The enigmatic decline of the Wood Warbler *Phylloscopus sibilatrix*: nest predation and habitat characteristics

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Summary

1. Among the greatest threats to biodiversity are habitat loss, degradation and fragmentation, but other factors such as predation may also impact populations. Many species of ground nesting birds are declining. They are especially exposed to nest predation. As meso-predators often have increasing population sizes, it remains difficult to disentangle the effects of habitat change vs. predation.

2. Using trail photographic cameras, we first investigated the effects of nest predation on the breeding success of the Wood Warbler, a woodland passerine that is declining in Central Europe. Second, we studied the links between breeding success and habitat characteristics. We monitored 45 natural nests and 32 artificial nests in 12 study areas in northern Switzerland.

3. Survival of Wood Warbler nests declined progressively during the approximately 32 days of nesting, resulting in an overall nest survival rate of 40.8% (n=49). Breeding success averaged 1.9 fledglings per initiated nest and 4.6 fledglings per successful (≥ 1 fledgling) nest (n=20). Predation was the primary cause of nest failure in 79% of 29 unsuccessful nests. Predators of real nests were *Vulpes vulpes* (n=9), *Martes spp.* (n=6), *Meles meles* (n=4), *Garrulus glandarius* (n=3) and *Strix aluco* (n=1). In constrast, artificial nests were predated by muroid rodents (n=26), *V. vulpes* (n=4) and *Sciurus vulgaris* (n=1).

4. There was a positive relationship between daily nest survival and nest concealment, as well as tree diameter. Daily nest survival showed a quadratic relationship with crown coverage, with a peak at 80-85%. It was negatively, but only weakly related to rodent density,

presumably because Wood Warblers settled in territories with low rodent densities.

4. Martens as well as jays left behind broken egg shells while *V. vulpes* destroyed or deformed nests. *Apodemus* mice (n=3) and *S. vulgaris* (n=2) inspected Wood Warbler nest content without causing depredation. Our findings contradict the claim that rodents may be major predators of Wood Warbler nests.

5*. Synthesis and applications*. Our study confirms that predation is a main factor of nest failure in the Wood Warbler, with meso-predators (carnivores, corvids) being the main agents. Although our results rule out a direct role of rodents as nest predators, further investigations are needed to see whether rodents abundance might favor meso-predators populations and thus influence nest predation risk. A preference of Wood Warblers for mature forest stands with a rather closed canopy provides initial guidance for forest management.

Key-words: artificial nests, experiment, GLMM, trail cameras, AIC, nest survival

1 Introduction

Conservation of threatened species is usually a daunting task because many factors may influence individual behavior and population dynamics. In order to develop sound conservation measures for a given species it is essential to thoroughly understand its ecology.

Currently, the greatest threats to the approximately 10'000 bird species occurring worldwide are habitat loss, degradation and fragmentation, which not only continue to affect 1146 already endangered bird species, but may also imperil many species not yet listed as threatened. Factors such as intensification of agriculture (1065 species concerned), logging and forestry practices (668 species concerned), invasive species (625 species concerned), residential and commercial development, hunting and trapping, changing fire regimes, pollution as well as climate change exacerbate the situation (BirdLife International 2008). Efforts should not only be put into reversing the status of already threatened species, but also into preventing more species from becoming threatened.

Taking all these factors into account in the study of a target species is difficult enough, but the situation is greatly aggravated when the species’ life cycle is spread over multiple habitats and continents, as is the case with migratory bird species. Migratory birds not only have to cope with afore mentioned threats on breeding grounds, but are additionally affected by loss of important stop-over sites and possibly, deteriorating conditions on wintering grounds. Individuals occupying stop-over sites and especially wintering grounds of low quality may return to their breeding grounds in suboptimal physical condition.

These carry-over effects may reduce survival and possibly reproductive performance and may ultimately lead to population declines (Weber *et al.*, 1999; Marra *et al.*, 1998).

An increasingly discussed issue, especially in the context of migratory species, is climate change, which may limit demography in several ways. Changing climatic conditions may shift the development of ground vegetation (Flade & Schwarz, 2004) or shift the peak in food availability away from when broods require most nutrition (Both *et al.*, 2009). Fluctuating climatic conditions may give populations of short-distance migratory species and species remaining in the breeding area a competitive advantage (Lemoine & Bohning-Gaese, 2003). Indeed, populations of long-distance migratory species have declined much more strongly since 1970 than populations of short-distance migratory species or resident species .

One such declining long-distance migrant, and the target species of this study, is the Wood Warbler *Phylloscopus sibilatrix*, which is classified as vulnerable (VU) on the current red list of breeding birds of Switzerland and considered a priority species for the Swiss species recovery program (Keller *et al.*, 2010a; Keller *et al.*, 2010b; Rehsteiner *et al.*, 2004). Throughout Western Europe, Wood Warbler populations have declined in the last three decades, while in Eastern Europe populations seem to stay relatively stable, with yearly fluctuations (Flade & Schwarz, 2004; Glutz von Blotzheim & Bauer, 1991; Škorpilová *et al.*, 2007; Wesołowski & Maziarz, 2009). The Wood Warbler has wintering grounds in tropical Africa and breeding grounds spanning Northern and temperate Europe as far east as the Ural Mountains (Stresemann, 1955).

Usually an important factor influencing reproductive performance is time of breeding, with nest age effects generally also differing greatly between species, habitat and geographic area. Several studies have reported no difference in nest survival between incubation and nestling stage (Roper and Goldstein, 1997), while others report higher nest survival during incubation (Best, 1978; Burhans et al., 2002; Suárez & Manrique, 1992; Young, 1963), higher nest survival during nestling stage (Dixon, 1978, Pietz & Granfors, 2000) or even seasonally oscillating trends throughout nesting (Grant et al., 2005). An effect of age on reproductive performance was here assessed by examining linear and quadratic relationships between daily nest survival and nest age. A negative linear relationship was predicted, under the assumption that parental activity increases during nestling stage, which may increase cues about nest existence and location given to predators (Martin et al., 2000). A possible quadratic relationship between daily nest survival and nest age may be caused by poorly hidden nests, which we predicted to be found and predated quickly during early nesting, i.e. egg-laying. During incubation, daily nest survival would increase due to well-concealed nests and little parental activity around the nest. Daily nest survival may decrease again once hatching occurred due to increased chick provisioning activity (Martin et al., 2000). Seasonal effects on nest success have been reported in many studies, with either increasing (Best, 1978; Young, 1963) or, more often, decreasing nest success as the season progresses (Grant et al, 2005; Müller et al., 2004; Naef-Daenzer et al., 2001; Peak, 2007). Seasonal effects may be linked to lower reproductive performance for late onset of reproduction, increasing nest predation due to increasing population sizes of predators after births, or to factors linked to climatic conditions. Therefore, decreasing trends were predicted for daily survival rates, clutch size and number of fledglings, as the breeding season progresses.

Nest concealment is very important, especially among ground nesting species that are exposed to the entire predator community. Several studies (Martin et al., 2000; Müller et al., 2004; Weidinger, 2002) but not all (Burhans et al., 2002; Howlett & Stutchbury, 1997) have found effects of concealment on reproductive performance. Yet, an absence of nest concealment effects often mirrors the difficulty to measure the impact of different predators, while these affects can further be masked by nest age and/or parental care behavior. Nest concealment and parental care behavior may act antagonistically, meaning that birds, which have not evolved low activity around the nest during nestling stage, may counteract nest concealment effects with parental care behavior and activity (Martin et al., 2000; Weidinger, 2002). As a ground nesting passerine species, which is exposed to the entire predator community and most likely cannot physically defend its nest against most predators, nest concealment may be a very important factor for nest survival of Wood Warbler nests. A positive relationship between daily nest survival rates and nest concealment was thus predicted.

Previous studies suggested a territory clustering effect in relation to habitat selection of male Wood Warbler (Herremans, 1993). Eight hypotheses, which can be divided into the two subcategories natural and sexual selection, have been proposed to explain territory clustering (reviewed in Tarof & Ratcliffe, 2004). In relation to reproductive performance, the subcategory sexual selection includes three main hypotheses: 1) “hidden lek”, which relates clustering to extra pair copulations (EPC) (Tarof & Ratcliffe, 2004; Wagner, 1998); 2) “social facilitation”, which relates clustering to stimulatory effects created by observing reproducing neighbors (Darling, 1938 in Tarof & Ratcliffe, 2004) and 3) “social mate choice”, which relates clustering to males’ increased chance of attracting the rarer females (Allee, 1951 in Tarof & Ratcliffe, 2004). Two variables were used, “distances to closest nest” and “number of nests within 300 m”, to investigate possible effects of clustering in relation to reproductive performance and pairing rates. A positive relation was predicted between pairing rates and clustering, referring to the “social mate choice” hypothesis as well as between clutch size and/or number of fledglings and clustering, referring to the “social facilitation” and “hidden lek” hypotheses. However, whether these predictions can be supported or not, it will not be possible to say whether Wood Warblers clustered due to reasons described in the three sexual selection hypotheses or whether they simply settled according to habitat availability.

Disturbance, either directly through human presence, e.g. recreational activities, or indirectly through habitat changes caused by infrastructure development such as hiking trails networks, also constitutes an ever increasing threat to bird species (Miller et al., 1998; Miller & Hobbs, 2000; Kangas et al., 2010). Human disturbance in form of recreational activity has largely negative effects on birds, especially ground nesting species (Boyle & Samson, 1985; Kangas et al., 2010; Arlettaz et al. 2007; Patthey et al. 2009). Hiking on and off trails and camping constitute the greatest disturbance, reported in 52 studies, followed by wildlife observation reported in 27 studies (Boyle & Samson, 1985). Trails not only affect birds through hikers but also increase habitat fragmentation and create habitat edges, which are preferred by some predators (Miller & Hobbs, 2000; Miller et al., 1998). As the principle predators of Wood Warbler nests in Switzerland remained unknown before this study, a positive relationship was predicted between daily nest survival rates and distance to the closest trail if avian predation predominates, whilst no such relationship would exist if mammals would be the main nest predators.

Habitat structure is not only important for territory selection but also for reproductive performance (Maguire, 2006; Penteriani et al., 2003). Wesołowski and Maziarz (2009) found that behavior, ecology and breeding success of Wood Warblers did not change significantly in pristine ecosystems like Bialowieza National Park in Poland, an environment little affected by humans, compared to the situation in Western European woodland where major habitat changes have occurred (Flade & Schwarz, 2004; Glutz von Blotzheim & Bauer, 1991). Habitat quality is high where crucial species-specific resources are available. Food availability (not measured in this study) is an essential component as it determines chick provisioning efficiency and may vary with various grades of canopy cover. Habitat structure also influences nest predation as nest concealment is micro-habitat dependent. Although the surrounding vegetation offers perches for singing, foraging trips and nest-approach, it may also be used by prospecting avian predators, such as Eurasian Jay Garrulus glandarius. Dense and closed canopies may also shield nest sites from adverse weather. On the other hand, too much canopy cover may create unfavorable conditions on the ground, where nests may not dry fast enough after severe weather (Hillig, 2009; Marti, 2007). Vegetation structure may also be important as it provides material for nest construction, e.g. grass tussocks. As several studies suggest that Wood Warblers are flexible when it comes to macro-habitat choice (Herremans, 1993; Marti, 2007), comparing patterns of habitat selection between successful and unsuccessful nests may provide decisive insights into optimal habitat profiles, i.e. deliver guidelines for Wood Warbler friendly forest management (Glutz von Blotzheim & Bauer, 1991; Quelle & Lemke, 1988; Hillig, 2009; Marti, 2007; Reinhardt & Bauer; 2009).

Wood Warblers exhibit very little site fidelity and a nomadic behavior typical of long-distance migrating, insectivorous forest passerines, which creates strong local fluctuations of populations (Wesołowski et al., 2009). This may be explained by the Wood Warblers’ systematic avoidance of areas with high nest predation risk, given that 95% of nest losses are due to predation (Glutz von Blotzheim & Bauer, 1991; Wesołowski et al., 2009). Wesolowski et al. (2009) report lower settlement of Wood Warbler during rodent outbreak years than during years with fewer rodents. Rodents themselves have been documented to predate nests of various bird species (Kirkpatrick & Conway, 2010; Walankiewicz, 2002). Therefore there are suspicions that rodents may prey on Wood Warblers' nests (Wesołowski & Maziarz, 2009; Mildenberger, 1949; Wesołowski, 1985), which is one of the major hypotheses tested in this study. However, high rodent abundances may not only increase direct predation on nests but may also attract rodent-hunting predators (Jędrzejewski &

Jędrzejewska, 1992; Jędrzejewski & Jędrzejewska, 1993), which may increase the risk of nests being found and predated by chance, due to increased activity of predators on the forest floor. These may not only be nest predators confined to forest habitats, but also nest predators entering from adjacent habitats. We thus investigated such an edge effect, generated by what is known as spillover predation (Oksanen et al., 1992; Storch et al., 2005), with a variable measuring distance from nests to closest forest edge, for which a positive correlation with daily nest survival rates was predicted. Note that a similar effect may arise from spreading urbanization, possibly causing increased predation through domesticated dogs (Canis lupus familiaris) and especially cats (Felis catus) as suggested by Rehsteiner et al. (2004) and Sanders (2001) near villages, towns or farms. A positive correlation between distance of a nest to the nearest building and daily nest survival rates was thus predicted. As spillover predation may be connected to rodent densities, a negative correlation was also predicted between reproductive performance and rodent densities. This prediction is not mutually exclusive, as it may also arise due to direct nest predation by rodents. Note finally, that high rodent density may also on the contrary dilute the effects of predators on Wood Warbler nests due to very abundant prey on which predators focus; in this case, no link between nest survival and rodent density should be observed. Nest predators were identified with trail cameras.

Finally, an artificial nest experiment was conducted in order to evaluate the capacity of Wood Warblers to deter some predators.

Hypotheses and predictions were principally the same as for real nests1.

All in all, the information gathered in this study should shed more light into the factors affecting the populations of the Wood Warbler in Western Europe, with the objective to provide guidance for evidence-based conservation management.

2 Materials and methods

2.1 STUDY AREAS

Based on several databases we determined areas with potential Wood Warbler territories. We considered data from the common breeding bird survey ("Monitoring Häufige Brutvögel", MHB) provided by the Swiss Ornithological Institute and atlas data from the Canton of Zurich (www.birdlife-zuerich.ch) to determine 9 initial regions throughout Northern Switzerland. All these regions showed a relatively high concentration of Wood Warbler territories in the past 10 years. However, during early field work, it became apparent that some of these areas no longer harbored birds, especially in the Canton of Zurich. By also checking www.ornitho.ch almost daily we ended up with 12 areas with Wood Warbler territories (Fig. 1). We used coordinates of sightings only as rough starting point, around which we checked a large area in at least one initial survey.

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[1] Field data for the breeding season 2010 was collected together with Michael Gerber from the University of Zurich, who focused on habitat selection at the territory level (Gerber, 2011). Subsequent analyses and theses were conducted and written separately.

2.2 TERRITORY LOCATION MAPPING

We started mapping territories in the above mentioned areas by listening for the distinct Wood Warbler songs from mid-April, 2010. To increase detection probability, we used playback of Wood Warbler songs (Schulze 2003) through a MP3 player (Cowon iAudio 7 and Sony Walkman NWZ-S616F) and portable speakers (iLuv iSP100). On average, we visited each study area once a week. A territory was classified as occupied when (a) we recorded a singing male twice in the same place with at least 7 days in between, (b) we observed a pair (two birds in the same territory showing no agonistic behavior) at least twice on two successive visits or (c) we found the nest. Due to limited time and resources we selected 27 territories harboring a nest for detailed analyses (i.e. recording of habitat structure variables and rodent density). The selection was made in such a way to get a representative number of successful, predated and abandoned nests, and a balanced sample from different study areas. The remaining territories with nests were only used for specific measurements (see below). Territories without a nest were not used for any further analyses, except in the calculation of pairing rates.

2.3 NEST SEARCH

Territory mapping and nest search occurred concurrently. Nests were best searched and found during the nest construction stage due to high activity and frequent calls of the female and the unambiguous change in behavior and song of the male (Glutz von Blotzheim & Bauer, 1991;

Martin and Geupel, 1993; Wesołowski & Maziarz, 2009; Reinhardt A. personal communication, 17.01.2010). However, nests were found throughout the nesting cycle, i.e. egg-laying stage, incubation and nestling stage until about the end of June. Upon finding, a nest was geo-located with hand held GPS devices (Garmin Quest, Garmin nüvifone M10 or Garmin eTrex Summit) and photographed from different perspectives.

