings. Nest status was determined at each visit (i.e. still nesting or empty) and nestlings were aged with pictures of reference nestlings from nests where exact hatching date was known. With weekly nest checks it was possible to visit each nest at least twice during each phase. During egg-laying we could determine the exact date the first egg was laid, since the laying interval is one day.

Visiting the nest immediately after hatching allowed us to determine the exact hatching date by witnessing hatching or aging nestlings through pictures as described above. Hatching rate was determined by dividing the number of hatched nestlings by number of eggs per nest. Visiting nests around day 6-7 and again at around day 10 allowed us to determine number of lost nestlings and how many young would fledge. We worked with the assumption that all nestlings seen at the age of 10 days would survive till fledging, unless predated, which would be captured by cameras. Date of fledging could be inferred via picture analysis. Once a nest was inactive (successful or unsuccessful), we measured vegetation parameters and rodent occurrence (details given in Table S1). We used the same field methods to map and monitor bird nests in the four additional study sites mentioned above. To evaluate whether breeding conditions were generally good or bad during the period of the experiment in 2013/14, we compared mean reproductive performance (number of eggs, nestlings and fledglings) of nests in unmanipulated study areas in 2013/14 (unmanipulated others13/14 hereafter; $n_{\text{study areas}} = 4$), to nests in all areas but Blauen and Erschwil in the three years preceding the experiment 2010-12 (others10-12 hereafter; $n_{\text{study areas}} = 15$). We also compared reproductive performance in nests on control plots of the two manipulated study areas (Blauen and Erschwil) of 2013/14 (BL/EW(c) hereafter; $n_{\text{study areas}} = 2$) and nests in the same two areas (Blauen and Erschwil) when they were unmanipulated in 2010-12 (BL/EW hereafter; $n_{\text{study areas}} = 2$).

Responses measured

The measured response was the number of wood warbler territories in the song and control plots (i.e. the 5-ha circles), respectively, in the same breeding season the experiment took place. A territory was defined to occur if either 1) a nest was found, 2) a pair was seen at least once or 3) a singer was recorded on at least 3 consecutive visits. All birds were captured, ringed and color banded, which allowed detecting within- or between-study area movements. Reproductive performance was evaluated with four components of reproduction: clutch size (number of eggs of a completed clutch), number of nestlings (young that successfully hatched), number of fledglings (young that left the nest) and daily nest survival rate (*dnsr* hereafter). We also assessed hatching rate (eggs that successfully hatched), nestling success (number of fledglings divided by number of hatchlings) and fledging success (proportion of eggs that produced a fledgling).

Table 1. Summary statistics for thirteen microsatellites analyzed for wood warblers in 2014. Marker names correspond to Dawson et al. (2010) and (2013), respectively. Hobs = observed heterozygosity, Hexp = expected heterozygosity, PIC = polymorphic information content, NE-1P = average non-exclusion probability for one candidate parent, NE-2P = average non-exclusion probability for one candidate parent given the genotype of a known parent of the opposite sex, NE-PP = average non-exclusion probability for a candidate parent pair, HW = significance of deviation from Hardy-Weinberg equilibrium (NS = not significant, * = significant at the 5% level, ** = significant at the 1% level, *** = significant at the 0.1% level, ND = not done), F(null) = estimated null allele frequency for each locus. Loci with significant deviation from HW (cam-06, cam-12, TG04-012) were excluded from subsequent analysis.

Marker	**Multiplex assay**	**Primer sequence 5' – 3'**	**BP size**	**Nr. of alleles**	**Nr. of typed adults**	**Hobs**	**Hexp**	**PIC**	**NE-1P**	**NE-2P**	**NE-PP**	**HW**	**F(null)**
cam- 06	M1	GTGATGGTCCAGGTCTTGC CAAGAGGAACAGATGAGGGTC	273-303	11	75	0.520	0.673	0.634	0.728	0.547	0.347	*	0.1416
cam-10	M1	TATCCMGAGAATGGGCATC KGCTCTCATTGTCATGCTG	194-196	2	84	0.464	0.502	0.375	0.875	0.813	0.719	NS	0.0364
cam-18	M1	TTAAGAAGTTTACACCCAGCG GCTAAATAACAGAGCCAGGAAG	337-343	4	82	0.329	0.375	0.329	0.93	0.82	0.705	ND	0.0606
cam-24	M1	CCCACTTCAGTCTTCAGAGC TGGAGTATTTGGGATTGGAG	129-147	9	84	0.679	0.681	0.62	0.737	0.574	0.394	NS	-0.0116
cam-23	M2	CTCCACTTAGCTTGTAAATGCAC CCAAGRAGTGCCCTAGATGTC	138-156	9	84	0.679	0.834	0.811	0.5	0.329	0.149	NS	0.0983
cam-07	M2	AAATGATGAGRTCTGGGTGAG CCATTTCCAAGWGATTTGC	230-234	5	84	0.417	0.456	0.409	0.893	0.758	0.613	NS	0.0337

cam-12	M2	TGGCARTAAWTCCAGAGATTACC CTGRCATTTGTCTTAAGCGTG	344-358	12	61	0.230	0.668	0.636	0.722	0.536	0.324	***	0.5036
cam-15	M2	SGACGACTCCTTTATTTCCC TTCTGACTTCCYCAGGTAACAC	267-293	14	81	0.753	0.831	0.805	0.509	0.338	0.16	NS	0.0449
TG04-012	M2	TGAATTTAGATCCTCTGTTCTAGTGTC TTACATGTTTACGGTATTTCTCTGG	131-137	7	82	0.220	0.576	0.535	0.817	0.648	0.462	***	0.4480
cam-19	M3	TCTTGGAGGCAGATARGAAGTG GAGCAAGCAAAGATCACAAGC	241-252	10	84	0.702	0.755	0.711	0.647	0.471	0.285	NS	0.0345
cam-02	M3	GAATTAAAGAYAGCAGATGCAGG AGCTGATGAAATGAGAATGCAG	378-401	16	81	0.765	0.84	0.817	0.483	0.316	0.138	NS	0.0442
cam-03	M3	ATTAGCATAGCTCAGCATTGCC CGAGCATTCAAMCCTGTCATC	148-174	14	78	0.859	0.885	0.868	0.39	0.241	0.088	ND	0.0115
cam-01	M3	AAAGGCCAAGRCCAGTATG CTCTCATCCACCCTGTTAGC	300-313	6	83	0.59	0.649	0.574	0.785	0.637	0.481	NS	0.0472

DNA sampling

Based on the outcome of the playback experiment in 2013, we hypothesized opportunity for extra-pair copulations (EPC) to be a potential driver of settling near conspecifics, and we thus investigated patterns of extra pair parentage (EPP) of wood warblers that settled and bred on song and control plots in 2014. To test the utility of conserved avian microsatellite markers for use with the wood warbler (see below for more details), we captured 15 males, punctured the brachial vein and collected a drop of blood with Whatman® grade 4 filter paper. All subsequently captured individuals ($n_{\text{males}} = 11$, $n_{\text{females}} = 7$, $n_{\text{nestlings}} = 54$ from 10 nests) were sampled using the buccal swab method (Handel et al. 2006). For an extended analyses of extra-pair parentage in wood warblers (presented elsewhere), additional individuals ($n_{\text{males}} = 24$, $n_{\text{females}} = 32$, $n_{\text{nestlings}} = 151$ from 29 nests) from four other study areas were sampled and used here for the allele frequency analysis (Table 1). Samples were stored in 96% ethanol and kept at 5° C. Capturing and ringing were done with permits from the Federal Office of Environment (FOEN), Switzerland, taking blood samples and buccal swabs with permission for animal experimentation from the Cantonal Veterinary Office, Basel-Landschaft (permission number BL468).

DNA extraction from buccal swabs and blood samples was performed with the DNeasy Blood and Tissue kit, Qiagen. Tests of markers' polymorphism, multiplex development, genotyping, and molecular sexing were done by Ecogenics GmbH, Schlieren, Switzerland. We tested for utility of 24 microsatellite markers in the set of Conserved Avian Microsatellites (CAM) described by Dawson et al. (2013), and of markers TG02-088 und TG04-012 (Dawson et al. 2010) in 15 samples of wood warbler. For this, the procedure originally described by Schuelke (2000) using the fluorophore-labeled universal M13 primer was followed. Products were analyzed on an ABI3730 sequencer using an internal size standard. Based on the level of polymorphism and the band patterns in the wood warbler, we chose 13 markers for the subsequent genotyping of the samples in three multiplex-PCR reactions (Table 1) using HotStarTaq Master Mix, Qiagen, and the following cycling protocol: 35 cycles with 94°C for 30 s, 56°C for 90 s, and 72°C for 60 s; before the first cycle, a prolonged denaturation step (95°C for 15 min) was included and the last cycle was followed by a 30 min extension at 72°C. Sex was determined by PCR with the primers P2/P8 and visualization of the products in agarose gel (Griffiths et al. 1998).

Statistical analyses

We pooled data from silent and noise control plots as there was no significant difference in occupancy rate between the two treatment types (t-test, p = 1, n = 14). Even though experimental plots were set up in areas with wood warbler territories in previous years, we tested whether habitat varied between treatment types. We used MANOVA with the three dependent variables rodent occurrence, number of trees, number of grass tussocks (see Table S1 for more details) and one independent variable treatment type (2 levels: wood warbler song plots vs. control plots). We ran separate analyses for both years (2013, 2014), due to possible variation in rodent occurrence between the years. As none of the three dependent variables differed significantly between song and control plots (Table S2), none were included in subsequent analyses.

From a total of 22 nests, 21 could be used for the analyses of clutch size and *dnsr*, and 14 for the analysis of number of fledglings. One nest had to be omitted from all analyses due to incomplete data.

We analyzed settlement, clutch size, number of nestlings, number of fledglings of successful nests and *dnsr* in relation to treatment type with generalized linear mixed effects models (GLMM, package lme4, Bates and Maechler 2010) and likelihood ratio tests in R (R Development Core Team 2008). For the analysis of settlement we modeled the number of territories per plot as dependent variable in relation to treatment (wood warbler song playback or control) and year (2013 or 2014) as independent variables (fixed effects), assuming a Poisson distribution of errors and a log link. We also included “study site” as a random effect to account for the data dependency arising from using multiple experimental plots in each of the two study sites. We repeated the same analysis for the dependent variables clutch size, number of nestlings and number of fledglings, respectively, but additionally included laying date (number of days since the first egg of the first clutch per season of both study areas was laid) as fixed effect to account for the known seasonal decrease in clutch size and number of fledglings (Grendelmeier et al. 2015). For the analysis of *dnsr*, each exposure day constituted one line of data (controlled for with a random variable “nestID”), which was coded and modeled as a binomial dependent variable indicating success (= 1) or failure (= 0) per nest and day. We modeled *dnsr* in relation to treatment, year and nest age (Grendelmeier et al. 2015) as fixed effects, and “study site” and “nest ID” as random effects assuming a binomial error distribution and a logit link. For each analysis we first evaluated whether there was a significant interaction between treatment type and year, comparing a model with both main effects plus their interaction to a model without interaction. There was no evidence for a significant interaction between treatment type and year in any of the five analyses (see results). We continued to evaluate the significance of treatment type by comparing the full model and a reduced model missing treatment type with likelihood ratio tests. For the analyses of clutch size, number of nestlings, number of fledglings and *dnsr*, we also evaluated the significance of laying date by comparing the full model to a reduced model missing laying date. *Dnsr* per treatment type and the corresponding standard errors were calculated according to Mayfield (1961) and Johnson (1979).

To evaluate extra-pair parentage we used parental genotypes from six study sites. First we tested the assumption of a homogenous population using Arlequin (Excoffier and Lischer 2010), which was met. We proceeded by determining expected and observed heterozygosity, and deviations from Hardy-Weinberg equilibrium using Cervus 3.0.7 (Kalinowski et al. 2007) and subsequently had to omit 3 of 13 microsatellite loci due to high null allele frequencies (Table 1). Parent-offspring relationships were analyzed using Wang’s (2004) maximum likelihood method implemented in Colony 2.0.5.6., allowing for a 0.01 error rate. All offspring are simultaneously partitioned into paternal and maternal family clusters, to which candidate parents are assigned at 95% confidence. For missing parent data, Colony will reconstruct parental genotypes and give an index to each missing parent ID. To compare outputs, we conducted four heats with the following input settings: “update allele frequency”, “inbreeding absent”, “polygamy”, “no clones”, “10 runs”, “very long run”, “full-likelihood”, “very high precision”. All four heats produced the same output.

RESULTS

Settlement response to playback

Song plot occupancy amounted to 7% after the first week, compared to 0% control plot occupancy in 2013. In 2014 song plot occupancy amounted to 57% one week after the experiment had started compared to 7% control plot occupancy in the same week. Peak occupancy for song plots occurred five weeks after the onset of the experiment in both years and amounted to 73% and 71% in 2013 and 2014

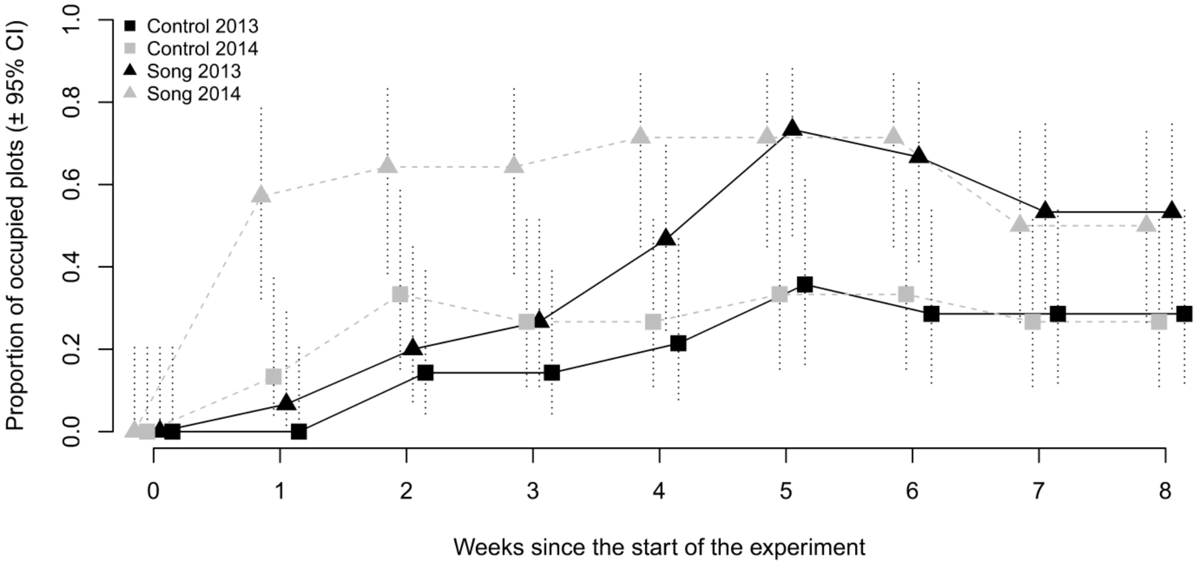

Fig. 1 Proportion of study plots occupied by wood warblers following the start of the experiment with respect to treatment type (triangles: song plots; squares: control plots; black: 2013; grey: 2014). A plot was considered as occupied if at a least one territory had been established. N = 29 plots.

respectively. Occupancy rate of control plots never exceeded 36% in both years (Fig. 1).

For the analysis of settlement, there was no significant difference for models with and without the interaction between treatment and year (likelihood ratio test, $\chi^2 = 0.042$, df = 1, p = 0.84). At the end of the experiment (both years pooled), we recorded 1.2 ± 0.3 territories (mean ± SE, n = 52) on song plots compared to 0.4 ± 0.14 territories on control plots ($\chi^2 = 13.682$, df = 1, p = 0.0002; Fig. 2). Number of territories on song and control plots ranged from 0 to 4 and from 0 to 1,

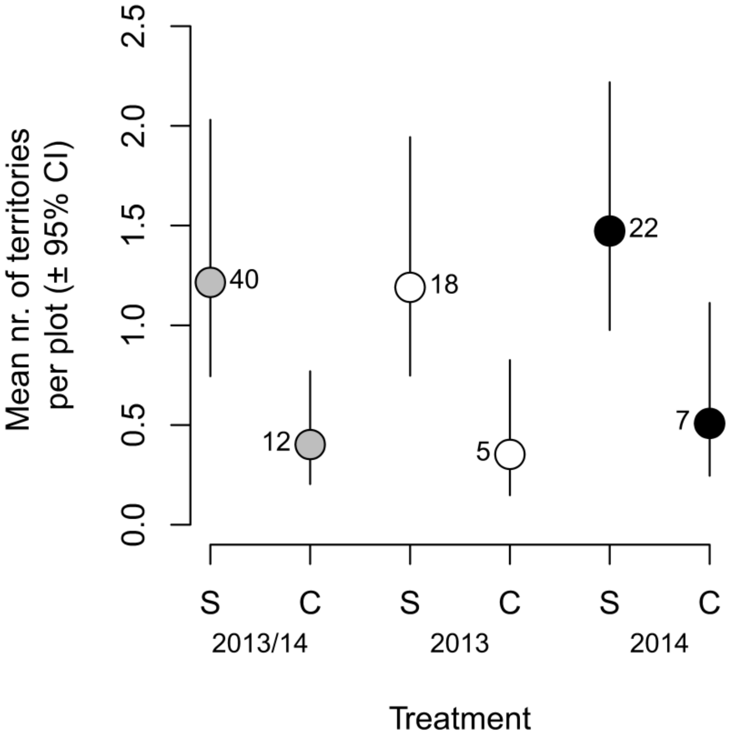

Fig. 2 Mean (± 95% confidence interval) number of territories observed on song plots (S) and control (C) plots for both years together (grey), and separate for 2013 (white) and 2014 (black). Values next to dots indicate the territory sample size the model and graph are based on.

respectively.

Breeding ecology

In total, 23 (2013) and 29 (2014) males set up territories on experimental plots.

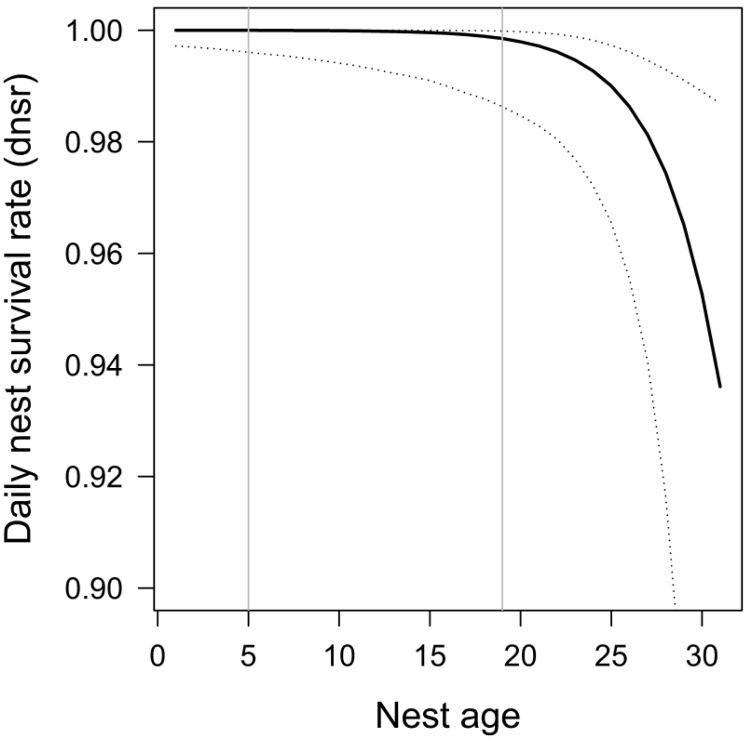

Fig. 3 Daily nest survival rate in relation to nest age (in days). Plot shows fitted values (solid lines) and 95% confidence intervals (dashed lines) based on a model combining 21 nests on song and control plots of 2013 and 2014. Vertical grey lines at nest age five and 19 depict end of egg-laying and incubation, respectively, based on average egg laying, incubation and rearing durations in our study.

On song plots 17 males found a mate and 23 males remained unpaired. On control plots four males found a mate and eight males remained unpaired. There was no significant difference in the number of paired and unpaired males on song and control plots (Fisher's exact test, p = 0.7407). We found 14 nests on song plots and seven nests on control plots, meaning that three pairs or females moved to control plots to build their nests, after pairing on song plots. *Dnsr* over an average nesting period of 31 days was negatively related to nest age (Fig. 3), but did not differ for nests on song plots (mean ± SE: 0.984 ± 0.007, n = 13) and control plots (0.988 ± 0.009, n = 8) (likelihood ratio test, $\chi^2 = 0.596$, df = 1, p = 0.44). Treatment type also had no significant influence on average clutch size ($\chi^2 = 0.06$, df = 1, p = 0.81; Fig. 4) or average number of fledglings of successful broods ($\chi^2 = 0.02$, df = 1, p = 0.89; Fig. 4). The date a clutch was initiated (i.e. first egg being laid) had no significant effect on average clutch size ($\chi^2 = 0.17$, df = 1, p = 0.68, n = 21), average number of fledglings ($\chi^2 = 0.4$, df = 1, p = 0.54, n = 14) or *dnsr* ($\chi^2 = 0.082$, df = 1, p = 0.775, n = 21). The total numbers of eggs produced on song and control plots were 90 and 43 (2 years, $\chi^2 = 7.86$, df = 1, p = 0.005, Fig. 5), respectively. The total numbers of fledglings produced on song and control plots were 43 and 29 (2 years, $\chi^2 = 1.01$, df= 1, p = 0.315, Fig. 5), respectively. Fledging success was thus lower on song plots compared to control plots (48% vs. 67%, Fisher's exact test, p = 0.041, n = 21) when

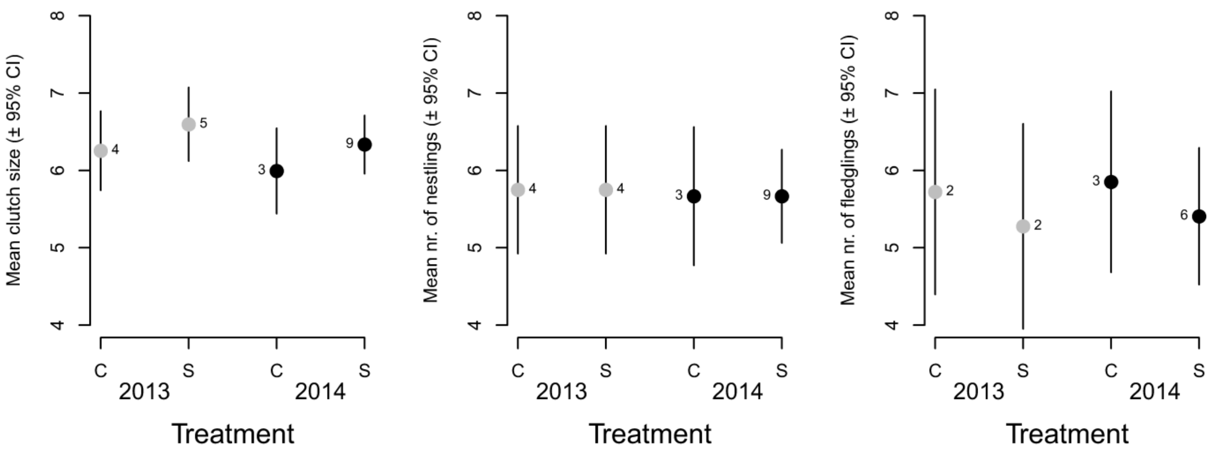

Fig. 4 Mean (± 95% confidence interval) clutch size (n = 21 nests), mean number of nestlings (n = 20 nests) and fledglings (n = 13 nests) on song plots (S) and control plots (C) for 2013 (grey) and 2014 (black). Values next to dots represent the nest sample size the model and graph are based on.

analyzing all nests together. Hatching rate on song and control plots did not differ with 82% and 93%, respectively (p = 0.117, n = 21). Nestling success on song and control plots did not differ with 58% and 73%, respectively (p = 0.157, n= 21). When nests lost to predation are omitted from the dataset, hatching rate (song: 80% vs.

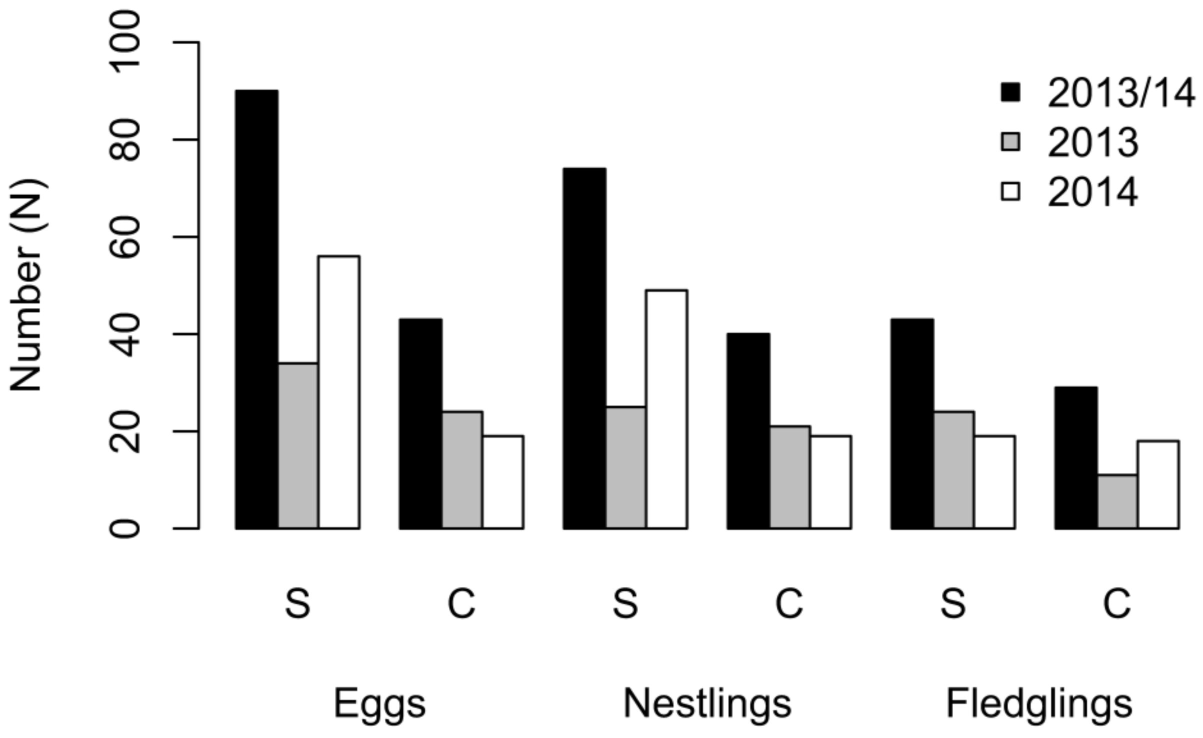

Fig. 5 Number of eggs (21 nests), nestlings (20 nests) and fledglings (13 nests) on song plots (S) and control (C) plots in 2013 (grey bars), 2014 (white bars) and summed up for both years (black bars).

