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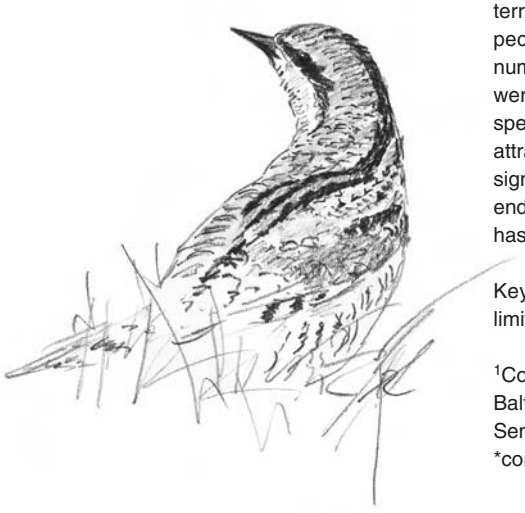
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Nestboxes are a popular measure to support populations of endangered secondary-cavity breeding birds. Yet, studies of the impact of nestbox abundance and design on bird breeding ecology in intensive farmland remain scarce. We experimentally studied nestbox preferences in a Wryneck *Jynx torquilla* population in SW Switzerland. Initially designed for the larger Hoopoe *Upupa epops*, voluminous nestboxes installed at 269 locations within the study area were checked for Wryneck breeding since 2002. In 2008, we installed smaller sized, Wryneck compatible nestboxes at 135 locations (50%) randomly selected from these 269 locations. 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. Wrynecks settled in territories equipped with the more suitably designed nestboxes more than expected by chance and preferentially used them for raising their broods. The number of fledged young did not depend on nestbox design, although nestlings were slightly heavier in the smaller nestboxes, probably due to reduced interspecific competition with Hoopoes. This study shows that in particular territory attractiveness 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

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Intensification of agriculture in the past century is a main reason for the decline of cavity breeding farmland birds as the removal of trees and hedges resulted in a dramatic reduction of nesting sites (Newton 1994a). The provisioning of nestboxes to support populations of secondary cavity-breeders has therefore become a popular conservation tool (Newton 1994b), but surprisingly few studies have assessed the effect of nestbox provisioning on bird population ecology (Møller 1992, Pöysä & 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.*, unpubl. data) thanks to nestbox provisioning. The review by Newton (1994b) 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 adapted to nestboxes, others such as Blue Tits *Cyanistes caeruleus* or Nuthatches *Sitta europaea* did not (Lõhmus & Remm 2005). Habitat features other than cavities can also play a role. Nestboxes

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in high quality habitat are more likely to increase population size than nestboxes in low quality habitats (Brawn & 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 1994b, Pöysä & Pöysä 2002, Mänd *et al.* 2005, Mänd *et al.* 2009). Finally, it is 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 & 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, Lõhmus & Remm 2005). Often, nestboxes are preferred over natural cavities because reproductive output is typically higher. Risks of drowning of eggs or nestlings after strong rainfall and of predation are often lower in nestboxes than in natural cavities (Fargallo *et al.* 2001, Mitrus 2003, Radford & Du Plessis 2003, Llambías & Fernández 2009). However, studies about the effect of cavity quality (Lõhmus & Remm 2005, Radford & Du Plessis 2003) and about the effect of different nestbox designs on bird populations are rare (but see Summers & 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 & 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 studied 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 in the area (Arlettaz *et al.* unpubl. data). Hoopoe nestboxes are relatively large with respect to the body size of Wrynecks, and larger competitors such as Hoopoes and predators such as Stoats *Mustela erminea* can easily enter them. In 2008, we added smaller nestboxes which were both predator and Hoopoe proof. This enabled us to address the following questions: First, did the new Wryneck nestboxes have a positive effect on the occupancy of a territory (settlement decisions)? Second, was the smaller nestbox design preferred over the larger one by Wrynecks? Third, did reproductive output, nestling body mass and tarsus length differed between the two nestbox types? And fourth, 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 & Bauer 1980, Reichlin *et al.* 2009). In the last decades Wrynecks have declined strongly all over Europe (Tucker & 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 (Mermod *et al.* 2009). The diet mainly contains ground-dwelling ants in all developmental stages (Glutz von Blotzheim & 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 & Bauer 1980). Wrynecks also remove old nest material.