2.4 RECORDING OF THE HABITAT STRUCTURE VARIABLES

For each territory we recorded several structural variables that possibly influence Wood Warbler habitat selection (Gerber, 2011) and reproductive performance between May 15 and September 2, 2010. Recording while the nest was still active was omitted to reduce disturbance and was therefore done as soon as the nest was inactive. As territory center of occupied territories we considered the nest position. From each territory center we measured 17 m in each intercardinal direction (NE, SE, SW, NW) to obtain 4 points in total. From each point we again measured 5 m in each intercardinal direction to finally get 5 sample areas (central point and four intercardinal points) each measuring approximately 50 m^2 (Fig. 2). This way we defined all Wood Warbler territories to span over an area of approximately 968 m^2, of which 250 m^2 were used to measure most variables, as described below (Wood Warbler breeding territories have been reported to span between 500 and 1900 m^2; Glutz von Blotzheim & Bauer, 1991). To measure vegetation cover and count grass tussocks we used a 1 m^2 frame in each corner and the center of each 50 m^2 sample area (Fig. 2), also described below.

2.4.1 *Habitat structure variables*

The following variables were recorded at the territory center: coordinates (measured with handheld GPS), elevation (measured in ecoGIS (http://www.ecogis.admin.ch) based on coordinates), distance (m) to closest building (inhabited farms and buildings of urbanized areas, measured in ecoGIS based on coordinates), distance (m) to closest path (ranging from foot paths to paved roads, but not game trails, measured in ecoGIS based on coordinates or in the field in the case of paths not shown on maps), distance (m) to closest edge of forest (measured in ecoGIS based on coordinates). For territory clustering (Herremans, 1993; Tarof & Ratcliffe, 2004) we measured: distance to closest nest (calculated from nest coordinates) and number of occupied territories within 300 m (calculated from nest coordinates; 300 m is based on hearing range of humans). The following variables were recorded in each of the five 50m2 sample areas and later averaged, over each territory separately, for analysis: inclination and exposition (measured with a compass), sky visibility (ratio white/black pixels from photograph, see 2.6.2), number of bushes > 0.5 m in height and young trees with stem circumference < 25.1 cm, number of trees with stem circumference at breast height > 25.1 cm. If circumference at breast height > 25.1 cm we also recorded: tree species, tree diameter (calculated from circumference at breast height, measured with a measuring tape; hereafter called "avg. diameter"), number of trees branched below 4 m (hereafter called "branched below

4 m), number of trees branched below 10 m (hereafter called "branched below 10 m), number of crown contacts with other trees (if the tree reached the top canopy layer), number of dead trees

For practical reasons we measured stem circumference in the field, which we later converted to stem diameter to comply with forestry practice. In the field we used a benchmark circumference of 25.1 cm (2 x Pi x (8 cm/2)) to determine whether a tree falls below or above 8 cm diameter. The following variables were recorded in five 1 m^2 areas in the corners and at the center of each 50 m^2 sample area and later averaged, over each territory separately, for analysis: percentage of vegetation cover smaller than 0.5 m (estimated based on a reference table by Gehlker, 1977 in Dierschke, 1994; see appendix 1) and number of grass and sedge tussocks.

2.4.2 *Sky visibility photography*

The percentage of canopy cover at each sample area was recorded from pictures of the tree canopy. We followed a method described by Coch *et al.* (2005), with the following adaptations and additions: We used a DSLR camera (Nikon D2Xs) with a standard zoom lens (18-70 mm f3.5-4.5G ED-IF AF-S DX Zoom Nikkor) at a focal length of 35 mm. To take the pictures, the camera was held 1.5 m above ground, lens pointing vertically up, camera ground plate facing towards the territory center (or towards south east for the pictures at the territory center).

The pictures were taken in camera RAW format and imported to Photoshop CS5 for editing. Import was performed with standard camera RAW settings, except that brightness of green colors was lowered to the minimum and brightness of blue colors heightened to the maximum to increase contrast between sunlit green leaves and blue sky. The pictures were edited as described by Coch *et al.* (2005), downscaled to 1500 x 1000 pixels and transformed to b/w bitmap before being processed by a self-written php-script to calculate the black/white pixel ratio.

2.5. DESCRIPTION OF NEST POSITION

Each real and artificial nest (2.9.2) was assigned one of the following four categories: 1) Concealed by grass or sedge tussocks, 2) concealed by a single small plant < 50 cm in height besides grass or sedge tussocks and 3) hidden in dense herb layer with > 2 small plants < 50 cm in height besides grass or sedge tussocks. The fourth category, “other” includes nests that are: concealed or covered by leaves or deadwood (< 8 cm in diameter), wedged between tree roots, wedged between or under boulders and wedged under dead tree trunk > 8 cm in diameter.

2.6. CONCEALMENT INDEX

Each nest was assigned to one concealment category, which denotes whether the nest was concealed from the four cardinal directions at a distance of 1.5 m and from a point situated 1.5 m vertically above the nest. “0” (lowest) denoted the nest was not concealed from any of the five directions. “5” (highest) denoting the nest was concealed from all 5 directions and therefore not visible.

2.7. RODENT DENSITY

2.7.1 *Live-trapping, marking and identification of rodents*

We conducted live-trapping to estimate rodent density in occupied territories between June 30 and September 3. To avoid disturbance, trapping was not done while nests were still active. For logistic reasons we waited until at least 2 nests in one study area became inactive. We used the same grid for trapping as for recording habitat variables. In each of the five 50 m^2 sample areas, five traps were placed near structures or near rodent trails and covered with foliage. We used Longworth traps (Penlon Ltd., Abingdon, UK) made of steel and aluminum and "Field Trip Trap Live Catch Trap" (Alana Ecoloty, Bishops Castle, UK) made of plastic. Trapping efficacy of these two types of traps varies only slightly (Arlettaz et al, 2010). To allow calculation of capture probabilities, we used a capture-recapture protocol during 48 hours per trapping session with control intervals of 8 hours. We provided bedding and bait in form of commercial pet hay and apple pieces, oatmeal, peanut butter and hazel nuts (Douglass *et al.*, 1996; pers. comment Prof. Airoldi). Caught animals, were tipped into a plastic bag, classified on species and genus level, marked by hair clipping and then released immediately. We marked the animals using a nose hair trimmer at 5 different parts of the body, which we assigned to each of the 5 capture events (CE). CE 1: left thigh; CE 2: left shoulder; CE 3: right shoulder; CE 4: right thigh; CE 5: base of tail. From these markings we later obtained individual capture histories. Despite identifying rodents to the species level, numbers of caught animals of each species were too low for species-specific analysis and therefore pooled.

2.8. NEST PREDATION

In order to obtain information about the influence of nest predation on Wood Warbler nests, we used trail cameras to monitor both real and artificial nests. The latter were installed in occupied and control areas to compare predator guild and predation pressure or risk in inhabited vs. non-inhabited areas. They were also intended to increase sample size in case of few real nests found. A real nest was classified as predated if 1) during the egg-laying and/or incubation stages all eggs were missing or broken, 2) during nestling stage all nestlings disappeared before the expected fledging date, 3) nests were destroyed 4) female could be observed being predated. A nest was considered successful if at least one nestling fledged. For the definition of artificial nest predation, see 2.8.2.

2.8.1 *Trail camera surveillance*

We used four units of the type "Reconyx RC55 RapidFire Color IR" (Reconyx, Inc., Holmen, Wisconsin, USA), provided by KORA Switzerland and 20 units of the type "Reconyx PC900 HyperFire Professional High Output Covert" (Reconyx, Inc., Holmen, Wisconsin, USA) provided by the University of Bern. Immediately upon nest discovery, one trail camera was placed 1-2 m away (depending on topography, ground type and vegetation surrounding the nest), pointing directly at the nest. The cameras were set up to take 10 images per motion detection, which is triggered by moving infrared signals, at a rate of 1 image per second. Additionally, the cameras took 1 image every 15 minutes independent from infrared motion. A pilot study showed that cameras could detect animals as small as Bank Voles *Myodes glareolus*. This approach allowed us to get accurate information about fledging and nest predation rates as well as predator identity. We checked cameras at least once a week for battery, operational and capacity status until nest predation, "hatching" (artificial nests) or fledging (real nests).

2.8.2 *Selection of control areas*

For the artificial nest experiment described below, we assigned a control area without Wood Warblers to each occupied territory. The control areas were located 200 m from the occupied territories (center to center, with the nest position as center of the occupied territories). We defined 8 possible control areas in the cardinal and intercardinal directions of each territory. To avoid trivial results, we ruled out control areas with a habitat known to be not inhabited by Wood Warblers, such as non-forest areas, large clearings, purely coniferous wood patches, young re-growths and tree plantations. Also, control areas closer than 50 m to other occupied territories were excluded. The remaining possible control areas were numbered clockwise starting in the North, and one was randomly selected.

2.8.2 *Artificial nest experiment*

We obtained a sample of 32 camera-monitored artificial nests, 16 in occupied territories and 16 in their corresponding control areas. We arbitrarily placed artificial nests in the center of the sample area located northeast of the real nest and in the center of the central sample area for control areas. We used pre-fabricated grass nests from pet market and placed them as naturally as possible to imitate real Wood Warbler nests. Each nest contained 5 plasticine eggs, which corresponds to the average clutch size of Wood Warbler (Glutz von Blotzheim & Bauer, 1991), attached to the nest by nylon thread to prevent removal by a predator (Lewis *et al.*, 2009). We checked artificial nests at least once a week until nest predation or until 13 days, which corresponds to the average incubation period of Wood Warbler (Glutz von Blotzheim & Bauer, 1991). All artificial nests could be monitored and all nest predations photographed by trail cameras. Artificial nest predation was defined to have occurred as soon as a nest predator interacted with a nest in some manner.

2.9. NEST AGE AND FIRS-EGG DATE

We defined the variable “first-egg date” as the day the first egg was laid. Nests found during construction were at the latest checked again after 3 days to determine true start of the egg-laying stage. Once the complete clutch was observed, the duration for the egg-laying stage could be determined with the assumption that female Wood Warblers lay one egg per day in the early morning (Glutz von Blotzheim & Bauer, 1991).

For nests found during the egg-laying stage, start of the incubation stage equaled the day the last egg was laid. For nests found after the egg-laying stage, an incubation period of 13 days was used (Glutz von Blotzheim & Bauer, 1991) with a minimum egg-laying stage duration adjusted to clutch size.

For eight nests found during the nestling stage, defined as the period between hatching and fledging, we first determined the hatching date by aging hatchlings based on own photographs of known-age hatchlings, from nests where the exact hatching date was known. For these nests, incubation periods were again assumed to be 13 days, and the minimum duration of the egg-laying stage was calculated so as to match the number of nestlings.

The date was coded as a continuous integer where 1 represents the date on which the first of all observed females laid her first egg. Fledging date was inferred by determining the presence or absence of feeding activity of adults as reconstituted from trail camera pictures. As we did not employ methods such as egg candling or floating (Reiter & Andersen, 2008), two nests found and predated during incubation could not be aged and therefore were not used for further analyses, except for calculation of mean clutch size and naïve nest success. "First-egg date" was only used in the analyses of "clutch size" and "number of fledglings". To analyze daily nest survival rates, we worked with exposure time as described in the statistical section "exposure time".

2.10 STATISTICS

2.10.1 *Rodent density estimates*

We analyzed capture-recapture data using Program CAPTURE (Rexstad & Burnham, 1991) run through Program Mark v6.0 (White and Burnham, 1999) and assumed demographically closed populations (White *et al.*, 1982), since we worked with a trapping time frame of only 48 hours. Even though we caught and identified several species, we pooled all captures for a single estimate of rodents per territory or control area. Program CAPTURE computes estimates of capture probability and population density for 1) a null model of no time, behavior or heterogeneity effect (M_o), assuming all individuals of a population are equally at risk of capture on every trapping occasion. 2) A model of heterogeneity effects (M_h), assuming capture probabilities vary by individual animal. 3) A model with time effects (M_t), assuming capture probabilities vary with time. 4) A model of behavior effects (M_b), assuming capture probabilities vary by behavioral response to capture. 5) A model of behavior and heterogeneity effects (M_{bh}), assuming capture probabilities vary by individual animal and by behavioral response to capture. 6) A model of time and heterogeneity effects (M_{th}), assuming capture probabilities vary with time and by individual. 7) A model of time and behavior effects (M_{tb}), assuming capture probabilities vary with time and with behavioral effects (trap happiness, trap shyness). Finally for a model of time, heterogeneity and behavior effects (M_{tbh}), for which however, there is currently no estimator (Rexstad and Burnham, 1991). These 7 models are then ranked by a model selection criterion between 0 and 1, where the most appropriate model scores a 1. We then used the rodent density estimate from the most appropriate model, calculated for each territory or control area for further analyses. For a detailed breakdown of the CAPTURE analysis results of rodent densities see Appendix 2.

2.10.2. *Exposure time*

Providing naïve nest success calculated by dividing the number of successful nests by the number of initiated nests may give biased estimates of nest survival, usually by underestimating it. In order to avoid this underestimation, which results from nests predated or fledged before they are found, we worked with exposure time for the analysis of daily nest survival rates (Mayfield, 1961). For nests found before the egg-laying stage, exposure time was the difference between the actual first-egg date and nest predation or fledging date. For nests found after the egg-laying stage, exposure time was the difference between finding date and fledging or nest predation date. By using trail cameras, the observation interval was always one day and we obtained exact predation and fledging dates. Therefore, I did not have assumptions about date of nest loss as is often the case when not using cameras. Furthermore, I did not have to use complex code in the analysis of daily nest survival rates, which is normally necessary (Shaffer, 2004).

2.10.3 *Coding the data set and model structure*

By using nest cameras we continuously monitored nests until nest predation or fledging occurred. Subsequently, a simple generalized linear mixed-effects model approach (GLMM) was used to assess the influence each variable has in relation to three different dependent variables: daily nest survival rates, clutch size and number of fledglings. As we had territories with their real and artificial nests, as well as control areas with their artificial nests in 12 different study areas, we accounted for data independence within study areas by including a random effect for this factor. Study areas with less than three nests were pooled into a new, single study area. All variables potentially influencing the dependent variables were modeled as fixed effects. I included a second random effect called "territory ID" to avoid pseudoreplication since each nest delivered multiple observations (Appendix 3). For example, the nest coded as BL03 could be observed from day 62 when it was 12 days old until its young fledged on day 80, when it was 30 days old. Therefore BL03 contributed 19 observations and each variable is replicated in the data set except for nest age and date, which both are continuous integers. Nest survival was the binomial dependent variable, where each day the nest was alive receiving a "1". This means that BL03, as successful nest, has a history with 19 observations of "1" ending on the date the young fledged, in this case day 80. Unsuccessful nests, like GH01, simply received an observation of "0" on the date they were predated.

Clutch size and number of fledglings typically are Poisson-distributed dependent variables. For analyses that included these variables, we thus used a differently coded data set, where each nest only contributed one observation, consisting of either known or back-calculated first-egg dates to examine seasonal effects on clutch size and number of fledglings. Abandoned nests (n = 5) were omitted from these analyses..

2.10.4 *Candidate models and handling of variables*

To evaluate the eight hypotheses I assigned all variables to their respective hypotheses: 1) disturbance hypothesis (distance to paths);

2) clustering hypothesis (distance to closest nest, number of nests within 300 m); 3) habitat hypothesis (vegetation cover, number of grass tussocks, number of bushes, crown coverage, number of trees, branched below 4 m, branched below 10 m, avg. diameter); 4) nest predation hypothesis (rodent density, distance to forest edge, distance to building); 5) nest site hypothesis (concealment index, nest position); 6) nest age hypothesis (linear and quadratic terms for nest age); 7) seasonal hypothesis (linear and quadratic term for date) and 8) geographic hypothesis (elevation, inclination). The only variable I excluded *a priori* was exposition from the geographic hypothesis, since occupied territories were generally exposed to the south. Because the three variables "number of trees", "branched below 4 m" and "branched below 10 m" were highly correlated (correlation coefficient > 0.7) (Appendix 5), they were never used together in a single model. The two highly correlated variables "avg. diameter" and "branched below 4m" were also never used in the same model. Except for the categorical variable "nest position", as well as the variables "nest age" and "date", all variables were standardized prior to analysis.

2.10.5 *Model selection*

Model selection was used to determine the variables potentially influencing daily nest survival rates, clutch size and number of fledglings. To rank models the Akaike Information Criterion (AIC) (Akaike, 1974) was applied, or rather its derivative AICc which corrects for small sample size (Sugiura, 1978). The AICc approach ranks models by taking into account their goodness of fit using their log-likelihood and penalizing for the number of variables included to explain models' dependent variable (Akaike, 1974). We first assessed each hypothesis separately by evaluating models with all possible combinations of the respective variables (see 2.10.4) and comparing them to a null model containing only the random effects. If there were multiple models with an AICc smaller than 2 compared to the highest ranked model (ΔAICc), they were deemed to have equal support to explain the dependent variable. To account for this model selection uncertainty model averaging was carried out for estimates and standard errors of all variables contained in models with ΔAICc < 2. Variables with model averaged estimates greater than their model averaged standard errors are likely to have an effect (Burnham and Anderson, 2002, Mazerolle, 2006) and were included in the across-hypothesis analyses (hereafter called AHA) to examine effects of variables from different hypotheses in relation to reproductive performance. Model selection and model averaging of estimates and standard errors to find variables relating to reproductive performance were conducted in the same manner for AHA as was done for the assessment of the separate hypotheses.

