

**Nestbox design influences territory occupancy
and reproduction in a declining, secondary
cavity-breeding bird**

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Table of contents

Summary.....	4
Introduction.....	5
Materials & Methods.....	7
Results.....	11
Discussion.....	12
Acknowledgements.....	16
References.....	17
Tables.....	20
Figure legends.....	24
Figures.....	25

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Summary

1. Nestboxes are a popular measure to support populations of endangered secondary-cavity breeding birds. Yet, studies of the impact of nestbox abundance and design on bird breeding ecology in intensive farmland remain scarce.
2. We experimentally studied nestbox preferences in a wryneck *Jynx torquilla* population in SW Switzerland. Initially designed for the larger hoopoe *Upupa epops*, voluminous nestboxes installed at 269 sites within the study area were checked for wryneck breeding since 2002. In 2008, we installed smaller sized, wryneck compatible nestboxes at 135 sites (50%) randomly selected from these 269 sites. We recorded the nestbox design preferences of wrynecks, and measured reproductive output, nestling body mass and tarsus length, while assessing patterns of intra- and interspecific competition.
3. Wrynecks settled in territories equipped with the better designed nestboxes more than expected by chance and preferentially used them for raising their broods. Reproductive output did not depend on nestbox design, although nestlings were heavier in the smaller nestboxes, probably due to reduced interspecific competition with hoopoes.
4. This study shows that territory attractiveness and reproductive performance can be enhanced when artificial cavities with an appropriate design are provided. Nestbox provisioning is an efficient conservation measure for endangered bird species but attention should be paid to nestbox design which has to be tailored to species-specific requirements.

Key-words: competition, conservation, *Jynx torquilla*, management, nest-site limitation, wryneck.

Introduction

Intensification of agriculture in the past century is a main reason for the decline of cavity breeding farmland birds (Newton, 1994b) as the removal of trees and hedges resulted in a dramatic reduction of nesting sites (Newton, 1994b). In order to 'reduce' this limiting resource, the provisioning of nestboxes to support populations of secondary cavity-breeders has become a popular conservation tool (Newton, 1994a), but surprisingly few studies have assessed the effect of nestbox provisioning on bird population ecology (Møller, 1992; Pöysä and Pöysä, 2002; Mänd et al., 2005; Mänd et al., 2009). If breeding cavities are a limiting resource, provisioning of nestboxes usually results in an increase of the focus population. The population increases can be very spectacular and fast. A population of Eurasian Kestrels (*Falco tinnunculus*), for example, doubled within six years (Fargallo et al., 2001), whilst a population of hoopoes (*Upupa epops*) increased by a factor of six within nine years (Arlettaz et al. in prep.) thanks to nestbox provisioning. A review by Newton (1994) revealed that in 30 out of 32 studies on cavity-breeding birds the provisioning of nestboxes resulted in an increased breeding density. However, not all cavity breeding species respond in the same way to nestboxes. While some secondary cavity breeders such as great tits *Parus major* easily adapt to nestboxes, others such as blue tits *Parus caeruleus* or nuthatches *Sitta europaea* do not (Lõhmus and Remm, 2005). Habitat features other than cavities can also play a role. Nestboxes in high quality habitat are more likely to increase population size than nestboxes in low quality habitats (Brawn and Balda, 1988; Mänd et al., 2005). Competition for other resources may prevent bird populations from increasing in size even if additional nestboxes are provided (Newton, 1994a; Pöysä and Pöysä, 2002; Mänd et al., 2005; Mänd et al., 2009). Finally, it is even possible that nestbox provisioning has negative effects on the population. Birds may be attracted by nestboxes to habitats of low quality, which can result in a decrease of reproductive output and even to population extinction (Mänd et al., 2005; Klein et al., 2007).

Not only the quantity of cavities, but also their quality can have an impact on populations. Usually birds select cavities with reduced predation risk and that allow high brood survival (Wesołowski, 2002; Lõhmus and

Remm, 2005), with the consequence that many cavities remain unoccupied. A number of unoccupied cavities is therefore not necessarily an indication that breeding cavities are a non-limiting resource (Bai et al., 2003; Löhmus and Remm, 2005). Often, nestboxes are preferred over natural cavities because reproductive output is typically higher. Risks of drowning after strong rainfall and of predation are usually lower in nestboxes (Fargallo et al., 2001; Mitrus, 2003; Radford and Du Plessis, 2003; Llambías and Fernández, 2009). However, studies about the effect of cavity quality (Radford and Du Plessis, 2003; Löhmus and Remm, 2005) and about the effect of different nestbox designs on bird populations are rare (but see Summers and Taylor, 1996; Browne, 2006; García-Navas et al., 2008). Different nestbox designs can have differential effects on reproduction. Large entrance holes allow predators and competitors to enter the cavity (Wesołowski, 2002), whilst the size of the brood chamber can influence clutch size and thermoregulation (Löhrl, 1973; Van Balen, 1984; Gustafsson and Nilsson, 1985), the latter impacting on egg and nestling development (Browne, 2006; García-Navas et al., 2008). For efficient conservation it is therefore essential to use the most suitable nestbox designs.