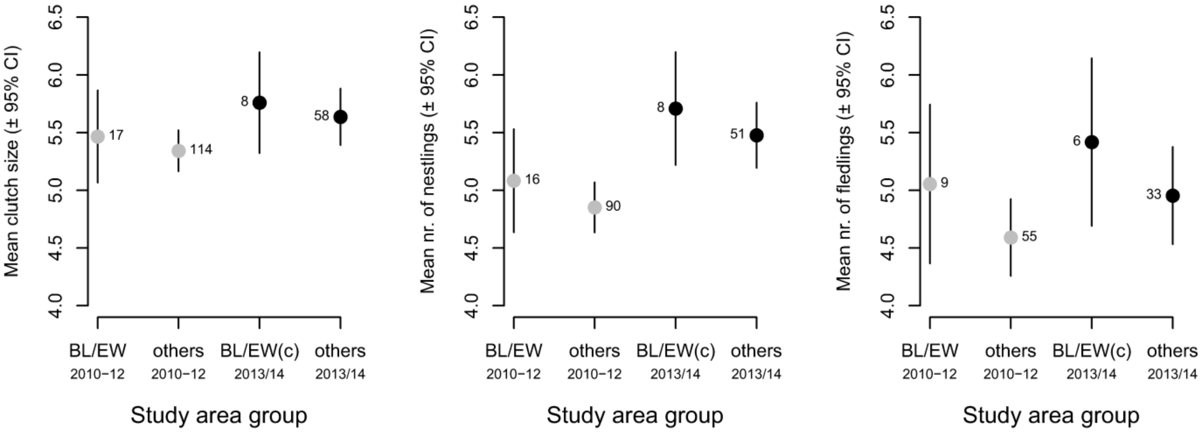

Fig. 6 Mean (± 95% CI) clutch size, number of nestlings and fledglings with respect to experimental manipulation and time period. Each panel is divided by four categories: 1) The two study areas Blauen and Erschwil when they were unmanipulated in 2010-2012 ($n_{\text{study areas}}$ = 2), 2) all other areas besides Blauen and Erschwil in 2010-2012 ($n_{\text{study areas}}$ = 15), 3) the two study areas Blauen and Erschwil when they were manipulated in 2013/14 ($n_{\text{study areas}}$ = 2, data from control plots only), and 4) unmanipulated study areas in 2013/14 ($n_{\text{study areas}}$ = 4). Values next to dots represent the nest sample size the model and graph are based on.

control: 97%; p = 0.034, n = 16), nestling success (75% vs. 97%; p = 0.015, n = 16) and fledging success (61% vs. 94%; p = 0.0007, n = 16) were all lower on song plots compared to control plots.

General breeding conditions in 2013/14 appeared to have been better than in 2010-2012. We found increased clutch sizes and number of nestlings in unmanipulated areas of 2013/14 compared to the same areas in 2010-2012, and number of fledglings tended to differ (Fig. 6). Clutch sizes, number of nestlings and number of fledglings also tended to be higher on control plots of the two manipulated areas in 2013/14 than before, though 95% confidence intervals are large due to small sample sizes once nests on song plots are omitted.

Extra-pair parentage

All loci were polymorphic (number of alleles 2 – 16) and observed heterozygosity ranged from 0.220 to 0.859 per locus (Table 1). Based on the best (ML) configuration under the full likelihood model, Colony detected extra-pair young (EPY) in one out of seven nests on song plots and in one out of three nests on control plots, respectively. Two of the six nestlings in the nest with EPY on song plots were from another male than the social-pair male. In the control plot nest with EPY, one of six nestlings was sired by a male other than the social-pair male. No evidence for extra-pair maternity was found.

DISCUSSION

Settlement

The presence of conspecifics appears to be a key component for the settlement of wood warblers. Plots with experimental playback of wood warbler song had more than three times as many territories and were settled faster compared to control plots without wood warbler song playback. These findings are in line with results reported in most playback experiments carried out over the past four decades in the context of artificial attraction (20 out of 24 studies reviewed by Ahlering et al. 2010). Of the studies providing evidence for artificial attraction, two used post-breeding cues, whereas 18 used pre-breeding cues as in the present work. However, the occurrence of reproduction was mentioned (and investigated) in only seven of the 20 studies reporting successful artificial attraction.

Breeding ecology

Information about reproductive performance following artificial attraction is crucial for the potential applicability of the method in species conservation, especially given the inherent risk of creating ecological traps. As mentioned above, reproduction could be confirmed in seven of the studies employing artificial (visual and/or acoustic) attraction methods, of which two concerned songbirds. Nest success of the black-capped vireo (*Vireo atricapilla*) attracted to song plots was higher than on plots with unmanipulated populations, but only if the brood-parasitizing Brown-headed Cowbird (*Molothrus ater*) was managed (Ward and Schlossberg 2004). The second study investigated least flycatchers (*Empidonax minimus*), for which patch size is a limiting factor for settlement. The sensitivity to patch size vanished when artificial social attractants were used, resulting in flycatcher settlement in all patches, but nest success did not vary between treatments (Fletcher 2009). Among the five studies conducted on species other than songbirds, artificial attractants (sound decoys, bird replica decoys and/or mirrors) were used to achieve various conservation goals such as colony relocation (Crouch et al. 2002), reintroducing or boosting populations and even promote increased breeding and reproduction (Kress 1983, Kotliar and Burger 1984, Kress and Nettleship 1988, Parker et al. 2007).

In our study, more eggs were laid on song plots compared to control plots due to more nests on song plots. We did however not detect any difference in mean clutch size, total and mean number of nestlings, total and mean number of fledglings, or *dnsr* between song and control plots. Even though increased territory density on song plots appeared to result in a higher cumulative breeding output, the difference of 43 fledglings on song plots compared to 29 fledglings on control plots was not significant. In contrast, the overall loss of potential young was significantly larger on song plots, where 47 eggs did not survive to produce fledglings compared to 14 eggs on control plots. When nest predation was accounted for, the difference of lost potential young between song and control plots became even larger, meaning that reasons other than nest predation primarily affected breeding performance, such as nest abandonment, which occurred only on song plots, or density-dependence (see below).

Even though more eggs were laid in total on song plots, density-dependent regulation may have affected subsequent nesting phases (incubation and rearing) resulting in the pattern of increased overall loss of potential young on song compared to control plots. Density-dependent regulation can impact incubation and rearing (e.g. Hixon and Johnson 2001), negatively affecting hatching rate, nestling success and fledging rate. Density dependent reproduction has previously been found, for example in Great Tits (*Parus major*; Both 1998) or Seychelles Warblers (*Acrocephalus sechellensis*; Brouwer et al. 2009). The artificially created high density of territories and nests in our study might have surpassed the local carrying capacity, compromising the success of any single nest. That the density in our song plots (maximum of 8 territories per 10 ha) and control plots (maximum of 2 territories per 10 ha) remained below that reported in most other wood warbler studies (up to 15.3 breeding pairs per 10 ha; (Glutz von Blotzheim et al. 1991) does not weaken the hypothesis of negative density dependence for two reasons: 1) we do not know local carrying capacity in our study system and 2) comparing density across studies is difficult, as density typically varies with habitat quality (Van Horne 1983).

Complementary to density dependent regulation, quality of attracted individuals may also play a role in reproductive performance. It is hypothesized that mainly young, inexperienced individuals, for example first-year males, use public information (Nordell and Valone 1998) and respond to conspecific cues, including artificially provided ones (Nocera et al. 2006). We have no data on age and very limited data on body condition of wood warblers during the period of the experiment, making it impossible to assess individual quality further.

Mating system

The observed clustering of territories did apparently not result in increased reproductive output as discussed above. Territory clustering also did not increase the chance of finding a mate, as pairing rates on song and control plots did not differ. Even with no apparent direct benefit, clustering may facilitate promiscuity thereby increasing the chance of individuals to pass on genes to the next generation, essentially via extra-pair copulation. Although work carried out in central Sweden on wood and willow warbler (*Phylloscopus trochilus*) concluded that extra-pair copulations are rather uncommon in these two species (Gyllensten et al. 1990),a recent study in Russia provided evidence for frequent extra-pair offspring in wood warblers: from 12 out of 23 wood warbler nests, 38 out of 130 young were not related to their social father (Moskalenko et al. 2014). In our study, we found extra-pair young in one of seven nests on song plots and in one of three nests on control plots, with young from two fathers in each case. The low rates of extra-pair young could be an artifact of the relatively low wood warbler abundance in 2014 (when blood samples and buccal swabs were taken), compared to other years. The low rate of extra-pair paternity precludes a robust test of the hidden lek hypothesis. Whether social factors or food availability underlie territory clustering, experimentally induced in this study and previously reported in observational studies (Herremans 1993, Wesołowski et al. 2009), remains to be studied.

Conclusion

Conspecific attraction is often overlooked in studies investigating settlement behavior, but may in fact be one of the most important factors in many species. We experimentally demonstrated that conspecific attraction and public information play a role in the settlement process of the wood warbler. Although individual reproductive performance in artificially created territory clusters following conspecific song playback was altered, overall reproductive output was comparable to control plots. While our results on fledgling production indicate that our experiment did not create an ecological trap, increased rates of brood reduction on song plots give reason to further evaluate the usefulness of this method for conservation purposes. This study exemplifies how important social cues are in territory selection of birds but also how crucial it is to monitor / evaluate reproductive performance during and following experimental treatments.

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Table S1 List of possibly confounding factors shown to be related to territory selection (after Pasinelli et al. accepted, BMC Ecology) and how they were measured.

Variable	**Measurement location**	**Measurement method (description if applicable)**
Number of grass tussocks	At center of experimental plot, as well as 100 m from the plot center in each of the four cardinal and each of the four intercardinal directions. Total of 9 measurement points per plot.	Tussock count on a 14 m transect line on a W-E alignment. Resulting in the average number of grass tussocks per experimental plot.
Number of trees	(same as number of grass tussocks)	Tree count on an area with 14 m radius. Resulting in the average number of trees per experimental plot
Rodent occurrence	Over the experimental plot with 125 m radius we laid a grid with 50 m spacing. This resulted in 21 intersection points where one track plate was placed near habitat structure such as trees, stumps, rock piles, bushes, etc.	Measured with a slightly altered track plate method described in Connors et al. (Connors et al. 2009). We used 20 x 30 cm PVC plates. We covered each plate with a mixture of 99% ethanol (80 volume %), graphite powder (17 volume %) and paraffin oil (3 volume %). We applied the mixture with water spray bottles. We collected the plates after three days, counted the rodent tracks on each plate and averaged all tracks per plot.

Table S2 The first two rows show that the overall MANOVAs for each year were significant or marginally so. Subsequent rows show MANOVA results for the three possibly confounding factors number of grass tussocks, number of trees and rodent occurrence.

year	**Wilk's lambda**	**Pillai**	**approx. F**	**Df**	**P-value**
2013	0.68423	0.31577	3.8458	1	0.02
2014	0.74657	0.25343	2.8288	1	0.06

year	**factor**	**x^2**	**Residual df**	**F value**	**P-value**
2013	rodent tracks	85.123	$1,_{27}$	2.6194	0.1172
	grass tussocks	8373.4	$1,_{27}$	0.7813	0.3854
	number of trees	1235.48	$1,_{27}$	3.6099	0.06817
2014	rodent tracks	56.387	$1,_{27}$	1.9403	0.175
	grass tussocks	6428.6	$1,_{27}$	0.5959	0.4469
	number of trees	1283.68	$1,_{27}$	3.7704	0.06267

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Reproductive performance of a declining forest passerine in relation to environmental and social factors: implications for species conservation

Reproductive performance of a declining forest passerine in relation to environmental and social factors: implications for species conservation

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ABSTRACT

Identifying factors influencing a species' ecological niche and demography is a prerequisite for species conservation. However, our understanding of the interplay between demographic rates and biotic/abiotic factors is still poor for most species of conservation concern. We evaluated relevance of eight hypotheses relating to timing of breeding, temporal nest exposure, nest concealment, topography, tree structure, predation risk and disturbance, density dependence and weather for explaining variation in reproductive performance of the declining wood warbler *Phylloscopus sibilatrix* in northern Switzerland. Reproductive performance was monitored with cameras at 136 nests from 2010 to 2012 and was associated to temporal exposure, timing of breeding and concealment of nests. Daily nest survival was positively related to the number of grass and sedge tussocks, nest concealment and nest age. Clutch size and number of fledglings decreased, the later in the season a nest was initiated. Nest survival over an average nesting period of 31 days was 46.9 ± 0.07 % (mean ± SE), daily nest survival rate was 0.976 ± 0.002. As for many ground-breeding birds, nest predation was the principal cause of nest failure, accounting for 79 % of all nest losses. Conservation measures should aim at increasing the area of relatively homogenous forest stands featuring suitable habitats characterized by abundant and accessible grass and sedge tussocks. In managed forests, such conditions can be found in stands of middle age (i.e. pole wood) with little to no shrub layer.

INTRODUCTION

Population dynamics is driven by the four vital rates fertility, survival, immigration and emigration (Williams et al. 2002). Which vital rate is most important for population dynamics remains largely species-specific. Population growth rate in many large, long-lived animal species is mostly affected by (adult) survival, whereas population growth rate in small, short-lived species is usually most strongly influenced by fertility, reproductive performance and recruitment (Mills 2012). In the case of small passerines, reproductive performance can itself be sub-divided into different components, such as clutch size, number of hatchlings, number of fledglings or nest survival. Understanding the relative contribution of each component to reproductive success and population growth is crucial, but remains poorly understood in most species (Schaub et al. 2012). Clutch size gives information about how much a female can allocate to reproduction, which may be influenced by her body condition, perceived predation risk, inter- and intraspecific competition, natural and anthropogenic disturbance, food availability, habitat suitability and interactions among these aspects (Lack 1954, Slagsvold 1984, Jetz et al. 2008, Zanette et al. 2011). Number of fledglings provides a reproductive performance value per individual, breeding pair or population. It further results from nestling survival, which itself depends upon weather conditions, food availability, parents’ quality, perceived predation risk and actual predation (Murphy 1983, Monaghan and Nager 1997, Brown and Brown 1999, Sutherland et al. 2004, de Heij et al. 2006, Zanette et al. 2011). Nest survival thus represents an overall estimate of breeding success within a population. Examining these three components of reproductive performance in relation to potentially influential environmental factors may provide important information on an animal’s life-history (Hatchwell et al. 1996, Burke and Nol 2000, Maguire 2006) and should help in creating management plans for species of conservation concern. Using data from 3 years and 136 nests, this study evaluates thematically grouped hypotheses, introduced separately below, regarding the relationships between three components of wood warbler (*Phylloscopus sibilatrix*) reproductive performance – clutch size, number of fledgling and nest survival – and various environmental and social factors.

Timing of breeding

Reproductive performance has been shown to depend on when in the season breeding is initiated (Young 1963, Best 1978, Naef-Daenzer et al. 2001, Grant et al.

2005, Müller et al. 2005, Peak 2007, Arlettaz et al. 2010b). Males can increase their fitness by securing high quality territories, and high-quality territories are typically among the earliest occupied in the season (Hansson et al. 2000). In many animal species, females select mates based on both specific male traits and habitat cues (Buchanan and Catchpole 1997, Haley et al. 2004, Robertson and Monteiro 2005). Females then choose the time of breeding based on environmental cues. Females should time their broods so that the peak food availability matches the highest demands of nestlings (Both et al. 2006) and periods of increased predator abundance late in the breeding season are avoided (Naef-Daenzer et al. 2001). Thus, we predicted decreased clutch sizes, number of fledglings and nest survival as the breeding season progresses.

Temporal exposure

The relationship of nest survival with nest age appears to differ among species. While several studies have reported no difference in nest survival between incubation and nestling stage (Roper and Goldstein 1997), others have reported either higher nest survival during incubation (Martin et al. 2000, Pasinelli and Schiegg 2006), higher nest survival during nestling stage (Dixon 1978, Pietz and Granfors 2000) or even multimodal distributions of nest survival throughout the nesting phase (Grant et al. 2005). Under the assumption that parental food provisioning activity increases with nest age due to increased food requirements of maturing nestlings (Glutz von Blotzheim et al. 1991), which in turn increases predation risk (Martin et al. 2000), we predicted a negative relationship between nest survival and nest age.

Nest concealment

As nest predation is the principal cause of nest failure in many bird species, nest concealment and nest substrate choice are very important, especially for ground nesting species (Signorell et al. 2010). Some studies have found positive effects of nest concealment on reproductive performance (Martin et al. 2000, Weidinger 2002, Müller et al. 2005, Pasinelli and Schiegg 2006), whereas others have not (Howlett and Stutchbury 1997, Burhans et al. 2002). We predicted a positive relationship between nest survival and nest concealment.

Topography

Exposition, elevation and inclination can be important topographical factors affecting reproductive performance via weather conditions and/or solar radiation. In relation to reproductive performance, these factors may especially influence temperature stress of incubating females and their nestlings at both low and high ambient temperatures. In temperate forest birds, reproductive performance is often increased at lower elevations due to more favorable temperatures, with a lower likelihood of freezing to death (LaHaye et al. 1997, Smith et al. 2005, Heltzel and Earnst 2006). Inclined slopes exposed to the south generally receive more solar radiation than flat terrain or slopes exposed to the north. By building nests on south-east exposed slopes, high midday temperatures and/or prevailing west winds can be avoided, which may increase nestling survival (Verbeek 1981, Burton 2006). We predicted a negative relationship of nest survival, clutch size and/or number of fledglings with elevation. Moreover, nests on slopes exposed to south-east were expected to have increased survival, larger clutches and more fledglings than nests with other expositions.

Tree structure

Forest and tree structure can play a role in relation to daily nest survival rate, correlating with canopy cover (Bakermans et al. 2012) or basal area of trees (Newell and Rodewald 2011). As discussed in the previous paragraph, incubating females and their nests can be sensitive to temperature stress. Assuming microclimatic weather conditions are not only influenced by topographical factors but also by tree structure, we predicted a quadratic relationship between nest survival and canopy cover. Territories in open stands could be subject to solar radiation that is too high, while completely closed stands would allow almost no solar radiation and exhibit microclimatic conditions that are too humid and cool.

Predation risk and disturbance

Nest predation is the most important cause of nest failure in most bird species worldwide, including ground nesting forest birds (Martin 1995, Sanders and Maloney 2002, Langgemach and Bellebaum 2005, Emmering and Schmidt 2011), and is therefore a major force driving avian demography and evolution. We investigated the relationship between reproductive performance and rodent abundance, as negative relationships between rodent and wood warbler abundances (Wesołowski et al. 2009), as well as between settlement probability of wood warblers and rodent abundance have been found (Gerber). It is also known that varying rodent numbers trigger numerical and/or behavioral responses of rodent hunting predators (Schmidt and Ostfeld 2008). It may be possible that birds use rodent abundance as a proxy for general predation risk. Whether through direct rodent predation or predation through rodent hunting predators, we predicted a negative relationship between nest survival and rodent abundance. Zanette et al. (2011) have shown that females exposed to experimentally simulated predation risk produced smaller clutches and fewer fledglings than females not exposed to simulated predation risk. Accordingly, we predicted smaller clutches and fewer fledglings with increasing rodent abundance.

Nest predation may also increase due to edge effects connected to outer (i.e. forest edge) or inner (i.e. forestry trails) habitat edges (Patthey et al. 2008, Signorell et al. 2010). Certain predators are known to use habitat edges to travel and forage (Miller et al. 1998, Miller and Hobbs 2000). Habitat edges can also be connected to spillover predation, a process where nest predators cross over from adjacent habitats (Storch et al. 2005). We assessed increased predation risk connected to habitat edges with the variables “distance to closest forest edge” and “distance to closest human used trail”. However, human used trails may not only be linked to predator abundance but also to disturbance via recreational activity, which is known to have mostly negative effects on birds, especially on ground nesting species (Boyle and Samson 1985, Arlettaz et al. 2007, Steven et al. 2011). According to a review by Steven et al. (2011) dealing with non-motorized disturbance on birds, 61 out of 69 studies showed negative impacts. Hiking/touring had the highest negative impact, reported in 45 out of 51 studies. Accordingly, we predicted increased nest survival, clutch sizes and number of fledglings with increased distances from forest edges and from human used trails, respectively.

Density dependence

Previous studies have suggested that cues received from conspecifics to be just as important as or sometimes even more important than habitat quality in terms of settlement (Pasinelli and Walters 2002, Betts et al. 2008, Ahlering et al. 2010). Conspecific cues may provide readily available information about a specific habitat or conspecifics themselves and if individuals subsequently decide to settle close to conspecifics, a clustering of territories and nests may result. Clustered conspecifics may also have effects on each other post settlement by influencing reproductive performance (Tarof et al. 2004, Berec et al. 2007). Territory clustering can be looked at in the context of positive density dependence or the Allee effect, a positive correlation between population density and fitness (Mills 2012). Clustering could arise due to sexual selection mechanisms that increase an individual’s fitness such as chances for extra pair parentage or due to natural selection mechanisms such as anti-predator strategies (Tarof et al. 2004, Berec et al. 2007). As territory clustering has been observed in wood warblers (Herremans 1993), we investigated whether reproductive performance was positively related to population density. We evaluated models including two variables related to population density, namely the distance to the closest nest and the number of nests within 300 m from a focal nest in relation to our three components of reproductive output. We predicted positive non-linear relationships (Courchamp et al. 2008) between population density and clutch size, number of fledglings and/or nest survival, respectively. However, negative density dependence has been shown to occur in a variety of taxa(Mills 2012), and we therefore also tested for a negative relationship between population density and our three measures of reproductive performance.

Weather

Variation in reproductive performance could also be explained by weather factors, such as ambient temperature, rainfall or solar radiation. High amounts of rainfall and low temperatures can affect food resources (Baxter 1994, Arlettaz et al. 2010b) and/or chick provisioning performance by parents, predator activity (Morrison and Bolger 2002) and even parental fitness, including life span und lifetime reproductive success (Krüger 2002). Rodriguez and Bustamante (2003) found that nest success of the lesser kestrel (*Falco naumanni*) was positively influenced by winter rainfall but negatively by rainfall during the nestling period. Arlettaz et al. (2010b) demonstrated that, in the hoopoe (*Upupa epops*), food provisioning activity of chicks by parents was dramatically affected by adverse weather (heavy rainfall and low ambient temperature) conditions, resulting in decreased number of fledglings per brood. Thus, we predicted decreased clutch sizes, number of nestlings and nest success with increased rainfall and decreasing ambient temperature just before and/or during nesting.

METHODS

Study species and area

The wood warbler is a long-distance migratory, insectivorous forest passerine, exhibiting very little site fidelity (ring return percentages reviewed in (Wesołowski et al. 2009)). Exhibiting great annual local population fluctuations, the species' nomadic behavior is hypothesized to be a response to annually varying local rodent densities (Wesołowski et al. 2009). This species has wintering grounds in tropical Africa (Hobson et al. 2014) and breeding grounds spanning northern and temperate Europe as far east as the Ural Mountains (Stresemann 1955, Glutz von Blotzheim et al. 1991). Breeding sites are typically occupied between April and July. Across Europe, the population trend of this species is moderately negative. Regionally, however, the species has dramatically declined, as for example in the UK, Germany or the Netherlands (Flade and Schwarz 2004, Škorpilová et al. 2007, Wesołowski and Maziarz 2009). It is classified as “Least concern” on the current IUCN red list due to a large breeding range and high number of breeding pairs (BirdLifeInternational 2014). However, similar as in the aforementioned countries, the decline of this species in Switzerland is strong and the species is classified as vulnerable (VU) on the current red list of breeding birds of Switzerland. In addition, the wood warbler is considered a priority species for the Swiss species recovery program (Keller et al. 2010b, Spaar et al. 2012).

The study took place along northern Switzerland’s Jura mountain chain, as well as at one sitenear Lake Constance and one site in the pre-alpine valley of Glarus: 1. Bänkerjoch (Canton Aargau (AG); N 47° 26.2’ E 8° 2.1’), 2. Staffelegg (AG; N 47° 25.4’ E 8° 4.1’), 3. Blauen (Basel Landschaft (BL); N 47° 27.6’ E 7° 31.7’), 4. Dittingen (BL; N 47° 26.9’ E7° 28.8’), 5. Langenbruck (BL; N 47° 21.3’ E 7° 47.0’), 6. Lauwil (BL; N 47° 22.5 E 7° 39.7), 7 Oltingen (BL; N 47° 25.8’ E 7° 56.5’), 8. Ennenda (Glarus (GL); N 47° 2.3’ E 9° 5.0’), 9. Montsevelier (Jura (JU); N 47° 22.1’ E 7° 29.5’), 10. Belchen (Solothurn (SO); N 47° 21.7' E 7° 48.6'), 11. Erschwil (SO; N 47° 22.7 E 7° 33.3'), 12. Hochwald (SO; N 47° 27.5' E 7° 39.7'), 13. Homberg (SO; N 47° 21.5', E 7° 50.9'), 14. Kleinlützel (SO; N 47° 26.3’ E 7° 25.9’), 15. Scheltenpass (SO; N 47° 20.8’ E 7° 37.1’), 16. Gündelhart (Thurgau (TG); N 47° 38.7’ E 8° 56.4’). Using data from the common breeding bird survey (the standardized Swiss national bird monitoring program, http://www.vogelwarte.ch/en/projects/monitoring/monitoring-common-breeding-birds.html) and from the Swiss ornithological information service (casual observations of rare breeding and visiting birds, http://www.vogelwarte.ch/en/projects/monitoring/information-service-monitoring-rare-breeding-and-visiting-birds.html), regions with wood warbler occurrence in the past decade were localized and used as a rough starting point to map wood warbler territories. This approach yielded a total of 16 study areas, which range in size from 1.4 to 21 ha, in elevation from 430 to 1132 m a.s.l., and in inclination from 2 to 50 degrees. Most wood warbler territories, and hence the study areas, were located on slopes exposed to the south and consisted of deciduous and mixed-forest stands dominated by European beech (*Fagus sylvatica*), with coniferous tree species interspersed (*Picea abies, Abies alba, Pinus sylvestris*). Stands predominantly consisted of old pole wood and young timber with a relatively closed canopy and a sparse shrub layer. Generally, the field layer consisted of grass and sedges and/or herbaceous species. Several study areas had been declared as forest reserves, or were privately owned, meaning they were subjected to no or very limited forestry interventions in the past decades (personal communication of landowners and foresters).

Field methods

Data was collected between April and September from 2010 to 2012. Each study area was visited at least once a week to map singing males, pairs and nests. Upon finding a nest, one trail camera (Reconyx PC900 HyperFire Professional High Output Covert; Reconyx, Inc., Holmen, Wisconsin, USA) was installed, pointing directly at the nest entrance at a distance of 1-2 m, depending on topography, and was set up to take 10 images over 10 s per motion detection and one image every 15 min. Trail cameras allowed to survey activity of adults and (old) nestlings, to identify nest predators and to simultaneously monitor many nests, while keeping researcher disturbance at a minimum (Ibanez-Alamo et al. 2012). Once a week cameras were checked for operational, battery and capacity status until nest success (fledging) or failure (predation, unknown failure) was documented. During the camera checks, nest status was determined (i.e. still active or inactive) and, where applicable, hatchlings were aged with pictures of reference hatchlings from nests where daily visits had been conducted and a reference list given by Wesolowski & Maziarz (Wesołowski and Maziarz 2009). A nest was considered successful, when at least one young fledged. In turn, a nest was considered unsuccessful when it was predated (all eggs or hatchlings had disappeared before the expected fledgling date) or when it failed for unknown reasons (eggs still in the nest, but cold to the touch or dead young in the nest without parental activity evident). The exact date of fledging or failure of a nest, and whether it was predated or failed for unknown reasons, was inferred from picture footage. Daily nest survival rates (*dnsr*) and overall nest survival rates were then calculated by taking into account the duration of nest exposure (Shaffer 2004), as described in detail under “General statistics” below.