All statistics were performed in R (R Development Core Team 2010) using the packages lme4 (Bates and Maechler, 2010), AICcmodavg (Mazerolle, 2010) and arm (Gelman *et al.*, 2011) for model selection and averaging.

2.10.6 *Period nest survival rates*

To obtain period survival rates and standard errors, we ran a GLMM containing the variable "nest age" with a range of 1 to 32 (5 days egg-laying stage, 14 days incubation stage, 13 days nestling stage;

Appendix 5). From this GLMM we calculated predictor values and took their inverse logit, which multiplied with each other for a given stage or the entire nest period, gave period survival rates or nest survival rates, respectively, with standard errors.

3 Results

3.1 PHENOLOGY

We found 49 nests in 12 study areas, 21 during nest construction, none during the egg-laying stage, 19 during the incubation stage and 8 during the nestling stage. An additional nest was found after predation, with its stage remaining unknown. We found one monoterritorial, polygynous triplet with nests approximately 2 m apart, active at the same time. On three occasions replacement broods were likely, considering first-egg dates. The median first-egg date was May 22 (n = 41) and varied strongly among the 12 study areas (Table 1). Earliest and latest first-egg dates occurred on May 5 in Glarus and June 24 on Scheltenpass, respectively. The mean incubation and nestling stage durations were 14 days (n = 7, range: 13 – 16) and 13 days (n = 17, 11 – 15), respectively (Appendix 4).

Twenty-seven nests were built into a grass or sedge tussock, 12 nests were built beneath a single plant less than 50 cm in height and 4 nests were placed in a relatively dense herb layer, that is, beneath more than one plant less than 50 cm in height. The remaining 6 nests were pooled into a category called "other", containing 4 nests concealed or covered by either dead leaves or a combination of dead leaves and deadwood (< 8 cm diameter), while one nest wedged between tree roots and another one was placed underneath a boulder.

In total 49 of 81 territorial males got paired with a female (60%) (Table 2), of which at least one male had two females in the same territory (nests 2 m apart, see above). Pairing rates were not correlated to number of territories per study area (Spearman's rank correlation coefficient r_s -0.3, p = 0.295).

3.2 NEST FAILURE AND NEST PREDATORS

Forty-five out of 49 nests were monitored with trail cameras. Four nests could not be monitored due to 1) the nest already destroyed upon discovery, 2) too close proximity to hiking trail, 3) no cameras available initially and then nest abandoned or destroyed on the following visits. In total 24 of 49 nests (49%) were predated and five abandoned. Nest predation occurred during the egg-laying stage in four cases and during incubation in four cases (between the 6th and the 13th day). The other 15 nests were predated during nestling stage, and 11 of these nest losses occurred in the second half of the nestling stage (Table 3). For one nest, the stage it was predated on is unknown, but destruction manner clearly attributed it to Red Fox *Vulpes vulpes*.

Nest predators were Red Fox (n = 9), Pine Marten (*Martes martes*) and Stone Marten (*Martes foina*) (n = 6), European Badger (*Meles meles*) (n = 3), Eurasian Jay (n = 3) and one Tawny Owl (*Strix aluco*). There were no domesticated dogs seen near nests and only three cases of domesticated cats, none of which noticed the artificial nests (n = 2) or the real nest (n = 1). In 2 nests, predated by Pine Marten and

Eurasian Jay, respectively, remaining egg shells were present. In total 5 nests were abandoned for an unknown reason, only one during nestling stage.

Despite daily camera use we had to infer nest predator identities in nine cases. In two cases (Eurasian Jay, Tawny Owl) the cameras did not show a direct picking motion at fledglings, but the Tawny Owl was seen immediately in front of the nest, facing it, while the Eurasian Jay was seen flying away from the nest. However, after either nest predator was present at the nest, parental activity subsequently ceased and therefore nest predation was assumed and later confirmed through nest inspection. In two cases cameras were placed suboptimally, so no motion detection triggered and hence nest predator identity remains unknown. In both cases nests were predated but left intact. Finally, in 5 cases we could infer nest predator's identity from the typical condition, with total destruction indicating Red Fox, based on evidence of Red Fox nest predations caught on camera (n = 4). Neither of the Marten species, Jays, Badgers, nor the Tawny Owl caused any destruction or even deformation to the nest during predation.

3.3 RODENTS

Rodent densities varied between 2 and 34 (mean = 13.5) rodents in successful Wood Warbler territories (n = 13) and 6 and 37 (mean = 18.1) rodents in unsuccessful Wood Warbler territories (n = 14). The principal rodent species caught during the day was the Bank Vole *Myodes glareolus*, while, during the night, the Yellow-necked mouse *Apodemus flavicollis* was predominant. Other species caught, but to a much lesser extent, were Wood Mice *Apodemus sylvaticus*, House Mice

Mus musculus and the Edible Dormouse *Glis glis*. *Apodemus* mice and Red squirrels *Sciurus vulgaris* were found to inspect nest contents closely on three and two occasions, respectively, but were never observed predating nests. Furthermore, 10 cameras showed nine *Apodemus* mice and one Red Squirrel roaming around nests at ranges between approximately 20 cm and 1 m, again without predating eggs or nestlings.

3.4 NAÏVE NEST SUCCESS AND PERIOD NEST SURVIVAL

20 of 49 nests were successful in producing at least one fledgling, which resulted in a naïve nest success rate of 40.8%. Naïve nest success was highest at Staffelegg (100%, n = 1), followed by Glarus (83.3%, n = 6) and Scheltenpass (64.3%, n = 14) (Table 4). 5 of 12 areas had a naïve nest success of 0%, however four of these areas had a sample size of 1 nest and the fifth area a sample size of 3 nests. Nest survival over the entire nesting period was also 40.8% (± 13.8%) for 32 days, which can be broken down to 93.6% (± 5.3%) for the egg-laying stage, 74.2% (± 10.2%) for the incubation stage and 58.7% (± 14.4%) for the nestling stage. Daily and period nest survival rates varied in the absence of different predators, especially Red Fox predation, which lowered nest survival over the entire nesting period by 28.4 % (Table 5).

3.5 RELATIONSHIP BETWEEN DAILY NEST SURVIVAL RATE AND VARIABLES

For the assessment of influential variables in relation to daily nest survival rates we used only territories for which habitat structure and rodent density had been recorded (n = 27). By including a null model throughout assessing hypotheses separately it became apparent that many variables had some but rather little influence. In every hypothesis assessment, the null model was within a ΔAICc of 2 compared to the highest ranked model.

Nest site hypothesis – This hypothesis received some support, because there was one model ranked higher than the null model (Table 6). This highest ranked model contained the variable "concealment index". Models containing the variable "nest site" had no support.

Habitat hypothesis – This hypothesis received some support, because there were five models ranked higher than the null model (Table 6). The highest ranked model contained the variable "avg. diameter". However, there were 22 other models including the null model that had a ΔAICc < 2 compared to the highest ranked model, containing various subsets of all 10 variables (2.11.4). After model averaging, the five variables "number of bushes", "vegetation cover", "branched below 10 m", "number of grass tussocks" and "number of trees" were omitted. "Avg. diameter", "branched below 4 m", the linear term for "sky visibility", "crown contacts" and the quadratic term for "sky visibility" were considered for AHA.

Predation hypothesis – This hypothesis received weak support, because the null model was ranked highest. Only the linear model for rodent density was within a ΔAICc of 2. Model averaging supported that the linear term of "rodent density" could be considered for AHA. "Distance to forest edge" and "distance to building" had model averaged estimates smaller than their model averaged standard errors and were hence omitted.

Clustering hypothesis – This hypothesis received weak support, because both variables, "distance to closest nest" and "number of nests within 300 m" were present in models ranked lower than the null model. Subsequent model averaging revealed that "distance to closest nest", while weak, could be considered for AHA, whereas "number of nests within 300 m" was omitted.

Nest age hypothesis – This hypothesis received weak support, because the null model was ranked highest, but linear and quadratic models for "nest age" had an AICc difference of only 0.05 and 0.24, respectively. However, the model with the quadratic term for "nest age" was omitted after model averaging and only the linear model for "nest age" was considered for AHA (Table 7).

Seasonal hypothesis – This hypothesis received weak support, because the model containing the variable "date" was ranked lower than the null model, but still within a ΔAICc of 2. The model containing the quadratic term for "date" had to be deleted from analysis as it failed to converge. The linear model for "date" was omitted after subsequent model averaging (Table 7).

Geographic and disturbance hypothesis – These hypotheses received weak support, because the null models were ranked highest. However, model averaged estimates for all assessed variables were smaller than their model averaged standard errors and therefore not considered for AHA (Table 7).

Across hypotheses analysis – There was support, as 10 models, but not the null model, had ΔAICc of 2 (Table 6). The highest ranked model contained the three variables "nest age", the quadratic term for "sky visibility" and "nest concealment, which were present in all 10 highest ranked models. The second ranked model with a ΔAICc of just 0.11 additionally contained "avg. diameter". The remaining eight models additionally contained the variables "crown contacts", "branched below 4 m", "rodent density" and "distance to closest nest". After model averaging (Table 7), "distance to closest nest" was the only variable with an estimate smaller than its associated SE and hence omitted. The other seven variables "nest age" (Fig. 3a), "concealment index" (Fig. 3b), the quadratic term for "sky visibility" (Fig. 3c), "avg. diameter" (Fig. 3d), "rodent density" (Fig. 3e), "crown contacts", "branched below 4m" and "nest age" showed effects in relation to daily nest survival rate.

3.6 CLUTCH SIZE

A total number of 44 clutches in 12 areas contained 226 eggs. The mean clutch size over all areas was 5.1 (SD = 1.3) eggs. Clutch sizes varied from 2 eggs, which occurred twice (Langenbruck and Staffelegg) to 7 eggs, which occurred four times (twice in Montsevelier and twice on Scheltenpass) (Table 8).

3.7 RELATIONSHIP BETWEEN CLUTCH SIZE AND VARIABLES

To assess the influence of variables in relation to clutch size we used the data set containing all variables. This data set had a sample size of 23 and included habitat variables and rodent density variables. Assessing all hypotheses separately revealed two models with a ΔAICc < 2 compared to the highest ranked model, the null model. One model contained the variable "distance to path" from the disturbance hypothesis. The other model contained the variable "first-egg date" from seasonal hypothesis. After omitting "distance to path" (0.09 ± 0.09), only the variable "first-egg date" remained in a model inferior to the null model by an AICc of 1.17. All other hypotheses had no support in relation to clutch size, as there were no models with a ΔAICc < 2 compared to the highest ranked (null model. Similar as with the analysis of number of fledglings, habitat and rodent density variables had no effect in relation to clutch size. Hence I reanalyzed the "geographic", "disturbance", "clustering", "concealment" and "seasonal" hypothesis again with 38 nests, as variables from these hypotheses could be measured for all nests. Again, two models with "distance to path" and "first-egg date" had ΔAICc of 1.28 and 1.22, respectively, to the highest ranked model, the null model. A third model including only "nests within 300 m" had a ΔAICc 1.85 to the highest ranked model, the null model, but the variable had a smaller model averaged estimate than standard error.

AHA with the large data set revealed that the null model was not highest ranked, with the model with "first-egg date" having some support (Table 9). Using the larger data set, model averaged estimate and standard error of "first-egg date" have slightly "improved" compared to the model averaged estimate and standard error, from the smaller data set (Table 10), indicating a decline of clutch size with season (Fig. 4)

3.8 NUMBER OF FLEDGLINGS

Naïve average number of fledglings in relation to all nests was 1.9 (SD: ±2.4) fledglings per breeding pair over all study areas (Fig. 5). The minimum number of fledglings was 2 (observed once at

Staffelegg) and the maximum number of fledglings was 6, observed 5 times, twice in Glarus and three times on Scheltenpass. Disregarding predated and abandoned nests, the average number of fledglings amounted to 4.6 (SD: ±1.2) fledglings per successful breeding pair (n = 20).

3.9 RELATIONSHIP BETWEEN NUMBER OF FLEDLGINGS AND VARIABLES

To assess the influence of variables in relation to number of fledglings, only nests producing at least 1 fledgling were used. I used the data set which contained all variables, including habitat variables and rodent density variables, which could only be measured for 12 nests with fledglings. Assessing all hypotheses separately revealed no model within a ΔAICc of 2 compared to the highest ranked model, the null model. As habitat variables and rodent densities had no effect in relation to number of fledglings, I reanalyzed the data with the data set containing only variables that could be measured for all 20 nests with fledglings. This data set still contained variables from the "geographic", "disturbance", "clustering", "concealment", "nest age" and "seasonal" hypotheses. Even though the null model was again ranked highest (AICc 11.53), the model with the variable "number of nests with 300 m" (AICc of 12.86) from the "clustering" hypothesis received weak support (Fig. 6). All other hypotheses had no support in relation to number of fledglings. The variable "number of territories within 300 m" was weakly related to number of fledglings (0.13 ± 0.11).

3.10 ARTIFICIAL NEST EXPERIMENT

Seven of 38 artificial nests survived the "incubation" stage of 13 days. No area had an artificial nest success over 50% and four areas had an artificial nest success of 0% (Table 11). The most numerous nest predators, with 26 documented cases of predation, were rodents of the superfamily Muroidae, usually *Apodemus* mice, followed by Red Fox with four predations and Red Squirrel with one predation case.

3.11 RELATIONSHIP BETWEEN ARTIFICIAL NEST SUCCESS AND VARIABLES

Before assessing each hypothesis separately, we first checked whether there was a difference between artificial nests in occupied territories and artificial nests in control areas, which was not the case, for the null model was higher ranked (ΔAICc 2.1) than the model including the variable territory type (occupied territory vs. control area). Therefore artificial nests in occupied territories and control areas were pooled in all subsequent analyses.

Habitat hypothesis – This hypothesis received most support in relation to artificial nest success, with three models within a ΔAICc of 2 (Table 12). All three models contained the variables "vegetation cover", "number of bushes", "number of grass tussocks" and "avg. diameter". The model ranked second highest additionally contained "number of trees" and the model ranked third highest additionally contained "sky visibility". Model averaging estimates and standard errors for all variables revealed that "number of bushes", "number of tussocks”, “vegetation cover” and “number of trees” could be considered for AHA (Table 13).

Nest site hypothesis – This hypothesis received some support in relation to artificial nest success, with the highest ranked model containing “nest position”, followed by the null model (Table 12). The variable “concealment index” was also present in models, though inferior to the null model, but still within a ΔAICc of 2 to the highest ranked model. “Concealment index” had to be omitted as its model averaged estimate was smaller than its associated standard error, whereas “nest position” could be considered for AHA.

Seasonal hypothesis – This hypothesis received some support as the model containing the variable “date” was ranked higher than the null model (Table 12). Although the model averaged estimate for “date” was very small, it was greater than its model averaged standard error and hence considered for AHA (Table 13).

Nest age, predation, disturbance and geographic hypotheses – These hypotheses received weak support, as the null model was always ranked highest. The only variable considered for AHA was “distance to forest edge”, which was in a model with a ΔAICc of 0.17 compared to the highest ranked model, the null model and had a model averaged estimate greater than its model averaged standard error (Table 13).

Across hypotheses analysis – There was support, as four models, but not the null model were within a ΔAICc of 2 (Table 12), all containing the variables “nest position”, “number of tussocks” and “date”. Three models also contained the variable “number of trees”. “Vegetation cover” and “distance to forest edge” were present in the third and fourth ranked models, respectively. Model averaging revealed six variables with an effect on artificial nest success: “nest site” with its four levels “other”, “concealed by leaves/deadwood”, “beneath plants”, “concealed by grass/sedge”, “number of grass tussocks”, “number of trees” and “date”. For a complete overview of the model selection and model averaging refer to tables 12 and 13, respectively.

4 Discussion

4.1 METHODOLOGICAL ASPECTS

The fact that naïve nest success and overall nest survival calculated from daily nest survival rates over 32 days were very similar indicates that almost all nests could be found before they failed due to predation or abandonment. Still, we have to assume that some early first broods were not found, because we could not monitor all study areas from mid-April on due to logistic and time constraints (Table 1). Not knowing all fates of all nests from the beginning of the breeding season may influence the effect of “first-egg date” in relation to reproductive performance.

Since we did not ring the birds, we did not discriminate between primary, secondary or even tertiary territories or broods, which may cause overestimation of number of breeding males and females.

Obtaining precise estimations of daily nest survival is often a problem in nest success studies, which may overestimate nest success, due to nests that are predated in the last days or hours before fledging. Using continuous monitoring with trail cameras, late predations would not have gone unnoticed in this study. Trail cameras also proved to be very helpful for nest predator identification in 15 cases. Nevertheless, 7 nest predator identities were inferred according to nest condition or weak image evidence. While two nest predations were caused by unknown predators, Red Fox predations may have been overestimated by 5 animals. However, as described in detail in the result section "nest failure and nest predators", we remain confident that destroyed nests can be attributed to Red Foxes.