Using an experimental approach, we here study the effects of two different nestbox types on the performance of a wryneck *Jynx torquilla* population. In contrast to other woodpeckers, wrynecks are secondary cavity breeders, exclusively depending on old woodpecker holes, natural cavities or nestboxes. Our study population was in an intensively farmed area in the Swiss Alps where natural cavities are rare. Actually, our wryneck population breeds in the numerous nestboxes designed and installed for the larger-sized, endangered hoopoe (*Upupa epops*) in the area (Arlettaz et al. in prep.). Hoopoe nestboxes are relatively large with respect to the body size of wrynecks, and larger competitors such as hoopoes and predators such as stoats can easily enter them. In 2008, we added smaller nestboxes, better adapted to wrynecks requirements, which were both predator and hoopoe "proof". This enabled us to address the following questions: First, have the new wryneck nestboxes a positive effect on the occupancy of a territory (settlement decisions)? Second, is the smaller nestbox design preferred over the larger one by wrynecks? Third, do reproductive output, nestling body mass and tarsus length differ between the two nestbox types?

And finally, can intra- (local wryneck density) and interspecific (wryneck-hoopoe co-occurrence) competition be reduced by the provisioning of different nestbox designs? The results of this study shall set guidelines for provisioning appropriate nestboxes to support declining wryneck populations.

Material and Methods

Study site, design and species

The wryneck is a ground feeding woodpecker, wintering mainly in sub-Saharan Africa (Glutz von Blotzheim and Bauer, 1980; Reichlin et al., 2009). In the last decades wrynecks have declined strongly all over Europe (Tucker and Heath, 1994). They prefer semi-open landscapes with forests, orchards as well as vineyards, whereas open landscapes without trees and dense forests are generally avoided (Ehrenbold, 2004; Mermod, 2008). The diet mainly contains ground-dwelling ants in all developmental stages (Glutz von Blotzheim and Bauer, 1980; Freitag et al., 2001). Wrynecks are strong competitors against smaller or similar sized birds, being able to remove their clutches or nestlings, although this does not occur against the larger hoopoe (Glutz von Blotzheim and Bauer, 1980).

The study was conducted on the plain of the Upper Rhône River, in the canton of Valais (Switzerland, 46° 14' N, 7° 22' E, 460 - 520 m a.s.l.). The study area has an extension of about 64 km² (1.6 x 40 km) and is characterised by intensive agriculture, mainly fruit plantations, vineyards and vegetable cultures. Pastures and meadows are less frequent. Because old, tall trees are rare the area is characterized by a scarcity of natural cavities. Previous studies from the same study area have shown that food supply is not a limiting resource (Weisshaupt, 2007; Mermod, 2008) and that weather variation has relatively little impact on reproduction of wrynecks (Geiser et al., 2008). It is likely that nest sites are the main limiting resource. From 1998 to 2003 nestboxes were installed at 269 sites, here referred to as *territories*, which were monitored yearly since then. These wooden nestboxes have an entrance-hole diameter of 55 mm and a large brood chamber (20 x 20 cm). They are designed for hoopoes

(hereafter hoopoe nestboxes) but were also frequently used by wrynecks. The hoopoe nestboxes were fixed inside agricultural shacks and buildings. In order to avoid competition for access to nestboxes between sympatric bird species, a pair of nestboxes was installed at every site, totalling 490 boxes. In 2008 we installed 135 additional nestboxes (Schwegler Type 3SV) considered as particular suitable for the wryneck (hereafter wryneck nestboxes). The wryneck nestboxes were produced of wood concrete, have an entrance-hole diameter of 34 mm and the brood chamber is slightly concave with a radius of 14 cm. Due to its smaller size, larger potential competitors such as hoopoes cannot enter the box, while smaller passerines can be eliminated by wrynecks if necessary (great tits, tree sparrows). We randomly selected half of the territories, adding one wryneck nestbox at the same building already equipped with hoopoe nestboxes. In all nestboxes we recorded occupancy by wrynecks and hoopoes, their reproductive success and measured the body mass and tarsus length of the nestlings.