Evaluated variables in relation to components of reproductive performance

Once a nest had failed or succeeded, variables pertaining to the introduced thematically grouped hypotheses were measured at three sampling scales (Fig. 1) within a territory of 968 m^2, which lies within the reported wood warbler territory size of 500 and 1900 m^2 (Glutz von Blotzheim et al. 1991)

Variables evaluated, grouped by hypothesis, were: 1) “start of egg-laying” (timing of breeding hypothesis), 2) “nest age” (temporal exposure hypothesis), 3) “nest concealment index”, “nest location”, “number of bushes”, “number of grass and sedge tussocks”, “vegetation cover” (nest concealment hypothesis), 4) “elevation”, “inclination”, “exposition” (topography hypothesis), 5) “number of trees”, “average tree diameter”, “canopy cover” (tree structure hypothesis), 6) “rodent abundance”, “distance to forest edge”, “distance to trail” (predation and disturbance hypothesis), 7) “distance to closest territory”, “number of territories within 300 m” (density dependence hypothesis), 8) “daily mean temperature”, “total daily rainfall”, “mean temperature”, “mean rainfall”, “rainfall stretch” and “ratio rainfall” (weather hypothesis). Details and descriptions about the variables measured are presented in Table 1.

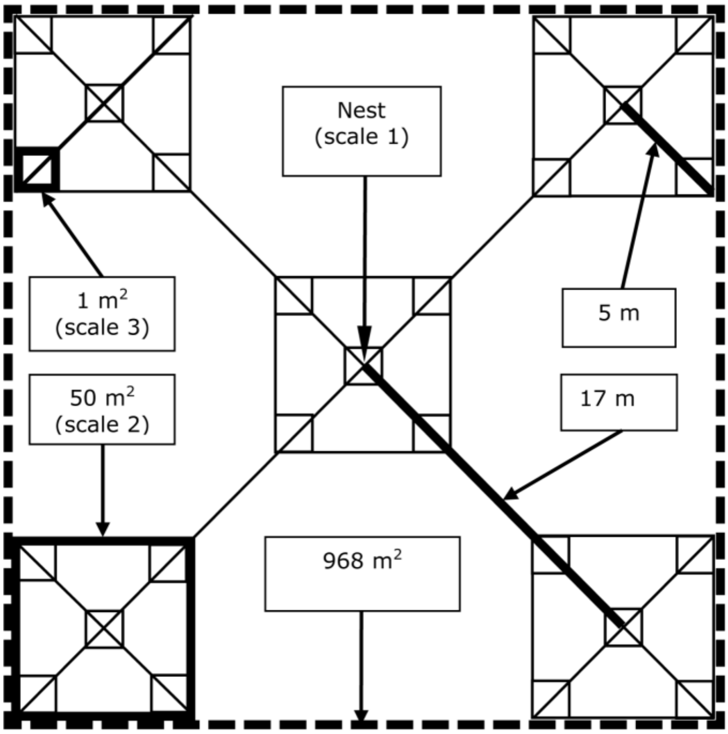


Fig. 1 Sampling design with three scales used to map and measure habitat variables and to trap rodents. Scale 1 = nest location (territory center); scale 2 = five 50 m^2 squares; scale 3 = twenty-five 1 m^2 squares.

Statistical procedures

General statistics

We worked with an exposure time method for the analysis of *dnsr* (Mayfield 1961). For nests found before egg-laying, exposure time was the number of days between the actual first-egg date and nest predation or fledging date. For nests found during and after the egg-laying stage, exposure time was the number of days between finding date and fledging or nest predation date. By using trail cameras, the observation interval was always one day

Table 1. Variables used in the modeling of components of reproductive performance in the Swiss wood warbler.

Hypothesis	Variable	Measurement method (description if applicable)	Scale*
Timing of breeding	start of egg-laying	- nest check after 3 days for nests found during building - back calculating based on age and nr. of fledglings for nests found after clutch completion - assuming one egg laid per day [#], 14 days incubation °	NA
Temporal exposure	nest age	- number of days based on actual or back calculated start of egg-laying	NA
Nest concealment	nest concealment index	- discrete variable from 0 to 5 denoting nest concealment from five viewpoints assessing whether the nest is visible or not from front (entrance hole), back, left, right and top of nest from a distance of 1.5 m 0 = visible from all 5 sides, 5 = not visible from any of the 5 sides	1
	nest location	categorical variable with four levels a) concealed by grass or sedge tussock b) concealed by single plant < 50 cm in height (other than grass/sedge tussock) c) concealed by 2 or more plants < 50 cm in height d) other (including all other concealment possibilities)	1
	number of bushes	- number of bushes and young trees > 50 cm in height and < 25.1 cm in stem circumference (territory mean)	2
	number of grass and sedge tussocks	- tussock count (territory mean)	3
	vegetation cover	- vegetation cover in 5%-classes (territory mean)	3
Topography	elevation	- extracted from ecoGIS, http://map.geo.admin.ch/	1
	inclination	- compass inclinometer (territory mean)	2
	exposition	- compass with values from 0 to 360 degrees (territory mean)	2
Tree structure	number of trees	- tree count (territory mean)	2
	tree diameter	- based on circumference at breast height (territory mean)	2
	canopy cover	method described by (Coch et al. 2005) with adaptions: - DSLR camera (Nikon D2Xs) with standard lens (18-70 mm f3.5-4.5G ED-IF AF-S DX Zoom Nikkor) and focal length: 35 mm - camera held 1.5 m above ground, pointing vertically up - camera ground plate pointing towards territory center or south east for picture at territory center - Import with raw format in Photoshop CS5 - brightness of green and blue colors lowered to minimum and increased to maximum, respectively, to increase contrast	2

		- pictures downscaled to 1500 x 1000 pixels and transformed to b/w bitmap - processed by self-written php-script for b/w pixel ratio	
Disturbance	distance to forest edge	- measured in meters in ecoGIS without considering topography	1
	distance to trail	- measured in meters in ecoGIS without considering topography (distance to closest human used trail)	1
Predation risk	rodent abundance	- by live-trapping with longworth traps (Penlon Ltd., Abingdon,+ UK) and “Field Trip Trap Live Catch Trap” (Alana Ecology, Bishops Castle, UK) [†] - 25 traps per territory for 48 hours with controls every 8 hours - 5 traps per 50 m^2 square (Fig. 1) placed without pattern at structures likely used by rodents (e.g. tree, stump, bush, rock, dead wood) - minimum known number alive (mna) used for analysis, due to low recaptures in certain years and/or territories	3
Density dependence	distance to closest territory	- calculated in meters based on nest coordinates	1
	number of territories within 300 m	- number of territories within 300 m of focal territory - calculated based on nest coordinates	1
Weather [§]	daily mean temperature	- mean temperature (°C) per day	NA
(in relation to *dnsr*)	total daily rainfall	- mm, between 5:40 a.m. and 5:40 a.m. of the following day	NA
Weather [§]	mean temperature	- mean temperature (°C) during each of the 3 periods [±]	NA
(in relation to clutch size	mean rainfall	- mean rainfall during each of the 3 periods [±]	NA
and number of fledglings)	rainfall stretch	- longest stretch of days with rainfall during each of the 3 periods [±]	NA
	ratio rainfall	- ratio of days with rainfall during each of the 3 periods [±]	NA

* refer to Fig. 1 for scale description; [#] Glutz von Blotzheim et al. 1991; ° own data; [†] see (Arlettaz et al. 2010a) for trap comparison, [§] all variables derived based on data obtain from SMI-MeteoSwiss stations (Buchs AG, Delemont JU, Glarus GL, Rünenberg BL, Wynau BE, Güttingen TG), which were on average 12.7 km away from study areas; [±] 1) pre-laying: period of 7 days before egg laying started; 2) pre-incubation: period of 7 days before egg-laying phase, plus the egg-laying phase (clutch size dependent); 3) rearing: period between hatching and fledging.

and we obtained exact predation and fledging dates. To obtain nest survival rates and standard errors from *dnsr*, we ran a generalized linear mixed-effects model (GLMM) containing the fixed effect “nest age” with values ranging from 1 to 31. 31 days was the average nesting period in our study (5 days egg-laying, 14 days incubation, 13 days rearing). Since incubation typically starts on the same the last egg is laid, we used 31 instead of 32 days for the average nesting period, Using the resulting intercept and estimate from this model, 31 predictor values on the logit scale were calculated through matrix multiplication. The inverse logits of these predictor values resulted in 31 daily nest survival rates. Nest survival rate for the entire nesting period was calculated in two ways: 1) all 31 *dnsr* were multiplied with each other, yielding the primary nest survival rate used in this paper and 2) calculating a mean *dnsr* across the 31 values, then taking this mean *dnsr* to the 31nd power, calculated to compare with Mallord et al. (2012b). To obtain survival rates for egg-laying, incubation and rearing stages, respectively, *dnsr* values for each period were multiplied with each other. Standard errors were obtained via calculation of upper and lower confidence intervals in R (R Development Core Team 2008).

Model selection

We modeled three components of reproductive performance (clutch size, number of fledglings from successful nests and daily nest survival) using generalized linear mixed effects models (GLMM) in R (R Development Core Team 2008), with the packages lme4 (Bates and Maechler 2010), AICcmodavg (Mazerolle 2010) and arm (Gelman et al. 2011). For each nest, nest survival was coded and modeled as a binary dependent variable (yes/no) on a day-by-day basis using a logit link function and binomial error structure. Thus, each nest provided multiple data points and we accounted for this dependency with a random effect “nestID”. The dependent variables “clutch size” and “number of fledglings” were modeled assuming a Poisson distribution of errors and a log link function. In all three analyses we included the random effects “study area” and “year” to account for the data dependency arising from using multiple nests per study area and year, respectively. We investigated each thematic hypothesis by building models of all possible combinations with the associated variables (no interactions), including a null model containing only the random effects. As there may be optima for each variable we also included quadratic effects of all variables. Using AICc, Aikake’s Information Criterion (Akaike 1974) corrected for small sample size (Sugiura 1978), all models were ranked, taking into account each model's goodness of fit using its log-likelihood (LL). The model with the lowest AICc was considered the most parsimonious model among all the candidate models examined. A common approach is to also consider models with a ΔAICc < 2 compared to the top ranked model, as they may have equal support to explain variation in the dependent variable (Burhans et al. 2002). We adopted this approach but added the following two criteria to select models: they had to 1) rank higher than the null model and 2) to have a LL Δ > 1 (compared to models with fewer predictors) or a LL Δ < 1 (compared to models with more predictors) (Burnham and Anderson 2002). Through model averaging over all candidate models, we obtained estimates and standard errors from all variables included in models that met the selection criteria described above (Mazerolle 2006). All predictor variables with model-averaged estimates larger than their model-averaged SEs were then used in an across-hypothesis analysis (AHA). Here, reproductive performance variables were related to predictor variables pertaining to different hypotheses, using the same GLMM structures as previously outlined. The same model selection approach as described above was applied.

RESULTS

General findings

Between 2010 and 2012 we found 136 nests of which 57 were classified as predated (42%) and 15 as "unknown failure" (11%). Picture evidence of the predator was available in 84% of the predated nests. Identified nest predators were Eurasian jay (*Garrulus glandarius*, n = 14), stone and pine martens (*Martes foina* and *Martes martes*, n = 13), red fox (*Vulpes vulpes*, n = 11), European badger (*Meles meles*, n = 5), tawny owl (*Strix aluco*, n =3), domesticated cat (*Felis catus*, n = 1) and Eurasian sparrowhawk (*Accipiter nisus*, n = 1). Across 3 years, nest survival (± SE) over an average nesting period of 31 days was 46.9 ± 0.07 % (Table 2) and mean daily nest survival (*dnsr*) 0.976 ± 0.002. Without fox or jay predation (main mammalian and avian nest predators), nest survival over 31 days would have been 57.4 ± 0.1 % (mean dnsr: 0.982 ± 0.002) and 55.7 ± 0.08 % (mean dnsr: 0.981 ± 0.002), respectively.

Table 2. Reproductive performance of Swiss wood warblers in 2010 – 2012. Shown are means ± SE, with sample sizes in parentheses.

Year	Clutch size	Number of fledglings		Naïve nest success[#]	Nest survival			
		over successful nests	over all nests		Egg laying	Incubation	Rearing	Whole nesting period*
2010	5.23 ± 0.20 (40)	4.55 ± 0.28 (23)	1.86 ± 0.34 (49)	40.8 (49)	95.5 ± 0.02 (40)	76.9 ± 0.06 (40)	61.5 ± 0.07 (40)	45.2 ± 0.07 (40)
2011	5.55 ± 0.10 (62)	4.71 ± 0.25 (34)	2.46 ± 0.32 (65)	52.3 (65)	99 ± 0.02 (57)	90.6 ± 0.06 (57)	69 ± 0.07 (57)	61.9 ± 0.08 (57)
2012	5.19 ± 0.22 (21)	4.70 ± 0.37 (10)	2.14 ± 0.52 (22)	45.5 (22)	99 ± 0.02 (22)	88.2 ± 0.06 (22)	52.1 ± 0.07 (22)	45.5 ± 0.08 (22)
2010-2012	5.38 ± 0.09 (123)	4.66 ± 0.17 (67)	2.19 ± 0.21 (136)	47.1 (136)	96 ± 0.02 (119)	78.5 ± 0.06 (119)	62.2 ± 0.07 (119)	46.9 ± 0.07 (119)

* whole nesting period is based on an average clutch size of 5 eggs, an average of 14 days of incubation and an average of 13 days of rearing

[#] Naïve nest success is the proportion of successful nests out of all sampled nests without considering exposure time

Table 3. Model selection results for the analysis of daily nest survival rate in relation to environmental and social factors. Models are separated into thematically grouped hypotheses, including an across-hypothesis-analysis at the end. Models with a ΔAICc < 2 to the highest-ranked model as well as null models are presented. K = number of parameters in the model (only fixed effects are shown in the table). Wt. = Akaike's weight; LL = Log likelihood of a model. "…" refers to additional models examined, but not listed in detail to avoid overlong table, as they were little informative. N = 115.

Hypothesis	Model	K	AICc	ΔAICc	Wt.	LL
Temporal exposure and timing of breeding	nest age	5	312.40	0.00	0.35	-151.17
	nestage^2	6	313.28	0.88	0.22	-150.60
	nest age + start of egg-laying	6	314.34	1.94	0.13	-151.13
	…					
	null model	4	315.22	3.89	0.05	-154.13
Nest concealment	nr of tussocks	5	312.75	0.00	0.17	-151.35
	nr of tussocks + concealment index	6	313.54	0.79	0.12	-150.73
	nr of tussocks + nr of bushes	6	313.6	0.81	0.12	-150.74
	nr of tussocks^2	6	313.65	0.91	0.11	-150.79
	nr of tussocks^2 + nr of bushes	7	314.02	1.27	0.09	-149.96

	nr of tussocks^2 + concealment index	7	314.7	1.91	0.1	-150.28
	nr of tussocks + nr of bushes + concealment index	7	314.7	1.93	0.07	-150.29
	…					
	null model	4	316.29	3.55	0.03	-154.13
Weather	null	4	316.29	0.00	0.30	-154.13
	rainfall	5	316.35	0.06	0.29	-153.15
	temperature + rainfall	6	318.03	1.74	0.1	-152.98
	temperature	5	318.18	1.88	0.12	-154.06
Topography	null	4	316.29	0.00	0.13	-154.13
	exposition^2	6	316.54	0.24	0.12	-152.23
	exposition	5	316.89	0.59	0.10	-153.42
	exposition^2 + inclination	7	317.30	1.01	0.08	-151.60
	inclination	5	317.78	1.49	0.06	-153.87
	inclination^2 + exposition^2	8	317.80	1.51	0.06	-150.84
	elevation	5	318.18	1.89	0.05	-154.06
	expsistion^2 + elevation	7	318.29	2.00	0.05	-152.10
Tree structure	null	4	316.29	0.00	0.18	-154.13
	nr of trees	5	317.22	0.92	0.12	-153.58
	average tree diameter	5	317.93	1.64	0.08	-153.94
	canopy cover^2	6	317.98	1.69	0.08	-152.95
	canopy cover	5	318.13	1.84	0.07	-154.04
Predation risk	null	4	316.29	0.00	0.66	-154.13
and	nr of rodents	5	318.29	1.99	0.24	-154.12
Disturbance	null	4	316.29	0.00	0.34	-154.13
	distance to forest edge	5	317.55	1.26	0.18	-153.75
	distance to closest path	5	317.78	1.49	0.16	-153.87
Density dependence	null	4	316.3	0	0.3	-154.13
	nr of territories within 300m	5	317.62	1.33	0.17	-153.79
	nr of territories within 300m^2	6	317.98	1.69	0.14	-152.96
	distance to closest territory	5	318.14	1.84	0.13	-154.04
Across-	nr of tussocks + nest age	6	307.95	0.00	0.54	-147.94
hypothesis-	nr of tussocks + nest age + concealment index	7	309.27	1.33	0.28	-147.59
analysis	…					
	null model	4	316.29	8.35	0.01	-154.13

Daily nest survival rate (dnsr)

Temporal exposure and timing of breeding

Model selection yielded three models with a ΔAICc < 2 to the top ranked model (ΔAICc of null model = 3.89, Table 3). These models contained the variables “nest age”, “nest age^2” and “start of egg-laying”. Based on model averaged estimates and SEs (Table 4), only “nest age” (-0.07 ± 0.03) was used for the subsequent AHA.

Nest concealment

Model selection yielded six models with a ΔAICc < 2 to the top ranked model (ΔAICc of null model = 3.94). These models contained the variables “number of grass and sedge tussocks”, “number of grass and sedge tussocks^2”, “number of bushes” and “concealment index”. Based on model averaged estimates and SEs, “number of grass and sedge tussocks” (0.62 ± 0.34) and “nest concealment index” (0.17 ± 0.16) were used for subsequent AHA (Table 3 and 4).

Weather

While model selection classified the null model as the highest ranked model, it is worth noting that one model had a ΔAICc very close to the null model (ΔAICc = 0.06) suggesting that total daily rainfall may well have an influence on *dnsr*. The model averaged estimate and SE for total daily rainfall was 0.35 ± 0.28. However, abiding by our selection criteria, we did not analyze total daily rainfall together with other variables in the AHA.

Topography, tree structure, predation risk, disturbance, density dependence

In all five thematic hypothesis groups, the respective null models were always ranked highest (Table 3) and therefore none of the variables were considered in the AHA.

Across hypotheses analysis

Model selection for the AHA yielded one model with a ΔAICc < 2 to the top ranked model (ΔAICc of null model = 8.35; Table 3). The top ranked model contained the variables “number of grass and sedge tussocks” and “nest age”, the second-best model “number of grass and sedge tussocks”, “nest age” and “nest concealment”. Based on model averaged estimates and SEs, *dnsr* was negatively related to “nest age” (-0.07 ± 0.03, Fig. 2a, Table 4) and positively related to “number of grass and sedge tussocks” (0.76 ± 0.41, Fig. 2b, Table 4) as well as to “nest concealment” (0.18 ± 0.16, Fig. 2c, Table 4).

Table 4 Model-averaged estimates and standard errors (SE) based on all models per hypothesis group. Only estimates and SE for variables in the top-ranked model and in models with ΔAICc < 2 to this one are shown. For the hypothesis groups topography, tree structure, predation risk, disturbance and density dependence, estimates and standard errors were not averaged as there were no models ranked better than the null model (see methods for variable exclusion criteria). Estimates (and SE) for the variables of these hypothesis groups are therefore not shown.

Hypothesis	Variable	Model averaged estimate	Model averaged SE
Temporal exposure	nest age	-0.07	0.03
	nest age (linear term)	0.03	0.10
	nest age (quadratic term)	0.00	0.00
timing of breeding	start of egg-laying	0.01	0.02
Concealment	nr tussocks	0.62	0.34
	concealment index	0.17	0.16
	nr bushes	0.22	0.23
	nr tussocks (linear term)	0.27	0.48
	nr tussocks (quadratic term)	0.43	0.49
Weather	mean daily temperature	0.08	0.17
	total daily rainfall	0.35	0.28
Across hypotheses	nr of tussocks	0.76	0.41
	nest age	-0.07	0.03
	concealment index	0.18	0.16

Clutch size and number of fledglings

Model selection for both clutch size and number of fledglings resulted in one top-model containing only “Start of egg-laying” (ΔAICc to null models: 2.48 for clutch size, 2.82 for number of fledglings). Estimates (and SE) for “Start of egg-laying” were -0.01 ± 0.00 in both analyses of clutch size (Fig. 3a) and number of fledglings (Fig. 3b). In the analyses of all other thematic hypotheses groups, the null models were always ranked highest and therefore no other variables were considered nor was an AHA necessary.

DISCUSSION

Reproductive performance of the wood warbler in our study area was associated to temporal exposure, timing of breeding and concealment of nests. Daily nest survival was positively related to the number of grass and sedge tussocks present in a given territory, nest concealment and nest age. Moreover, both clutch size and number of fledglings decreased, the later in the season egg-laying started.

Nest predation

Clutch sizes, nest survival, nest success and number of fledglings of Swiss wood warblers seem to be lower than in most other studies (Herremans 1993, Moreau

2001, Lippek 2009, Wesołowski and Maziarz 2009, Mallord et al. 2012b). Nest success and nest survival of wood warblers in Switzerland were furthermore lower than in other ground-nesting forest passerines of Europe (Yanes and Suarez 1995, Hölzinger 1999, Wesołowski and Tomialojc 2005) and North America (Martin 1993) (Table 5). In our study, the primary cause of nest failure was nest predation, amounting to 79% of all failures (n = 72). Increased predation pressure by foxes due to increasing fox populations has been discussed to contribute to the decline of wood warblers, but our data does not lend support to this suspicion. Omitting nests predated by foxes from our statistical calculations does result in higher nest survival over the three study years, but nest loss rate was still around 43%. Also, nest survival was higher in 2010 (year with most fox predation, n = 9 nests) than in 2012 (year with no fox predation). Indeed, the main predator of wood warbler nests in Switzerland was the Eurasian jay, similar to observations from Welsh oakwoods (Mallord et al. 2012b), where jays and birds of prey were responsible for 93% of all predation events, with only two cases of predation by mammals. Mammals in Switzerland caused as much as 52.6% of all predatory events, suggesting that predator guilds differed between the two regions.

Rodents are known to be important in territory selection of wood warbler (Gerber , Wesołowski et al. 2009). Furthermore, rodents have been documented to predate nests of several bird species (Walankiewicz 2002, Kirkpatrick and Conway 2010) and have been suspected to predate wood warbler nests as well (Mildenberger 1940, Wesołowski 1985, Wesołowski and Maziarz 2009). Apart from one instance where a red squirrel (*Sciurus vulgaris*) killed but did not eat all nestlings of a nest, there is no picture evidence of any single event of direct predation by smaller rodents such as *Apodemus* or *Myodes* species in our study or elsewhere (Mallord et al. 2012b). This is not due to a problem of detection as the photo footage revealed several occasions of rodents inspecting nests.

Temporal exposure

Higher nest survival during incubation than during rearing is documented in several studies (Young 1963, Best 1978, Suarez and Manrique 1992, Burhans et al. 2002). The negative relationship observed between *dnsr* and nest age most likely reflects a change in parental activity at the nest. The number of visits to the nest by parents dramatically increases from incubation to chick rearing due to the intense food provisioning (Glutz von Blotzheim et al. 1991), which will in turn augment nest

Table 5 Comparison of reproductive performance parameters of wood warblers across Europe and of other ground nesting forest birds of Europe and North America. Standard errors and sample sizes are provided, when extraction from the original publications was possible.

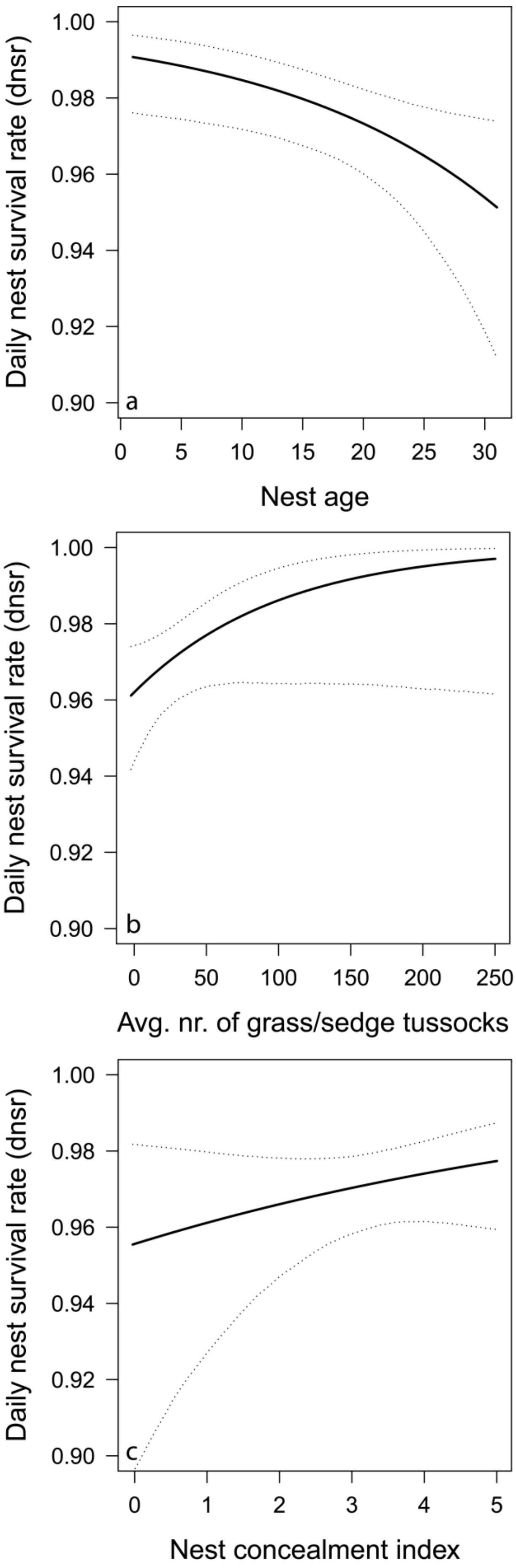
Study	Number of study years; country	Mean clutch size (sample size)	Mean number of fledglings per successful nest	Mean number of fledglings per nest	Naïve nest success in % (sample size)	Nest survival using exposure time methods in % (sample size)
Wood Warbler						
This chapter	3; Switzerland	5.38 ± 0.09 (123)	4.66 ± 0.17 (64)	2.19 ± 0.21 (136)	47.1 (136)	46.9* ± 0.07 (119) 47.1° ± 0.02 (119)
Herremans 1993	5; Belgium	-	5.64	-	-	-
Hillig 2009	1; Germany	5.77	4.77	2.63	57.35 (68)	-
Hölzinger 1999	-; Germany	5.84 (583)	-	3.3	-	-
Lippek 2009	5; Germany	5.36 ± 0.09	-	-	-	-
Mallord et al. 2012	3; Wales UK	-	-	-	-	50.7 †# (167)
Moreau 2001	5; France	5.6	5.36	3.16	59 (122)	-
Reinhardt 2003	1; Germany	6.11 ± 0.09	-	-	50 (5)	-
Wesolowski & Maziarz 2009	8, Poland	6.32	-	-	34.6 #	-
other species						
Wesolowski & Tomialojc 2005	Poland					
- *Phylloscopus collybita*	5	-	-	-	44 (169)	-
- *Troglodytes troglodytes*	4	-	-	-	40 (101)	-
Hölzinger 1999	Germany					
- *Phylloscopus bonelli*		4.9 (103)	-	2.86	-	-
- *Phylloscopus collybita*		5.24 (617)	-	2.48	-	-
- *Phylloscopus trochilus*		5.65 (77)	-	3.64	-	-
- *Erithacus rubecula*		5.14 (715)	-	3.64	-	-
Yanes & Suarez 1995	Iberian peninsula					
- *Erithacus rubecula*	12	-	-	-	-	61.2 (47) #
- *Luscinia megarhynchos*	13	-	-	-	-	74.8 (32) #
- *Phylloscopus collybita*	10	-	-	-	-	75.9 (88) #
Martin 1993						
Oreothlypis celata	-	-	-	-	66.7 (90)	50.1 #
Oreothlypis virginiae	-	-	-	-	69.2(26)	58 #
Cardellina rubrifrons	-	-	-	-	60 (30)	51.8 #
Junco hyemalis	-	-	-	-	69.1 (55)	47 #
Mniotilta varia	-	-	-	-	73.7 (19)	49.9 #
Helmitheros vermivorum	-	-	-	-	78.6 (14)	71 #
Seiurus aurocapilla	-	-	-	-	71.4 (14)	48.9 #

* multiplying all 31 *dnsr* values with each other (31 was the mean duration of the nesting period of wood warblers in Switzerland in this study)

° using a daily nest survival rate of 0.976 ± 0.002 and an exponent of 31 (this study)

† using a daily nest survival rate of 0.979 ± 0.003 (Mallord et al. 2012b) and an exponent of 31 (this study)

\# values from data sets with nest losses only due to predation



predation risk (Martin et al. 2000). In wood warblers, chick provisioning peaks on approximately day 9, with up to 650 adult visits in 15 h (roughly 43 times per h), compared to the incubation period when foraging trips by the female amount to once or twice per hour (Glutz von Blotzheim et al. 1991). Given the huge energy and protein demand of rapidly growing nestlings, parents cannot limit the cues inadvertently given to predators (Martin et al. 2000), thus essentially relying on nest concealment to overcome nest predation. Moreover, with advancing age, begging nestlings may further augment the risk of a nest being visited by predators (Haff and Magrath 2011). Finally, nest predation rates may also increase simply due to a temporal synchronization of the

Fig. 2 Daily nest survival rate in relation to a) nest age (in days), b) number of grass and sedge tussocks in a given territory, and c) nest concealment. Plots show fitted values (solid lines) and 95% confidence intervals (dashed lines) based on a model that includes nest age, number of grass and sedge tussocks and nest concealment (Table 3, AHA results, n = 115).

reproductive cycles of both predators and wood warblers: adult predators seek food to rear their own demanding young while early dispersing juvenile predators suddenly increase the number of predators present in wood warblers' environment (Burhans et al. 2002).