Linked to nest predation and nest survival is the question whether there was a researcher effect. Ortega (1997), Penn (2000) and Schiegg *et al.* (2007) could not find researcher effects in their studies, while e.g. Gutzwiller *et al.* (2002) and Whelan *et al.* (1994) did find researcher effects. Although we did not make any attempt in masking our scents on boots or hands, we always approached nests from the same route. Also, we were not required to manipulate nests, adults, eggs or nestlings. Similarly, we did not control for researcher effects during the analysis, since we walked up to every nest at a similar frequency and installed cameras at almost every nest (n = 45). Only 1 of 21 nests was predated within 24 hours after our visit. For this nest, predated by a Eurasian Jay, it remains unclear whether the nest predator reacted to the researcher, who was present at the nest 2 hours before nest predation or whether it was a random occurrence. Based on camera footage analysis, seven nest predators did not approach the nest from the same direction as the researchers did, which is half of all monitored nest predations. In four cases the nest predators did approach nests from the same direction as the researcher. However, it remains unknown whether the nest predators followed scent trails or whether they randomly approached nests from that direction.

Another methodological issue regarding partial nest predation may have caused overestimation of unsuccessful nests and therefore underestimation of fledged young. Based on trail camera footage it was not possible to determine whether there was partial nest loss, i.e. some young, late during nestling stage, may have managed to prematurely fledge during nest predation. Therefore, whenever a nest predation occurred it was deemed a complete nest predation for the purpose of this study. An ascertained partial nest predation may have occurred at least once, with five 12 days old hatchlings, where the nest predator, a Red Fox, conspicuously searched the vicinity after nest predation, possibly looking for dispersing fledglings. All other nest predations occurred when nestlings were 10 days old or younger.

Biased results in the artificial nest experiment may have arisen from the type of material we used to mimic eggs. As we initially thought we would not have enough trail cameras to monitor all artificial nests, we relied on plasticine eggs with the objective to identify nest predators from bite marks (Bayne *et al.*, 1997; Purger *et al.*, 2004), Yet, plasticine has a fairly strong scent that could attract unconventional, casual nest predators. This may explain why the principal nest predators of artificial nests were rodents of the superfamily Muroidea, which were never observed predating real nests. Muroid predation can however also be explained by an absence of parents that may defend nest against small intruders. In contrast to real nests, we handled artificial nests with our bare hands. Human scent may thus have atypically attracted olfactorily hunting predators to artificial nests (Whelan *et al.*, 1994).

Placing artificial nests remains a very subjective exercise, as experienced in this study. Our artificial nests were mostly placed in leaf litter, leading to the nest position “other” being over-represented in our sample (93.8%) compared to the other three types of nest site situation. Real nests were predominantly built in grass tussocks (55.1%), while only 12.2% (category “other”) were constructed within leaf litter, under rocks or between tree roots,.

4.2 PHENOLOGY AND REPRODUCTIVE SUCCESS

First-egg dates as well as the duration of the incubation and nestling stages complied with other studies (Glutz von Blotzheim & Bauer, 1991; Mildenberger, 1949; Stresemann, 1955; Wesołowski & Maziarz, 2009). Earliest and latest first-egg dates were May 4 and June 24, respectively, with a median first-egg date over all study areas on May 22. The mean incubation and nestling stage durations were 14 days (n = 7, range: 13 –16) and 13 days (n = 17, 11 – 15), respectively. A nesting success of 40.8%, calculated over a period of 32 days, also was within the reported range (Glutz von Blotzheim & Bauer, 1991; Wesołowski, 1985), with fluctuations occurring between years. Abandonment of nests (n = 5) always occurred during cold outbreaks lasting several days, though we did not model with weather circumstances. Note that only one nest was abandoned during the nestling stage. Contrary to observations by Mildenberger (1940), Wood Warblers in our study were not easily disturbed by researchers. For the nest abandoned during nestling stage it remains unclear whether abandonment followed predation on parents.

Mean clutch size (5.1; SD = 1.3; n = 42) over all study areas was smaller than reported elsewhere (6.2, n = 379, including clutches from deciduous and coniferous forest patches; Bialowieza NP; Wesołowski & Maziarz, 2009), 6.3 (Czechoslovakia; Bauer & Tichy, 1966 in Wesołowski, 1985) and 6.3 (Switzerland, Glutz von Blotzheim, 1964; in Wesołowski, 1985). These differences in clutch size may partly reflect the fact that some first broods might have been missed, which are generally larger than subsequent broods (Wesolowski, 1985). Biologically, these differences in clutch size may be explained by differences in females' quality and/or age, or by varying nest predator pressure in different study areas (Wesołowski, 1985). The weak seasonal effect on clutch size (Fig. 4), revealed by model selection, can be seen in the difference of average clutch sizes in May and June, which were 5.5 (SD = 1.2) and 4.3 (SD = 1.3), respectively. Most studies have showed clear declining seasonal trends of reproductive performance in Wood Warblers (Wesolowski & Maziarz, 2009) as in most other bird species (Grant *et al.*, 2005; Müller *et al.* 2004; Naef *et al.*, 2001). Mean hatching rate of Warbler Wood in this study amounted to 93.4% (n = 18).

Wood Warblers in this study only produced 1.9 fledglings per nest when considering all nests (n = 49) and 4.55 fledglings per successful nest (n = 20). Hillig (2009) reported higher number of fledglings per breeding pair of 2.63 from all nests (n = 68) and 4.77 from successful nests (n = 39). Wesolowski (1985) reported 2.36 fledglings over all females, mentioning that 7 fledglings per female might be achieved without predation.

Considering only nest predation as cause of nest loss, a nest success of 40.8% (± 13.8%) could be documented, which is lower than the Wood Warbler nest success of 57.4% observed by Hillig (2009). Both these nest success rates were calculated from data from one summer. Wesolowski and Maziarz (2009) reported a mean nest success of 34.6%, ranging from 13.3% to 56.9% between 1976 and 2005. With data from only one year it is impossible to determine how this parameter fluctuates among years in Swiss populations.

4.3 NEST AGE HYPOTHESIS

Several studies have showed higher nest survival during incubation (Best, 1978; Burhans *et al.*, 2002; Suárez & Manrique, 1992; Young, 1963) and by applying quadratic or cubic terms to the data even seasonally oscillating trends (Grant *et al.*, 2005). In this study no such seasonal oscillation was found, but a relatively weak, linear, negative relation between daily nest survival rates and nest age. Still, "nest age" was present in all 10 highest ranked models. Nest survival steadily decreased during the entire nesting period (Fig. 3a), likely reflecting parental care activity around the nest, which increases during the nestling stage (Glutz von Blotzheim & Bauer, 1991; pers. Observation) and in turn may increase predation risk.

There are several reasons for a decrease in nest survival over the nesting period: 1) At the peak of chick provisioning, approximately on day 9th, adults may visit nests up to 650 times in 15 hours, roughly 43 times per hour, whereas on average, foraging during incubation occurred once or twice per hour (Glutz von Blotzheim & Bauer, 1991; pers. obs.). Considering these feeding rates, it seems unlikely that

Wood Warblers adjust their behavior during nestling stage to limit cues given to predators (Martin *et al.*, 2000). Most probably, they rely solely on nest concealment. 2) Nestlings themselves give auditory, olfactory and visual cues to nest predators. 3) Nest predation rates may simply increase due to temporal overlap in the nesting cycles of both predators and Wood Warblers, with increased activity of food seeking adults and progressive dispersal of juvenile predators (Burhans *et al.*, 2002).

Insufficient egg concealment by adults (Grant *et al.*, 2005; Klett & Johnson, 1982) was unlikely to play a role in predation rate, since nest content is not equally visible in Wood Warbler nests as it is in open nesting bird species such as Mallards *Anas platyrhynchos* (Klett & Johnson, 1982). The interaction between nest age, nest concealment, adult activity and different predators is anyways complex (Martin *et al.*, 2000; Weidinger, 2002) and could not be disentangled in this observational study.

4.4 SEASONAL HYPOTHESIS

Decreasing reproductive performance as the season progresses has been reported in many bird studies (Grant et al, 2005; Müller *et al.*, 2004; Naef-Daenzer *et al.*, 2001; Peak, 2007). Seasonal effects may be linked to higher quality of early breeders that are usually the most experienced individuals – and those that arrive first on breeding grounds in migratory birds –, to changing nest predator abundances due to juvenile dispersal, or to factors linked with climatic conditions, such as food availability. Reproductive performance over the entire breeding season may be reduced for females starting to breed late, as there is little chance for replacement, or second broods, while offspring have anyway less development time (Müller *et al.*, 2004). We found no support for a relationship between nest survival and number of fledglings vs. season, but there was a weak, negative relationship between clutch size and season.

4.5 NEST SITE HYPOTHESIS

Nest site selection and nest concealment seem to be critical aspects of nest success in birds (Martin *et al.*, 2000; Müller *et al.*, 2004; 2000, Weidinger, 2002). The variable "concealment index" was present in all 10 highest ranked models and seems to be important in relation to daily nest survival (Fig. 5). This might in part explain why relatively few nests were predated by birds over the entire nesting stage (n = 4). Only about one third of all nest predations occurred during the egg-laying and incubation stages, when the presumed positive effect of nest concealment may not have been counteracted by parental activity yet. Martin *et al.* (2000) have shown that increasing parental activity acts antagonistically to nest concealment. On the other hand, interpreting concealment is difficult because nest predators did not usually aim for the nest directly, but rather inadvertently flushed the female by walking past the nest, then turned around to investigate. This could be observed on footage for at least 7 nest predations. Therefore, not only nest concealment but also female attitude may play an important role. In some instances a passing-by nest predator would not have noticed the nest would the female have stayed still, which became apparent from 3 cameras showing martens (n = 4), badgers (n = 4) and cats (n = 2) walking by the nest without noticing it. The number of predators not noticing nests is certainly underestimated, for cameras were directly aimed at nest, and most camera angles did not allow monitoring a wide enough area to pick up such roaming nest predators.

4.6 CLUSTERING HYPOTHESIS

Only three pairs occurred alone in their respective study areas during the entire breeding season. Although two more pairs occupied two separate study areas by themselves, they had neighboring singing males at least in the early stages of nesting. All other pairs had territories next to each other. Clustering territories may not only result from patterns of resources acquisition, but may be an essential component of Wood Warbler's settlement dynamics, under the control of sexual selection: 1) clustering may allow for extra pair copulations by males or females (hidden lek hypothesis, Wagner, 1998); 2) clustering gives reproductive stimuli by observing reproducing neighbors (social facilitation hypothesis, Darling (1938) in Tarof & Ratcliffe, 2004); 3) clustering increases the chance of attracting females, because there are more singing males that can be heard by females (social mate choice hypothesis, Allee (1951) in Tarof & Ratcliffe, 2004). The social mate choice hypothesis, sometimes also referred to as the super sexy unit hypothesis, can be rejected in our study since the correlation between total number of territories and pairing rates per study area was not significant. The hidden lek or social facilitation hypotheses on the other hand may apply for Wood Warbler territory clusters, as monoterritorial and polyterritorial polygyny have been reported (Herremans, 1993; Temrin, 1984; Temrin & Jakobsson, 1988; Temrin *et al.*, 1984; this study).

Model selection in this study supported a weak effect of clustering in relation to number of fledglings (Fig. 6). When territories of singing and paired males are clustered together, females have a greater chance of receiving help from either an unpaired single, or paired, polygynous male, which they frequently solicit to possibly improve reproductive performance (Herremans, 1993).

4.7 DISTURBANCE HYPOTHESIS

Disturbance by humans has largely negative effects on birds, affecting occurrence and composition of bird communities and populations (Boyle & Samson, 1985; Kangas *et al.*, 2010; Patthey et al. 2008). Hiking constitutes the greatest disturbance, as it increases trampling of habitat, noise pollution, garbage thrown away and may elicit a stress response in wildlife. Hunters, wildlife observers and photographers actively seek out animals, often rare species, thereby increasing nest loss through direct extirpation and trampling, and influencing predation rates and abandonment (Boyle & Samson, 1985). Connected to recreational activity is the network of trails used by humans, which increases habitat fragmentation by creating habitat edges used by some nest predators, which in turn increases nest predation of certain species (Miller & Hobbs, 2000; Miller *et al.*, 1998).

In our study, reproductive performance of Wood Warbler was not related to “distance to trails”. On two occasions Wood Warblers built nests within 1 m of trails and both were predated. On the other hand, one pair successfully bred between a rock climbing wall and a small trail used to get to the wall. Females seem to care little for human presence around the nest. Upon checking nests and installing trail cameras, generally all females returned to nests within 5 to 10 minutes. Females also continued feeding the brood, while researchers were standing as close as 5 m.

4.8 HABITAT HYPOTHESIS

The importance of forest type, canopy closure, branch structure and other habitat features for Wood Warbler territory choice has been studied and documented in numerous papers and books (Glutz von Blotzheim & Bauer, 1991; Gerber, 2011; Hillig, 2009; Marti, 2007; Quelle & Lemke, 1988; Reinhardt & Bauer, 2009). There is consensus that the preferred habitat usually consists of forests with a mix of deciduous tree species, but also forests with a mix of deciduous and coniferous tree species. Preferred are stands of medium age with trees between 20 and 40 cm in diameter at breast height, canopy closure with an optimum between 60 and 90 % and some branches at low to medium heights. Canopy cover seemed to have been the most important variable in relation to daily nest survival rate, for it was present in all 10 highest ranked models. Nest survival was highest between 80% and 85% canopy cover. Besides nest concealment per se, densely structured canopy may additionally help to hide nests from high-flying aerial nest predators such as birds of prey or corvids. Dense canopy cover may also mitigate effects of severe weather (Henrioux, 2007). However, canopy cover which is to dense may be related to ground climate not suitable for Wood Warbler nests, where they may not maintain conditions necessary to produce successful broods. Whether canopy cover is related to prey abundance such as caterpillars is unknown for Switzerland, but it has been shown that caterpillar abundance is not significantly correlated to Wood Warbler territory choice in other areas (Herremans, 1993; Wesołowski *et al.*, 2009) and Maziarz and Wesolowski (2010) found no correlation between caterpillar abundance and nestling development in Bialowieza National Park in Poland.

The age of a forest patch seems to relate to Wood Warbler reproductive performance. Tree diameter, an index for stand age, averaged for each territory, was present in only four models with ΔAICc < 2 but had the highest model averaged estimate of all variables during AHA (Table 7). Mean average tree diameter for territories with successful and predated nests were not far apart with 29.0 cm (SD = 5.3 cm) and 25.8 cm (SD = 4.4 cm), respectively. Mean average tree diameter in relation to reproductive performance cannot be compare to other studies, as other studies have never conducted a similar analysis. Even though averaged tree diameter varies in habitats selected by Wood Warbles, model selection supports a positive correlation between nest survival and increasing average tree diameter, at least within the observed range of tree diameters.

I found no relation between reproductive performance vs. geographical variables and vs. variables describing undergrowth and field layer such as "number of grass tussocks", "vegetation cover" and "number of bushes". Interestingly, Gerber (2011) also found no relation between habitat selection and the variable "branched below 4m" while this study found a negative relation between nest survival and the variable “branched below 4m”. This is surprising as trees branched below 4 m have been found to have a negative effect in relation to habitat selection (Hillig, 2009; Quelle & Lemke, 1988; Reinhardt & Bauer, 2009), which is difficult to interpret. It may be an artefactual effect caused by preference for middle forest stand age. The older a tree stand gets, the fewer branches at low to medium heights can be found. While branches at low to medium heights are used by Wood Warbler for starting their singing flight and for nest approach, they may serve as perches for avian predators which would decrease daily survival rate of Wood Warbler nests. It has to be noted that mean and SD for “branched below 4 m” between occupied territories and control areas were almost identical (Gerber, 2011) and mean and SD for successful (9.2 ± 5.4) and unsuccessful nests (12.7 ± 5.8) very similar. Furthermore, “branched below 4 m” was present in only two models (Table 6) and had a model averaged standard error almost identical as its model averaged estimate.