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 covers about 64 km^2 (1.6 × 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 have largely been removed for the purpose of efficient agriculture, 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 *et al.* 2009) and that weather variation has relatively little impact on reproduction (Geiser *et al.*

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2008). It is likely that nest sites are the main limiting resource. From 1998 to 2003 nestboxes were installed at 269 locations, 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 × 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. 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 Wrynecks (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 *Passer montanus*). We randomly selected half of the territories, adding one Wryneck nestbox at the same building already equipped with Hoopoe nestboxes (Fig. 1). 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 *Gryllotalpa gryllotalpa* (Fournier & Arlettaz 2001).



Figure 1. A typical agricultural shack with three nestboxes: a Wryneck nestbox (middle) and two Hoopoe nestboxes (right and left). Only the entrance holes of the Hoopoe nestboxes are visible, the nestboxes themselves are inside the shack (photo M. Schaub).

Data sampling

Prior to the start of egg-laying, we removed old nest material from all nestboxes. All nestboxes in the study area were then 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 majority of nestlings were ringed and measured 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 *conspecifics* 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 to account for differences in territory quality as the frequency of occupancy is correlated with habitat quality (Mermod *et al.* 2009). Candidate models contained all the possible combinations of the explanatory variables.

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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* presence (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 brood success, i.e. whether or not at least one fledgling was produced, hatching success (number of hatchlings/clutch size) and fledging success (number of fledglings/number of hatchlings) as response variables, with binomial error terms. Since second- and replacement-broods were also included (11 out of 43 broods), 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 strongly 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.

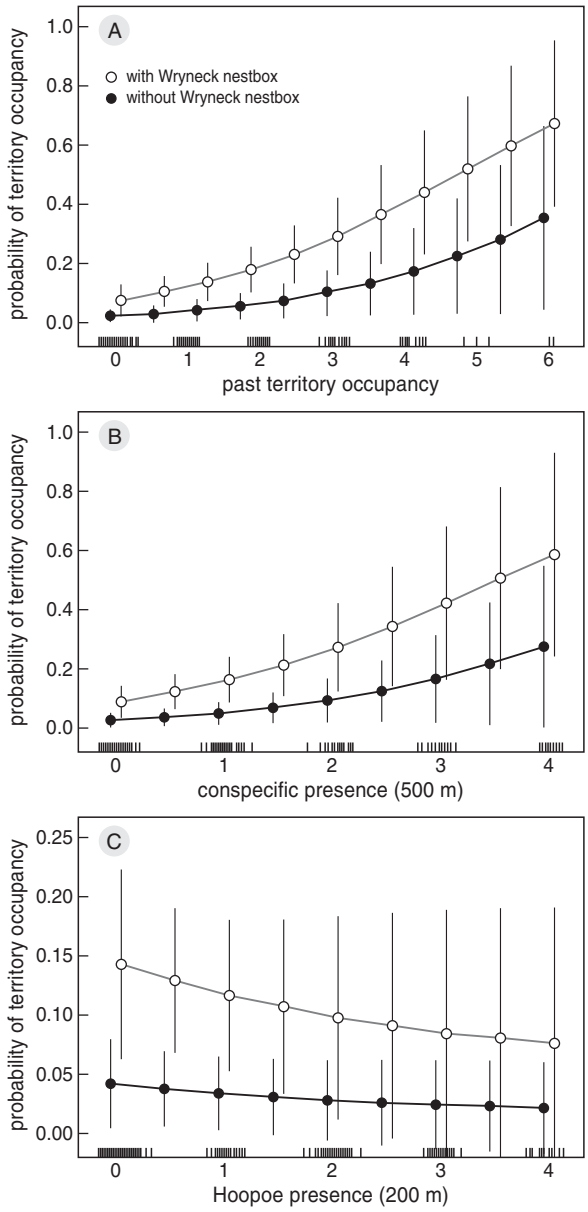


Figure 2. Model averaged probability that a territory is occupied by a Wryneck in relation to A) the past occupancy of the territory, B) the number of other Wryneck broods in a circle of 500 m around the focal nest, C) the number of Hoopoe broods in a circle of 200 m around the focal nest, this for territories with and without an additional Wryneck nestbox. The underlying model selection is given in Table 1. Vertical bars show the 95% confidence intervals.