The wryneck population inhabiting the hoopoe nestboxes declined from 72 broods in 2002 to 34 broods in 2007. This decrease may be due to competition with the increasing hoopoe population (1998: 20 broods, 2007: 160 broods). Competition between hoopoe and wryneck may occur among nest sites (Mermod et al., 2008), but not for food resources as hoopoes do not feed on ants but on molecrickets (Fournier and Arlettaz, 2001).

Data sampling

All nestboxes in the study area were checked every second week during the breeding season (April – August 2008). Nestboxes occupied by a wryneck where visited each 3-5 days. We recorded the date of first egg laying and hatching. The nestlings were ringed and measured approximately 13 days after hatching. We recorded body mass, tarsus length and exact age of each nestling.

Territory occupancy

We defined a territory to be occupied when in one of the 2-3 available nestboxes at least one egg of a wryneck was present. To study whether the occupancy of a territory was affected by the available nestbox types and or by inter- or intraspecific competition, logistic regressions with logit link

function and a binomial error distribution were used. The dependent variable was the *territory occupancy* (two levels: occupied or not) regardless of which nestbox type was eventually occupied. We modelled territory occupancy using four explanatory variables. The variable *conspicifcs* was defined as the number of wryneck broods within a 500 m radius of the focal territory and tested whether territory occupancy was affected by intraspecific competition. The variable *hoopoe* was defined as the number of hoopoe broods within a 200 m radius of the territory and tested whether interspecific competition affected territory occupancy. We assume that interactions with hoopoes take place on a narrower range than interactions with conspecifics, because wryneck and hoopoe only compete for nest sites but not for food resources. The variable *wryneck nestbox* indicated if a wryneck nestbox was present at the territory and tested whether an additional wryneck nestbox increased the attractiveness of a territory. Finally, the variable *past occupancy* is defined as number of years a given territory was occupied by a wryneck (between 2002 and 2007). This variable was always included in order to account for differences in territory quality as the frequency of occupancy is correlated with habitat quality (Mermod, 2008). Candidate models contained all the possible combinations of the explanatory variables.

Nestbox occupancy

We defined a nestbox to be occupied when at least one wryneck egg was present. To test whether wryneck nestboxes were preferred over hoopoe nestboxes, all available nestboxes in the occupied territories were considered. We used a generalized linear mixed model with logit link function. The occupancy of the nestbox was the binomial response variable and the territory identification number was included as random factor. The fixed effects were the *nestbox type* (two levels: wryneck or hoopoe) and *hoopoe* (see above). Candidate models contained the combinations of the two explanatory variables and their interaction. This allowed to test whether the occupancy of a given nestbox type is dependent on the presence of hoopoes (interspecific competition).

Reproductive output and nestling condition

The same explanatory variables as described for nestbox occupancy were used to study the impact of the nestbox design on reproductive output, nestling body mass and tarsus length. Candidate models contained all the possible combinations of these explanatory variables and the interaction *nestbox type* hoopoe*.

We used different components of reproductive success, namely overall success, i.e. whether or not at least one fledgling was produced (boolean), hatching success ($\frac{\text{clutch size}}{\text{number of hatchlings}}$) and fledging success ($\frac{\text{number of hatchlings}}{\text{number of fledglings}}$) as response variables, with binomial error terms. Since second- and replacement-broods were also included, the territory number was included as random effect. We included the laying date of the first egg in all models as an additional explanatory variable, because reproductive success declines strong during the course of the breeding season (Geiser et al., 2008).

Using a linear mixed model with a normally distributed error term we analysed nestling body mass and tarsus length to study the effect of nestbox type and competition. Since we measured all nestlings from a brood, the brood identification number was included as a random effect to account for possible dependence. All candidate models contained the exact age of the nestlings and the number of hatchlings per brood as additional explanatory variables.

Model selection

All analyses were conducted using R Version 2.7.2 (R Core Team 2008, libraries: nlme, lme4). All explanatory variables were tested for pair wise correlation. All correlations remained below $r = 0.5$, which has been defined as the maximal accepted limit. We ranked the models according to their support by the data using the Akaike Information criterion adjusted for small sample sizes (AICc) and the AICc-weights. Predictions were based on model averaging, using the best models whose AICc-weights summed up to 0.95. In addition we calculated an estimate for Goodness of fit for all linear mixed effect models (Xu, 2003). The coefficient of determination, $R^2 = 1 - ((\text{deviance}_i^2) / (\text{max. deviance}^2))$, is defined as the percent of the variance explained by a given model.