Timing of breeding

We found a negative relationship between both clutch size and number of fledglings and "start of egg-laying". Decreasing reproductive performance as the season progresses is a pattern found in many bird species (Naef-Daenzer et al. 2001, Grant et al. 2005, Müller et al. 2005, Peak 2007). As we never recorded partial predation, seasonal declines of clutch size and number of fledglings were mediated through factors pertaining to either the date or the quality hypotheses. According to the quality hypothesis, seasonal declines in reproductive performance occur due to late breeding individuals being of lower quality due to inexperience (e.g. first year breeders), worse physiological condition (senescent or injured individuals), or generally low foraging, predation avoidance or nest building skill compared to early breeding individuals. According to the date hypothesis, in contrast, a seasonal

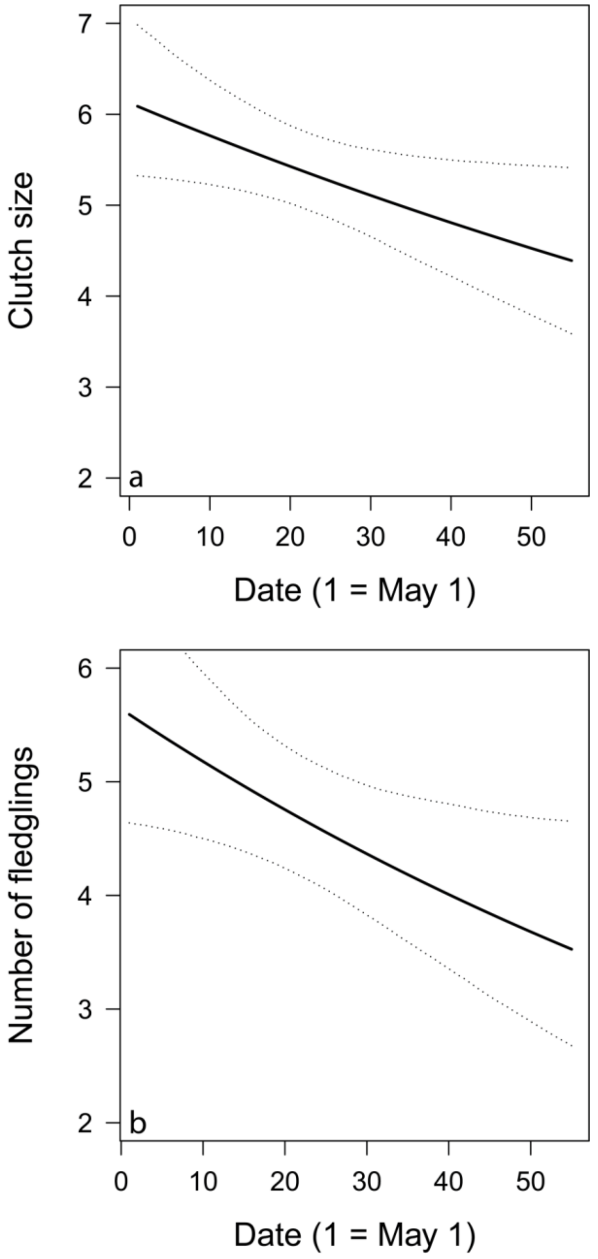


Fig. 3 a) Clutch size (n = 115 nests) and b) number of fledglings (n = 64 nests) plotted against start of egg laying. Data were pooled over the three years of study. Plots show fitted values (solid lines) and 95% confidence intervals (dashed lines) based on the highest ranked model including only start of egg-laying in both panels.

decline of reproductive performance may occur due to deteriorating environmental conditions for breeding as the season advances, such as worsening weather conditions, decreasing food availability and/or accessibility, or increasing predation pressure (Verhulst et al. 1995, Christians et al. 2001). Disentangling the two hypotheses is not possible with our data, but would require experiments, as conducted for example by Verhulst et al. (1995) on great tits (*Parus major*) and Christians et al. (2001) on European starlings (*Sturnus vulgaris*).

Food availability is not only intricately embedded in the two above hypotheses but also drives habitat selection of birds in general. In the wood warbler, the importance of food availability remains unclear, however. While Wesołowski and Maziarz (2009) found a positive correlation between abundance of wood warblers and caterpillars (main food source) (Glutz von Blotzheim et al. 1991), Herremans (1993) did not. The link between caterpillar abundance and reproductive success, while unclear for the wood warbler, has been shown for other bird species, such as great tits (*Parus major*) (Naef-Daenzer et al. 2001). However, caterpillars are not the sole food source for birds such as wood warblers or great tits. Great tits select spiders early in the breeding season, which may breed more than a month earlier than the wood warbler (Maumary et al. 2007), and exhibit prey switching once caterpillars reach body masses around 10-12 mg (Naef-Daenzer et al. 2000). Wood warblers may exhibit similar behavior where early breeding individuals attempt to match hatching of young with caterpillar peak abundance and late breeding individuals switch to spiders and/or other prey items as caterpillar abundance declines (Maziarz and Wesołowski 2010). Hence, wood warblers appear to exhibit very flexible foraging behavior and are unlikely to track only few specific food sources.

Nest concealment

Nest site selection and nest concealment influence nest survival in many bird species (Martin et al. 2000, Weidinger 2002, Müller et al. 2005). In the wood warbler, nest survival increased with nest concealment and availability of grass and sedge tussocks. The availability of grass and/or sedge tussocks alone is however not sufficient as they also have to be accessible for wood warbler, which is not the case if a shrub layer is present. Not only direct nest concealment seems to be important, but also the dominant ground vegetation surrounding the nest, with which successful nests appear to blend in. Thus, the existence of sufficient patches of grass and sedge appears to be an essential habitat requirement of the wood warbler. The positive correlation between *dnsr* and nest concealment may explain why only 31% of nest predation occurred during egg-laying and incubation, when parental activity around the nest is very limited and a concealment effect may fully unfold, compared to the rearing stage, when parental activity peaks and the majority (69%) of predation events took place ($z = 2.5$, p-value = 0.01). Martin et al. (2000) have shown that increasing parental activity at the nest can act antagonistically to nest concealment. Nests in the incubation stage might hence benefit most from nest concealment when the limited activity of the brooding females does not attract nest predators. Circumstantial evidence from our nest cameras for the incubation period suggests that mammalian predators mostly became aware of nest presence after inadvertently flushing the incubating female. We also assume that visually hunting predators like jays became aware of nests by observing feeding parents and not through detecting the nest itself.

Weather

The lack of evidence for a link between our reproductive performance variables and weather circumstances may have resulted from rather homogenous weather conditions throughout the breeding season without severe weather events such as prolonged cold, heat, rain or drought spells (Sergio 2003). Alternatively, predation may have been so strong that it masked weather effects.

Topography, tree structure, predation risk, disturbance, density dependence

Variables pertaining to topography, tree structure, predation risk and disturbance received no or only marginal support for an effect on reproductive performance. While several models ranked within a ΔAICc < 2 to the top ranked model, the null model was always ranked highest in all five groups. In the wood warbler, variables related to topography, tree structure and predation risk have been shown to strongly affect territory settlement within forest stands (Gerber , Marti 2007, Hillig 2009, Wesołowski et al. 2009). Differences pertaining to aforementioned variables between successful and unsuccessful territories may thus become negligible in later phases, such as reproduction. As nest abandonment seemed to have played a marginal role in our study, it is questionable whether disturbance, notably of anthropogenic origin, impacts reproductive success at all. Nests built close to hiking trails were not less successful than nests away from hiking trails ($x^2 = 0.203$, p-value = 0.65): nests built at > 11 m ($n = 115$ of 136 nests) and 1-10 m ($n = 21$ of 136 nests) from trails had a survival rate of 54.6% and 42.9%, respectively. Only one nest closer than 1 m from a trail was classified as “unknown failure”, i.e. might be attributed to direct human disturbance.

There was no evidence for an effect of density on reproductive performance: models with the two density indices were far worse supported than the null model. We had expected that at least one of the components of breeding output would be linked to density. Further studies are needed to understand the reasons of territory clustering reported in wood warbler populations elsewhere (Herremans 1993).

CONCLUSIONS

Using trail cameras, we were able to identify nest predators in 84% of all predation events, to accurately document the dates of nest predation or fledging and to estimate daily nest survival rates. By visiting our cameras only two or three times during the entire nesting period, we decreased the risk that the observer interferes with breeding, hence minimizing any observer bias in our data.

Although predation is the principal cause of nest failure in Swiss wood warblers, it is not yet possible to draw any conclusions about the potential impact of nest predation on the species’ demographic trends. An appropriate assessment of whether mortality via nest predation is (fully or partially) additive or compensatory would necessitate predator exclosure experiments. Therefore, it would be premature to claim that protecting nests against predators might be an option to improve the demographic status of the wood warbler in Switzerland, especially given the nomadic nature of the species (Wesołowski et al. 2009).

That reproductive performance of Swiss wood warblers is strongly related to the availability and especially accessibility of grass and sedge tussocks is a major finding of the present study and, combined with results on territory selection (Gerber , Mallord et al. 2012a), provides essential evidence-based guidance for planning forestry interventions that can benefit the species. Nevertheless, the implementation of our finding is not as straight forward as simple single tree removal to promote growth of the field layer. Depending on topographical factors (e.g. slope inclination or site elevation) and factors such as soil composition, grasses and sedges would grow, but so would other field layer vegetation (e.g. *Rubus* species or various shrubs), hence potentially decreasing habitat suitability for the wood warbler (Gerber , Mallord et al. 2012a). As there is evidence that wood warblers require large areas to allow for clustered settling of multiple individuals (Herremans 1993), conservation measures should aim at increasing the area of relatively homogenous forest stands featuring suitable habitats characterized by abundant grass and sedge tussocks (this study), high tree numbers, few bushes and an intermediate ground vegetation cover (Gerber) as well as a relatively closed canopy (Huber et al. 2016). Such conditions are typically found in forest stands of middle age (i.e. pole wood) in managed forests.

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Rodent-mediated numerical response of rodent-hunting predators affects reproductive performance in a ground-nesting forest passerine

Rodent-mediated numerical response of rodent-hunting predators affects reproductive performance in a ground-nesting forest passerine

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ABSTRACT

Avian population dynamics and fitness are strongly driven and shaped by predation. Predation pressure may vary in relation to annual fluctuations in density and assemblage of predator species, possibly mediated by intermittent resource pulses. Resource pulses in temperate forests often arise from seed masting of various tree species and are associated with strong growth and decline of populations of different taxa. Between 2010 and 2015, we monitored reproduction of a ground nesting forest passerine, the wood warbler (*Phylloscopus sibilatrix*), as well as abundances of rodents and rodent-hunting mammals (*Vulpes vulpes, Martes martes, M. foina*) in northern Switzerland. The aim was to test the hypotheses that 1) rodents influence wood warbler reproduction directly via predation; 2) rodents influence wood warbler reproduction indirectly by triggering a numerical response of rodent-hunting mammals, which incidentally prey on wood warblers and their nests; and 3) rodents influence wood warbler reproduction indirectly by triggering a behavioral response in rodent-hunting mammals, which switch from other prey to wood warblers and their nests. In rodent outbreak years, wood warbler daily nest survival rate was lower than in rodent crash years, but rodents were not important nest predators, in contrast to rodent-hunting mammals. In rodent outbreak years, abundance of and proportion of nests predated by rodent-hunting mammals were higher than in rodent crash years, confirming a rodent-mediated numerical response of rodent-hunting mammals, which incidentally prey on wood warbler nests. Fox, but not marten abundance was higher in rodent outbreak years, indicating that foxes but not martens are attracted to rodent-rich areas. Pine martens, the main nest predator, are forest bound and couldn’t be attracted from non-forested areas. We believe that pine martens, rather than being attracted like foxes, increase search intensity for rodents on the forest floor during rodent outbreaks, thereby explaining the increased nest predation rate by pine martens during rodent outbreak years. This study exemplifies how various species are connected to each other, taking on the roles of predators, primary prey, incidental and alternative prey in a complex food web driven by intermittent resource pulses.

Key words: numerical response, predation, carnivores, rodents, songbird,

INTRODUCTION

Predation is a prime determinant of avian fitness (Thompson 2007) and thought to be the principal force shaping avian population dynamics (Sæther and Bakke 2000). Predation may be committed by different species, each with annually varying densities possibly translating into varying levels of predation pressure exerted (Jędrzejewska and Jędrzejewski 1998). Variation in predator density and/or exerted predation pressure may be mediated by intermittent resource pulses, which are associated with strong growth and decline of populations of various taxa (King 1983, Jaksic et al. 1997, Schmidt and Ostfeld 2008). In temperate forest ecosystems, seed masting of various tree species constitute the most common primary resource pulse, resulting in various subsequent pulses, due to cascading effects up and down the food chain (Lalonde and Roitberg 1992, Clotfelter et al. 2007, Schmidt and Ostfeld 2008). An prominent secondary pulse consists of a numerical response by seed consuming small mammals. Cricetidae voles and Muridae mice (rodents hereafter) respond to seed masting with increased overwinter survival and overwinter breeding, resulting in larger spring and summer populations than in years without preceding seed masting (Ostfeld et al. 1996, Wolff 1996). Secondary pulses of rodents may lead to tertiary pulses of rodent-hunting predators, which may respond either numerically (increase in numbers) or behaviorally (prey-switching) (Abrams and Matsuda 2003), depending on the predator species and/or time since seed masting (Schmidt and Ostfeld 2003). While rodents constitute a key food source to a multitude of carnivores, rodents are not the sole possible prey species in an ecosystem. Various other species may face increased predation pressure as a consequence of past seed masting (Jędrzejewski and Jędrzejewska 1993, Jędrzejewski et al. 1994a, Brangi 1995, Martin 1995, Schmidt and Ostfeld 2003, Clotfelter et al. 2007, Sidorovich et al. 2010).

Rodent abundance is known to negatively influence wood warbler settlement and occurrence (Wesołowski et al. 2009, Szymkowiak and Kuczyński 2015, Pasinelli et al. accepted, BMC Ecology, chapter 4 of this thesis), but the exact mechanism underlying the avoidance of rodent-rich habitat by the wood warbler is unknown. Wood warblers may perceive rodents as direct threat or take them as proxy for general predation risk connected to rodent-hunting predators. We considered three hypotheses which may explain how rodents influence reproduction of the wood warbler and other similar songbirds occurring in mast-driven forest ecosystems. 1)

Rodents influence wood warbler reproduction directly via predation. 2) Rodents influence wood warbler reproduction indirectly, by triggering a numerical response (tertiary pulse) of rodent-hunting predators, which incidentally prey on wood warblers and their nests. 3) Rodents influence wood warbler reproduction indirectly, by triggering a behavioral response in rodent-hunting predators, which switch from other prey to wood warblers and their nests. In this study we tested expectations derived from these three hypotheses. 1) If direct effects of rodents underlie avoidance of rodent rich areas by wood warblers, then a negative relationship between wood warbler nest survival and rodent abundance is expected. In addition, rodents should account for a substantial fraction of the losses of wood warbler nests. 2) If indirect effects of rodents, under a scenario of a numerical response by rodent-hunting predators, underlie avoidance of rodent rich areas by wood warblers, then a negative relationship between wood warbler nest survival and rodent abundance is expected. However, rodent-hunting predators and not rodents should account for a substantial fraction of the losses of wood warbler nests in rodent outbreak years. 3) If indirect effects of rodents, under a scenario of a behavioral response by rodent-hunting predators, underlie avoidance of rodent rich areas by wood warblers, then a positive relationship between wood warbler nest survival and rodent abundance is expected. Rodent-hunting predators should account for a substantial fraction of the losses of wood warbler nests in rodent crash years.

METHODS

Study area and species

The study took place along northern Switzerland's Jura mountain chain, as well as at one site near Lake Constance and one site in the pre-alpine valley of Glarus (for more details on study site locations refer to Grendelmeier et al. 2015). Generally, the study areas were located on slopes exposed to the south, and consisted of mixed deciduous forest stands dominated by European beech (*Fagus sylvatica*), with other deciduous and coniferous tree species interspersed. Stands predominantly consisted of old polewood and young timber with a relatively closed canopy and a sparse shrub layer, if at all present.

The wood warbler has suffered long-term declines in many EU countries since at least 1980 (http://bd.eionet.europa.eu/article12/summary?period=1&subject=A314 (accessed February 5 2016). In Switzerland, it has been classified as vulnerable (VU) on Switzerland's red list (Keller et al. 2010a) and is considered a priority species for the Swiss recovery program for breeding birds (Keller et al. 2010b). This insectivorous forest-interior passerine winters south of the Sahara desert (Hobson et al. 2014) and exhibits very little breeding site fidelity (ring return percentages reviewed in Wesołowski et al. 2009), while avoiding areas with high rodent populations (Wesołowski et al. 2009, Szymkowiak and Kuczyński 2015; Pasinelli et al. accepted, BMC Ecology; chapter 4 of this thesis), resulting in strong annual fluctuations of local population size.

Assessing wood warbler reproduction

Each study area was visited twice a week to map singing males, pairs and nests. Each nest was monitored with one trail camera (Reconyx PC900 HyperFire Professional High Output Covert; Reconyx, Inc., Holmen, Wisconsin, USA), allowing to survey activity of adults and (old) nestlings, to identify nest predators and to determine the exact date of nest predation or fledging. Detailed methods on how nest status, nestling age, the date the first egg was laid, hatching date, number of fledglings and fledging date were determined, are outlined in Grendelmeier et al. (2015). Once a nest was inactive (successful or unsuccessful), we measured rodent occurrence and several environmental factors (details given below).

Assessing rodent abundance

We estimated rodent abundance based on live-trapping in breeding territories of wood warblers and in control areas without wood warblers 200 m away (paired design). In breeding territories and control areas, rodents were captured based on the same standardized sampling design of equal size (Pasinelli et al. accepted, BMC Ecology). We used longworth traps (Penlon Ltd., Abingdon, UK) and "Field Trip Trap Live Catch Trap" (Alana Ecoloty, Bishops Castle, UK), which have similar trapping efficacy (Arlettaz et al. 2010a). Between June and August, we conducted one trapping session with 25 traps per breeding territory and control area, respectively, during 48 hours with 12 hours control intervals. How rodent captures were processed for statistical use is described below under statistical procedures.

Assessing proportion of predations by rodent-hunting mammals

In this study, rodent-hunting predators include red fox (*Vulpes vulpes*), pine marten (*Martes martes*) and stone marten (*M. foina*) and are hereafter referred to as rodent-hunting mammals. Other animals that may be linked to rodents, such as common buzzards (*Buteo buteo*) or Tawny owls (*Strix aluco*) were not important predators of wood warbler nests (see results), hence their sample sizes were small and not included in the analysis. The proportion of nests predated by rodent-hunting mammals was calculated based on number of predations by rodent-hunting mammals and total number of predations per study area and year. Calculations were based on a sample of nests where predators could be identified. Adding nests with unidentified predators to either category would have biased the resulting values. 23 of 99 predated nests had to be omitted from the analysis, due to the unknown predator identity.

Assessing abundance of rodent-hunting mammals

Abundance of rodent-hunting mammals was assessed at the level of the study area to examine the possible links between wood warbler reproduction and predator abundance, as well as between rodent and predator abundance. Abundance of rodent-hunting mammals was estimated based on four camera traps installed along one line-transect in each study area between April and August of the years 2012-2015. Transects spanned the core of the study area (determined based on wood warbler nest coordinates of the years 2010-2011), with camera spaced 200 m apart. For each study area and year we summed all sightings (by camera) of red foxes and martens and divided by the summed number of days all transect cameras in a study area and year were recording. The result was multiplied by 100 to obtain number of rodent-hunting mammals during 100 trap nights per study area and year. Identification of martens to species level from transect-camera pictures, which photograph at greater distances than nest-cameras, was not possible. We did not include house cats (*Felis catus*), as their distribution and hunting behavior is strongly influenced by humans. Furthermore, house cats are not an important nest predator of wood warbler nests (see results). During four years, four Eurasian lynx (*Lynx lynx*) and two European wildcats (*Felis silvestris silvestris*) could be captured by transect camera traps. Neither of the two species were recorded as nest predator of wood warbler nests and therefore they were not included in the analyses.

Statistical procedures

Direct effects of rodents via predation

To assess our first hypothesis, we modeled daily nest survival rate (*dnsr* hereafter) in relation to rodent category (described below) using generalized linear mixed effects models (GLMM) in R (R Development Core Team 2008), implemented with the package lme4 (Bates and Maechler 2010). For each nest, nest survival was coded and modeled as a binary dependent variable (yes/no) on a day-by-day basis (accounted for with a random effect “nestID) using a logit link function and binomial error structure. Additionally we included random effects for study area and year to account for the data dependency arising from using multiple nests per study area and year. *Dnsr* was modeled in relation to rodent category, number of grass tussocks, nest age and nest concealment. The latter three covariates are known to be correlated with wood warbler *dnsr* and included in the model here, as they may explain part of the variance in *dnsr*: information on these three covariates and how they were measured can be found in Grendelmeier et al. (2015). Rodent abundance was based on number of rodents caught per 100 trap nights for each study area and year, thereby accounting for varying numbers of sampled breeding territories and control areas, in varying numbers of areas each year (Table 1). For each year, rodent abundance was then categorized as either high (outbreak year) or low (crash years) and called “rodent category”. Using Aikake’s Information Criterion (Akaike 1974) corrected for small sample size (Sugiura 1978), we compared a model with “rodent category”, “number of grass tussocks”, “nest age”, “nest concealment” and the three random effects to a model that also contained an interaction between rodent category and year, as well as to a null model containing only the intercept and the three random effects. The model with the lowest AICc and models with a ΔAICc < 2 compared to the top ranked model (Burhans et al. 2002) were considered for interpretation.

Indirect effects of rodents via predation by rodent-hunting mammals

To assess our second and third hypothesis, we model the proportion of nest predations by rodent-hunting mammals in relation to rodent category using GLMM (logit link function and binomial error structure). We followed the same information criterion approach as before and compared a model with “rodent category” and random effects for area and year to a model also containing an interaction between rodent category and year, as well as a null model containing only an intercept and the two random effects. Additionally, we ran the same analysis again, but included abundance of rodent-hunting mammals as additional covariate to see whether proportion of mammalian nest predation was related to abundance of rodent-hunting mammals. Because we had data on abundance of rodent-hunting mammals only for four years (2012-2015), sample size of this second analysis was only 15 (as opposed

Table 1 Shown are number of breeding territories and control areas in which rodents were captured by year and area.

year	area	number of breeding territories	number of control areas
2010	Bänkerjoch	1	1
	Gündelhart	1	1
	Glarus/Ennenda	4	4
	Kleinlützel	4	4
	Langenbruck	3	3
	Lauwil	4	4
	Montsevelier	2	2
	Oltingen	1	1
	Staffelegg	1	1
	Scheltenpass	6	6
2011	Belchen	3	3
	Blauen	3	3
	Glarus/Ennenda	4	4
	Homberg	4	4
	Hochwald	3	3
	Kleinlützel	4	4
	Lauwil	5	5
	Montsevelier	3	3
	Scheltenpass	2	2
2012	Blauen	4	4
	Erschwil	2	2
	Glarus/Ennenda	4	4
	Homberg	2	2
	Kleinlützel	4	4
	Langenbruck	2	2
	Lauwil	2	2
	Montsevelier	4	4
	Staffelegg	1	1
2013	Kleinlützel	4	4
	Langenbruck	1	1
	Lauwil	4	4
	Montsevelier	6	6
2014	Kleinlützel	4	4
	Lauwil	1	1
	Montsevelier	4	4
2015	Kleinlützel	4	4
	Lauwil	5	5
	Montsevelier	2	2
	Scheltenpass	6	6

to 31 in the first analysis without abundance of rodent-hunting mammals as covariate).

Proportion successful nests in relation to abundance of rodent-hunting mammals

In a post-hoc analysis we assessed whether wood warbler nest success was directly correlated with abundance of rodent-hunting mammals when rodent abundance was low or high. In a GLMM (logit link function and binomial error structure), we modeled proportion of successful nests (number of successful nests (produced at least one fledgling) to the total number of nests) per study area and year in relation to “rodent category”, “abundance of rodent-hunting mammals” and two random effects “area” and “year”. The candidate model set included a null model (intercept and the two random effects) and all possible combinations of the covariates “rodent category”, abundance of rodent-hunting mammals and their interaction. Models were compared with AICc as described above.