Model selection

We conducted all analyses with R Version 2.7.2 (R Core Team 2008, libraries: nlme, lme4). The pair-wise correlations of the explanatory variables were low ($r < 0.5$), and they could therefore all be considered in the analyses. We ranked the models according to their support by the data using the Akaike Information criterion (AIC) and the AIC-weights. From the best models whose AIC-weights summed up to 0.95 we computed model averaged predictions. In addition we calculated the coefficient of determination (R^2) as an estimate for

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Table 1. Summary results of Wryneck territory occupancy modelling. The 3 top-ranking models were used for model averaging. Given are ΔAIC, AIC weights w_i, the number of estimated parameters (NP), the residual deviance (Deviance) and the coefficient of determination (R^2). Variable *Past occupancy* was included in all models but not explicitly shown in the table. Variable *Conspecifics* is defined as the number of Wryneck broods within 500-m radius of the territory, *Hoopoe* is defined as the number of Hoopoe broods within a 200-m radius, and *Nestbox* indicates whether or not a Wryneck nestbox was present in the territory. 'Intercept' indicates the model that included none of the focal explanatory variables.

Model	w_i	ΔAIC	NP	Deviance	R^2
Conspecifics + Nestbox + Hoopoe	0.49	0.00	5	151.1	0.215
Conspecifics + Nestbox	0.46	0.14	4	153.3	0.192
Conspecifics	0.02	6.75	3	161.9	0.099
Conspecifics + Hoopoe	0.02	6.98	4	160.1	0.119
Hoopoe + Nestbox	0.01	7.64	4	160.8	0.111
Nestbox	0.01	9.11	3	164.3	0.073
Hoopoe	0.00	12.44	3	167.6	0.035
Intercept	0.00	13.42	2	170.6	0.0

goodness of fit for all linear mixed effect models (Xu 2003). R^2 is defined as the proportion of the variance explained by a given model i and is calculated as $R^2 = 1 - \text{deviance}_i^2 / \text{max. deviance}^2$.

RESULTS

Territory occupancy

Of the 269 monitored territories, 32 were occupied by a Wryneck in 2008. Twenty three 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.

Model-averaged probability that a territory was occupied by a Wryneck was higher if an additional Wryneck nestbox was present (Fig. 2A). 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. 2B), while the number of occupied Hoopoe territories had no impact (Fig. 2C). Territories that had been occupied in the past also had a higher probability to be occupied in the study year (Fig. 2A).

Nestbox occupancy

Within the 32 occupied territories a total of 78 nestboxes were available (56 Hoopoe and 22 Wryneck nestboxes). Nineteen Wryneck broods occurred in one of the 56 available Hoopoe nestboxes, 14 broods occurred in one of the 22 available Wryneck nestboxes. In one territory, the first, failed brood was conducted in the Hoopoe nestbox, the replacement brood in the Wryneck nestbox. Model selection revealed that models with *nestbox type* were clearly higher ranked than models without (Table 2).

Table 2. Results of Wryneck nestbox occupancy modelling. Given are ΔAIC, AIC weights, the number of estimated parameters (NP), the residual deviance (Deviance) and the coefficient of determination (R^2). Variable *Nestbox type* indicates in which nestbox (Wryneck or Hoopoe) a Wryneck brood was conducted. Variable *Hoopoe* is defined as in Table 1.