Results

Territory occupancy

Of the 269 monitored territories, 32 were occupied by a wryneck in 2008. 23 of the 32 occupied territories were equipped with a wryneck nestbox, nine had only hoopoe nestboxes. Two models clearly stood out for explaining territory occupancy (Table 1). Both models contained *conspecifics* and *wryneck nestbox*, but only one model also incorporated the variable *hoopoe*. Thus, there was uncertainty about whether territory occupancy was impacted by interspecific competition, but it became very evident that territory occupancy was affected by intraspecific interactions and the presence of a wryneck nestbox.

The probability that a territory was occupied by a wryneck was higher if an additional wryneck nestbox was present (Fig. 1a). The number of occupied wryneck territories within 500 m radius around the focal territory positively affected the probability that the focal territory was occupied (Fig. 1b), while the number of occupied hoopoe territories had almost no impact (Fig. 1c). Territories that had been occupied in the past also had a higher probability to be occupied in the study year (Fig. 1a).

Nestbox occupancy

Within the 32 occupied territories a total of 78 nestboxes were available (56 hoopoe and 22 wryneck nestboxes). Nine-teen wryneck broods occurred in one of the 56 available hoopoe nestboxes, 14 broods occurred in one of the 22 available wryneck nestboxes. Model selection revealed that models with *nestbox type* were clearly higher ranked than models without (Table 2).

Wryneck nestboxes were clearly preferred over hoopoe nestboxes (Fig. 2). The presence of hoopoes had no influence on the nestbox choice (Table 2).

Reproductive output and nestling condition

In the year 2008, 25 successful and 20 failed wryneck breeding attempts were recorded. The wryneck nestboxes had no effect on the reproductive output. The null model, only containing past occupancy of the territory and

the date when the first egg was laid, was the best model for all components of reproduction (Table 3).

The best model for nestling body mass contained the interaction of *nestbox type* and *hoopoe* (Table 4a). Models with *conspecifics* had lower support. By contrast, the best model for the variation of nestling tarsus length did not contain the focal explanatory variables (Table 4b). However, all models explained little of the observed variance.

In general, wryneck nestlings from broods in wryneck nestboxes had a higher body mass than wryneck nestlings of the same age in hoopoe nestboxes (Fig. 3). The presence of a hoopoe brood also had an impact, and this impact differed depending on which nestbox type a wryneck raised a brood in. When a brood was raised in a hoopoe nestbox, the presence of a hoopoe had a slightly negative impact on nestling body mass. However, the effect of hoopoe presence was generally small (Fig. 3).

Discussion

This study shows that the probability of territory occupancy by wrynecks was augmented when additional artificial cavities tightly matching species-specific requirements were available. An appropriate nestbox design is thus essential to increase territory attractiveness for these endangered cavity-nesting birds. While various components of reproductive success did not differ between the two types of nestbox tested in this study (hoopoe vs. wryneck nestboxes), nestlings were heavier in wryneck nestboxes, i.e. individual quality at fledgling was improved when the appropriate nestboxes were used (Naef-Daenzer et al., 2001). This may explain the strategic choice operated by wrynecks towards this type of nestbox.

Territories with an additional wryneck nest box were more likely to be occupied. Wrynecks outcompete all other sympatric, cavity-nesting birds in the study area – with the noticeable exception of the hoopoe (Mermod et al., 2008) – nevertheless many suitable nestboxes remained unoccupied. This suggests that the increased attractiveness of territories equipped with additional, smaller nestboxes is not just due to a greater availability of free nestboxes, but to an absolute greater number of nestboxes per se. Actually, the number of cavities (either artificial or natural) available within a

wryneck territory may be an important habitat clue to predict both territory and mate qualities as demonstrated for other bird species (Eckerle and Thompson, 2006; Llambías and Fernández, 2009). In a study of little owls (*Athene noctua*), for instance, the number of alternative cavities around a nest was the most important variable associated with territory selection (Tomé et al., 2004). A wide palette of alternative cavities in nest surroundings might reduce predation risk, both for resting adults and broods, due to a dilution effect. Additionally, the alternative cavities can also be used for roosting (Martin and Roper, 1988). Provisioning nestboxes that better match species-specific requirements may also simply improve breeding circumstances by providing cavities of a much higher standard. Actually, separating these two effects (higher number per se, or increased quality), which are not necessarily mutually exclusive, would request further experiments manipulating nestbox availability. Previous studies have shown either that the quality of cavities is important (Summers and Taylor, 1996; Browne, 2006; García-Navas et al., 2008) or that the quantity of them matters (Tomé et al., 2004; Eckerle and Thompson, 2006; Llambías and Fernández, 2009), probably pointing to the divergent, species-specific functions of cavities as mentioned above.