Abundance of rodent-hunting mammals in relation to rodent category

In a second post-hoc analysis we assessed whether “abundance of rodent-hunting mammals” was correlated with “rodent category”. With a linear mixed effect model, including two random effects “area” and “year”, we modeled “abundance of rodent-hunting mammals” in relation to “rodent category”. The candidate model set included a null model (intercept and the two random effects) and all possible combinations of the covariates “rodent category”, “abundance of rodent-hunting mammals” and their interaction. Models were compared with AICc as described above. We ran the same analysis for the response variables “abundance of red foxes” and “abundance of martens”.

RESULTS

During six years (2010-2015) we found 250 wood warbler nests of which 99 were predated (nests empty before possible fledging date), 22 failed due to unknown cause (eggs or nestlings dead in nest) and three had unknown fate (no camera installed or camera failure). In 76 of 99 predations, the predator could be identified. We recorded 23 pine martens, 2 stone martens, 18 Eurasian jays (*Garrulus glandarius*), 13 red foxes, seven European badgers (*Meles meles*), three tawny owls, three Eurasian sparrowhawks (*Accipiter nisus*), two *Apodemus* mice, one common blackbird (*Turdus merula*), one house cat, one honey buzzard (*Pernis apivorus*), one wild boar (*Sus scrofa*) and one Eurasian red squirrel (*Sciurus vulgaris*). In 23 cases predators could not be identified because no camera could be installed or due to camera failure.

We identify three rodent outbreak years (high rodent abundance) and three rodent crash years (low rodent abundance), based on a boxplot with number of rodents by year (Fig. 1).

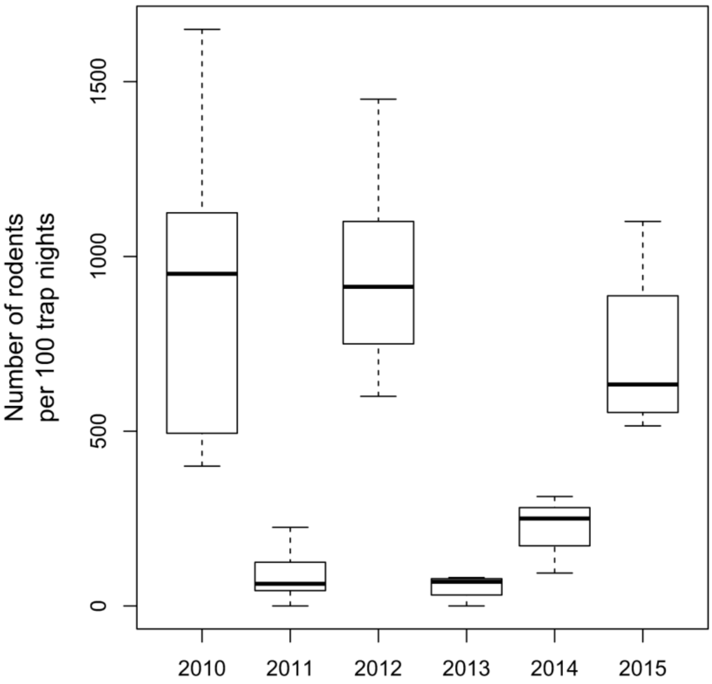

Fig. 1 Boxplot depicting number of rodents per 100 trap nights for each of the six study years. N = 39 areas.

Direct effects of rodents via predation

The highest-ranked model contained the covariates "rodent category", "nest age", "territory grass tussocks" and "nest concealment". No other model had a ΔAICc < 2 compared to this best model (Table 2). In relation to *dnsr*, rodent category and nest age were most important, while "number of grass tussocks" and "nest concealment" appeared to be less important (estimate < SE). Mean *dnsr* was lower in rodent outbreak years compared to rodent crash years (Fig. 2).

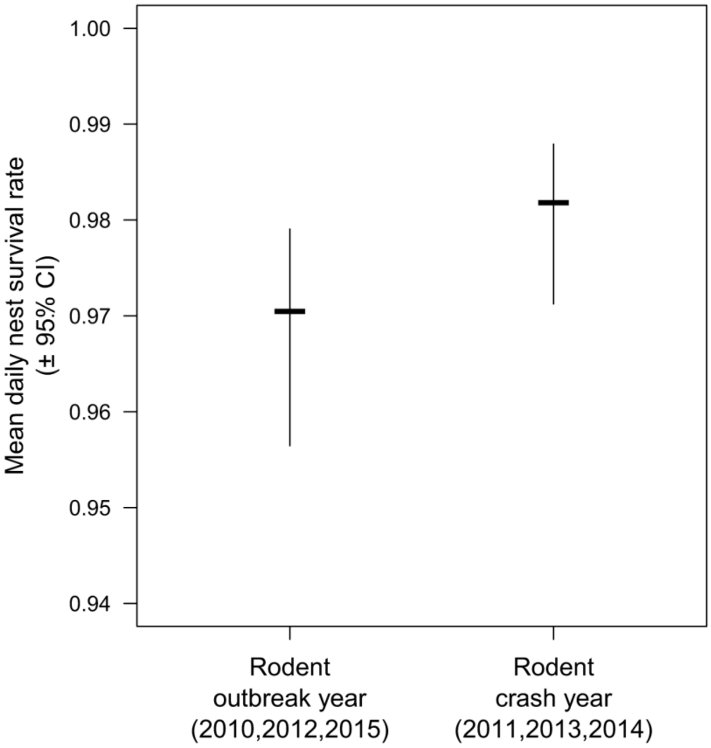

Fig. 2 Mean daily nest survival rate (± 95% confidence interval) in rodent outbreak years (high rodent abundance in 2010, 2012, 2015) and in rodent crash years (low rodent abundance in 2011, 2013, 2014). N = 228 nests.

Indirect effects of rodents via predation by rodent-hunting mammals

The highest-ranked model was the null model, followed by a model containing the covariate rodent category with a ΔAICc of 0.408 (Table 2). The proportion of predations by rodent-hunting mammals was higher in rodent outbreak years than in rodent crash years (Fig. 3). The analysis based on the reduced data set but including abundance of rodent-hunting mammals also as covariate yielded the null model as best ranked model with no other model having a ΔAICc < 2.

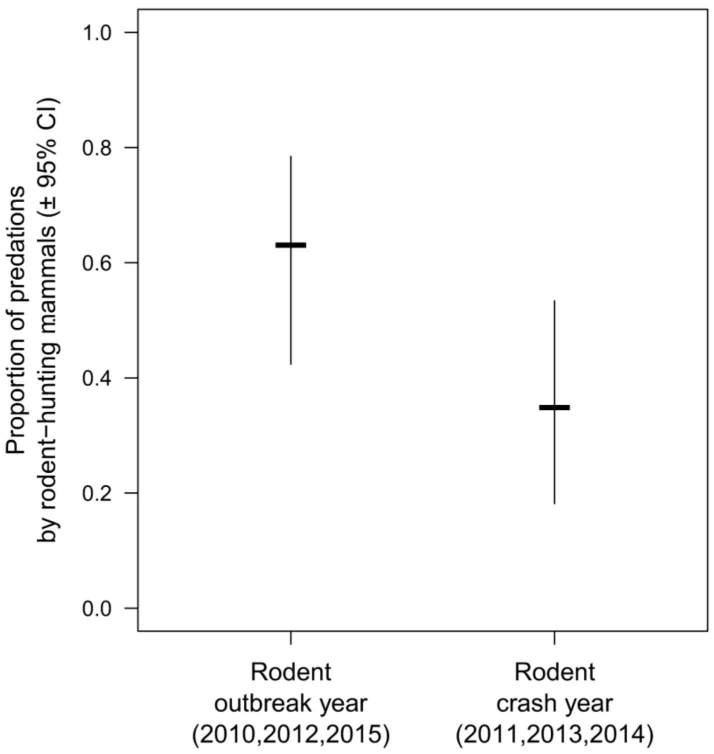

Fig. 3 Proportion of wood warbler nest predations by rodent-hunting mammals (± 95% confidence interval) in rodent outbreak years (high rodent abundance in 2010, 2012, 2015) and in rodent crash years (low rodent abundance in 2011, 2013, 2014). N = 31 areas.

Proportion of successful nests in relation to rodent-hunting mammals

Nest success was not related to abundance of rodent-hunting mammals. All models containing abundance of rodent-hunting mammals had ΔAICc > 2 to the highest-ranked null model (Table 2).

Abundance of rodent-hunting mammals in relation to rodent category

The null model was ranked highest followed by the model containing the covariate “rodent category” with a ΔAICc < 2 of 0.45 compared to the best model (Table 2). Mean number of rodent-hunting mammals was higher in rodent outbreak years compared to rodent crash years (Fig. 4).

Abundance of red fox in relation to rodent category

The model containing the covariates “rodent category” was ranked highest follow by the null model with had a ΔAICc < 2 of 0.4 compared to the best model (Table 2). Mean number of red foxes was higher in rodent outbreak years compared to rodent crash years (Fig. 5).

Table 2. Model selection results and covariate coefficients for the analyses with response variables *dnsr*, proportion of predations by rodent-hunting mammals, proportion successful nests, abundance of rodent-hunting mammals, abundance of red foxes and abundance of martens. For each analysis, the covariates are shown first, followed by their estimates (Est) ± standard errors (SE). The intercept of each model is only shown for null models. Models highlighted in grey, contained the interaction between the fixed effect rodent category and the random effect year. The coefficients are followed by the model selection information: K = number of parameters, AICc = Akaike's information criterion corrected for small sample size, ΔAICc = Difference of AICc compared to best ranked model, AICc weight = Akaike's weight, LL = log likelihood of a model.

Model	**1**	**2**	**3**	**4**	**5**
Analysis					
Daily nest survival rate ~					
(n = 228 nests)					
(intercept)				3.72 ± 0.19	
rodent category (high)	5.79 ± 0.78	5.49 ± 0.75	3.47 ± 0.19		3.47 ± 0.18
rodent category (low)	6.44 ± 0.93	6.28 ± 0.95	3.96 ± 0.26		4.13 ± 0.42
nestage	-0.11 ± 0.03	-0.10 ± 0.03			
territory grass tussocks	0.11 ± 0.18	0.10 ± 0.16			
nest concealment	0.45 ± 0.28	0.43 ± 0.25			
model information					
K	8	10	5	4	7
AICc	471.70	475.00	486.24	486.76	489.03
ΔAICc	0.00	3.30	14.54	15.06	17.33
AICc weight	0.84	0.16	0.00	0.00	0.00
LL	-227.82	-227.45	-238.10	-239.37	-237.49
Proportion fox/marten predations ~					
(n = 31 areas)					
(intercept)	-0.29 ± 0.48				
rodent category (high)		0.47 ± 0.42	0.07 ± 0.84		
rodent category (low)		-0.69 ± 0.44	-0.75 ± 0.47		
model information					
K	3	4	6		
AICc	71.44	71.85	77.16		
ΔAICc	0.00	0.41	5.72		

AICc weight	0.53	0.44	0.03		
LL	-32.28	-31.16	-30.83		
Proportion successful nests ~					
(n = 135 nests)					
(intercept)	0.10 ± 0.25				
rodent abundance		-0.32 ± 0.22		0.01 ± 0.27	-0.17 ± 0.32
fox/marten abundance			-0.25 ± 0.32	-0.82 ± 0.46	-0.28 ± 0.23
rodent abundance : fox/marten abundance				0.67 ± 0.38	
model information					
K	3	4	4	6	5
AICc	77.03	78.20	79.29	80.75	81.08
ΔAICc	0.00	1.17	2.25	3.72	4.04
AICc weight	0.46	0.26	0.15	0.07	0.06
LL	-34.97	-34.15	-34.69	-32.16	-34.04
Abundance of rodent-hunting mammals ~					
(n = 26 areas)					
(intercept)	4.26 ± 1.71				
rodent category (high)		6.72 ± 1.90	6.57 ± 2.06		
rodent category (low)		2.42 ± 1.80	2.40 ± 1.80		
model information					
K	4	5	7		
AICc	182.78	183.23	190.44		
ΔAICc	0.00	0.45	7.66		
AICc weight	0.55	0.44	0.01		
LL	-86.44	-85.12	-85.11		
Abundance of red foxes ~					
(n = 26 areas)					
(intercept)		2.43 ± 0.54			
rodent category (high)	3.29 ± 0.63		3.29 ± 0.63		
rodent cagetory (low)	1.75 ± 0.60		1.75 ± 0.60		
model information					
K	5	4	7		
AICc	124.41	124.80	131.63		
ΔAICc	0.00	0.40	7.22		

AICc weight	0.54			0.44			0.02		
LL	-55.70			-57.45			-55.70		
Abundance of martens ~									
(n = 26 areas)									
(intercept)	2.06	±	1.22						
rodent category (high)				3.56	±	1.72	3.56	±	1.72
rodent category (low)				0.76	±	1.60	0.76	±	1.60
model information									
K	4			5			7		
AICc	177.58			179.24			186.46		
ΔAICc	0.00			1.66			8.88		
AICc weight	0.69			0.30			0.01		
LL	-83.84			-83.12			-83.12		

Abundance of martens in relation to rodent category

The null model was ranked highest followed by the model containing the covariate “rodent category” with a ΔAICc < 2 of 1.66 compared to the best model (Table 2). Mean number of martens did not differ between rodent outbreak years and rodent crash years (Fig. 6).

DISCUSSION

In six years of monitoring wood warbler nests in our study, the main nest predators were mammalian carnivores, responsible for almost half of all nest predations. The proportion of nest predations by mammalian carnivores was positively related to rodent abundance, while daily survival rate of wood warbler nests was negatively related to rodent abundance, which has not been shown before for this species.

Direct effects of rodents via predation

That rodent abundance is important for wood warbler settlement and occurrence has been shown in previous studies on several scales. Wood warbler settlement at the territory scale in Switzerland (Pasinelli et al. accepted, BMC Ecology), wood warbler numbers at the forest stand scale in Białowieża Forest, Poland (Wesołowski et al. 2009) and wood warbler densities at the landscape scale in Poland (Szymkowiak and Kuczyński 2015) and Germany (chapter 4 of this thesis) were all negatively related to rodent abundances. In our study, we additionally found that also a measure of reproductive success was negatively correlated to rodent abundance. Daily survival rate of wood warbler nests was higher in years with low rodent abundances compared to years with high rodent abundance. To our knowledge, this is the only study documenting a direct, but not necessarily causal (see below), relationship between wood warbler nest survival and rodents. Analyzing short-term data, Wesołowski (1985) found a positive relationship between wood warbler nest loss and rodent abundance, which disappeared however when analyzing a long-term data set. Currently we cannot discuss whether the observed correlation between wood warbler nest survival and rodent abundance in Switzerland would also be found in a data set longer than six years. Apart from these wood warbler studies, evidence for a correlation between nest survival and rodents has also been found for other systems and species. Schmidt and Ostfeld (2003) found that daily nest mortality rate (the inverse of *dnsr*) of veeries (*Catharus fuscescens*), red-eyed vireos (*Vireo olivaceus*) and wood thrushes (*Hylocichla mustelina*) was positively related to rodent density in the Hudson Valley, New York, USA. Our study and other cited studies exemplify how strongly life-history of some songbird species is affected by rodents, negatively influencing reproduction even after causing avoidance behavior and thereby decreasing settlement, occurrence and abundance of focal songbirds (Jędrzejewska and Jędrzejewski 1998, Schmidt and Ostfeld 2003, Clotfelter et al. 2007, Schmidt and Ostfeld 2008, Wesołowski et al. 2009, Grendelmeier et al. 2015, Szymkowiak and Kuczyński 2015). While we could confirm our first hypothesis that wood warbler reproduction is directly related to rodent abundance, we cannot confirm that the reason behind this relationship is direct rodent predation. Rodents have been documented to predate and/or destroy nests of several bird species in general (Walankiewicz 2002, Kirkpatrick and Conway 2010) and have been suspected to predate wood warbler nests in particular (Mildenberger 1940, Wesołowski 1985, Wesołowski and Maziarz 2009), though concrete evidence has been lacking. In our study, predation by rodents was not important as only 2% of all nest predations were caused by rodents (own unpublished picture evidence). Such a low predation rate by rodents, at least in Switzerland, is astonishing, considering that rodents moved around and even inspected nests without predation occurring on many occasions (own unpublished picture evidence). Moreover, 26 of 31 unsuccessful artificial nests (84%) monitored with cameras were predated by rodents (Grendelmeier 2011). It is unclear whether wood warblers consider rodents as direct threat, given their low predations rates in Switzerland. Alternatively, nomadic wood warblers may face increased predation by rodents elsewhere and therefore track rodent abundances where ever they settle. We agree with other authors that rodents are most likely taken as proxy for overall predation risk, but argue that the underlying mechanism behind the observed negative relationship between rodents and wood warbler reproduction is found in rodent-mediated effects of predators.

Rodent-mediated numerical response and predation by rodent-hunting mammals

The proportion of nest predations by rodent-hunting mammals on wood warbler nests was higher in rodent outbreak years compared to rodent crash years (Fig. 3). We could therefore confirm our second hypothesis that rodents have an indirect effect on wood warbler reproduction by triggering a numerical response of rodent-hunting mammals. Furthermore we have direct evidence for the numerical response of rodent-hunting mammals in relation to rodent abundances (Fig. 4). Numerical responses of predators to rodent abundances are found in various ecosystems and various predator-prey systems. In a temperate forest ecosystem in New York, USA, abundances of cooper's (*Accipiter cooperii*) and sharp-shinned hawks (*A. striatus*) both showed a positive relationship with rodent densities the previous year (Schmidt and Ostfeld 2003). In high arctic Greenland, arctic fox (*Alopex lagopus*), stoat (*Mustela erminea*), long-tailed skua (*Stercorarius longicaudus*) and snowy owl (*Nyctea scandiaca*) exhibited numerical responses in relation to densities of the collared lemming (*Dicrostonyx groenlandicus*), albeit to varying degrees (Gilg et al. 2006). And in semiarid neotropical Chile, five out of ten studied predator species (four and one species from the orders Falconiformes and Strigiformes, respectively) showed numerical responses in relation to densities of small mammals (Jaksic et al. 1992). While other rodent-hunting predators including common buzzards and Tawny owls are also known to be strongly linked to rodent abundances (Jędrzejewski and Jędrzejewska 1993, Jędrzejewski et al. 1994a, Jędrzejewski et al. 1994b), they played a minimal role in wood warbler nest predation in this study and were therefore not included in the analyses.

Numerical responses of rodent-hunting predators in relation to rodent abundance result in other species becoming incidental prey. All three carnivorous mammals considered in this study are generalist predators and use rodents as staple food source. A numerical response through population increase in the same year as a rodent outbreak, as observed in this study, is not possible for any of the three species, due to their long reproductive cycle. Though red foxes may breed as early as December, juvenile

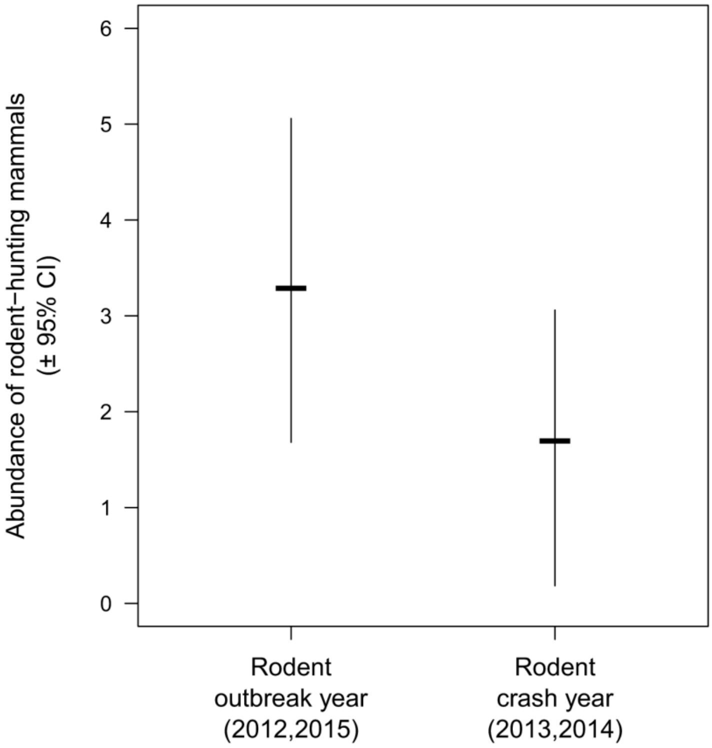

Fig. 4 Abundance of rodent-hunting mammals (± 95% confidence interval) in rodent outbreak years (high rodent abundance in 2012, 2015) and in rodent crash years (low rodent abundance in 2013, 2014). N = 26 areas.

independence and dispersal does not occur until early fall (Feldhamer et al. 2003). Stone and pine marten reproduce in late summer, but due to delayed implantation, parturition does not occur until spring in the following year and juvenile independence takes even longer (Zalewski et al. 1995, Heptner and Sludskii 2002). We therefore propose that the numerical response of rodent-hunting mammals in the same year of a rodent outbreak is a result of rodent-hunting mammals being attracted to rodent-rich forests. Increased occurrence of predators hunting for rodents on the forest floor may then result in increased finding rates of incidental prey, including wood warblers and their nests. Red foxes in particular are known to be edge habitat predators (Brangi 1995, Silva et al. 2009). Fragmented landscapes with many edges, like in our study, therefore offer ideal foraging habitat. In forest-rodent crash years, open habitat, such as meadows and agricultural fields, offer more abundant small mammal populations than forest habitats (Jędrzejewski and Jędrzejewska 1992). However, in forest-rodent outbreak years, red foxes are known to change foraging habitat from open to forested areas (Jędrzejewski and Jędrzejewska 1992, 1993). In this study, we found that red foxes occurred more frequently in forests during rodent outbreak years compared to rodent crash years (Fig. 5).

Stone martens are also opportunistic predators like red foxes, foraging in various habitats including forests, meadows and urban areas (Delibes 1983, Rondinini and Boitani 2002, Posłuszny et al. 2007). During rodent outbreak years, stone martens may increase foraging in forests compared to rodent crash years, similar to red foxes. In our study however, transect-camera pictures revealed that marten abundance during rodent outbreak and crash years did

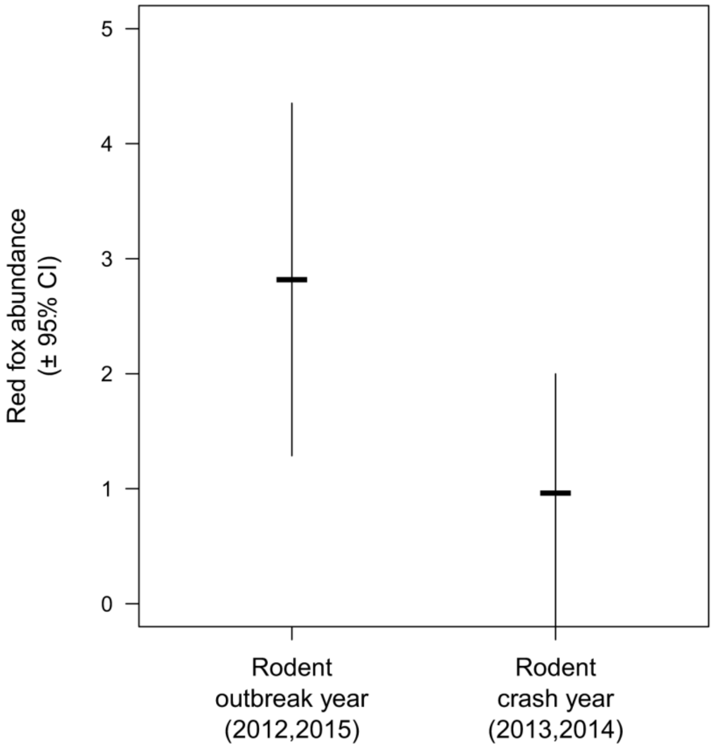

Fig. 5 Abundance of red foxes (± 95% confidence interval) in rodent outbreak years (high rodent abundance in 2010, 2012, 2015) and in rodent crash years (low rodent abundance in 2013, 2014). N = 26 areas.

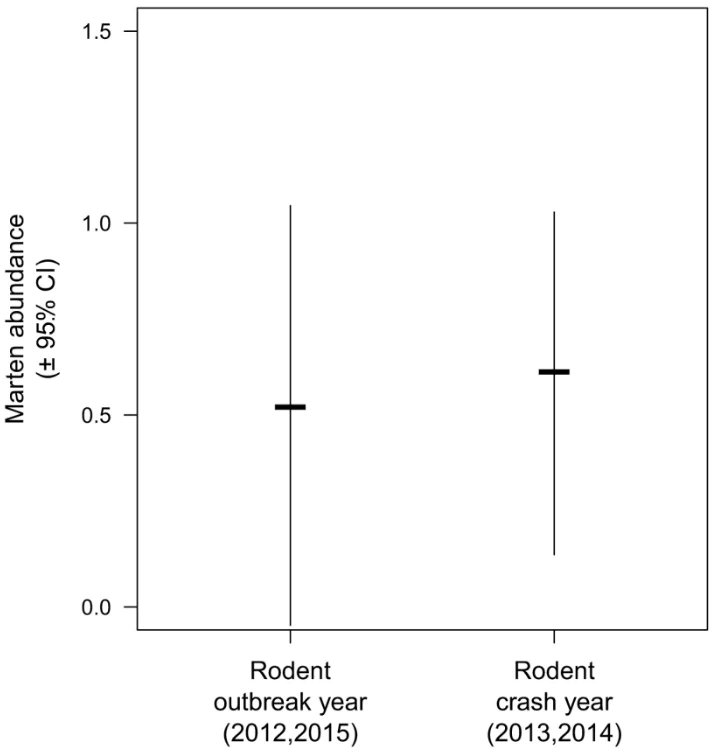

Fig. 6 Abundance of martens (± 95% confidence interval) in rodent outbreak years (high rodent abundance in 2012, 2015) and in rodent crash years (low rodent abundance in 2013, 2014). N = 26 areas.

not differ (Fig. 6). Since pine martens are bound to forested areas (Zalewski et al. 1995) and couldn't be attracted to rodent-rich forests from non-forested areas, only stone marten attraction could explain a difference in marten occurrence between rodent outbreak and crash years. As there was no such difference, we assume that predominantly pine martens were photographed by transect-cameras and that stone martens are not attracted to a great extent. This assumption is supported by nest-camera pictures, showing that pine martens are the main predator of wood warbler nests with 23 predations and not stone martens with twp predations. Furthermore, rodents are a staple food source for especially pine martens. In central Poland, the food niche of both marten species highly overlapped, but there were large quantitative differences in their food composition (Posłuszny et al. 2007). Stone martens predominantly fed on fruits, with rodents, birds and insects as complementary food, while pine martens relied on rodents as staple food. Following our assumption that we recorded predominantly pine martens with transect cameras, thereby explaining the equal occurrence of martens during rodent outbreak and crash years, we propose a second mechanism responsible for a rodent-mediated predation on wood warbler nests: search intensity. During rodent outbreak years, pine martens, but also red foxes, most likely increase search intensity on the forest floor while hunting for rodents. Due to increased search intensity incidental prey, including nests of ground breeding birds would be found more frequently than in rodent crash years. In rodent crash years, foxes may cross forest habitat with the primary intent of getting to adjacent, non-forested foraging patches and not with the intent of searching for food within the forest. Pine martens would not switch foraging habitats but would probably have to invest more time seeking out other food sources in addition to rodents (Posłuszny et al. 2007), thereby decreasing search intensity on the forest floor.