4.9 NEST PREDATION HYPOTHESIS

Nest predation is one of the major causes for reduced reproductive performance, especially for ground nesting species (Langgemach & Bellebaum, 2005), and may influence habitat selection (Hatchwell et al., 1996; Martin, 1988), nest site selection (Martin & Roper, 1988), clutch size (Jetz et al., 2008; Mönkkönen, 2009; Slagsvold, 1984) and parental care behavior (Martin, 2000). Also phenological and life history traits of Wood Warblers are affected by nest predation. Nest predation is the main cause of nest loss and can amount up to 95%

(Wesołowski *et al.*, 2009). Nest predation rate in this study was higher than in a study conducted in parts of Germany in 2007 (Hillig, 2009), but smaller than mean predation rates reported by Wesolowski and Maziarz (2009), who's data set spans almost 30 years. Wesołowski and Maziarz (2009) have also found that Wood Warbler settlement decreases as rodent numbers increase. Therefore we assessed rodent density per territory in relation to habitat selection (Gerber, 2011) and reproductive performance. Model selection revealed a weak, negative relation between nest survival and rodent density (Fig. 3e) and suggests that the effect is negligible. However, the fact that I found an effect, even if weak, after taking into account that Wood Warblers only settle in territories with low rodent numbers to begin with (Wesołowski et al; 2009), which we can confirm for our research system (Gerber, 2011), seems to support a role of rodents, possibly indirect, on Wood Warbler nest success. "Clutch size" and "number of fledglings" were not related to rodent density. We observed nest predation in all Wood Warbler study areas with at least two breeding pairs.

4.9.1 *Nest predation mechanisms*

Before discussing each predator separately, I first discuss possible mechanisms responsible for nest predation. 1) High rodent abundance during rodent outbreak years constitutes a readily available food source and can increase the abundance of rodent-hunting nest predators predominantly found or breeding in forest habitat, such as Pine Martens, Tawny Owls and Common Buzzards *Buteo buteo*. 2) Generalist nest predators such as Stone Marten and Red Fox may also be attracted by rodent outbreaks in forests but may also occur due to spillover predation (Oksanen *et al.*, 1992), connected to landscape fragmentation (Storch *et al.*, 2005). In either mechanism, Wood Warbler nests are not the primary targets sought, but are found by chance due to increased nest predator presence on the forest floor.

The first mechanism may be a form of hyperpredation (Smith & Quin, 1996). Hyperpredation usually occurs on islands, where one prey species increases in abundance and therefore enables a predator species to do the same. A secondary species is subsequently under increased predation pressure (Courchamp *et al.*, 1999; Courchamp *et al.*, 2000; Roemer *et al.*, 2002). During rodent outbreak years, forest patches may take the role of islands, where rodents greatly increase in numbers. Thereby, reproductive performance of animals using rodents as food source increases as well. As numbers of Pine Martens and birds of prey, such as Tawny Owls, increase, the chance of them accidentally coming across and predating Wood Warbler nests supposedly increases as well. Such a dynamic in relation to rodent outbreak years may explain annual fluctuations of Wood Warbler reproductive performance (Wesolowski et al, 2009; Wesolowski & Maziarz, 2009). However, due to a general, long-term increase of Red Fox and possibly also Stone Marten populations (Breitenmoser *et al.*, 2000; Contesse *et al.*, 2004; Langgemach & Bellebaum, 2005), further discussed below, hyperpredation may not be limited to but aggravated by rodent outbreak years and exert increased predation pressure on Wood Warbler reproductive independent of rodent outbreak years. Against such aggravated predation conditions, Wood Warblers may have not had enough time to adapt patterns of habitat and nest site selection, clutch size or parental care behavior.

The second mechanism possibly playing a role in nest predation and possibly aggravated by hyperpredation may be found in one type of spillover predation, where generalist predators not only penetrate into but completely traverse adjacent habitat patches to get to different foraging grounds or resting sites and opportunistically take prey along the way (Andren & Angelstam, 1988; Batáry & Báldi, 2004; Lidicker, 1999; Oksanen *et al.*, 1992; Rodewald & Yahner, 2001; Storch *et al.*, 2005; Wilcove, 1985). Studies on spillover predation, where predator and prey operate on different spatial scales (Lidicker, 1999), have to take entire landscape mosaics into consideration and not only single patches as is done when studying edge effects (Storch *et al.*, 2005). Hence, spillover predation is related to landscape fragmentation. As forest fragmentation has not increased much for over a century due to efficient protection of Swiss woodlands (SR 921.0, "Bundesgesetz über den Wald"), reduced reproductive performance of Wood Warblers in Switzerland can certainly not be attributed to forest fragmentation. However, Swiss forests are fragmented nonetheless after millennia of deforestation, as well as spreading agricultural and urbanized land. Furthermore internal forest fragmentation still occurs, creating a mosaic of different tree communities or age classes, which may favor generalist species and certain predators, but puts Wood Warblers under pressure. We hypothesize that spillover predation may have gained importance in connection with the eradication of rabbis in Red Fox (Breitenmoser *et al.*, 2000; see below). To analyze spillover predation it is necessary to measure and analyze patch size, landscape patchiness and/or predator density in relation to reproductive performance of Wood Warbler, which was not done during this study.

We did however measure distance from Wood Warbler nests to closest forest edge to investigate the presence of an edge effect. Edge effects are a type of spillover predation (Storch *et al.*, 2005) and can be created by trails (Miller *et al.*, 1998; Miller *et al.*, 2000), but are usually studied in connection with edges along different habitats (Batáry & Báldi, 2004; Paton, 1994; Storch *et al.*, 2005). Unlike spillover predation caused by predator traversal of entire habitat patches, edge effects are caused by predators living predominantly in one habitat, but temporarily crossing into adjacent habitats to forage (Andren & Angelstam, 1988). In his review, Paton (1994) found that studies proposing the occurrence of edge effects within 50 m of an edge to be most convincing, whereas studies proposing the occurrence of edge effects beyond 50 m to be less convincing. Storch *et al.* (2005) found edge effects in relation to nest fates at over 4 km from edges. Model selection in this study did not support an edge effect using the variable "distance to forest edge". Mean and range of "distance to forest edge" over all fledged (169 m, range: 63 – 516 m) and unsuccessful nests (185 m, 50 – 558 m) were quite similar, respectively.

A third mechanism, the prey switching hypothesis, has to be mentioned at this point. Prey switching is frequency-dependent prey selection by predators, meaning predators concentrate on the most abundant prey and ignore less abundant prey (Abrams & Matsuda, 2003; Allen & Greenwood, 1988). In the context of this study this hypothesis would imply that with high rodent densities, Wood Warbler nests would face much less predation due to satiation of predators through rodents. There was indication that the summer of 2010 was a rodent outbreak year, as can been seen from very favorable conditions for Tengmalm's Owls *Aegolius funereus*, *S. aluco* and Long-eared Owls *Asio otus* (Media communication, Swiss Ornithological Institute, July 21, 2010). According to the switching hypothesis, Wood Warbler nests should have had high nest survival during this alleged rodent outbreak summer. Whether or not nest survival was in fact high or low cannot be answered based on nest predation rates and rodent densities from one year only.

4.9.2 *Nest predators*

Taking into account some uncertainty regarding 9 nest predator identities, the principal nest predator of Wood Warbler nests in Switzerland was Red Fox (n = 9), followed by Stone and Pine Martens (n = 6), European Badger (n = 4), Eurasian Jay (n = 3) and Tawny Owl (n = 1). Principal nest predators listed by stage were European Badgers and martens during the egg-laying and incubation stages and Red Fox and avian predators during the nestling stage. Of 15 nest predations during nestling stage, 11 occurred in the second half of nestling stage, of which six were caused by Red Fox (Table 3). Interestingly, with respect to nest destruction, the only nest predated by Red Fox during nest construction or very early during the egg-laying stage was located within 10 m of a Red Fox den, which was one of only two Red Fox dens found throughout this study.

Red Foxes have increased in several European regions. In Switzerland this increase is attributed to the eradication of rabies since 1999 (Breitenmoser *et al.*, 2000). Fox populations increased in almost every habitat including urbanized areas since the 1980s (Contesse *et al.*, 2004; Langgemach & Bellebaum, 2005), which coincides with increased kills by hunters since the 1980s, followed by a decrease in the past 15 years while hunting pressure on Red Fox may have decreased due to societal changes (Appendix 5).

Red Foxes are habitat generalists and opportunistic nest predators, often called edge habitat predators (Brangi, 1995; Silva *et al.*, 2009). Their home range and habitat selection depends on factors such as distribution and abundance of prey and other food sources, as well as den site availability (Silva *et al.*, 2009). Fragmented landscapes offer ideal habitat to Red Foxes for foraging, which occurs predominantly in open habitat, such as meadows and agricultural fields, where small mammals, especially *Microtus* voles, are normally in much higher abundance than in forest habitats (Jędrzejewski & Jędrzejewska, 1992). However, Red Fox den and resting sites are often situated in forests (Silva *et al.*, 2009). Despite a preference to forage in open habitats, Red Foxes also forage in forests, where seasonal vegetal matter and, during winter, carrion is preferred. However, Red Foxes are also attracted to high rodent concentrations (Jędrzejewski & Jędrzejewska, 1992; Jędrzejewski & Jędrzejewska, 1993), which occur in forests predominantly during rodent outbreak years related to mast seeding (Ostfeld et al, 1996; Schnurr, 2002). As a generalist predator, Red Foxes will forage in and switch among many habitat patches, including open and forest habitat. Such switching and traversing of habitat patches is described in the spillover predation hypothesis above (Oksanen *et al.*, 1992; Storch *et al.*, 2005), which is favored by fragmented landscapes (Storch *et al.*, 2005). As discussed above, forest fragmentation in Switzerland has not changed much more for over a century, but in connection with the eradication of rabies and the resulting increase of Red Fox populations, nest predation pressure may have increased. We could not statistically analyze spillover predation, but from picture analysis we see that Red Foxes do not specifically search for ground nests, but rather take notice of them only after flushing the female by accident. Calculating nest survival in the absence of Red Fox predation revealed that this predator is responsible for a decreased nest survival of 28.4% over the entire nesting period.

Mustelids together accounted for as many predations as Red Fox. Considering mustelid predator species separately, the predation by this group of carnivores is less intense, as suggested by Langgemach & Bellebaum (2005). Species identification from picture analysis turned out to be difficult for Stone and Pine Marten, but they committed 4 and 2 nest predations, respectively, while European Badgers predated three nests. Should these identifications be correct, surprisingly, Pine Martens, as forest dwellers and preferring Bank Voles as main prey (Lanszki *et al.*, 2007; Zalewski *et al.*, 1995), are not responsible for many nest predations. On the other hand Stone Martens, as opportunistic habitat generalists often residing near human settlements accounted for twice as many predation events, though both species can live sympatric in the same habitat (Poslusny *et al.*, 2007). The

European Badger spends most of its time rummaging the ground in search of its favorite prey, earth worms (Kruuk, 1978; Kruuk and Parish, 1981), thereby coming across Wood Warbler nests and profiting of an easy meal. As Red Foxes, mustelids did not seem to search for ground nests specifically, as at least three martens did not noticed the nest until flushing the female. Furthermore, martens in four cases and European Badgers in four cases walked by nests without noticing them.

Corvids and birds of prey played only a small role as nest predators. The only nest predation by a bird of prey was committed by a Tawny Owl, which uses rodents, predominantly the nocturnal Yellow-necked Mouse (Jędrzejewski *et al.*, 1994), as staple food source. With the exception of the Eurasian Jay, corvids predominantly hunt along edges and do not penetrate into the forest interior often (Miller *et al.*, 1998; pers. observation). Apparently, corvid nest predation has been regularly overestimated before the usage of modern devices such as thermo-loggers and cameras (Langgemach & Bellebaum, 2005).

Domesticated dogs and cats were not observed as predators of Wood Warbler nests in our study. Dogs were never even seen on camera and cats did not notice artificial nests (n = 2) or real nests (n = 1). Using "distance to buildings" as proxy for possibly increased nest predation pressure by domesticated pets, especially cats, we hypothesized that there may be an effect of "distance to buildings" in relation to reproductive performance, which however was not supported by model selection.

Rodents were present in the Wood Warbler territories, as can been seen from captures and on 10 cameras, where rodents, including Red Squirrels, roamed around nests without approaching them. Furthermore, *Apodemus* mice and Red Squirrels could be observed investigating nest content closely on three and two occasions, respectively, but nest predation did not occur in these cases. We suspect that Wood Warblers are able to chase off rodents as big as squirrels, which has been observed by Whelan *et al.* (1994) for other passerine species. Mildenberger (1940) observed lower nest success during rodent outbreak years, but did not per se observe nest predation by rodents. Wesołowski *et al.* (2009) also observed lower nest success in rodent outbreak years, and attributed predated, but intact nests to rodent predation. Using nest condition may lead to biased results, as shown in this study, because only Red Foxes destroyed nests. Not even the similar sized European Badger even deformed nests. Other studies have used cues like small broken egg shell pieces found in the nest to attribute nest predation to rodents (Walankiewicz, 2002). While Walankiewicz (2002) also used other cues like shredded nest material for identification of nest predator, we warn against using such cues, for we have found small broken egg shells in nests predated by Eurasian Jays and martens. Nest survival negatively correlated with rodent density, possibly due to spillover predation and/or hyperpredation.

4.10 ARTIFICIAL NEST EXPERIMENT

There were several differences between artificial and real nests in relation to predator community, nest success rates and influencing variables. One major difference were the survival rates of real nests during incubation and artificial nests during 13 days (corresponding to incubation), which amounted to 74.2% (± 10.2%) and 18.4%, respectively. This large difference of period survival rate can be attributed to massive rodent predation upon faked nests, which was not observed for real nests. Interestingly though, if we disregard rodent predation on artificial nests, survival rate of artificial nests during 13 days would have been 73.7%, almost identical to survival rates of real nests during incubation.

Apart from muroids as nest predators of artificial nests, the second difference were the different mesopredator communities between real nests during incubation and artificial nests during 13 days corresponding to incubation. While four real nests were predated by avian predators, their absence as nest predators on artificial nests supports the hypothesis that avian nest predators, especially diurnal ones, such as the Eurasian Jay, react to adult Wood Warbler activity around the nest. Red Foxes and Red Squirrels could not be observed predating real nests during incubation or at all (Red Squirrel), but they predated artificial nests four times and once, respectively.

The third major difference between real and artificial nests however, can be found in the variables related to real and artificial nest success. While real nest success was mainly related to nest concealment, habitat structures related to forest stand age (average tree diameter, canopy closure) and weakly to nest age and rodent density, artificial nest success was mainly related to nest position, number of grass tussocks and weakly to date. Whether artificial nests are adequate surrogates for real nests is frequently debated and may depend on how elaborate the study design for an artificial nest experiment is (Faaborg, 2004; Villard *et al.*, 2004). If questions concerning Wood Warbler reproductive ecology are addressed, using artificial nests can at the most be used to determine nest predation rates, but only if muroid predation is disregarded as established here.

5. Implications for conservation

Flade and Schwarz (2004) showed that 7 out of a selected sample of 10 declining species are long-distance migrants, which may indicate problems in the wintering habitats and/or during migration. For the Wood Warbler there seem to be different population trends between Western Europe (declining) and Eastern Europe (stable). It is possible that Wood Warblers from Eastern and Western Europe also use different wintering grounds and/or different migration routes. But even if these different wintering grounds and/or migration routes vary in quality, the decline of Wood Warblers in Western Europe can most likely not only be sought in wintering habitats and/or during migration as Flade and Schwarz (2004) showed that 17 of 21 forest species with increasing populations did so in urbanized areas and not in closed forests, indicating a forest habitat problem. It is likely that complex interactions between breeding habitat availability, quality and patchiness of breeding habitat, nest site, as well as nest predation affect Wood Warbler reproductive performance. Once a forest stand has reached the age and succession stage sought out by Wood Warblers, the forest stand usually becomes subject to some form of logging. Even though we do not know the optimal breeding habitat conditions for the Wood Warbler, several studies suggest that the species does not typically breed in very young or very old stands; likewise in our study areas, we did not find any Wood Warblers in very young and old mature stands (Gerber, 2011. Therefore, the relation between nest survival and stand age found in this study can most likely be observed only within a certain range of stand ages. Through removal of single trees to open up the closed forests and/or achieve forest rejuvenation, as is common in Swiss forestry, stands are managed in a way that may favor many other species, but limits Wood Warblers. Opening forest stands entails opening the canopy. As a consequence of open canopies, more light can penetrate to the forest floor and allow underbrush, i.e. young trees and shrubbery, to grow. Underbrush may 1) interfere with the Wood Warbler's aerial maneuverability and approach of the nest, 2) create unfavorable ground conditions for constructing nests, including lack of nest concealment and/or 3) attract more predators than open ground habitats. Interestingly five of our seven study areas with major Wood Warbler aggregations, i.e. more than one breeding pair, are not subject to forestry. Blauen, Langenbruck, Lauwil are forest reserves and Glarus and Scheltenpass cannot be logged cost efficiently, so only fallen trees or trees posing a threat to humans or roads are removed.

Taking into consideration the results of this study concerning habitat structure in relation to reproductive performance as well as Gerber's (2011) results concerning habitat structure in relation to habitat selection, one strategy to support Wood Warbler populations may be to maintain many more medium aged forest stands, possibly in form of forest reserves or alternatives to the current forestry practice of single tree removal (forest gardening).