The presence of other wrynecks in the nest surrounding had a strong positive influence on territory occupancy. This may be due to either social attraction by conspecifics, or, alternatively, habitat quality which leads to local aggregations of breeders. Conspecific attraction seems to be frequent even in non-colonial birds (Doligez et al., 1999; Doligez et al., 2004). Some more elaborated design than in this study would be needed to confirm it in wrynecks. For now we simply note that intraspecific competition does not seem to be a secondary effect of these local aggregations since neither territory occupancy nor reproductive output were negatively affected by density.

Wrynecks preferred the new smaller nestboxes than the first-installed hoopoe nestboxes. Apparently the former better fit to species ecological requirements. The two nestbox types mainly differ regarding material and size. In tits and tree sparrows, nestboxes made of wood concrete (comparable to the wryneck nestboxes described here) were preferred over nestboxes made of wood (Browne, 2006; García-Navas et al., 2008): the better insulating properties of wood concrete (internal temperature 1.5°C

higher on average) resulted in a shorter incubation period and a higher reproductive success, but in no variation of clutch size and number of nestlings in one of the above studies (García-Navas et al., 2008). Actually, temperature in our wryneck nestboxes was on average (\pm SE) 0.87°C ($\pm 0.16^{\circ}\text{C}$, $n = 12$) higher than in wooden hoopoe nestboxes (Zingg 2008, unpubl. data). Increased nest temperature may decrease post-hatching female brood attendance during the early phase of growth when chicks cannot thermo regulate by themselves. This may provide them with more time for food provisioning (Pérez et al., 2008). Also, larger nestlings, as found here for wrynecks in the more adapted nestboxes, can fledge earlier and have a higher survival probability (Naef-Daenzer et al., 2001).

Previous studies have shown that larger and deeper cavities are usually preferred, because they allow larger clutches to be laid (Löhrl, 1973; Van Balen, 1984; Gustafsson and Nilsson, 1985; Rendell and Verbeek, 1996), as well as better thermal environment (Summers and Taylor, 1996; Mazgajski and Rykowska, 2008). We observed the contrary in our study, most probably because the hoopoe nestboxes were noticeably too big to offer optimal brooding conditions for the wryneck. This is supported by the observation that there was no clutch size reduction in the smaller compared to the larger nestboxes. Furthermore, the small entrance hole of the wryneck nestboxes also limits the risk of costly agonistic interactions with larger cavity-nesting birds (Krist, 2004), while limiting the access to predators (e.g. stoats). Resource competition in form of direct interaction occurs frequently when two species compete on nesting cavities (Minot and Perrins, 1986; Merilä and Wiggins, 1995). We observed no clear effect of hoopoe density on nestbox occupancy by wrynecks, but hoopoe density exerted some weak negative effect on the body mass of wryneck nestlings. Interestingly, our results showed that the negative effect of hoopoes on wryneck chicks operated only in broods situated in hoopoe nestboxes but not in wryneck nestboxes. This suggests that wrynecks had to defend their nests against intrusions by hoopoes, a behaviour which seemed to have entailed some reproductive costs (chick quality).

The two nestbox types used in this study not only differ regarding size and material, but also regarding age. Parasitic load could be an additional factor, influencing both, nest site choice and nestling condition (Merino and Potti, 1995; Rendell and Verbeek, 1996; Tomás et al., 2007).

Anyways, it has been shown that the re-use of the same cavities over time has actually no negative effects on reproduction, with parasite intensity in one year being independent of the infestation in the previous year (Wesołowski, 2006). Therefore and also because wrynecks often remove building material brought by other cavity breeders, we think that ectoparasites are not an issue in the present study.

The three main advantages of the smaller nestboxes for the wrynecks (better thermal environment, protection against predators and exclusion of competitors) may explain their nest site selection pattern. By provisioning different nestbox types, competition for nest sites can be dramatically reduced in secondary cavity breeding bird species (Remm et al., 2008).