CONCLUSIONS

Negative relationships between occurrence and/or reproduction of birds (often incidental prey) and rodent abundance have been found in various studies, with different pathways how incidental or alternative prey is affected. In our study system, where at least rodents (secondary pulse species), mammalian predators (tertiary pulse species) and wood warblers (incidental prey) are linked, the pathway, by which secondary and tertiary pulse species responded, were numerical responses. Tertiary pulses and secondary pulses are results of primary resource pulses, which in our system are initiated by seed masting. These resource pulses are an important ecosystem process with consequences for a multitude of species, as evident from this study. Drawing conclusions as to how resource pulses affect local demography of the wood warbler is difficult, due to the wood warbler’s nomadic behavior. Nomadism however, appears to be a behavioral response of wood warblers to cope with intermittent resource pulses allowing wood warblers to minimize negative consequences of predation by avoiding areas with high predation risk.

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Of seed mast, rodents and songbirds: how populations relate to resource pulses

Of seed mast, rodents and songbirds: how populations relate to resource pulses

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ABSTRACT

Wide ranging ecosystem processes such as resource pulses can be very influential, initiating cascading effects up and down the food chain, sometimes over multiple years. Resource pulses in temperate forests are most often initiated through seed masting of one or several tree species, providing a key food source to a multitude of species. In this study we tested several hypotheses regarding how primary and secondary resource pulses connect forest rodents, Eurasian jays (*Garrulus glandarius*), caterpillars and wood warblers by means of a 17-year data set from Germany. Using the *lasso* procedure, a model reduction and variable selection method, we were able to reduce a large set of candidate covariates down to the important ones. We found that rodent abundance was positively related to seed mast in the previous year and to number of snow days, and negatively related to frost days. Jay abundance was positively related to seed mast two years ago and negatively related to mean onset date of hazel (*Corylus avellana*) bloom in the previous year. Wood warbler (*Phylloscopus sibilatrix*) abundance was positively related to cumulative rainfall in April and May and to caterpillar abundance, and negatively related to rodent abundance and jay abundance. Wood warbler abundance was thus indirectly and negatively related to seed masts via numerical responses of rodent populations (one year post-mast) and jay populations (two years post-mast). Jays, but much less rodents, are known to depredate wood warbler nests, possibly explaining why wood warbler numbers correlate negatively to rodent and jay abundances. This study adds to the knowledge of how complex interactions among multiple taxa at multiple trophic levels, directly and indirectly, link various members of a temperate forest ecosystem community.

Key words: resource pulses, seed mast, rodents, Eurasian jay, wood warbler, lasso procedure

INTRODUCTION

Resource pulses are among the most influential ecosystem processes in nature, initiating cascading effects up and down the food chain, sometimes over multiple years (King 1983, Ostfeld et al. 1996, Jaksic et al. 1997, Clotfelter et al. 2007, Schmidt and Ostfeld 2008). Resource pulses in temperate forests occur, for example, due to timed emersion of insects (Yang 2004) or seed masting of one or several tree species (Lalonde and Roitberg 1992), triggered by climatic and environmental cues and providing key food sources to a multitude of species (King 1983, Schmidt and Ostfeld 2008). Whether seed masting evolved to maximize seed dispersal or to minimize seed predation, it has a large impact on the entire ecosystem by creating several subsequent secondary pulses of seed consuming animals (Ostfeld et al. 1996, Wolff 1996). These secondary pulses of, for example, rodents can lead to tertiary pulses of rodent-hunting predators, which may respond either numerically (population increase) or behaviorally (prey-switching), depending on the predator species and/or time since the seed mast. While rodents constitute a key and often primary food source for many carnivores, they are typically not the sole possible prey in an ecosystem. As predator populations grow or predators switch to alternative prey, species normally not directly influenced by seed mast events may face increased predation pressure. Birds have often been documented to become alternative prey to various predators affected by resource pulses. (Jędrzejewski and Jędrzejewska 1993, Jędrzejewski et al. 1994a, Schmidt and Ostfeld 2003). Predators and predation are also thought to be major drivers of avian life history, evolution and population dynamics (Jędrzejewski and Jędrzejewska 1993, Brangi 1995, Martin 1995, Schmidt and Ostfeld 2003, Clotfelter et al. 2007, Sidorovich et al. 2010). In this study we evaluated how populations of Eurasian jays (*Garrulus glandarius*) and rodents (*Cricetidae* voles and *Muridae* mice) relate to seed masts and other environmental factors. In a second step, we evaluated how populations of an alternative prey species in this resource pulse system, the wood warbler (*Phylloscopus sibilatrix*), are related to rodent populations, jay populations and other environmental factors. We tested several hypothesis introduced below by means of a 17-year data set from Germany.

Following seed masting of angiosperm trees in fall, one of the first taxon affected is rodents. Owing to seed caches from seed masts, rodents not only exhibit increased overwinter survival, but populations can even increase due to overwinter breeding

(Wolff 1996). We therefore expected a positive relation between rodent abundance in spring and seed mast in the previous fall. Another predictor of rodent abundance is winter weather, which may negatively influence rodent abundance via temperature (e.g. Ergon et al. 2004) or positively via snow cover (e.g. Hansson and Henttonen 1985). We expected a negative relation between rodent abundance and covariates pertaining to temperature and a positive relation between rodent abundance and covariates pertaining to snow fall.

How important seed masting is for Eurasian jays (*Garrulus glandarius*; jays hereafter), is unclear as they exploit various other food sources such as fruits, cereal crop, young birds and different small mammals, reptiles and amphibians (Glutz von Blotzheim et al. 1991). Nonetheless, tree seeds are known to be stored by jays as winter supplies (Nilsson 1985, Patterson et al. 1991) and even serve as supplementary food during nesting and post-fledging parental care (Bossema 1979). As opposed to rodents, which can increase their population through overwinter breeding (Wolff 1996), jays would benefit from seed masts only through increased overwinter survival, hence population reduction due to overwinter mortality may be dampened compared to winters without preceding seed masts. In the spring following a seed mast, more individuals than in other years could breed, resulting in increased offspring production in summer and peak abundances in fall. Even with overwinter mortality returning to pre-mast levels, populations in spring two years after a mast should be relatively large due to increased offspring production in the previous year. We hypothesized that jay populations exert peak predatory pressure on wood warbler nests in the second spring after seed masting. A similar pattern was found for other avian predators in seed pulse-driven forest ecosystems (Jędrzejewska and Jędrzejewski 1998, McShea 2000, Schmidt and Ostfeld 2003). We therefore assumed that jay breeding populations could be positively related to seed masting two years ago. We also expected that jay breeding populations were positively related to caterpillar abundance during the nestling period of the previous year, as caterpillars are a main food item fed to jay nestlings (Bossema 1979, Glutz von Blotzheim et al. 1991). Even though we evaluated jay abundance in relation to caterpillar abundance, we also assessed the possible role of spring plant phenology, as it may be linked to other important environmental covariates not represented in our data. We hypothesize that juvenile recruitment of jays may increase the earlier breeding commences and therefore result in larger jay populations one year later. We expected that jay populations were larger with earlier onset of spring phenology in the previous year. In mostly sedentary species like the jay (Glutz von Blotzheim et al. 1991), density dependent regulation of population size may also play a role in explaining annual variation of abundance (Sibly et al. 2005). We therefore expected that jay populations were negatively related to jay populations in the previous year.

Seed masts may also influence the abundance of caterpillars, a prime food source for many animals in the spring. A general rule of life history theory is that reproduction comes at a cost to other fitness traits (Obeso 2002). However, there is ambiguity about the importance and strength of such a trade-off between reproduction and other fitness components for angiosperm trees (Gross 1972, Yasumura et al. 2006, Sánchez-Humanes et al. 2011). If seed masting comes at a cost to trees in our study system, we hypothesized that vegetal matter of trees following a seed mast offers a less reliable and/or nutritional food source to caterpillars, because leaves contain for instance less nitrogen, which was allocated to seeds. Decreased nutritional value of leaves may in turn decrease caterpillar abundances. We predicted that caterpillar abundance was negatively related to the occurrence of a seed mast in the previous year. Climatic factors such as temperature and rain may also affect caterpillar spring abundance (Hagstrum and Milliken 1988, Smith et al. 2011), so we expected that caterpillar abundance would be positively related to spring temperature and spring rainfall.

Seed masts may directly affect various taxa such as rodents, birds or caterpillars as hypothesized above. By influencing populations of potential predator and/or prey species, seed masts may also affect other species indirectly. The wood warbler may be one such example. The avoidance of areas with high rodent densities by wood warblers has been conclusively shown (Wesołowski et al. 2009; Pasinelli et al. accepted, BMC Ecology). It remains unclear whether wood warblers perceive rodents as direct threat or whether they connect rodents to meso-predator occurrence. Rodents have been documented to predate nests of several bird species (Walankiewicz 2002, Kirkpatrick and Conway 2010) and have been suspected (Mildenberger 1940, Wesołowski 1985, Wesołowski and Maziarz 2009) and recently observed (own unpublished picture evidence) to predate wood warbler nests. As one of the main predictors of wood warbler occurrence we evaluated whether wood warbler numbers were negatively related to rodent abundance of the same year. While the mechanisms underlying avoidance of rodent-rich areas by wood warblers remain unclear, jays have been shown to be a main predator of wood warbler nests in Europe (Mallord et al. 2012b, Grendelmeier et al. 2015). Avoiding areas with high jay abundance would therefore seem to be beneficial to wood warblers. We thus expected that wood warbler abundance was negatively related to jay abundance of the same year.

Perceived or actual predation risk may be a main driver of wood warblers' nomadic behavior, but territory selection may also be affected by other factors. How far along plant phenology has progressed in spring may be a crucial determinant for at least early returning wood warbler males in terms of habitat selection. Spring plant phenology affects the emergence of various insects and marks the beginning of canopy closure, which in turn regulates microclimate on the ground where wood warblers build their nests. Early plant phenology as indicator of an early spring could therefore mean the difference between settlement and continued migration and may therefore determine annual, local or regional population size. We expected that wood warbler abundance was negatively related to spring plant phenology on the breeding sites, that is, wood warbler abundance should be higher in years with earlier onset of plant phenology.

Weather conditions can have direct detrimental effects on birds (Holland and Yalden 1995, Newton 1998). If prevailing spring weather upon arrival may be deemed suboptimal to ensure survival or raise a brood, a nomad like the wood warbler may just keep migrating. We therefore expected that wood warbler abundance was negatively related to temperature and rain in April/May. Finally, population size of insectivorous passerines (Jędrzejewska and Jędrzejewski 1998, Holmes 2011), including the wood warbler (Wesołowski et al. 2009, Kühn 2015), have been shown to positively correlate with caterpillar abundance. We therefore expect that wood warbler abundance was positively related to caterpillar abundance in the same year.

METHODS

Bird data

Data on wood warbler and jay abundance were collected from 1989 to 2010 as part of the German common bird census (DDA monitoring program) and are based on point-stop-counts and territory mapping (Flade and Schwarz 1992). The DDA monitoring program uses 5 standard counting periods between mid-March and mid-

June, at higher altitudes extended with a 6th period in the second half of June. Jays were recorded on three visits between March 16th and May 15th and wood warblers on 2-3 visits between May 16th and June 30th (Flade and Schwarz 2004). Count data was processed with program TRIM (Trends and Indices for Monitoring Data, Pannekoek and Van Strien 1998).

Rodent data

Rodent data was collected from 1990 to 2010 as part of a rodent monitoring program of the state forestry research institutes of some federal states in NW Germany in Southern Saxony/Northern Hessen (by Nordwestdeutsche Forstliche Versuchsanstalt Göttingen) and in NE Germany in Mecklenburg-Vorpommern and Brandenburg (by Landeskompetenzzentrum Forst Brandenburg). In NE Germany, trapping was performed at an annually varying number of trapping sites per year (average: 266, range: 74 to 524), with on average 57-63 live traps and 1-3 nights of capture at each site. In NW Germany, trapping was performed in 7-15 forest districts per year with a total of 1100 to 8700 trap nights per year. Rodents were categorized as *Cricetidae* voles (hereafter voles) or *Muridae* mice (hereafter mice) and jointly processed as number of individuals per 100 trap nights.

Mast data

Seed mast data from central and northern Germany for the study period between 1990 and 2010 was provided by the Brandenburg State Agency for Forestry (J. Steigleder, Landeskompetenzzentrum Forst Eberswalde) and is based on blooming scores and seed crop yields of the certified state seed tree stands. Seed crop yield of *Quercus robur*, *Q. petraea* and *Fagus sylvatica* were categorized as follows: full mast (70-100% hanging seeds), half mast (40-69% hanging seeds), low mast (10-39% hanging seeds) and no mast (<10% hanging seeds). For more details see elaborations in Flade and Schwarz (2004). The resulting covariate is called “fructification” in all analyses, tables and figures.

Caterpillar data

Caterpillar data from the whole area of the federal state of Brandenburg (29,000 km^2) were provided for the years 1991 to 2010 by the Landeskompetenzzentrum Forst Eberswalde. For each year, the area in hectares with noticeable to strong frass damage by *Dendrolimus pini*, *Lymantria monacha* and *Trotrix viridana* separately was reported by the Brandenburg state forest administration (via foresters of the state forest districts).

Phenology

As a proxy for spring phenology we used mean blooming date of hazel (*Corylus avellana*), with data spanning a period between 1992 and 2010 provided by the „German weather service“ (http://www.dwd.de/DE/klimaumwelt/klimaueberwachung/phaenologie/produkte/langereihen/langereihen.html?nn=575800.

Weather data

Weather data were based on measurements from 44 stations distributed throughout Germany and were provided by the “German weather service”. Stations are located at elevations of 0 above sea level (a.s.l.) to 2960 m a.s.l., with an average elevation of 314 m a.s.l. All variables pertaining to temperature are based on degrees Celsius. Further variable details and which variables were used in relation to each response variable are given below.

Statistical procedures

Covariates used by response variable

In relation to rodent abundance we evaluated “fructification in previous year” and several weather-related factors: 1) “cold sum” (sum of negative daily mean temperatures in °C; a measure of winter harshness often used to evaluate freezing behavior of standing water bodies (German weather service)), 2) “snow days” (number of days with snow cover > 0 cm), 3) “snow height” (sum of daily snow cover in cm), 4) “frost days” (number of days with minimum daily temperature < 0 °C), 5) “ice days” (number of days with maximum daily temperature < 0 °C). We evaluated each of the five covariates during two time periods: period one (p1) was defined to last from November 1st to March 31st and period two (p2) from January 16th to March 31st.

In relation to jay abundance we evaluated “fructification two years ago”, “caterpillar abundance in previous year”, “mean onset date of hazel bloom in previous year” and “jay abundance in previous year”.

In relation to caterpillar abundance we evaluated “fructification in previous year”, “mean onset date of hazel bloom”, “mean temperature in °C in April/May” and “cumulative rainfall in mm in April/May”.

In relation to wood warbler abundance we evaluated “jay abundance”, “rodent abundance”, “caterpillar abundance”, “mean onset date of hazel bloom”, “mean temperature in °C in April/May” and ” cumulative rainfall in mm in April/May”.

Model reduction

For the analyses of wood warbler and rodent abundance, using all desired covariates in one statistical model would cause over-parameterization (Burnham and Anderson 2002, Crawley 2012).Therefore, model reduction was necessary to avoid over-parameterization and to allow identification of a subset of ”best” covariates. To fit a model with more covariates than observation points, a regression shrinkage procedure (e.g. Hastie et al. 2005), such as *lasso* ("least absolute shrinkage and selection operator"; Tibshirani 1996) can be used. The *lasso* method puts a constraint on the covariates’ coefficients within the model, where the sum of the absolute values for the slope parameters are not allowed to exceed a specific value, the constraint, or they collapse to zero. The constraint is obtained by multiplying the sum of the absolute values of the coefficients by a shrinkage factor. If this shrinkage factor is zero, the constraint equals zero as well and therefore constitutes the largest possible constraint. Visualizations of *lasso* regressions (e.g. Fig. 1) are best read from right to left, where a value of “1” (right side of the graph) constitutes a constraint of 0% and a value of “0” (left side of graph) constitutes a constraint of 100%. This means that at a constraint of 0%, we would allow all covariates to have an effect on the response variable. As we increase the constraint along the constraint range to the left, all the covariates’ coefficients start to shrink towards zero at the same time, as the method considers all covariates together. Considering all covariates together is an advantage of this method, since correlated variables can and should be entered in the same *lasso* model. As we approach a maximal constraint of 100%, more and more coefficients of covariates collapse to zero, meaning that the last covariate whose coefficient collapses to zero has the largest effect in relation to the response variable (Korner-Nievergelt et al. 2015). To account for year effects we included year as a (categorical) fixed effect on which no constraint was placed, so that it was always present in the model. In order to make the models more robust and force all covariates to have the same unit, they were z-transformed with a mean of zero and a standard deviation of one. The *lasso* method is implemented in the package lasso2 (Lokhorst et al. 2014) and run through the software R (R Development Core Team 2008).

Covariate selection

Sometimes *lasso* has to be run for multiple iterations for a response variable: upon a visual inspection of the first iteration (e.g. Fig. 1a), covariates whose coefficient crossed zero (Hastie et al. 2005) or varied strongly across the constraint range (F. Korner-Nievergelt, pers. communication) were identified and dropped from the set of candidate covariates. The *lasso* model was then rerun with the remaining set of covariates in a second iteration (Fig. 1b). Since every covariate whose coefficient collapses to zero has to be omitted from the model, a threshold, after which no more covariates are dropped, has to be selected at this point. Covariates that collapse after this threshold, usually at a high constraint (left side of the graph), can be looked at as important in relation to the response variable. We selected a threshold of four variables, meaning that the last four covariates whose coefficients collapsed to zero were regarded as important in relation to the response variable. We chose to select four covariates based on recommendations by Crawley (2012), stating to use one variable for every three observation points to avoid over-parameterization. Based on 17 years of data, therefore 17 observation points, and including the response variable and year, no more than four additional covariates should be selected. For the analyses of jay abundance and caterpillar abundance, it was possible to reduce the set of covariates with *a priori* hypotheses, so that no model reduction was necessary. Nevertheless, we ran *lasso* models for both response variables to evaluate whether any of the four selected covariates could be omitted from further analyses due to them crossing zero or varying across the constraint range as described above.

RESULTS

Rodents

After inspection of the model reduction graph, we identified and dropped four candidate covariates (“coldsum p1”, “icedays p1”, “snow days p2”, “frost days p2”, Fig. 1a) according to selection criteria described above, shrinking the set of initially 11 candidate covariates to seven for the second iteration. No third iteration was necessary and we found that “fructification in previous year”, “snow days p1”, “frost days p1” and “cold sum p2” were the four most important covariates in relation to “rodent abundance” (Fig. 1b). “Rodent abundance” was positively related to “fructification in previous year” and “snow days p1” and negatively related to “frost days p1”. “Rodent abundance” was not related to “cold sum p2”, based on large uncertainty (95% CI, Fig. 2) and model estimate < standard errors (Table 1).

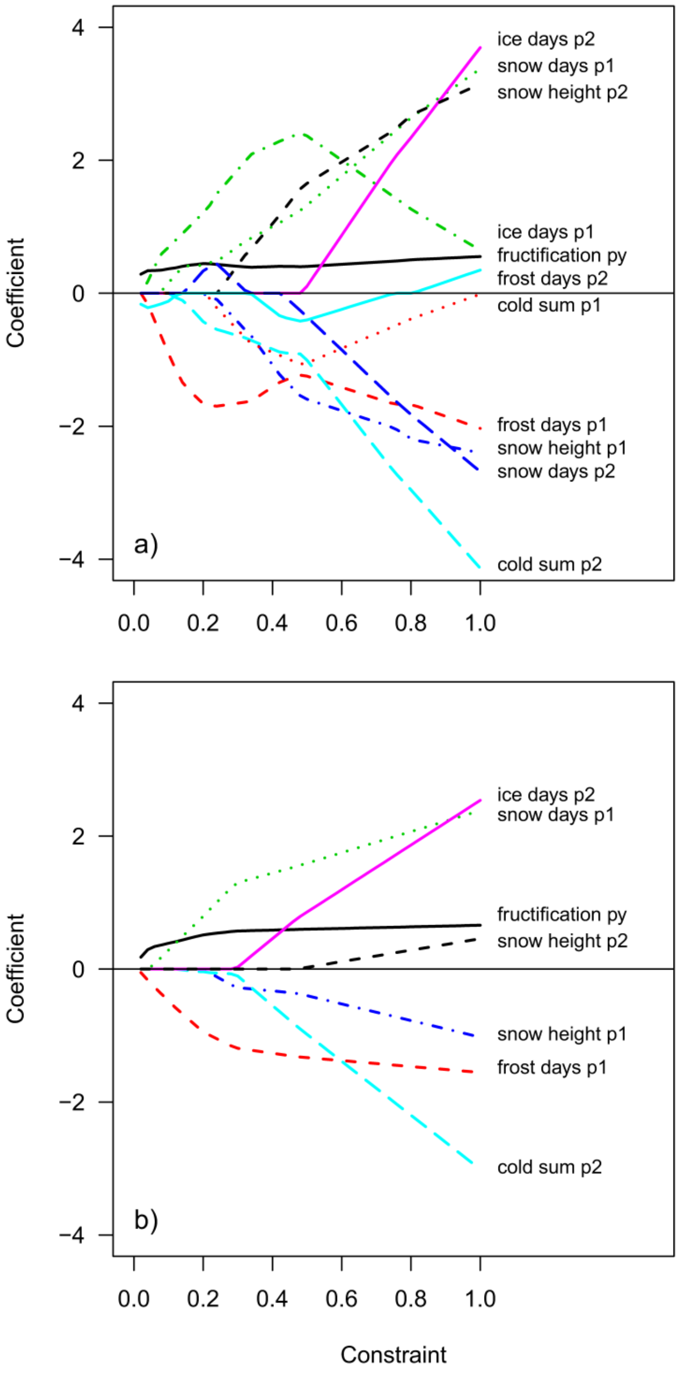


Fig. 1 Model reduction for the response variable “rodent abundance” using the *lasso* procedure. Each line, labeled with the covariate’s name on the right, represents the model coefficient per covariate across a constraint range from zero to one, where zero represents a constraint of 100% and one represents a constraint of 0%. Covariates shown in panel a) represent the maximum model assessed after the first iteration, during which covariates that crossed zero or varied strongly across the constraint range were dropped. Panel b) shows the result of the second iteration, where the *lasso* model was recomputed with the remaining set of covariates from iteration one. Year is included in the maximum and the reduced model but not shown as it is not put under the constraint.

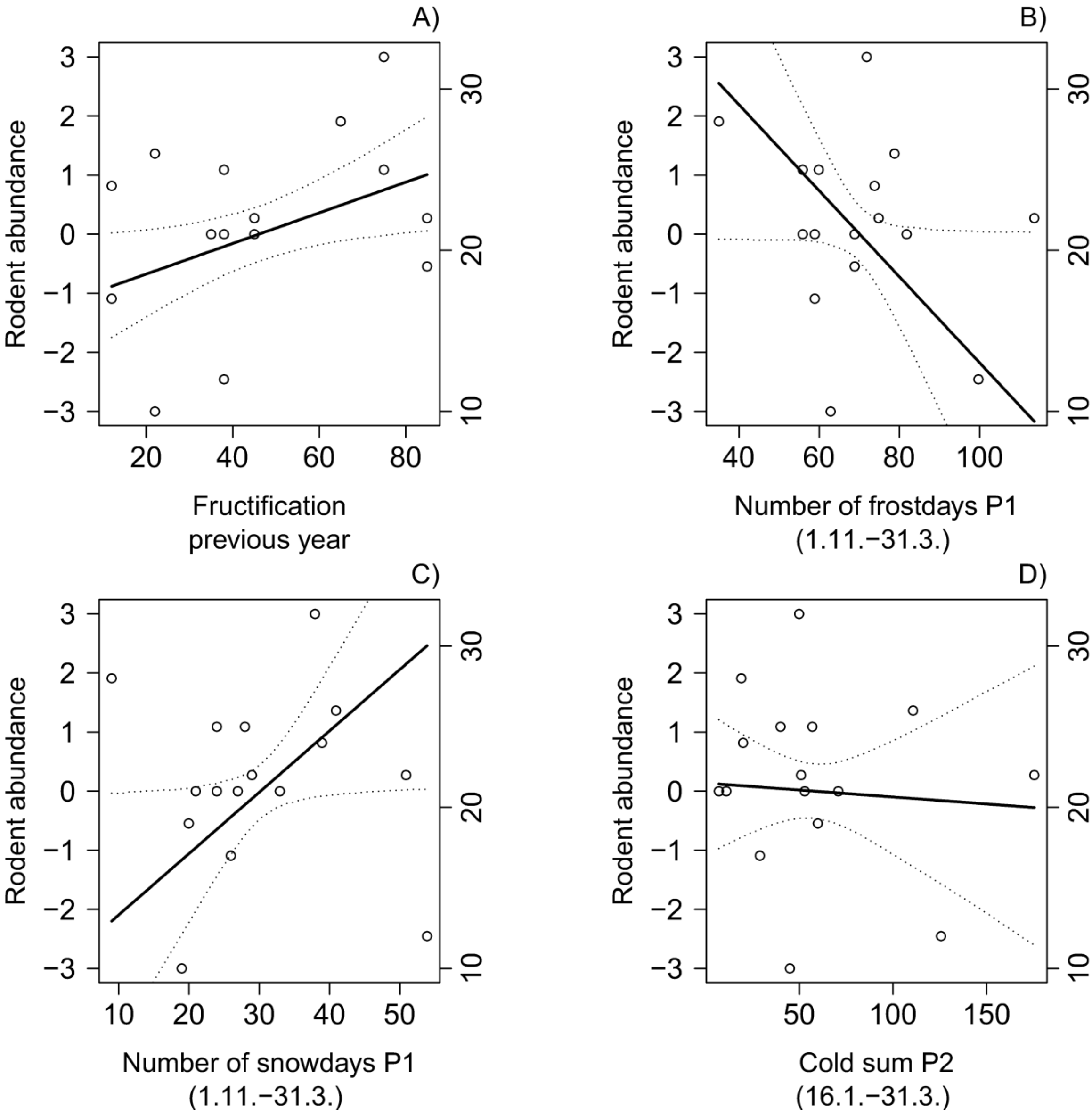
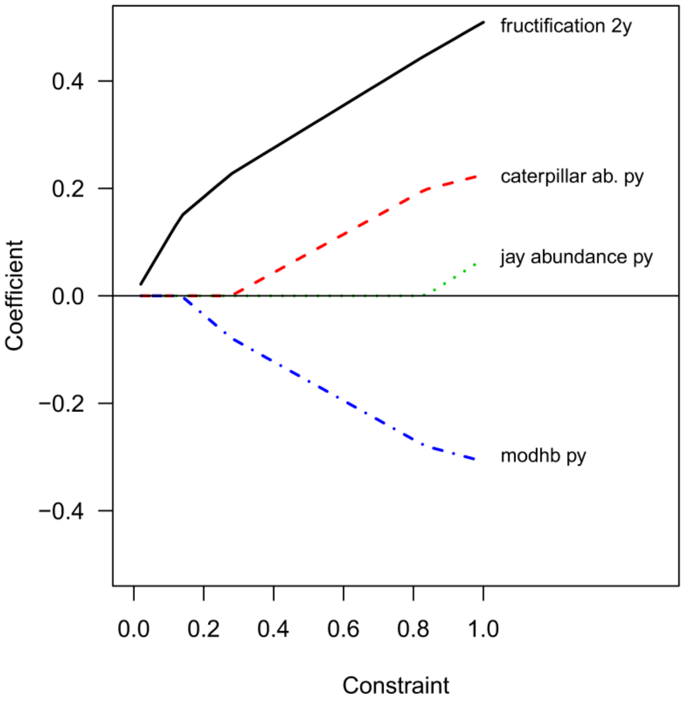


Fig. 2 “Rodent abundance “ in relation to A) “fructification previous year“, B) “number of frost days p1“, C) “number of snow days p1“ and D) “cold sum p2“. Each plot shows observed values (open dots), fitted values (solid lines) and 95% confidence intervals (dashed lines) based on a model including the four pictured covariates and year (Table 1). Covariates other than the one drawn were set to their mean. The left and right y-axes depict the scales for fitted and real values, respectively. Figure is based on the model detailed in Table 1.