Besides factors related to habitat selection which are further discussed by Gerber (2011), nest predation may have had a substantial impact on Wood Warblers nest success. Since rodents were not observed depredating Wood Warbler nests directly, the presence of rodents probably determines predator abundance, indirectly affecting the survival of Wood Warbler nests. Mesopredators, especially Red Foxes, have increased throughout the past decades and may thus aggravate declines of Wood Warblers. Future studies must investigate whether there is a relationship between nest predator occurrence and habitat fragmentation and how strong it is. Nest survival from one year documented in this study was actually lower than nest survival from one year reported by Hillig (2009), but higher than mean nest survival from several years reported by Wesolowski and Maziarz (2009) for the Bialowieza NP in Poland. Nest survival from one year should not be compared to mean nest survival from several years, therefore it is difficult to conclude how much of an impact predation has on Wood Warbler nesting. Also comparing clutch sizes and number of fledglings from this study to other studies should be done with caution. While both, clutch size and number of fledglings, were lower than what other studies reported, the results are again from only one, maybe bad year. Should it become apparent that predation really does have a substantial impact on Wood Warbler reproductive performance, possibly increased hunting effort concerning especially Red Fox may be conceivable. Red Fox predation lowered nest survival over the entire nesting period by 28.4%. Whether or not Red Fox predation on Wood Warbler nests is additive or compensatory is as yet unknown.

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Table 1. Earliest, latest and median first-egg dates by study area and in total (sorted by median first-egg date).

Study area	Elevation a.s.l. (m)	First survey of area	Median date	Earliest date	Latest date	Number of nests
Montsevelier	731	23.04.	12.05.	09.05.	15.05.	2
Glarus	663	21.04.	14.05.	04.05.	24.05.	6
Bänkerjoch	688	12.05.	18.05.	-	-	1
Staffelegg	595	14.06.	19.05.	-	-	1
Gündelhart	585	24.05.	20.05.	-	-	1
Oltingen	693	13.05.	22.05.	-	-	1
Lauwil	1008	23.04.	26.05.	16.05.	05.06.	5
Kleinlützel	656	29.04.	02.06.	12.05.	24.06.	5
Langenbruck	947	30.04.	03.06.	26.05.	11.06.	4
Scheltenpass	877	13.05.	03.06.	14.05.	24.06.	12
Blauen	690	27.05.	07.06.	22.05.	23.06.	2
Dittingen	612	08.06.	13.06.	-	-	1
Overall	**792**	**09.05.**	**22.05.**	**04.05.**	**24.06.**	**41**

Table 2. Pairing rates by study area, sorted by canton, including territories of unpaired males. South and north areas are separated from each other by large agricultural areas.

Study area	**Males only**	**Pairs**	**Total territories**	**Pairing rate (%)**
Bänkerjoch (south) AG	0	1	1	100
Bänkerjoch (north) AG	1	0	1	0
Staffelegg (south) AG	0	1	1	100
Staffelegg (north) AG	2	0	2	0
Blauen BL	2	3	5	60
Dittingen BL	1	1	2	50
Langenbruck BL	7	5	12	42
Lauwil BL	5	7	12	58
Oltingen BL	0	1	1	100
Ennenda GL	0	6	6	100
Montsevelier JU	6	3	9	33
Kleinlützel SO	4	6	10	60
Scheltenpass SO	5	13	18	72
Gündelhart TG	0	1	1	100
Niderholz ZH	0	0	0	-
Zürichberg ZH	0	0	0	-
Zürcher Oberland ZH	0	0	0	-
Total	**33**	**48**	**81**	**60**

Table 3. Nest losses due to predation sorted by nesting stage and day predated, also showing nest predator and territory. For SP14 and KL03 nests the predator is unknown but both nests were left intact. LB02 was found destroyed.

Nest predation stage	**Egg-laying**				**Incubation**				**Nestling stage**															-[2]
Day predated	2	2	6	6	6	6[1]	7[1]	11[1]	1	1	2	2	7	8	8	9	9	9	10	10	10	10	12	-
Territory	LB05	KL02	OL01	GH01	MS01	SP14	KL03	MS03	BL01	LB01	KL01	KL05	MS02	BJ01	LW02	BL02	GL03	KL06	LW06	SP01	SP05	SP11	LB04	LB02
Nest predator	Badger	Fox	Marten	Badger	Marten	Unknown	Unknown	Marten	Jay	Marten	Jay	Fox	Jay	Fox	Fox	Marten	Fox	Tawny Owl	Fox	Marten	Fox	Badger	Fox	Fox

[1] indicates that the nests were predated between given day and end of stage; [2] stage not known

Table 4. Fates of real nests by study area and naïve nest success

Study area	**Number of nests**	**Number of nests predated**	**Number of nests fledged**	**Number of nests abandoned**	**Average number of fledglings**	**Number of fledglings**	**Naïve Nest success (%)**
Bänkerjoch	1	1	0	0	0	0	0
Blauen	3	2	1	0	1	3	33.3
Dittingen	1	0	0	1	0	0	0
Gündelhart	1	1	0	0	0	0	0
Glarus	6	1	5	0	4.3	26	83.3
Kleinlützel	6	5	1	0	0.8	5	16.7
Langenbruck	5	4	1	0	1	5	20.0
Lauwil	7	2	2	3	1.3	9	28.6
Montsevelier	3	3	0	0	0	0	0
Oltingen	1	1	0	0	0	0	0
Staffelegg	1	0	1	0	2	2	100.0
Scheltenpass	14	4	9	1	2.9	41	64.3
Total:	**49**	**24**	**20**	**5**	**1.86**	**91**	**40.8**

Table 5. Nest survival by period in relation to presence or absence of different predators

	Egg-laying (5 days)	Incubation (14 days)	Nestling (13 days)	Overall (32 days)
Nest survival considering all predations	93.6 %	74.2 %	58.7 %	40.8 %
Nest survival in the absence of Red Fox predation	96.3%	86.9 %	82.7 %	69.2%
Nest survival in the absence of Mustelid predation	98.6%	89.1 %	64.4 %	56.5%
Nest survival in the absence of Marten predation	96.6%	82.5 %	64.3 %	51.2%
Nest survival in the absence of Badger predation	96.5%	81.9 %	62.5 %	49.4%

Table 6. Model selection results for the analysis of daily nest survival rates, showing models with ΔAICc < 2 compared to the highest ranked model for all hypotheses except for tree structures (only showing the five highest ranked models). n = 27 nests. K: number of parameters in the model, including intercept and two random effects; LL: log likelihood.

Hypothesis	**Model**	**K**	**AICc**	**ΔAICc**	**Wt.**	**LL**
Nest site	concealment index	4	122.63	0.00	0.49	-57.27
	null	3	123.79	1.16	0.27	-58.87
Habitat	avg. diameter	4	122.79	0.00	0.02	-57.35
	branched below 4m	4	122.81	0.01	0.02	-57.36
	branched below 4m + crown contacts	5	122.98	0.18	0.02	-56.42
	crown contacts + avg. diameter	5	123.23	0.44	0.02	-56.55
	sky visibility + avg. Diameter	5	123.28	0.49	0.02	-56.57
	null model (17 more models with ΔAICc < 2 compared to top model, containing subsets of all proposed habitat variables are not shown)	3	123.79	1.00	0.01	-58.87
Predation	null	3	123.79	0.00	0.27	-58.87
	rodent density	4	124.93	1.13	0.15	-58.42
	distance to forest edge	4	125.44	1.65	0.12	-58.68
	distance to buildings	4	125.78	1.99	0.1	-58.85
Clustering	null	3	123.79	0.00	0.44	-58.87
	distance to closest nest	4	124.70	0.91	0.28	-58.31

	number of nests within 300m	4	125.75	1.96	0.17	-58.83
Nest age	null	3	123.79	0.00	0.57	-58.87
	nest age	4	123.84	0.05	0.32	-57.88
	nest age + nest age^2	5	124.04	0.24	0.11	-56.95
Seasonal	null	3	123.79	0.00	0.64	-58.87
	date	4	124.94	1.15	0.36	-58.43
Geographic	null	3	123.79	0.00	0.50	-58.87
	elevation	4	125.46	1.67	0.22	-58.69
	inclination	4	125.66	1.86	0.20	-58.78
Disturbance	null	3	123.79	0.00	0.73	-58.87
	distance to path	4	125.74	1.94	0.27	-58.82
Across	sky visibility + sky visibility^2 + nest age + concealment index	7	119.04	0.00	0.02	-52.4
	sky visibility + sky visibility^2 + nest age + concealment index + avg. diameter	8	119.14	0.11	0.02	-51.41
	sky visibility + sky visibility^2 + nest age + concealment index + avg. diameter + crown contacts	9	119.94	0.90	0.01	-50.77
	sky visibility + sky visibility^2 + nest age + concealment index + branched below 4m	8	120.16	1.12	0.01	-51.92
	sky visibility + sky visibility^2 + nest age + concealment index + rodent density + avg. diameter	9	120.61	1.58	0.01	-51.11
	sky visibility + sky visibility^2 + nest age + concealment index + crown contacts	8	120.73	1.70	0.01	-52.21
	sky visibility + sky visibility^2 + nest age + concealment index + distance to closest nest + avg. diameter	9	120.79	1.75	0.01	-51.19
	sky visibility + sky visibility^2 + nest age + concealment index + branched below 4m + crown contacts	9	120.81	1.77	0.01	-51.21

sky visibility + sky visibility^2 + nest age + concealment index + distance to closest nest	8	121.01	1.97	0.01	-52.35
sky visibility + sky visibility^2 + nest age + concealment index + rodent density	8	121.02	1.98	0.01	-52.35

Table 7. Model averaged estimates and standard errors from variables included in models with ΔAICc < 2 (compared to the highest ranked model) from the analysis of daily nest survival rates. * indicate variables considered for across-hypothesis analysis (AHA).

Hypothesis	**Variable**	**Term (if applicable)**	**Model averaged estimates**	**Model averaged SE**
Nest site	concealment index*		0.43	0.20
Habitat	avg. diameter*		0.56	0.38
	branched below 4 m*		-0.49	0.31
	sky visibility (linear model) *		0.47	0.40
	crown contacts*		-0.35	0.29
	sky visibility (quadratic model) *	linear	0.52	0.37
		quadratic	-0.35	0.25
	number bushes		0.53	0.91
	vegetation cover		-0.38	0.39
	branched below 10 m		-0.29	0.41
	number of tussocks		-0.15	0.41
	number of trees		-0.01	0.49
Predation	rodent density (linear model) *		-0.64	0.56
	distance to forest edge		-0.18	0.29
	distance to building		-0.02	0.32
Clustering	distance to closest nest		0.33	0.30
	number nests within 300 m		0.08	0.31
Nest age	nest age (linear model) *		-0.05	0.03
	nest age (quadratic model)	linear	0.12	0.13
		quadratic	-0.01	0

Seasonal	Date	-0.02	0.02
Geographic	elevation	0.21	0.39
	inclination	0.10	0.35
Disturbance	distance to path	0.10	0.30
Across hypotheses	avg. diameter	0.59	0.36
	rodent density	-0.58	0.51
	sky visibility^2	-0.50	0.27
	concealment index	0.49	0.30
	branched below 4 m	-0.46	0.44
	crown contacts	-0.35	0.30
	nest age	-0.07	0.04
	distance to closest nest	0.21	0.43

Table 8. Breakdown of clutch sizes by study area, unsuccessful and successful nests.

Study area	**Number of clutches**	**Total number of eggs**	**Mean clutch size**	**Mean number eggs in unsuccessful clutches**	**Mean number eggs in successful clutches**
Bänkerjoch	1	5	5.0	5	-
Blauen	3	11	3.7	4	3
Dittingen	1	5	5.0	5	-
Gündelhart	1	6	6.0	6	-
Glarus	6	34	5.7	6	5.6
Kleinlützel	5	27	5.4	5.3	6
Langenbruck	4	18	4.5	4.3	5
Lauwil	5	28	5.6	5.7	5.5
Montsevelier	3	19	6.3	6.3	-
Oltingen	1	6	6.0	6	-
Staffelegg	1	2	2.0	-	2
Scheltenpass	13	65	5.0	5.3	4.9
Total	**44**	**226**	**5.1**	**5.3**	**5.0**

Table 9. Model selection results for the analysis of clutch size, showing models with ΔAICc < 2 compared to the highest ranked model. K: number of parameters in the model, including intercept and one random effect; LL: log likelihood. The “small” data set contains all variables, including habitat and rodent density variables which could be measured for only 23 nests with clutches. This data set is therefore smaller than the “large” data set which contains only variables that could be measured for all 38 nests with clutches, which excludes habitat and rodent density variables.

Data set	**Hypothesis**	**Model**	**K**	**AICc**	**ΔAICc**	**AICcWeight**	**LL**
“small”	Disturbance	null	2	13.61	0.00	0.43	-4.50
n = 23		to path	3	15.40	1.79	0.17	-4.07
	Temporal	null	2	13.61	0.00	0.58	-4.50
		first-egg date	3	14.78	1.17	0.32	-3.76
“large”	Disturbance	null	2	18.47	0.00	0.37	-7.06
n = 38		to path	3	19.75	1.28	0.19	-6.52
	Clustering	null	2	18.47	0.00	0.55	-7.06
		nests within 300m	3	20.32	1.85	0.22	-6.81
	Seasonal	first-egg date	3	17.25	0.00	0.65	-5.27
		null	2	18.47	1.22	0.35	-7.06

Table 10. Model-averaged estimates and standard errors from variables included in models with ΔAICc < 2 compared to the highest ranked model, from the analysis of clutch size. The “small” data set contains all variables, including habitat and rodent density variables which could be measured for only 23 nests with clutches. This data set is therefore smaller than the “large” data set which contains only variables that could be measured for all 38 nests with clutches, which excludes habitat and rodent density variables. * indicate variables considered for across-hypothesis analysis (AHA); * indicates the variable, which has an effect in relation to clutch size.

Data set	**Hypothesis**	**Variable**	**Model averaged Estimate**	**Model averaged SE**
Small	Disturbance	distance to path	0.09	0.09
n = 23	Seasonal	first-egg date *	-0.009	0.008
Large	Disturbance	distance to path	0.073	0.069
n = 38	Clustering	number nests within 300 m	0.05	0.07
	Seasonal	first-egg date *	-0.01	0.006

Table 11. Nest predators of artificial nests by study area.

Study area	n	Nest success rate (%)	successful	unsuccessful	Muroids	Fox	Squirrel
Bänkerjoch	2	0.0	0	2	2	0	0
Gündelhart	2	50.0	1	1	1	0	0
Glarus	10	30.0	3	7	7	0	0
Kleinlützel	8	12.5	1	7	6	1	0
Langenbruck	8	25.0	2	6	5	0	1
Montsevelier	4	0.0	0	4	1	3	0
Oltingen	2	0.0	0	2	2	0	0
Staffelegg	2	0.0	0	2	2	0	0
Total	**38**	18.4	**7**	**31**	**26**	**4**	**1**

Table 12. Model selection results for the analysis of artificial nest success, showing models with ΔAICc < 2 (compared to the highest ranked model) for all hypotheses. K: number of parameters in the model, including intercept and two random effects; LL: log likelihood. n = 32 artificial nests.

Hypothesis	**Model**	**K**	**AICc**	**ΔAICc**	**Wt.**	**LL**
Habitat	vegetation cover + number of bushes + number of tussocks + avg. diameter	7	98.80	0.00	0.08	-42.24
	vegetation cover + number of bushes + number of tussocks + avg. Diameter + number of trees	8	100.64	1.83	0.03	-42.11
	vegetation cover + number of bushes + number of tussocks + sky visibility + avg. Diameter	8	100.67	1.86	0.03	-42.12
Nest site	nest site	6	102.00	0.00	0.37	-44.88
	null	3	102.67	0.67	0.27	-48.30
	nest site + concealment index	7	103.35	1.35	0.19	-44.51
	concealment index	4	103.61	1.61	0.17	-47.75
Seasonal & Nest age	date	4	101.95	0.00	0.34	-46.91
	null	3	102.76	0.72	0.23	-48.30
	date + nest age	5	103.65	1.70	0.14	-46.74
Predation	null	3	102.67	0.00	0.24	-48.30
	distance to edge	4	102.85	0.17	0.21	-47.36
	distance to building	4	104.18	1.51	0.11	-48.03
	rodent density + distance to edge	5	104.39	1.72	0.10	-47.11
	rodent density	4	104.57	1.90	0.91	-

						48.23
Disturbance	null	3	102.67	0.00	0.70	-48.30
	distance to trail	4	104.35	1.67	0.30	-48.12
Geographic	null	3	102.67	0.00	0.50	-48.30
	elevation	4	104.20	1.53	0.23	-48.04
Across	nest position + # tussocks + date + # trees	9	97.17	0.00	0.08	-39.32
	nest position + # tussocks + date	8	97.54	0.37	0.07	-40.56
	nest position + # tussocks + date + # trees + vegetation cover	10	98.36	1.18	0.04	-38.85
	nest position + # tussocks + date + # trees + distance to forest edge	10	99.16	1.99	0.03	-39.25

Table 13. Model-averaged estimates and standard errors from variables included in models with ΔAICc < 2 (compared to the highest ranked model) from the analysis of artificial nest success. * indicate variables considered for across-hypothesis analysis (AHA).