Before nestbox programmes are implemented in population conservation and restoration projects it should be clarified whether nest sites are a main limiting factor and whether other key resources are still available (Newton, 1994b). Then, it must be ensured that nestbox design is really adapted to the focal species, with different nestbox designs necessary when the target consists of multiple species. Finally, the quantity of nestboxes should also be sufficient locally as this may increase habitat attractiveness for some species, as illustrated here by the wryneck.

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Tables

Table 1: Summary results of the territory occupancy modelling. The 3 best models were used for the model averaging. Given are the $\Delta AICc$, the AICc weights ($w_i = \exp(-0.5 \cdot \Delta AICc_i) / \sum \exp(-0.5 \cdot \Delta AICc)$), the number of parameters (K), the residual deviance and the coefficient of determination (R^2). The variable past occupancy was included in all models. The variable conspecifics is defined as the number of wrynecks broods within 500 m radius of the territory, hoopoe is defined as the number of hoopoe broods within a 200 m and wryneck nestbox indicates whether or not a wryneck nestbox was present in the territory. '1' indicates the model that included none of the focal explanatory variables.

Model	$\Delta AICc$	w_i	K	deviance	R^2
Conspecifics + Nest box + Hoopoe	0.00	0.48	5	151.15	21.5%
Conspecifics + Nest box	0.05	0.47	4	153.28	19.2%
Conspecifics	6.61	0.02	3	161.90	9.9%
Conspecifics + Hoopoe	6.89	0.02	4	160.12	11.9%
Hoopoe + Nest box	7.55	0.01	4	160.78	11.1%
Nest box	8.97	0.01	3	164.26	7.3%
Hoopoe	12.30	0.00	3	167.59	3.5%
1	13.24	0.00	2	170.57	0.0%

Table 2: Results of the nestbox occupancy modelling. Given are the AICc, the AICc weights ($w_i = \exp(-0.5 \cdot \Delta \text{AICc}_i) / \sum \exp(-0.5 \cdot \Delta \text{AICc}_i)$), the number of parameters (K), the residual deviance and the coefficient of determination (R^2). The variable nestbox type indicates in which nestbox (wryneck or hoopoe) a wryneck brood was conducted. For the meaning of the other variables, see table 1.

Model	w_i	ΔAICc	K	deviance	R^2
Nestbox type	0.50	0.00	3	100.6	12.8%
Nestbox type + Hoopoe	0.26	1.32	4	99.7	14.3%
Nestbox type* Hoopoe	0.11	3.11	5	99.2	15.2%
1	0.09	3.54	2	106.3	2.6%
Hoopoe	0.04	4.90	2	107.7	0.0%

Table 3: Model selection of different components of reproduction in relation to covariates. The date when the first egg was laid and the past occupancy of the territory were included in all models but not explicitly shown in the table. Given are the Δ AICc and the AICc weights ($w_i = \exp(-0.5 \cdot \Delta \text{AICc}_i) / \sum \exp(-0.5 \cdot \Delta \text{AICc}_i)$). For the meaning of the variables, see tables 1 and 2.

Model	Brood success		Hatching success		Fledging success	
	w_i	Δ AICc	w_i	Δ AICc	w_i	Δ AICc
1	0.44	0.0	0.32	0.0	0.46	0.0
Conspecifics	0.15	2.1	0.09	2.5	0.13	2.5
Nest box type	0.13	2.4	0.17	1.2	0.14	2.4
Hoopoe	0.12	2.5	0.18	1.1	0.13	2.6
Conspecifics + Nest box type	0.05	4.4	0.06	3.5	0.04	4.9
Hoopoe + Conspecifics	0.04	4.8	0.06	3.5	0.03	5.5
Hoopoe + Nest box type	0.04	4.9	0.06	3.4	0.04	4.9
Nest box type + Hoopoe + Conspecifics	0.01	7.2	0.02	5.8	0.01	7.8
Nest box type* Hoopoe	0.01	7.3	0.04	4.2	0.02	6.8
Nest box type* Hoopoe + Conspecifics	0.01	8.9	0.01	7.4	0.00	9.4

Table 4: Summary results of the nestling body mass (a) and tarsus length (b) modelling. The age of the nestlings and the number of hatchlings per brood were included in all models. Given are the Δ AICc, the AICc weights ($w_i = \exp(-0.5 \cdot \Delta \text{AICc}_i) / \sum \exp(-0.5 \cdot \Delta \text{AICc}_i)$) and the coefficient of determination (R^2). For the meaning of the variables, see tables 1 and 2.