Eurasian jays and caterpillars

For the analyses with response variables “jay abundance” (Fig. 3) and “caterpillar abundance” (Fig. 4), *lasso* modeling showed that none of the considered covariates had to be dropped according to criteria. We found that “jay abundance” was positively related to “fructification 2 years ago” and negatively related to “mean onset date of hazel bloom in previous year”. “Jay abundance” was not related to “caterpillar abundance in previous year" or to "jay abundance in previous year", based on large uncertainty (95% CI, Fig. 5) and model estimates < standard errors (Table 1). "Caterpillar abundance" was not related to "fructification in previous year", "mean onset date of hazel bloom" and spring temperature or rain (Fig. 6). The uncertainties (95% CI) for all four covariates evaluated in relation to "caterpillar abundance" were so large that the weak relationships between "caterpillar abundance" and the respective covariates were trivial (Fig. 6).



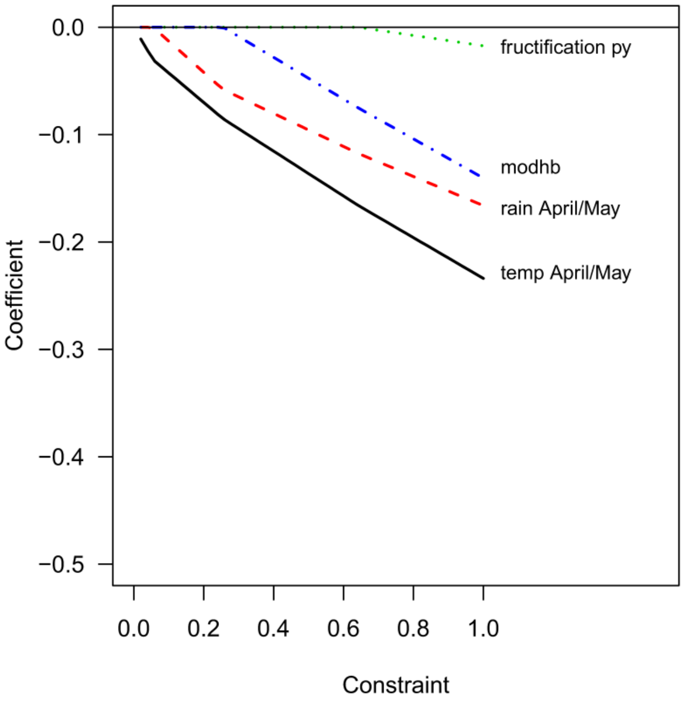


Fig. 3 Model reduction for the response variable "jay abundance" using the *lasso* procedure. Each line, labeled with the covariate's name on the right, represents the model coefficient per covariate across a constraint range from zero to one, where zero represents a constraint of 100% and one represents a constraint of 0%. Covariates, representing the full model, from top to bottom with explanation if necessary: "fructification 2y" = fructification of deciduous trees two years ago, "caterpillar ab. py" = caterpillar abundance in previous year, "jay abundance py" = jay abundance in previous year, "modhb py" = mean onset date of hazel bloom in previous year", year (this fixed effect is not shown as it is not put under the constraint).

Fig. 4 Model reduction for the response variable "caterpillar abundance" using the *lasso* procedure. Each line, labeled with the covariate's name on the right, represents the model coefficient per covariate across a constraint range from zero to one, where zero represents a constraint of 100% and one represents a constraint of 0%. Covariates, representing the full model, from top to bottom with explanation if necessary: "fructification py" = fructification of deciduous trees in previous year, "modhb" = mean onset date of hazel bloom", "rain April/May" = cumulative rainfall in mm in April/May, "temp April/May" = mean temperature in°C in April/May, year (this fixed effect is not shown as it is not put under the constraint).

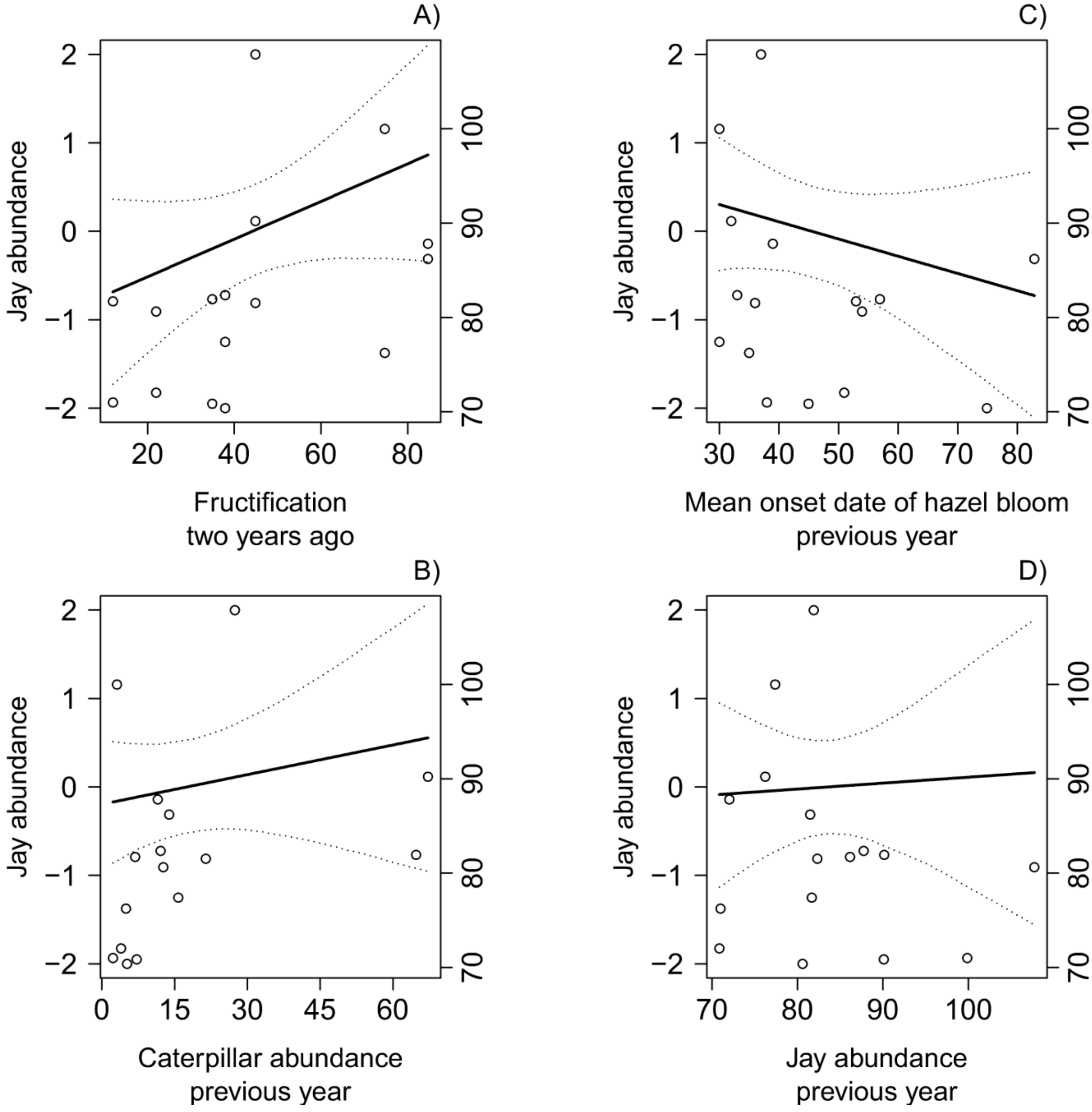


Fig. 5 “Jay abundance“ in relation to A) “fructification two years ago“, B) “mean onset date of hazel bloom previous year “ (1 = January 1^{st}), C) “caterpillar abundance previous year“ (scale = area fed on in ha x1000) and D) “jay abundance previous year“. Each plot shows observed values (open dots), fitted values (solid lines) and 95% confidence intervals (dashed lines) based on a model including the four pictured covariates and year (Table 1). Covariates other than the one drawn were set to their mean. The left and right y-axes depict the scales for fitted and real values, respectively. Figure is based on the model detailed in Table 1.

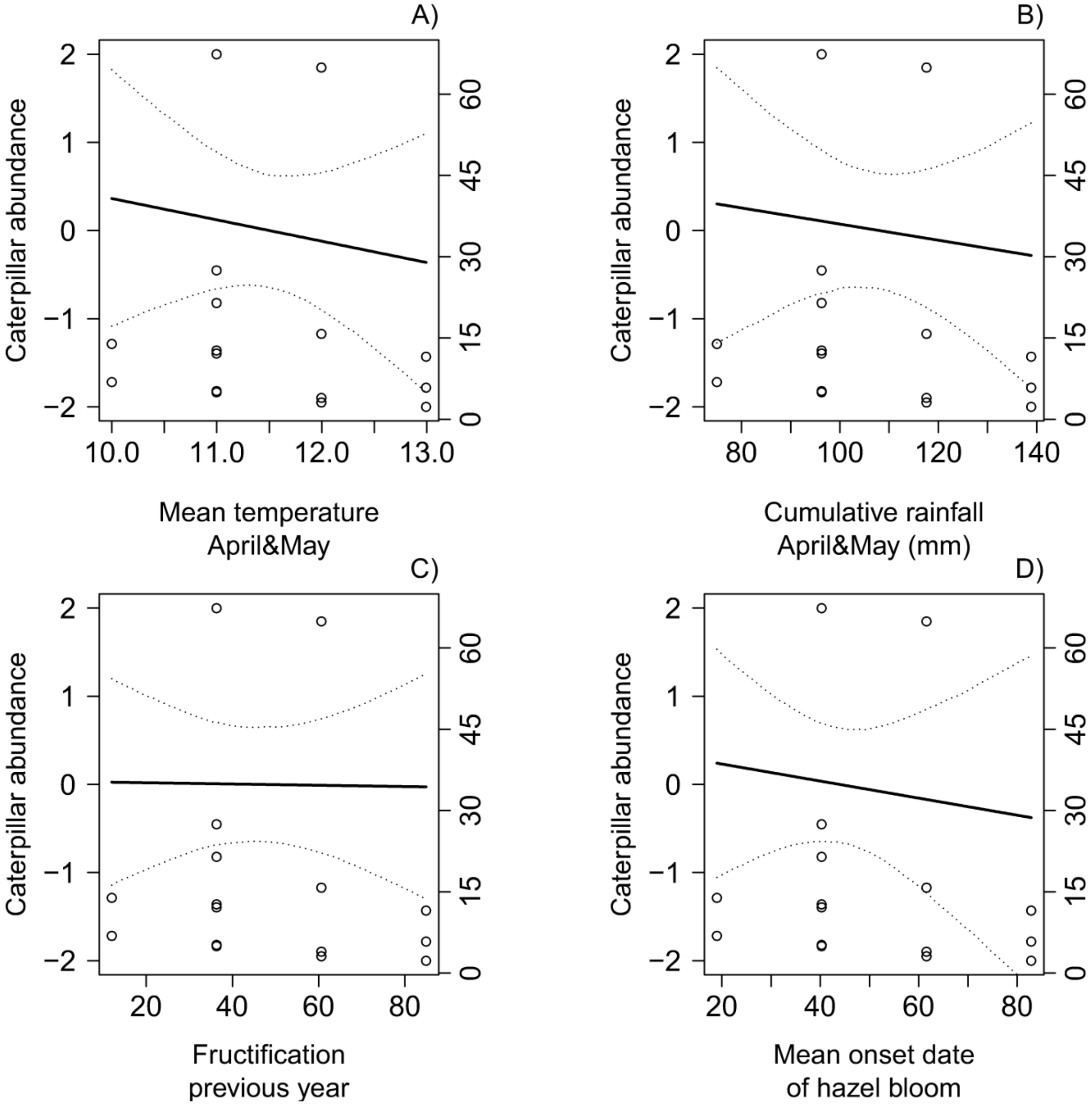


Fig. 6 “Caterpillar abundance“ in relation to A) “mean temperature in°C in April/May“, B) “cumulative rainfall April/May“, C) “fructification previous year“ and D) “mean onset date of hazel bloom “ (1 = January 1st). Each plot shows observed values (open dots), fitted values (solid lines) and 95% confidence intervals (dashed lines) based on a model including the four pictured covariates and year (Table 1). Covariates other than the one drawn were set to their mean. The left and right y-axes depict the scales for fitted and real values, respectively. Figure is based on the model detailed in Table 1.

Table 1. Final model for each of the four analyses, based on results from model reduction through *lasso*. Shown are model estimates and standard errors for each coefficient. Important covariates (estimate > standard error) are accentuated in grey. “py” stands for “previous year”, “2y” stands for “two years ago”, “p1” stands for winter period 1 (1.11. – 31.3.), “p2” stands for winter period 2 (16.1. – 31.3.).

Response variable	**Predictor variables**	**Estimate**	**Standard error**
Rodent abundance	frost days p1	-1.34	0.58
	snow days p1	1.24	0.51
	fructification py	0.63	0.23
	cold sum p2	-0.11	0.38
	year	0.15	0.21
Jay abundance	fructification 2y	0.51	0.29
	mean onset date of hazel bloom py	-0.31	0.24
	caterpillar abundance py	0.23	0.25
	jay abundance py	0.07	0.30
	year	0.24	0.26
Caterpillar abundance	fructification py	-0.02	0.29
	mean temperature April/May	-0.23	0.36
	cumulative rainfall April/May	-0.17	0.33
	mean onset date of hazel bloom	-0.14	0.35
	year	0.28	0.31
Wood warbler abundance	rodent abundance	-0.37	0.08
	cumulative rainfall April/May	0.33	0.09
	jay abundance	-0.12	0.08
	caterpillar abundance	0.09	0.08
	year	-0.89	0.09

Wood warblers

Only one *lasso* iteration was necessary to assess wood warbler abundance in relation to the selected covariates. “Rodent abundance”, “cumulative rainfall in mm in April/May”, “jay abundance” and “caterpillar abundance” were the four most important covariates for explaining variation in “wood warbler abundance”. “Rodent abundance” was the most important covariate, as its coefficient collapsed to zero last (Fig. 7). Specifically, “wood warbler abundance” was higher in years with low rodent numbers (Fig. 8a). An almost equally important covariate in relation to “wood warbler abundance” was “cumulative rainfall in mm in April/May. “Wood warbler abundance” increased with the amount of rain, at least within the measured range of rainfall (Fig. 8b). “Jay abundance” and “caterpillar abundance” were less important covariates in relation to “wood warbler abundance” as their coefficients collapsed to zero at larger constraints (Fig. 7). Due to small uncertainties (95% CI) the relationships between wood warbler abundance and jay abundance (Fig. 8c) as well as between “wood warbler abundance” and “caterpillar abundance” (Fig. 8d) were weak but statistically relevant (Table 1).

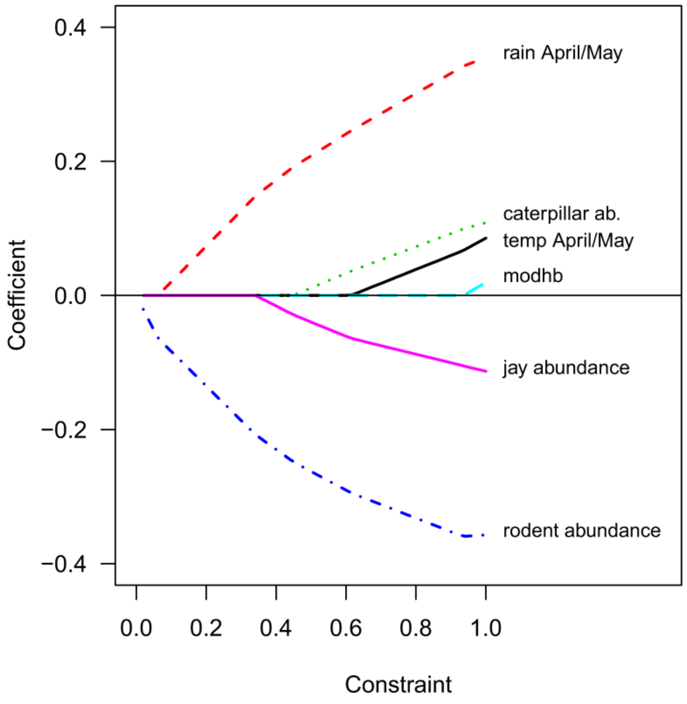


Fig. 7 Model reduction for the response variable “wood warbler abundance” using the *lasso* procedure. Each line, labeled with the covariate’s name on the right, represents the model coefficient per covariate across a constraint range from zero to one, where zero represents a constraint of 100% and one represents a constraint of 0%. Covariates, representing the full model, from top to bottom with explanation if necessary: “rain April/May” = cumulative rainfall in mm in April/May, “caterpillar ab.” = caterpillar abundance, “temp April/May” = mean temperature in°C in April/May, “modhb” = mean onset date of hazel bloom”, “jay abundance”, “rodent abundance”, year (this fixed effect is not shown as it is not put under the constraint).

DISCUSSION

Rodents

In a resource pulse driven temperate forest ecosystem, rodents are among the first to profit from seed masts. As hypothesized, rodent abundance in our study increased with increasing fructification of deciduous trees in the previous fall. This finding is in line with results of other studies investigating the connection between seed mast and rodent abundance. Following a seed mast in eastern U.S. oak forests, rodent numbers increased 15-fold compared to the previous year without preceding mast (Jones et al. 1998). In our study system, we recorded a three-fold increase in rodent numbers. Such an increase is explained by the interaction between increased overwinter survival and overwinter breeding, resulting in larger summer densities compared to years without preceding mast (Wolff 1996). *Apodemus sylvaticus* and *Myodes glareolus* extended their breeding season into winter only following a seed mast (Smyth 1966, Watts 1969). Rodent densities peaking about 1 year and crashing to a very low level about 1.5 years after acorn mast was a typical pattern observed by Ostfeld et al. (1996) over at least a decade.

Winter climate appeared to be another important covariate explaining variation in rodent abundance. We found that rodent abundance was positively related to number of days with snow cover between November and March, but was not related to cumulative snow height in the same period. These findings suggest that a continuous snow cover resulting from more snow days is more important than snow cover that may have variable height throughout the winter. It has to be noted here, that snow days and (cumulative) snow height strongly and positively correlated with each other ($r(14) = 0.904$, $p < 0.001$). Snow cover has been suggested to be important for rodent winter survival, as it probably decreases hunting efficiency and success of predators. Lindström and Hörnfeldt (1994) found that weight of small rodent remains in stomachs of foxes was negatively correlated to snow depth, indicating reduced hunting of rodents resulting from snow cover. Hansson and Henttonen (1985) found positive correlations between all indices of rodent density and duration, as well as thickness of snow cover, indicating that rodents suffered decreased mortality when protected by snow cover. On the other hand, snow cover has also been found to have negative effects on rodents by encasing vegetation in ice and thereby limit access to food sources above ground (Korslund and Steen 2006). In winters following seed masts, however, rodents benefit from stocked underground seed caches and therefore might not suffer from reduced access to vegetation by snow cover, but profit from the snow cover's anti-predation effect. Despite seed caches after seed masts, winter is a demanding time for small mammals, as energy expenditure increases with decreasing temperatures (Ergon et al. 2004). We found number of frost days between November and March to be an important covariate related to rodent abundance, with rodent populations decreasing as number of frost days increased.

Jays

We could confirm our hypothesis that seed mast two years ago was positively related to jay abundance. We speculated that increased overwinter survival probably lead to more breeding pairs in the following spring and consequently resulted in higher juvenile recruitment. While cached seeds are used by adult birds to better cope with increased energy demands during winter, cached seeds may play an even more important role as supplementary food during nesting and post-fledging parental care (Bossema 1979). Most young jays fledge in June (Glutz von Blotzheim et al. 1991) and are still fed by their parents for several weeks, with tree seeds and their cotyledons making a large portion of the food provided (Bossema 1979). In contrast to rodent populations, which first increase to very high levels and subsequently crash to very low levels within about one year after a seed mast, jay populations may follow a pattern similar to that of rodent-hunting raptors described in Schmidt and Ostfeld (2003). In their study, Cooper's hawk (*Accipiter cooperii*) and Sharp-shinned hawk (*Accipiter striatus*) showed positive numerical responses to seed masts two years ago and rodent densities one year ago. After a jay population increases due to increased juvenile recruitment in the summer following a seed mast, jay numbers appear to remain relatively high until the next spring even without another seed mast.

Jay abundance was negatively related to mean onset date of hazel bloom in the previous year, that is, jay abundance was higher, the earlier hazel bloom had commenced in the previous year, as we hypothesized. The timing of breeding with spring plant phenology has been shown in various bird species. Both great tits (*Parus major*) and blue tits (*Parus caeruleus*) for example, adjusted their egg-laying according to leafing out of deciduous trees (Nilsson and Kallander 2006), with further species-specific adjustments of laying date in relation to the main tree species used for foraging. We do not claim that jays use onset of hazel bloom directly as cue to start breeding. We used onset of hazel bloom as proxy for the beginning of spring and argue that jays have increased reproductive success in years with an “earlier spring”. We hypothesize that the earlier breeding commences, the more time juveniles have establish a territory and prepare for winter (put on fat reserves, stock food caches). Our hypothesis is supported by the timing-of-breeding-hypothesis predicting decreasing reproductive performance as the season progresses, a pattern found in many bird species (Naef-Daenzer et al. 2001, Grant et al. 2005). As a result of earlier breeding, juvenile recruitment of jays may increase and result in larger jay populations one year later.

Caterpillars

We found no evidence that caterpillar abundance was linked to seed masting in the previous year. We had hypothesized that caterpillar abundance would be negatively related to seed masts. Decreased leave quality, due to reduced nutrient concentration following seed masts (Obeso 2002), can negatively impact certain developmental traits of caterpillars such as growth rate (Barbehenn et al. 2015), thereby rendering caterpillars more vulnerable to predation (slow-growth-high-mortality-hypotheis; Benrey and Denno 1997). As there is general consent that caterpillar development is linked to leaf quality, but less consent concerning the link between vegetal growth and/or quality and seed masting, we suspect that deciduous trees considered in our study did not exhibit decreased leaf quality in favor of reproductive growth: consequently, caterpillar abundances were not negatively affected by seed masts of these trees.

Caterpillar development is linked to rain (Hagstrum and Milliken 1988), spring plant phenology (e.g. Thacker et al. 1997) and especially temperature (Bell 1975, Hagstrum and Milliken 1988). Since we found no link between caterpillar abundance and temperature, rainfall or spring plant phenology, we suspect that variation in these factors was not large enough to influence caterpillar phenology in our study system, or that they only affect development but not abundance. Alternatively, we may not have found a pattern in the data because caterpillar abundance was measured at a smaller spatial scale than mast, hazel bloom, temperature and rainfall.

Wood warblers

The consequences of resource pulses for populations of songbirds have been described in various studies. Over a 24-year study period, nests of the dark-eyed junco (*Junco hyemalis*) in the southern Appalachian Mountains, USA, were more likely to fail in years with increased rodent and raptor abundance, where raptor abundance was related to rodent abundance and rodent abundance related to seed mast in the previous year (Clotfelter et al. 2007). In southeastern New York, USA, predation on nests of veeries (*Catharus fuscescens*), red-eyed vireos (*Vireo olivaceus*) and wood thrushes (*Hylocichla mustelina*) increased with increasing rodent densities following a seed mast. Increased rodent densities triggered a numerical response of raptors, thereby decreasing songbird abundance (Schmidt and Ostfeld 2003). And in Virginia, USA, abundances of worm-eating warblers (*Helmitheros vermivorus*) and hooded warblers (*Wilsonia citrina*) were negatively correlated to seed masts two years ago, mediated through increased rodent and nest predator abundances (McShea 2000). We found a similar pattern in Switzerland, where high rodent numbers in rodent outbreak years triggered a numerical response by rodent-hunting mammalian predators. In rodent outbreak years, occurrence of rodent-hunting mammals was higher, proportion of predations on wood warbler nests by rodent-hunting mammals was higher and daily nest survival rate of wood warbler was lower compared to rodent crash years (chapter 3 of this thesis).