Hypothesis	**Variable**	**Level (if applicable)**	**Model averaged Estimate**	**Model averaged SE**
Habitat	numbre of bushes *		1.25	1.04
	number of tussocks *		1.22	0.73
	vegetation cover *		-0.90	0.54
	number of trees *		-0.41	0.38
	avg.diameter		0.72	0.47
	sky visibility		0.00	0.62
Nest site	nest position	Other *	3.52	1.39
		leaves/deadwood *	1.81	0.94
		beneath plants *	1.70	1.38
	concealment index		-0.34	0.38
Seasonal and Nest age	date *		-0.03	0.02
	nest age		-0.09	0.25
Predation	distance to edge *		0.80	0.60
	rodent density		0.13	0.55
	distance to building		0.11	0.69
Disturbance	distance to trail		-0.29	0.38
Geographic	elevation		0.34	0.49
Across	nest position	other	4.85	1.74
		beneath plants	3.53	1.89
		leaves/deadwood	3.44	1.44
	number of tussocks		1.20	0.73
	number of trees		-0.58	0.37
	date		-0.03	0.02
	vegetation cover		-0.40	0.50
	Distance to forest edge		0.33	0.66

Figure captions

Fig. 1. Study areas in Northern Switzerland from West to East – “Dots”: study areas with breeding pairs, including number of nests (KL: Kleinlützel, DI: Dittingen, MS: Montsevelier, BL: Blauen, SP: Scheltenpass, LW: Lauwil, LB: Langenbruck, OL: Oltingen, BJ: Bänkerjoch, SE: Staffelegg, GH: Gündelhart, GL: Glarus; “Crosses”: study areas with no breeding birds or territorial males (EW: Erschwil SO, EP: Eptingen BL, ZB: Zürichberg ZH, ZO: Zürcher Oberland ZH).

Fig. 2. Layout of sample areas (bold lines indicate measured distances) used to measure habitat structure variables and rodent densities. Territory center is the nest.

Fig. 3. Daily nest survival rates in relation to nest age (a), nest concealment (b), crown coverage (c), average tree diameter (d) and rodent density (e). Crown coverage is the inverse of sky visibility. Graphs are based on a model containing all five variables. For each graph, the target variable is set within the observed range and the other four variables fixed at their means. Dotted lines represent upper and lower 95% CI.

Fig. 4. Effect of first-egg date in relation to clutch size (n = 40)

Fig. 5. Mean number of fledglings per study area over all nests. BJ Bänkerjoch (n = 1 nest), BL Blauen (n=3), DI Dittingen (n=1), GH Gündelhart (n=1), GL Glarus (n=6), KL Kleinlützel (n=6), LB Langebruck (n=5), LW Lauwil (n=7), MS Montsevelier (n=3), OL Oltingen (n=1), SE Staffelegg (n=1), SP Scheltenpass (n=14).

Fig. 6. Boxplot showing median (bold line), range (box) and outliers (whiskers) of "number of fledglings" in relation to "number of nests within 300 m".

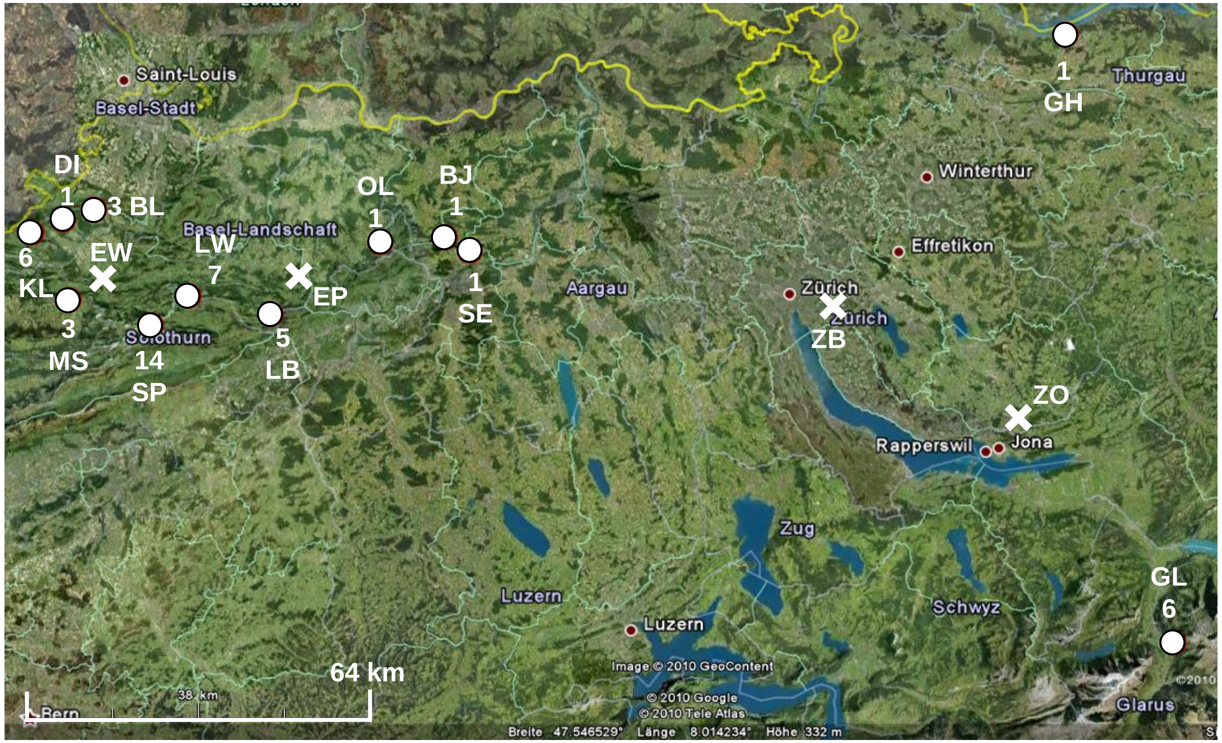

Saint-Louis
Basel-Stadt
1
GH
Thurgau
DI
1
3 BL
6
KL
EW
3
MS
Basel-Landschaft
LW
7
Solothurn
14
SP
5
LB
EP
OL
1
BJ
1
1
SE
Aargau
Winterthur
Effretikon
Zürich
Zürich
ZB
ZO
Rapperswil
Jona
Zug
Luzern
Luzern
Schwyz
GL
6
Glarus
64 km
38 km
Bern
Image © 2010 GeoContent
© 2010 Google
© 2010 Tele Atlas
Breite 47.546529° Länge 8.014234° Höhe 332 m

Fig.1

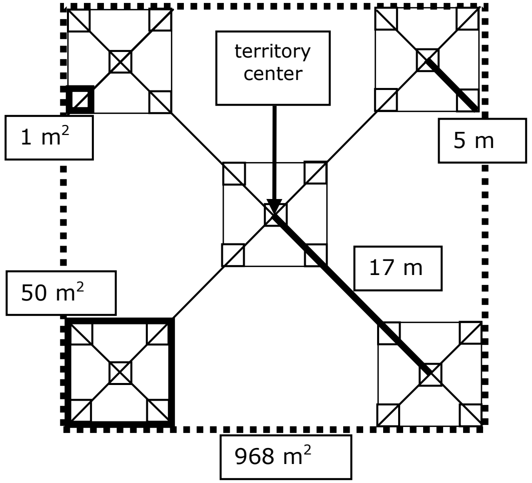


Fig. 2

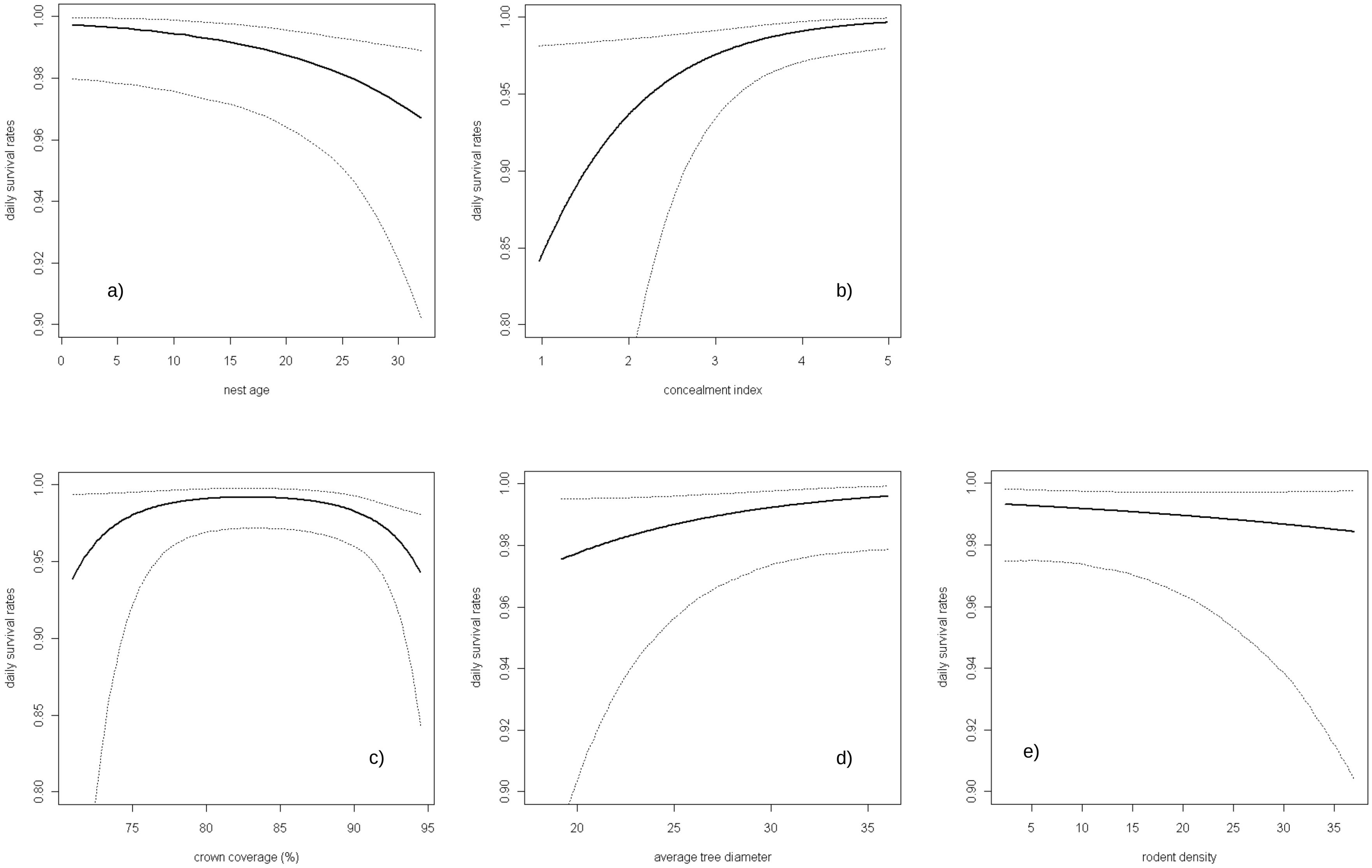

a)
daily survival rates
1.00
0.98
0.96
0.94
0.92
0.90
0
5
10
15
20
25
30
nest age
b)
daily survival rates
1.00
0.95
0.90
0.85
0.80
1
2
3
4
5
concealment index
c)
daily survival rates
1.00
0.95
0.90
0.85
0.80
75
80
85
90
95
crown coverage (%)
d)
daily survival rates
1.00
0.98
0.96
0.94
0.92
0.90
20
25
30
35
average tree diameter
e)
daily survival rates
1.00
0.98
0.96
0.94
0.92
0.90
5
10
15
20
25
30
35
rodent density

Fig. 3

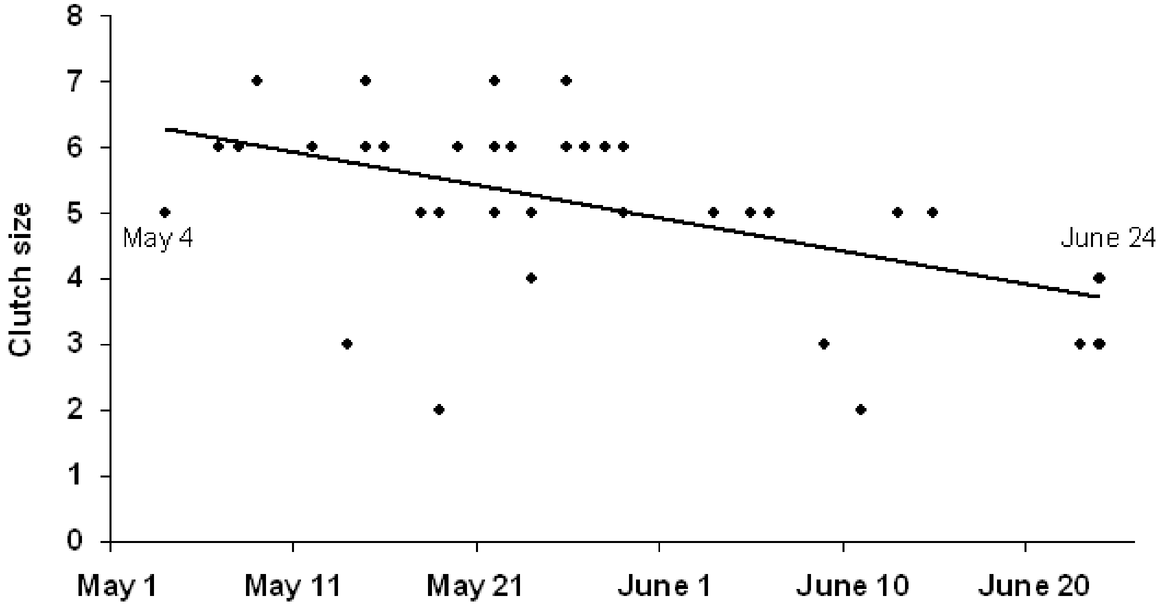
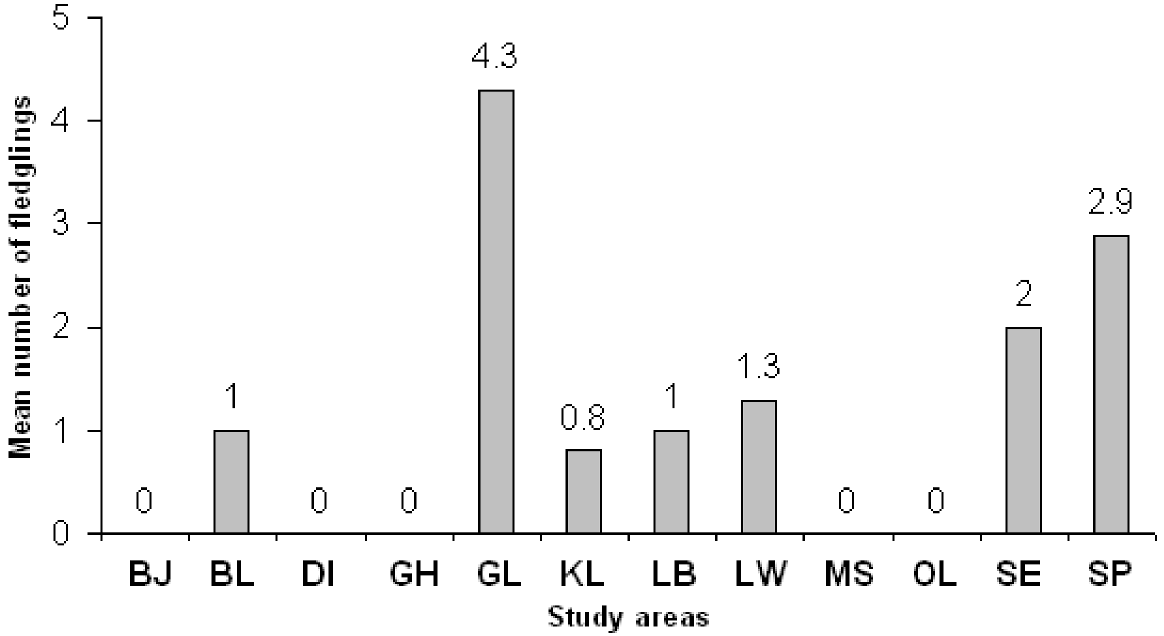

8
7
6
5
4
3
2
1
0
Clutch size
May 4
June 24
May 1
May 11
May 21
June 1
June 10
June 20

Fig. 4



Mean number of fledglings
5
4
3
2
1
0
0
1
0
0
4.3
0.8
1
1.3
0
0
2
2.9
BJ
BL
DI
GH
GL
KL
LB
LW
MS
OL
SE
SP
Study areas