a) Model	Nestling body mass		
	w_i	Δ AICc	R^2
Nest box type * Hoopoe	0.33	0.00	2.8%
Nest box type * Hoopoe + Conspecifics	0.19	1.12	3.1%
Nest box type	0.14	1.66	1.3%
Nest box type + Hoopoe	0.14	1.76	1.8%
Nest box type + Conspecifics	0.06	3.25	1.5%
Nest box type + Hoopoe + Conspecifics	0.06	3.33	2.0%
Hoopoe	0.03	4.62	0.6%
1	0.03	4.72	0.0%
Conspecifics	0.01	6.22	0.2%

b) Model	Nestling tarsus length		
	w_i	Δ AICc	R^2
1	0.46	0.00	0.00%
Nest box type	0.18	1.91	0.32%
Hoopoe	0.13	2.52	0.11%
Conspecifics	0.09	3.32	0.56%
Nest box type + Hoopoe	0.05	4.50	0.04%
Nest box type * Hoopoe	0.04	4.75	0.46%
Nest box type + Conspecifics	0.03	5.27	0.37%
Nest box type + Hoopoe + Conspecifics	0.01	7.76	1.03%
Nest box type * Hoopoe + Conspecifics	0.01	8.30	0.53%

Figure legends

Fig. 1: Model averaged probability that a territory is occupied by a wryneck in relation to a) the past occupancy of the territory, b) the number of other wryneck broods in a circle of 500 m around the focal nest, c) the number of hoopoe broods in a circle of 200 m around the focal nest, this for territories with and without an additional wryneck nestbox. The underlying model selection is given in Table 1. Vertical bars show the 95% confidence intervals.

Fig. 2: Predicted probability that a wryneck settled in a wryneck and hoopoe nestbox, respectively. In 56 hoopoe nestboxes there were 19 broods, whereas in only 22 wryneck boxes 14 broods occurred. The underlying model selection is given in Table 2. Vertical bars indicate the 95% confidence intervals.

Fig. 3: Model-averaged nestling body mass in relation to the number of hoopoes (200 m radius around the focal nest) for broods in wryneck and hoopoe nestboxes. The underlying model selection is given in Table 4. Vertical bars show the 95% confidence intervals.

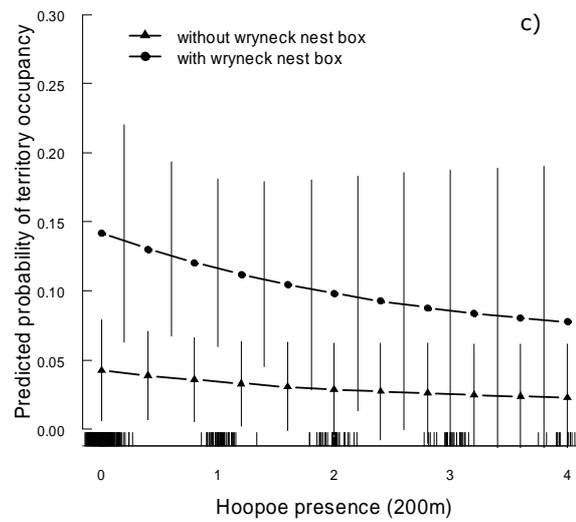
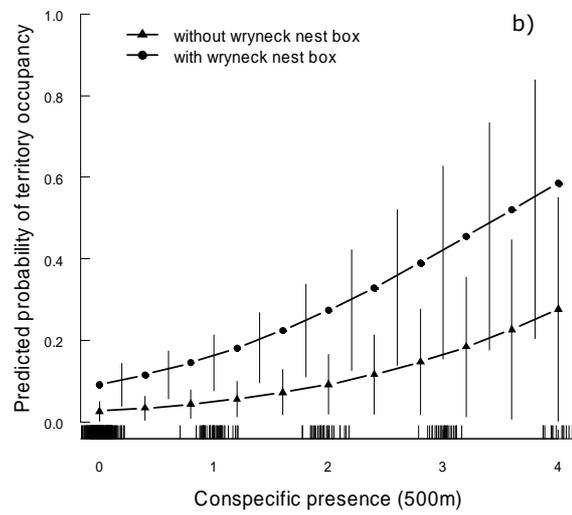
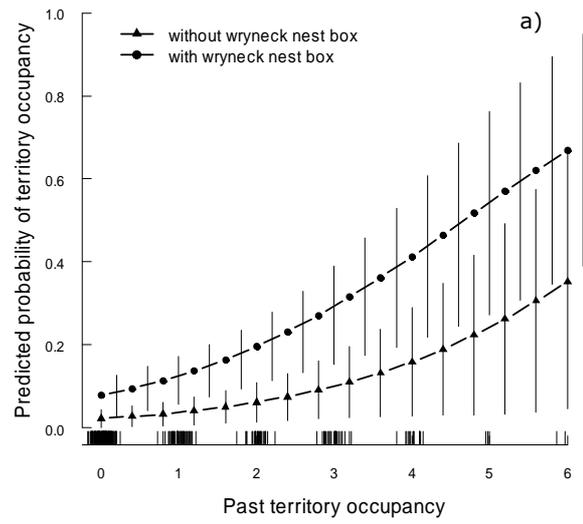