Model	w_i	ΔAIC	NP	Deviance	R^2
Nestbox type	0.48	0.00	3	100.6	0.104
Nestbox type + Hoopoe	0.27	1.14	4	99.7	0.120
Nestbox type × Hoopoe	0.13	2.65	5	99.2	0.128
Intercept	0.08	3.69	2	106.3	0.0
Hoopoe	0.04	5.13	3	105.7	0.0

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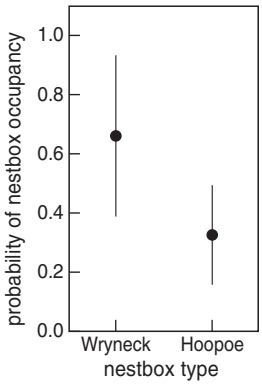


Figure 3. Model-averaged probability that a Wryneck settled in a Wryneck and Hoopoe nestbox, respectively. In 56 Hoopoe nestboxes there were 19 broods, whereas in only 22 Wryneck boxes 14 broods occurred. The underlying model selection is given in Table 2. Vertical bars indicate the 95% confidence intervals.

Wryneck nestboxes were clearly preferred over Hoopoe nestboxes (Fig. 3). The presence of Hoopoes had no influence on the nestbox choice (Table 2).

Reproductive output and nestling condition

Twenty-four successful and 19 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 *nestbox type* (Table 4A). Models with presence of *Hoopoes* and *conspecifics* had lower support. By contrast,

Table 4. Summary results of Wryneck 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 but not explicitly shown in the table. Given are the ΔAIC, the AIC weights (w_i) and the coefficient of determination (R^2). For the meaning of the variables, see Tables 1 and 2.

	Nestling body mass		
A) Model	w_i	ΔAIC	R^2
Nestbox type	0.32	0.00	0.008
Intercept	0.19	1.04	0.0
Nestbox type + Hoopoe	0.12	1.97	0.008
Nestbox type + Conspecifics	0.12	1.98	0.008
Hoopoe	0.08	2.86	0.0
Conspecifics	0.07	3.02	0.0
Nestbox type × Hoopoe	0.05	3.68	0.009
Nestbox type + Hoopoe + Conspecifics	0.04	3.96	0.004
Nestbox type × Hoopoe + Conspecifics	0.02	5.63	0.009

	Nestling tarsus length		
B) Model	w_i	ΔAIC	R^2
Intercept	0.30	0.00	0.0
Conspecifics	0.19	0.91	0.004
Nestbox type	0.14	1.56	0.002
Hoopoe	0.13	1.66	0.001
Nestbox type + Conspecifics	0.09	2.47	0.005
Nestbox type + Hoopoe	0.06	3.33	0.002
Nestbox type + Hoopoe + Conspecifics	0.04	4.10	0.006
Nestbox type × Hoopoe	0.04	4.28	0.006
Nestbox type × Hoopoe + Conspecifics	0.02	5.86	0.007

Table 3. Model selection of different components of Wryneck reproduction success 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 ΔAIC, the AIC weights (w_i) and the coefficient of determination (R^2). For the meaning of the variables, see Tables 1 and 2.

	Brood success (n = 43)			Hatching success (n = 33)			Fledging success (n = 33)		
Model	w_i	ΔAIC	R^2	w_i	ΔAIC	R^2	w_i	ΔAIC	R^2
Intercept	0.18	0.00	0.0	0.13	0.29	0.0	0.17	0.00	0.0
Conspecifics	0.14	0.52	0.17	0.09	1.14	0.003	0.13	0.56	0.014
Nestbox type	0.12	0.82	0.006	0.15	0.00	0.024	0.11	0.92	0.024
Hoopoe	0.11	0.94	0.002	0.10	0.85	0.008	0.11	0.87	0.004
Conspecifics + Nestbox type	0.10	1.14	0.031	0.12	0.54	0.034	0.09	1.32	0.021
Hoopoe + Conspecifics	0.08	1.52	0.017	0.07	1.54	0.014	0.08	1.53	0.015
Hoopoe + Nestbox type	0.08	1.66	0.012	0.10	0.93	0.025	0.07	1.69	0.010
Nestbox type + Hoopoe + Conspecifics	0.07	1.87	0.034	0.08	1.30	0.037	0.06	2.23	0.024
Nestbox type × Hoopoe	0.07	1.74	0.032	0.11	0.73	0.047	0.14	0.42	0.079
Nestbox type × Hoopoe + Conspecifics	0.06	2.12	0.081	0.05	2.05	0.042	0.05	2.56	0.045