In this study, wood warbler abundance was positively related to caterpillar abundance and cumulative rainfall in April/May and negatively related to jay abundance and rodent abundance. That wood warbler abundance was negatively related to number of rodents in the same year is a recurring result found by every study investigating the link between wood warbler settlement or abundance and rodent abundance. In Switzerland, breeding territory occupancy of wood warblers was strongly and inversely related to rodent abundance (Pasinelli et al. accepted, BMC Ecology), illustrating the negative effect rodents appear to have on wood warblers at the territory scale. At the forest stand scale, wood warbler numbers were negatively correlated to rodent numbers in Białowieża Forest, Poland (Wesołowski et al. 2009), with low wood warbler numbers in rodent outbreak years. Finally, at the landscape scale in Poland, wood warbler densities were strongly and negatively related to rodent occurrence (Szymkowiak and Kuczyński 2015). The specific mechanisms underlying the avoidance of rodent-rich habitats by wood warblers remain unclear. Rodent predation on wood warbler nests has been argued to be important (Mildenberger 1940, Wesołowski et al. 2009), but tangible evidence such as pictures from camera surveillance is scarce: there were no rodent predations reported by Mallord et al. (2012b) or Grendelmeier et al. (2015). However, in the last of six years monitoring wood warbler nests, two predations by rodents could be

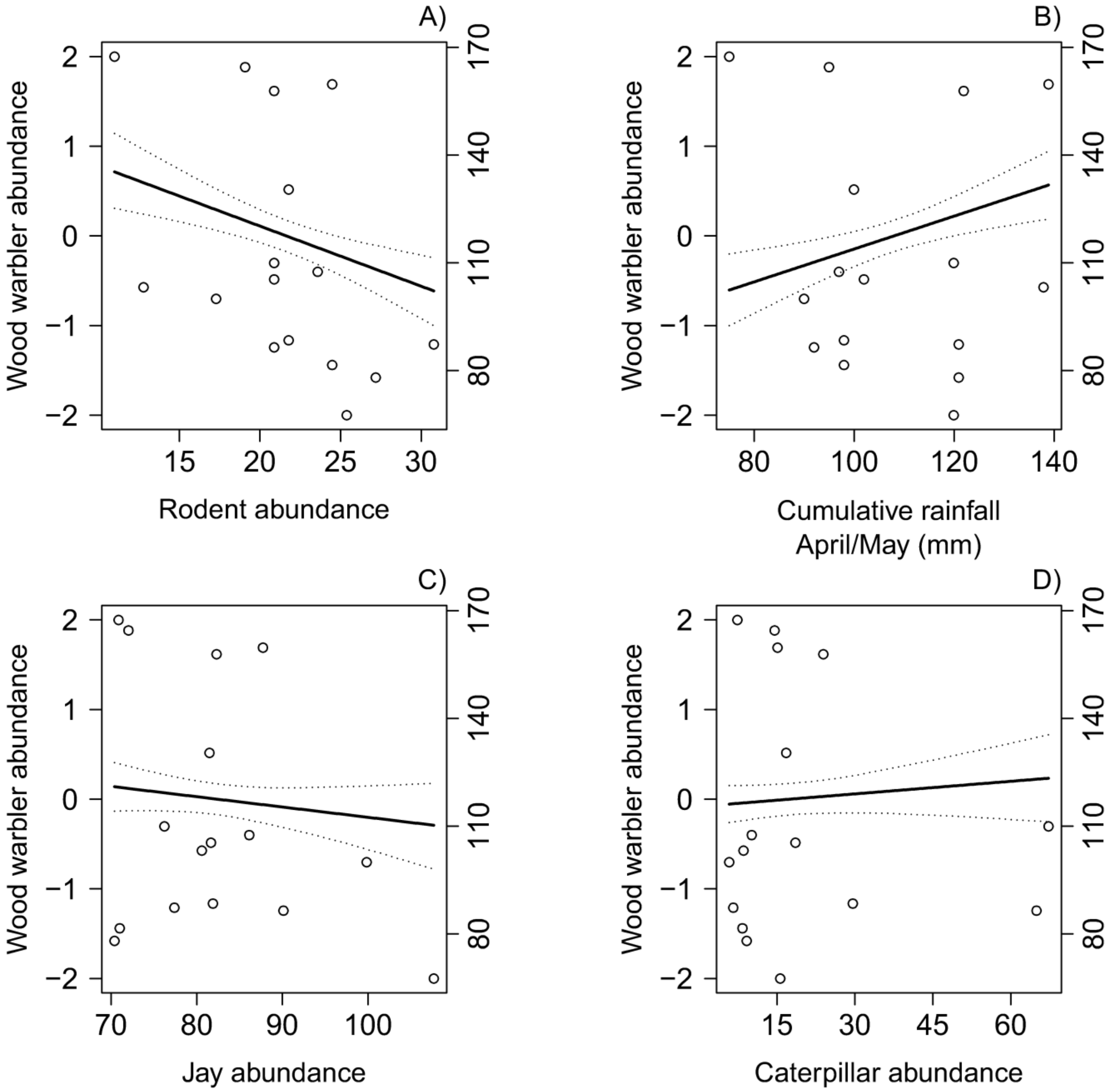


Fig. 8 “Wood Warbler abundance“ in relation to A) “cumulative rainfall April/May“, B) “rodent abundance“, C) “jay abundance“ and D) “caterpillar abundance“ (scale = area fed on in ha x1000). Each plot shows observed values (open dots), fitted values (solid lines) and 95% confidence intervals (dashed lines) based on a model including the four pictured covariates and year (Table 1). Covariates other than the one drawn were set to their mean. The left and right y-axes depict the scales for fitted and real values, respectively. Figure is based on the model detailed in Table 1.

filmed in Switzerland (own unpublished data). Scarce rodent predations on wood warbler nests are not due to cameras not triggering, as rodents are often seen bypassing and even inspecting active wood warbler nests without predation occurring. Moreover, 26 of 31 unsuccessful artificial nests (84%) monitored with cameras were predated by rodents (Grendelmeier 2011). We thus argue that rodents are not an important predator of wood warbler nests per se, but may be perceived as threat by wood warblers regardless. Whether wood warblers are able to connect fluctuating rodent numbers to rodent-hunting predators remains to be studied.

We hypothesized that wood warblers may evaluate prevailing weather conditions upon arrival on the breeding grounds in spring. Wood warbler abundance was not related to mean temperature, but, contrary to our hypothesis, positively related to the amount of rainfall in April/May. Multiple studies showed that breeding performance was related to amount and/or duration of rain in spring, often with a negative relationship (Krüger 2002, Rodriguez and Bustamante 2003, Bordjan and Tome 2014, Oberg et al. 2015). However, published evidence for a relationship between breeding abundance and weather conditions as assessed here is scare. Breeding abundance is generally regulated by a combination of survival, reproduction, emigration and immigration (Mills 2012), but for a local wood warbler population, analyzing the relative contributions of the above factors seems to be pointless due to its nomadic behavior. We propose three hypotheses to explain the positive relationship between wood warbler abundance and spring rain. 1) Water is of great importance for plants, due to the process of photosynthesis; and for ecosystem in general as water is a principal driver of ecosystem productivity (Taiz and Zeiger 2006) which consequently also shapes wood warbler habitat. 2) Water is important for development of insect larvae. Hagstrum and Milliken (1988) argue that moisture is important in altering feeding rate of larvae or the efficiency with which larvae can assimilate and convert their diet. In our study, wood warbler abundance was positively related to Lepidoptera larvae, further discussed below. 3) As plant phenology and insect development, respectively, are linked to rain, spring rain may simply be one of the cues wood warblers use to select their territory.

Wood warbler abundance was negatively related to jay abundance, as also found in Poland (Szymkowiak and Kuczyński 2015). Jays are important predators of nests of various bird species in general (Stevens et al. 2008, Weidinger 2009) and of wood warblers in particular (Mallord et al. 2012b, Grendelmeier et al. 2015). Birds have been shown to assess avian predator occurrence by simply eavesdropping on their vocalizations (Eggers et al. 2005). Arriving from migration in spring, wood warblers might be able to assess jay abundance and keep migrating to find saver breeding grounds if jay abundance is deemed too high.

Lastly, we found evidence that wood warbler abundance was positively related to caterpillar abundance, as hypothesized. Even though wood warbler diet includes imago stages of Lepidoptera, Diptera, Mecoptera, Neuroptera, Ephemeroptera, Dermeptera, Hymenoptera, Hemiptera, Arachnida, Gastropoda and very seldom vegetal matter (Glutz von Blotzheim et al. 1991), caterpillars constitute the most important food components fed to nestlings, even when caterpillar abundance decreases with progressing season (Maziarz and Wesołowski 2010). There is no apparent overlap of wood warbler territories with areas of increased caterpillar abundance (Herremans 1993), but wood warbler abundance has been shown to be positively correlated with caterpillar abundance (Wesołowski et al. 2009, Kühn 2015).

CONCLUSION

We found that resource pulses initiated by seed masts are also found in Germany’s temperate forests. Our results suggest that a seed mast event appears to negatively influence wood warbler abundance for up to two years. Rodents are an important component of forest ecosystem food webs. They may be regarded as direct threat by wood warblers or taken as proxy for overall predation risk. Indeed wood warbler abundances are related to both rodent and jay abundances, with rodent abundances being more important. Wood warblers likely track rodent abundances in the spring following a seed mast and jay abundances two springs after a seed mast to avoid areas of high predation risk stemming from different predators. This study adds to the knowledge of how multiple taxa at multiple trophic levels interact in a temperate forest ecosystem community.

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Synthesis

General aims

The main goal of this PhD thesis was to examine several aspects associated with demography and life-history of the wood warbler. Wood warbler populations have declined since the 1980ies in many European countries, with short term (since 2000) stabilization of populations in some countries (http://bd.eionet.europa.eu/article12 /summary?period=1&subject=A314, accessed February 28, 2016). A long term decline with short term stabilization of wood warbler populations can also be observed in Switzerland (http://www.vogelwarte.ch/de/voegel/voegel-der-schweiz/ waldlaubsaenger.html). In some areas of Switzerland however, especially on the central plateau, the species has almost completely disappeared from (example: Canton of Zürich; http://www.birdlife-zuerich.ch/vogelfinder/atlas-nach-vogelarten/ vogel/waldlaubsaenger/, accessed February 28, 2016). To investigate this decline and to ultimately develop evidence-based conservation measures, the project, of which this PhD is a part of, was conceived to acquire base line data on the ecology and behavior of the wood warbler and its niche requirements in Switzerland. Though basic ecological requirements were already known for the wood warbler from other countries, Switzerland at the periphery of the distribution range may exhibit different biotic and abiotic influences (Lesica and Allendorf 1995), warranting an additional assessment of basic ecological needs of the species.

The wood warbler spends only about a fourth of the year in Europe with the specific goal to reproduce. So research and conservation efforts limited to Europe have to focus on aspects surrounding reproduction: is there enough breeding habitat available, how is the breeding habitat selected, is available breeding habitat adequate for successful reproduction, how does reproduction compare to other areas and what are the limiting factors to reproduction (e.g. predation, competition, disturbance). Therefore this PhD project examined several aspects pertaining to territory selection and reproduction alongside various partner studies within the same project.

As one partner study already assessed the relationship between wood warbler settlement and various biotic / abiotic factors, I assessed in more detail the evidence for a social component in territory selection. Using playback of wood warblers song, I experimentally tested the conspecific attraction hypothesis and followed up with an evaluation of reproductive performance. In relation to reproductive performance, I evaluated various biotic and abiotic factors. One such factor often discussed in relation to wood warblers is rodents. While it has repeatedly been shown that wood warbler abundances relate negatively to rodent abundances from the territory to the landscape scale (Wesołowski et al. 2009, Szymkowiak and Kuczyński 2015; Pasinelli et al. accepted, BMC Ecology, chapter 4 of this thesis), the underlying mechanisms have remained unknown. I assessed the relationship between wood warbler reproduction and rodent abundance and factored in the role of rodent-hunting predators. Biotic and abiotic factors influencing settlement and reproduction ultimately determine local and annual abundance. It is important however to evaluate various factors at different spatial scales, as the importance of factors may depend on the spatial scale considered. Based on a long term dataset on the landscape scale I therefore assessed wood warbler abundance in relation to rodents, predators, seed mast, caterpillars, phenology and weather.

Wood Warblers

Long distance-migrants like the wood warbler have to make a decision where to settle very quickly upon arrival on the breeding grounds. Evaluating a potential breeding habitat in terms of biotic and abiotic factors may be lengthy and inefficient. The experience and interaction with the physical environment of other birds can be exploited by conspecifics to make a settlement decision (Valone 2007, Ahlering et al. 2010). As outlined in chapter one, I found that on average three times more territories were established on plots with song playback compared to control plots without song playback. On song plots, settlement occurred faster and maximum plot occupancy was higher compared to control plots. Overall reproductive performance and output did not differ between song and control plots, but I found increased brood reduction on song plots. I found evidence for extra pair copulations both on song and control plots. My results suggest that public information from conspecifics is an important factor for wood warblers during territory selection. Similar reproductive output on song and control plots and increased rates of brood reduction on song plots give reason to further evaluate the usefulness of this method for conservation purposes. The ability to rule out the creation of an ecological trap is imperative, should conspecific attraction be used as conservation measure. Nonetheless, social cues are an important factor in territory selection of birds, which research has recognized and answered with increasing incorporation in studies (Ahlering et al. 2010). This chapter also exemplifies the importance to monitor and evaluate reproductive performance during and following experimental treatments.

Monitoring reproductive performance is important not only following experimental treatment, but also to generally understand the demography of a species. Based on three years of data (chapter two), I found that clutch size and number of fledglings decreased, the later in the season a nest was initiated, a trend found for many bird species (Naef-Daenzer et al. 2001, Grant et al. 2005, Müller et al. 2005, Peak 2007). I also found that daily nest survival was positively related to the number of grass and sedge tussocks, nest concealment and nest age. Number of grass tussocks in a territory may be important in providing adequate nest building material. It is conceivable that number of grass tussocks also factors into nest concealment, which is an important anti-predation mechanisms (Martin et al. 2000, Weidinger 2002, Müller et al. 2005). Increasing nest age also increases the chance of a nest being found by predators just by chance. Furthermore, nestlings become increasingly active and vocal, further increasing the chance of attracting predators (Martin et al. 2000, Burhans et al. 2002, Haff and Magrath 2011).

As for many bird species, reproductive success of wood warbler is mostly limited by predation, committed by different predator species. Annually varying predator assemblages may be tightly linked to intermittent resource pulses in form of seed mast by various deciduous tree species. By monitoring wood warbler nests, I could confirm that, apart from number of grass tussocks, nest concealment and nest age, wood warbler daily nest survival rate was negatively related to rodent abundance. Even in rodent outbreak years, rodents are however not an important predator of wood warbler nests, but I found a rodent-mediated numerical response by rodent-hunting mammals. In forest-rodent outbreak years, number of rodent-hunting mammals is higher and the proportion of nests predated by rodent-hunting mammals is also higher than in forest-rodent crash years (chapter three). Collectively, these findings suggest that rodent-hunting mammals exhibit a numerical response to rodent outbreaks and that there is no behavioral response by the species studied in this thesis that affects wood warblers. After a numerical response, it is possible that in some predator prey systems, rodent-hunting predators exhibit an additional behavioral response (prey switching). This change in response types may occur when rodent-hunting predators numerically increase due to high rodent abundances, but fail to sustain rodent predation once rodent populations crash. Predators may then switch to alternative prey such as song birds (Jedrzejewska and Jedrzejewski 1998). In our study systems, prey switching does occur, but not with wood warblers as alternative prey. Because our study sites are situated within a fragmented landscape, especially red foxes and possibly stone martens switch from mainly foraging in forest patches back to mainly foraging in adjacent agricultural fields and meadows (Jędrzejewski and Jędrzejewska 1992). Though mammalian carnivores (red foxes and martens) were the most abundant predators of wood warbler nests in Switzerland, I also identified a wide variety of avian and other mammalian generalists and specialists.

It is known that the underlying mechanism behind rodent outbreak and crash years are resource pulses initiated by seed mast of various deciduous tree species (Ostfeld et al. 1996, Wolff 1996). Resource pulses can be very influential in an ecosystem, initiating cascading effects up and down the food chain, over multiple years. In chapter four I tested how primary and secondary resource pulses, together with other biotic and abiotic factors, are connected to wood warbler abundance. I found that wood warbler abundance was negatively related to rodent and jay abundance and positively related to cumulative rainfall in April and May and caterpillar abundance. Though not directly, seed masts appear to negatively influence wood warbler abundances for up to two years, by triggering numerical responses of rodents, jays and rodent-hunting mammals (discussed below). Wood warblers may view rodents as direct threat, which they are to some degree, or take their presence as proxy for overall predation risk to avoid rodent-rich areas. In the first breeding season of wood warblers in the spring of year t+1 after seed masting (year t), wood warblers may primarily track rodent populations, as rodents may be perceived as the greatest threat at that point. Because rodent populations crash roughly one year after seed masting, one may think that wood warbler populations should be larger in the second breeding season (year t+2). However, coinciding with the rodent crash in fall of year t+1, jay populations reach peak abundance. I hypothesized that peak jay abundances in fall of year t+1, suffer only small declines during winter. Consequently jay populations would still be higher than normal (no seed masting two years ago) in the second breeding season of the wood warbler in year t+2. Upon arrival on breeding grounds, that exhibited seed masting two years ago, wood warblers would find habitats with low rodent numbers but high jay numbers and therefore still avoid these areas. I propose that wood warblers assess predation risk based on some threshold, by tracking rodent and jay abundances. Finding this threshold was not aim of this thesis, but could be a subject for future research to further understand the interplay between wood warbler settlement and predation risk.

Rodents

I found that rodent abundance increased with increasing fructification of deciduous trees in the previous fall (chapter four), a result found in various studies investigating the connection between seed masts and rodents (Ostfeld et al. 1996, Wolff 1996). Rodent abundance was also positively related to number of days with snow fall between November and March but not to cumulative snow height in the same period. A continuous snow cover has been shown to increase rodent survival as it decreases hunting efficiency and success of predators. Despite increased food availability from seed caches and predation protection from snow cover, winter is a demanding time for small mammals. Rodent abundance was negatively related to number of frost days between November and March. Rodents are an important taxon for an ecosystem for multiple reasons. Rodents are important seed disperser for various plants, by relocating seeds farther away than abiotic dispersal (e.g. wind) could achieve (Vander Wall 2001). Seeds are of such importance to rodents that years with high seed crops (mast years) result in increased spring rodent populations due to increased over-winter survival and breeding. Rodents also play a vital role as staple food source for various carnivores. Rodent populations can influence growth and decline of various rodent-hunting predators (Jedrzejewska and Jedrzejewski 1998), or attract rodent-hunting predators to areas where they would normally occur less frequently. Due to rodent-mediated predation by rodent-hunting predators, rodents can also influence abundance and reproduction of alternative prey species such as certain song birds, like the wood warbler in this thesis (chapters three and four).

Mast, predators and prey

Seed masts are important ecological events within an ecosystem, often constituting a primary resource pulse that can result in subsequent secondary and tertiary pulses of seed consumers and predators hunting these seed consumers (Schmidt and Ostfeld 2008). I found that jay abundance was positively related to seed masting two years ago and negatively related to mean onset date of hazel bloom in the previous year (chapter four). Jays are another important tree seed disperser besides rodents.

Jays' radius of operation exceeds that of rodents, thereby dispersing seeds even farther from the parent plant compared to rodents (Vander Wall 2001). While trees profit from jays' dispersal of tree seeds, jays profit from tree seeds as a staple food source during winter, but also in spring and summer, especially following a seed mast (Bossema 1979, Glutz von Blotzheim et al. 1991). Despite being a secondary pulse species that utilizes seeds directly, jays take longer to show a numerical response linked to seed masting compared to rodents. Such a delayed response is a consequence of slower reproductive cycles of larger animals compared to reproductive cycles of rodents. Similar delayed numerical responses, such as the one of jays, can be observed in tertiary pulse species, specifically rodent-hunting birds of prey (Schmidt and Ostfeld 2003). How important the above described response pathway is for mammalian rodent hunters (red foxes and martens) is difficult to say, as these generalist predators can utilize a wide variety of food items, including vegetal matter (Lanszki et al. 2007, Posłuszny et al. 2007), during rodent crash phases. In this thesis, I found that the occurrence of red foxes, but not martens, as well as the proportion of predated nests by foxes and martens, was higher in rodent outbreak years compared to rodent crash years (chapter three), suggesting a numerical response by these rodent-hunting mammals. It has to be noted that a numerical response does not necessarily mean a population increase. The reproductive cycle of rodent-hunting mammals can be similarly long to that of birds of prey discussed in Schmidt and Ostfeld (2003) or even longer due to delayed implantation in martens (Zalewski et al. 1995). Rodent-hunting mammals are therefore not able to respond with an immediate, intrinsic population increase. A numerical response, as referred to in this thesis, can also occur when rodent hunting mammals are attracted to forest patches due to increased rodent numbers during outbreak years. Rodent-hunting mammals do occur in wood warbler habitat during rodent crash years, but to a lesser extent. In addition, it is conceivable that rodent-hunting mammals' search intensity is increased when hunting rodents in forests during rodent outbreak years. As a side effect, incidental prey, such as wood warblers and their nests, is also found at a higher rate.

Wood warblers themselves are predators of various insects, especially Lepidoptera larvae fed to nestlings. The size of local wood warbler populations has been shown to correlate positively with caterpillar abundance (Wesołowski et al. 2009, Kühn 2015, chapter four of this thesis). Caterpillars are not only an important food item for wood warbler, but also for jays (Bossema 1979) and many other bird species (Glutz von Blotzheim et al. 1991), so caterpillars play an important role in the forest food web. Caterpillar abundance was not related to any of the covariates (onset date of hazel bloom in spring, spring temperature, spring rain) examined in this thesis.

Resource pulses

Resource availability is important in relation to structure and dynamics of ecosystems, determining consumer density, biomass and growth rates (Nowlin et al. 2008). Sometimes, resource availability increases drastically within a very short time and for a short duration. Such resource pulses can be triggered by biotic or abiotic factors and affect various trophic levels in various ecosystems: agricultural and arid landscapes, tropical, temperate and boreal forests, freshwater and marine habitats, riparian and wetland habitats (Yang et al. 2010). It has been suggested that there may be large differences how consumers respond to resource pulses between ecosystems, especially between aquatic and terrestrial systems (Nowlin et al. 2008). In their review, Yang et al. (2010) suggest that aquatic and terrestrial systems exhibit differences in the characteristics of their resource pulse and consumers, but also similarities in their resource-pulse-consumer dynamics. Terrestrial systems show longer response lags, but also longer response durations to resource pulses compared to aquatic systems. Longer response lags and durations are in part a consequence of longer generation times of terrestrial consumers and reduced effects of top-down control in terrestrial ecosystems (Nowlin et al. 2008, Yang et al. 2010).

Our findings on seed masting, rodent outbreaks and numerical responses of rodent-hunting mammals fit in well with findings of Yang et al. (2010) concerning factors influencing consumer responses. They found that consumer response magnitude was related to resource pulse magnitude and resource trophic level and that consumer response lag and duration were related to consumer body mass. In our study, seed masting (a large magnitude primary pulse) triggered a numerical response of rodents and jays (secondary pulses). Rodents are of small body mass and their populations can increase within weeks following seed masting compared to larger bodied jays with longer generation times. Rodent-hunting mammals (tertiary pulse) also require at least one year following seed masting to increase their population, although a quicker numerical response of rodent-hunting mammals is possible via temporary attraction to resource-rich habitat (as observed in this thesis).

Management recommendations

Based on results from this thesis and partner studies within the wood warbler project, I can draw some conclusions for management recommendations with the aim of improving the wood warbler's demographic status in Switzerland. I will quickly outline the major findings of this thesis and of partner studies if necessary, and discuss possible uses of the results for management.

In a partner study (Pasinelli et al. accepted, BMC Ecology) and in this thesis, occurrence probability and daily nest survival rate, respectively, were related to number of grass tussocks in a territory. Number of grass and sedge tussocks may be important for various reasons. 1) Grass is an important nest building material. 2) Nests are predominantly built under grass tussocks in my study areas. 3) Grass tussocks may be a proxy for a specific habitat type preferred by the wood warbler. The habitat type referred to is characterized by high tree numbers, few bushes and an intermediate ground vegetation cover consisting of grass tussocks, as well as a relatively closed canopy (Huber et al. 2016; Pasinelli et al. accepted, BMC Ecology). Such conditions are typically found in forest stands of middle age (i.e. pole wood) in managed forests. However, management cannot consist of promoting the field layer via methods such as single tree removal, as other field layer vegetation (e.g. Rubus spp., various shrubs and tree regrowth) could grow as well and thereby decrease habitat suitability for the wood warbler (Marti 2007, Mallord et al. 2012a; Pasinelli et al. accepted, BMC Ecology). A possible short term approach to be tested is removal of the shrub layer in forest patches with adequate canopy closure, so that the shrub layer cannot grow back immediately. A mid-term approach consists of not altering current occupied habitat.

I found that wood warblers are attracted to conspecifics resulting in territory clustering (Herremans 1993). This means that the above proposed measures should be implemented on a large enough area that allows for several territories to be established. The utility of using conspecific playbacks to attract wood warblers to suitable habitat remains to be tested further. Based on my data, attraction would work, but there was also increased brood reduction on playback plots during my experiment.

Wood warbler occurrence probability (Pasinelli et al. accepted, BMC Ecology) and daily nest survival rate were negatively related to rodent abundance (chapter three). However, excluding or eradicating natural populations of rodents in seemingly suitable wood warbler habitat to promote wood warbler populations would be logistically difficult and ethically untenable and may have far reaching and negative consequences for the entire ecosystem, including wood warblers. I was also able to determine that the principal cause of nest failure in Swiss wood warblers was predation. Nonetheless, predation on wood warblers in Switzerland seems comparable to predation on wood warblers elsewhere. Naïve nest success (proportion of successful nests; 51%; n = 247) and daily nest survival rate based on Mayfield (1961; 0.97647; n = 228) were mostly lower for Swiss wood warbler compared to other species, but similar compared to wood warblers elsewhere (reviewed in Grendelmeier et al. 2015). I am not able to determine whether or how predation pressure on wood warbler nests has changed in the past decades, potentially negatively influencing local wood warbler abundance. Testing a change of predation pressure would require historical data on nest predation, which rarely exist. In summary, it would be inadequate to claim that the species' decline in Switzerland is linked to nest predation and premature to claim that nest protection against predators might be an option to improve the demographic status of the wood warbler in Switzerland, especially given the nomadic nature of the species (Wesołowski et al. 2009).

Future research

While wood warbler populations have declined in Switzerland and Europe, Bonelli's warbler (Phylloscopus bonelli) populations have mostly increased in the past two decades throughout the species' distribution range (http://www.vogelwarte.ch/de/voegel/voegel-der-schweiz/berglaubsaenger.html, accessed February 28, 2016). The different demographic trends for these two species are striking, considering their similar ecology. Despite differences in preferred habitat, in my study areas, wood warblers and Bonelli's warblers often occurred sympatrically. Both species were observed foraging in the same trees, sometimes at the same time, and active ground nests of both species were found within few meters of each other on at least one occasion. The difference in demographic trends may be found in the difference in breeding habitat or wintering habitat. Nevertheless, investigating how Bonelli's warblers cope with forest rodents and predators may allow us to draw further conclusions on how predation impacts ground nesting passerines.

Wood warblers not only share their habitat with Bonelli's warblers but also with numerous other insectivorous bird species. Based on my findings that wood warblers are attracted to conspecifics, resulting in clustered territories and increased local density, an assessment of intra- and interspecific competition for food may be an adequate future research topic to assess whether competition may be a limiting factor in territory selection and rearing of young.

Questions also remain concerning the underlying mechanisms of territory clustering and conspecific attraction. The hidden lek hypothesis predicts that clustering occurs to increase chances for promiscuity (Wagner 1998). Assessing promiscuity can be difficult in small populations where sample size is small to begin with, but becomes even smaller due to nest predation. Using predator exclosures, nests would be protected and the importance of extra-pair paternity could be evaluated much more accurately.

Aspects of wood warbler demography and life-history are subject to research in many countries, but Europe wide research has received little attention. Considering the wood warblers nomadic behavior, various comparisons across countries seem necessary to increase our knowledge of the species. A comparison of body size metrics and possibly condition of individuals settling and breeding in fringe and core populations may be appropriate to draw conclusions on age and quality structure of local populations. Due to the nomadic behavior however, wood warblers may settle and breed in different countries every year, which could partially explain why local population sizes vary annually. To this end, analyzing spatial variation of population sizes and movements among countries may allow us to draw further conclusions about the impact nomadism has in this species.

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MAMMUT

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Erklärung

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Leiter der Arbeit:	Prof. Dr. R. Arlettaz PD Dr. G. Pasinelli

Ich erkläre hiermit, dass ich diese Arbeit selbständig verfasst und keine anderen als die angegebenen Quellen benutzt habe. Alle Stellen, die wörtlich oder sinngemäss aus Quellen entnommen wurden, habe ich als solche gekennzeichnet. Mir ist bekannt, dass andernfalls der Senat gemäss Artikel 36 Absatz 1 Buchstabe o des Gesetztes vom 5. September 1996 über die Universität zum Entzug des auf Grund dieser Arbeit verliehenen Titels berechtigt ist.

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References are gladly provided upon request

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Peer reviewed English

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Grendelmeier, A., R. Arlettaz, M. Gerber, and G. Pasinelli. 2015. Reproductive performance of adeclining forest passerine in relation to environmental and social factors: Implications for species conservation. PloS one 10:e0130954.

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