Fig. 1

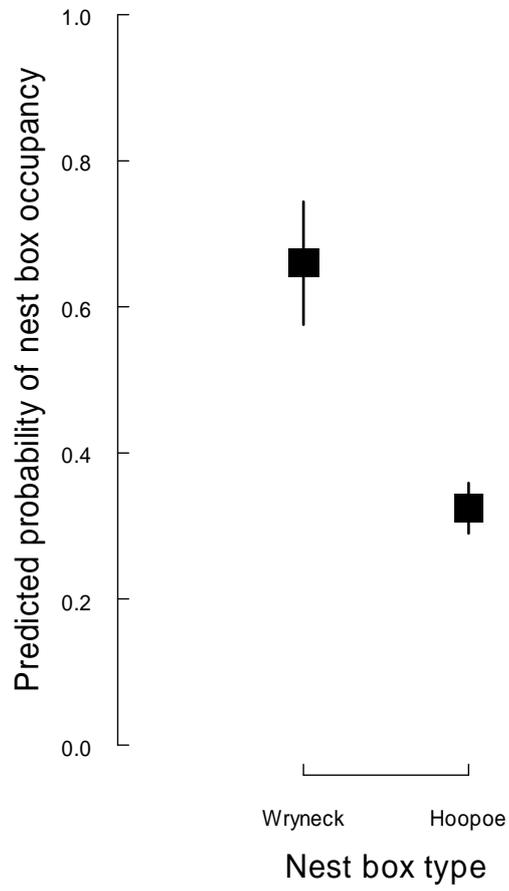


Fig. 2

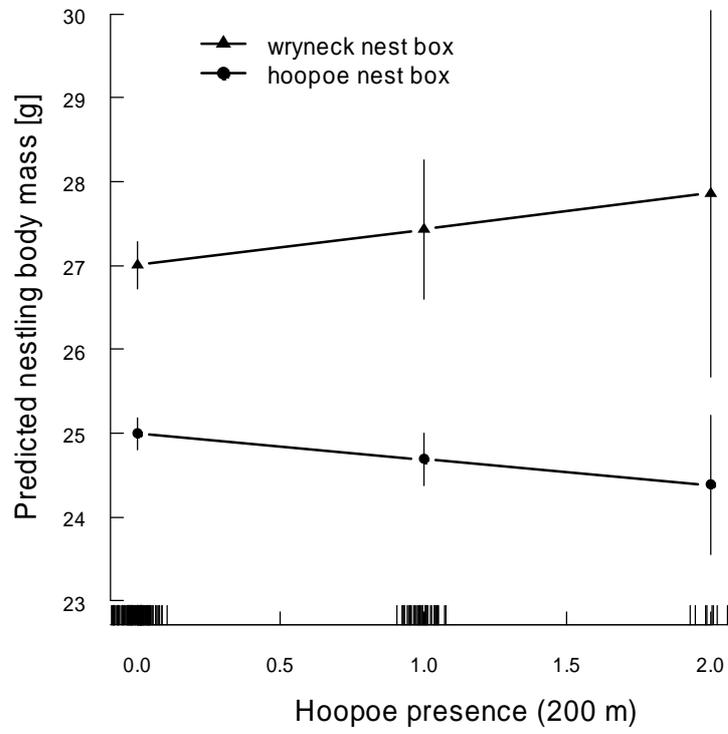


Fig. 3

Erklärung

gemäss Art. 28 Abs. 2 RSL 05

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Studiengang: Biologie

Bachelor

Master

Dissertation

Titel der Arbeit: Nestbox design influences territory
occupancy and reproduction in a declining,
secondary cavity-breeding bird

LeiterIn der Arbeit: Prof. Dr. Raphael Arlettaz
PD Dr. Michael Schaub

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

Bern 12.05.09

Ort/Datum

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Unterschrift