Fig. 5

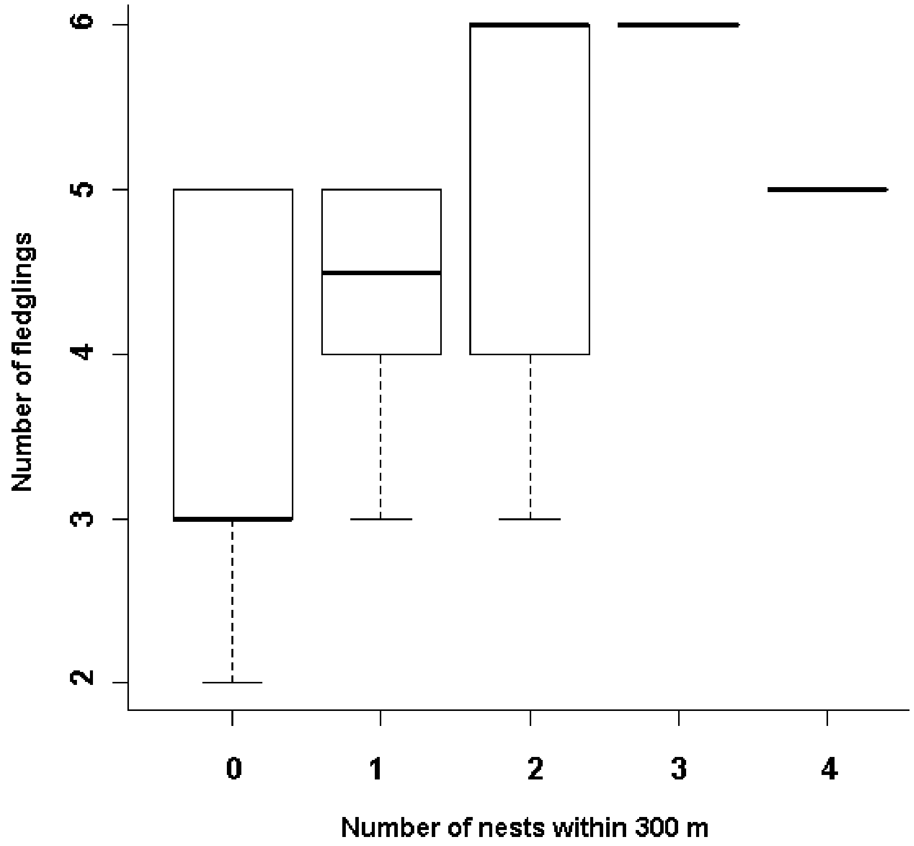

Number of fledglings
6
5
4
3
2
0
1
2
3
4
Number of nests within 300 m

Fig. 6

Appendix 1 Reference table by Gehlker (1977) in Dierschke (1994) to estimate percentage of vegetation cover smaller than 0.5 m

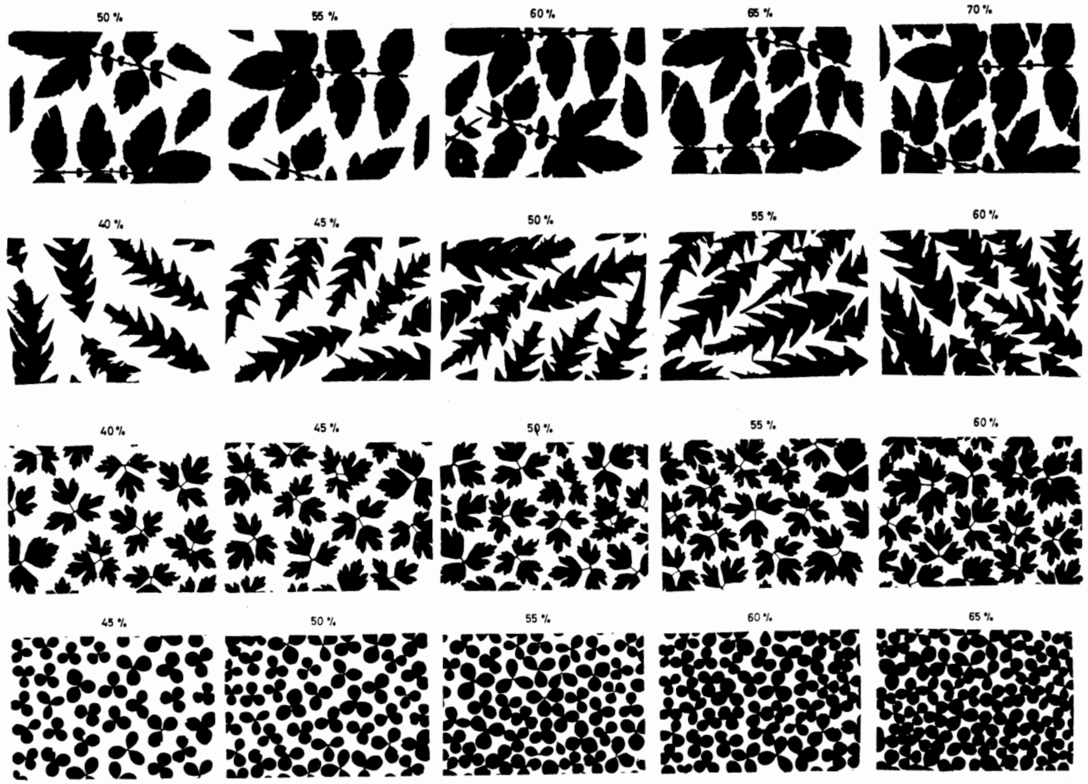


Abb. 76. Schätzskalen zur Erfassung der Blattflächen-Deckungsgrade von Wiesenpflanzen (aus GEYGER 1964). Von oben: *Filipendula ulmaria, Taraxacum officinale, Ranunculus repens, Trifolium repens*.

Appendix 2 Capture probabilities (p) and density estimates (N) of rodents calculated with program CAPTURE (2.12.1). BJ: Bänkerjoch (Canton of Aargau), GH: Gündelhart (Thurgau), GL: Glarus (Glarus), KL: Kleinlützel (Solothurn), LB: Langenbruck (Basel-Landschaft), LW: Lauwil (Basel-Landschaft), MS: Montsevelier (Jura), OL: Oltingen (Basel-Landschaft), SE: Staffelegg (Aargau), SP: Scheltenpass (Solothurn). M(o): null model, M(t): time model, M(h): heterogeneity model, M(th): time-heterogeneity model; For explanation of models, see methods.

Territory	Animals captured	Capture probability (p)	Density estimate (N)	SE	95% CI		Most appropriate model
BJ01	30	0.242	37	3.9	33	49	M(o)
GH01	8	0.055	27	22.5	12	126	M(o)
GL01	23	0.192	34	6.4	27	54	M(t)
GL02	4	0.330	4	2.5	4	4	M(h)
GL03	4	0.167	6	1.8	5	13	M(h)
GL04	24	0.295	26	1.5	25	31	M(t)
KL02	16	0.116	33	8.1	23	57	M(h)
KL03	17	0.138	27	6.9	20	50	M(t)
KL04	8	0.250	10	3.2	9	25	M(th)
KL05	16	0.193	22	4.3	17	36	M(o)
LB01	7	0.115	13	7.6	8	47	M(th)
LB04	9	0.250	10	2.6	10	25	M(h)
LB05	5	0.250	6	1.8	6	15	M(h)
LW01	9	0.233	10	2.6	10	25	M(h)
LW03	8	0.233	10	2.6	9	22	M(h)
LW06	6	0.250	6	2.2	6	19	M(h)
LW07	5	0.233	5	2.2	5	20	M(h)
MS01	10	0.235	12	3.5	11	29	M(th)
MS02	9	0.208	12	2.3	10	20	M(h)
OL01	19	0.173	25	4.5	21	41	M(t)
SE01	23	0.185	31	4.8	26	46	M(t)
SP02	6	0.263	7	2.1	7	19	M(th)
SP07	2	0.250	2	0.9	2	2	M(o)
SP08	3	0.133	5	1.8	4	12	M(h)

SP09	6	0.167	10	5.7	7	37	M(th)
SP11	15	0.220	17	1.8	15	25	M(t)
SP13	8	0.292	10	3.0	9	25	M(th)
BJ11	36	0.145	58	10.4	46	89	M(o)
GH11	35	0.100	85	15.0	64	123	M(h)
GL11	18	0.220	21	2.3	19	29	M(t)
GL12	17	0.307	19	2.6	18	31	M(th)
GL13	12	0.119	21	5.7	16	39	M(h)
GL14	17	0.199	23	4.2	18	36	M(o)
KL12	20	0.122	37	7.9	27	60	M(o)
KL13	22	0.148	33	6.8	26	55	M(t)
KL14	18	0.130	29	7.8	22	56	M(t)
KL15	23	0.067	65	13.3	47	100	M(h)
LB11	3	0.333	3	0.6	3	3	M(o)
LB14	7	0.128	13	4.3	9	28	M(h)
LB15	19	0.200	23	2.9	20	33	M(t)
LW11	7	0.262	7	0.0	7	7	M(t)
LW13	11	0.278	11	0.7	11	14	M(t)
LW16	20	0.085	45	18.0	28	108	M(t)
LW17	13	0.308	13	0.0	13	13	M(t)
MS11	25	0.235	30	3.1	27	40	M(t)
MS12	38	0.112	71	15.6	52	117	M(t)
OL11	34	0.059	104	16.7	79	145	M(h)
SE11	22	0.173	31	5.5	25	48	M(t)
SP22	6	0.097	12	4.2	8	26	M(h)
SP27	4	0.167	6	1.8	5	13	M(h)
SP28	4	0.167	7	5.0	5	32	M(th)
SP29	15	0.123	27	10.6	18	67	M(th)
SP31	6	0.271	8	1.8	7	15	M(h)
SP33	21	0.177	31	5.8	25	49	M(h)

Appendix 3 A section of the “nest success” data set. NA indicates values of variables which were not recorded. To control for the multi-line coding per nest, I included a random effect in the GLMM as is described in section 2.11.3. For an explanation of the variables, see methods. Nest pos. csp means “concealed by small plant”. Nest fate f means fledged, nest fate p means predated. Nest history describes whether the nest was still active (1) or predated (0) on a given day.

Nest ID	Study area	Dist. to forest edge	Nr. terr with 300m	Canopy cover	Veg. cover	Nr. tussocks	Nr. trees	Branched Below 4m	Avg. Diameter	Crown Contacts	Rodent density	Nest Type	Nest pos.	Nest Fate	Nest predator	Nr. fledglings	Nest History	Nest age	Initiation date
BL03	BL	88	0	NA	NA	NA	NA	NA	NA	NA	NA	natural	csp	f	np	3	1	12	62
BL03	BL	88	0	NA	NA	NA	NA	NA	NA	NA	NA	natural	csp	f	np	3	1	13	63
BL03	BL	88	0	NA	NA	NA	NA	NA	NA	NA	NA	natural	csp	f	np	3	1	14	64
BL03	BL	88	0	NA	NA	NA	NA	NA	NA	NA	NA	natural	csp	f	np	3	1	15	65
BL03	BL	88	0	NA	NA	NA	NA	NA	NA	NA	NA	natural	csp	f	np	3	1	16	66
BL03	BL	88	0	NA	NA	NA	NA	NA	NA	NA	NA	natural	csp	f	np	3	1	17	67
BL03	BL	88	0	NA	NA	NA	NA	NA	NA	NA	NA	natural	csp	f	np	3	1	18	68
BL03	BL	88	0	NA	NA	NA	NA	NA	NA	NA	NA	natural	csp	f	np	3	1	19	69
BL03	BL	88	0	NA	NA	NA	NA	NA	NA	NA	NA	natural	csp	f	np	3	1	20	70
BL03	BL	88	0	NA	NA	NA	NA	NA	NA	NA	NA	natural	csp	f	np	3	1	21	71
BL03	BL	88	0	NA	NA	NA	NA	NA	NA	NA	NA	natural	csp	f	np	3	1	22	72
BL03	BL	88	0	NA	NA	NA	NA	NA	NA	NA	NA	natural	csp	f	np	3	1	23	73
BL03	BL	88	0	NA	NA	NA	NA	NA	NA	NA	NA	natural	csp	f	np	3	1	24	74
BL03	BL	88	0	NA	NA	NA	NA	NA	NA	NA	NA	natural	csp	f	np	3	1	25	75
BL03	BL	88	0	NA	NA	NA	NA	NA	NA	NA	NA	natural	csp	f	np	3	1	26	76
BL03	BL	88	0	NA	NA	NA	NA	NA	NA	NA	NA	natural	csp	f	np	3	1	27	77
BL03	BL	88	0	NA	NA	NA	NA	NA	NA	NA	NA	natural	csp	f	np	3	1	28	78
BL03	BL	88	0	NA	NA	NA	NA	NA	NA	NA	NA	natural	csp	f	np	3	1	29	79
BL03	BL	88	0	NA	NA	NA	NA	NA	NA	NA	NA	natural	csp	f	np	3	1	30	80
GH01	GH	50	0	94	11.2	51	30	18	26	4	27	natural	csp	p	Badger	0	1	1	17

GH01	GH	50	0	94	11.2	51	30	18	26	4	27	natural	csp	p	Badger	0	1	2	18
GH01	GH	50	0	94	11.2	51	30	18	26	4	27	natural	csp	p	Badger	0	1	3	19
GH01	GH	50	0	94	11.2	51	30	18	26	4	27	natural	csp	p	Badger	0	1	4	20
GH01	GH	50	0	94	11.2	51	30	18	26	4	27	natural	csp	p	Badger	0	1	5	21
GH01	GH	50	0	94	11.2	51	30	18	26	4	27	natural	csp	p	Badger	0	1	6	22
GH01	GH	50	0	94	11.2	51	30	18	26	4	27	natural	csp	p	Badger	0	1	7	23
GH01	GH	50	0	94	11.2	51	30	18	26	4	27	natural	csp	p	Badger	0	1	8	24
GH01	GH	50	0	94	11.2	51	30	18	26	4	27	natural	csp	p	Badger	0	1	9	25
GH01	GH	50	0	94	11.2	51	30	18	26	4	27	natural	csp	p	Badger	0	0	10	26

Appendix 4 Correlation matrix showing spearman correlation coefficients. For details about the variables see methods.

Elevation	-0.70	0.60	-0.28	0.29	0.22	-0.13	0.04	0.61	-0.18	0.10	0.25	0.23	-0.26	-0.04	-0.53	-0.09
	Exposition	-0.57	0.09	0.00	-0.08	0.31	0.18	-0.43	0.29	0.06	0.05	-0.04	0.01	-0.22	0.31	-0.02
		Inclination	-0.17	0.10	0.08	0.13	0.24	0.59	0.03	-0.24	0.05	-0.05	-0.06	0.06	-0.08	-0.21
			distance to forest edge	0.07	0.34	0.00	0.04	-0.01	-0.17	-0.10	-0.40	-0.30	0.19	0.12	0.21	0.38
				distance to trail	0.22	0.21	0.59	0.42	0.01	0.10	0.24	0.09	-0.21	-0.31	-0.35	0.18
					distance to building	0.21	0.35	0.38	-0.05	0.17	0.11	0.08	-0.09	-0.35	-0.10	0.10
						Sky visibility	0.42	0.24	0.27	-0.43	-0.25	-0.35	0.11	-0.37	-0.15	0.01
							vegetation cover	0.53	0.46	-0.16	0.01	-0.13	-0.05	-0.33	0.00	0.24
								number of grass tussock	0.04	-0.14	0.00	-0.02	0.00	-0.17	-0.35	0.13
									number of bushes	0.01	0.01	-0.03	0.00	-0.31	0.36	0.33
										number of trees	0.80	0.93	-0.63	-0.21	0.18	-0.29
											branched below 4 m	0.89	-0.73	-0.15	-0.05	-0.42
												Branched below 10 m	-0.67	-0.21	0.03	-0.38

tree diameter	0.07	0.08	0.31
	Crown contacts	0.05	-0.28
		rodent density	-0.13
			concealment index

Appendix 5 Median incubation and nestling stage duration with sample size, minimum and maximum. BJ: Bänkerjoch (Canton of Aargau), BL: Blauen (Basel-Landschaft), GL: Glarus (Glarus), KL: Kleinlützel (Solothurn), LB: Langenbruck (Basel-Landschaft), LW: Lauwil (Basel-Landschaft), MS: Montsevelier (Jura), SP: Scheltenpass (Solothurn).

Incubation		**Nestling stage**	
Territory	Duration	Territories	Duration
BJ01	14	BL03	15
KL01	13	GL01	13
LW02	14	GL02	13
LW03	14	GL04	13
LW05	13	GL05	13
MS02	13	GL06	13
SP02	16	KL04	13
Mean	**14**	LB03	15
n	7	LW03	12
max	16	LW07	14
min	13	SP02	13
		SP03	14
		SP04	15
		SP07	11
		SP09	14
		SP12	13
		SP13	13
		Mean	**13**
		n	17
		max	15
		min	11

Appendix 6 Federal hunting statistics, showing shot V. vulpes between 1933 and 2009