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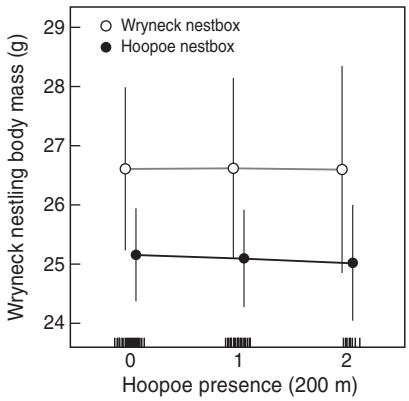


Figure 4. Model-averaged Wryneck nestling body mass in relation to the number of Hoopoes (200-m radius around the focal nest) for broods occurring in Wryneck and Hoopoe nestboxes. The underlying model selection is given in Table 4. Vertical bars show the 95% confidence intervals.

the best model for the variation of nestling tarsus length did not contain the focal explanatory variables (Table 4B). However, all models explained very 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. 4). The presence of a Hoopoe brood had virtually no impact on Wryneck nestling body mass (Fig. 4).

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 slightly heavier in Wryneck nestboxes, possibly improving the individual quality of fledglings in terms of survival when the appropriate nestboxes were used (Naef-Daenzer *et al.* 2001). This may explain the strategic choice by Wrynecks towards this type of nestbox.

Territories with an additional Wryneck nestbox 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 & Thompson 2006, Llambías & 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 & Roper 1988) and provide nesting sites for replacement broods. 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 & Taylor 1996, Browne 2006, García-Navas *et al.* 2008) or that the quantity of them matters (Tomé *et al.* 2004, Eckerle & Thompson 2006, Llambías & 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 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, small nestboxes over the first-installed, large Hoopoe nestboxes. Apparently the former better fit to species ecological requirements. The two nestbox types mainly differ regarding material and size. Tits and Tree Sparrows preferred nestboxes made of wood concrete (comparable to the Wryneck nestboxes described here) over nestboxes made of

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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. Actually, temperature in our Wryneck nestboxes was on average (± SE) 0.87°C (± 0.16°C, $n = 12$) higher than in wooden Hoopoe nestboxes (Zingg, unpubl. data). Increased nest temperature may decrease post-hatching female brood attendance during the early phase of growth when chicks cannot thermoregulate by themselves. This may provide them with more time for food provisioning (Pérez *et al.* 2008). Also, heavier 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, Rendell & Verbeek 1996, Gustafsson & Nilsson 1985), as well as better thermal environment (Summers & Taylor 1996, Mazgajski & 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. The small entrance hole of the Wryneck nestboxes 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 & Perrins 1986, Merilä & Wiggins 1995). However, we observed no clear effect of Hoopoe density on Wryneck nestbox occupancy and on the body mass of Wryneck nestlings.

The three main advantages of the smaller nestboxes for 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 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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SAMENVATTING

Nestkasten worden veel gebruikt als steun in de rug voor holenbroeders waar het niet goed mee gaat. Toch is er weinig onderzoek gedaan naar de invloed van de dichtheid en het ontwerp van nestkasten op broedvogels in het boerenland. Dit onderzoek richtte zich op de voorkeur voor bepaalde nestkasttypes door de Draaihals *Jynx torquilla* in het zuidwesten van Zwitserland. Het eerste type kast was oorspronkelijk ontworpen voor de grotere Hop *Upupa epops*. De kasten van dit type waren op 269 plekken opgehangen en werden vanaf 2002 gecontroleerd op broedende Draaihalzen. In 2008 werd een kleiner type nestkast opgehangen, die speciaal voor de Draaihals was ontworpen. Dit type werd geplaatst op de helft van de plekken waar al een grotere kast hing. De onderzoekers registreerden in welk type kast de Draaihals broedde, hoeveel jongen er werden geproduceerd en hoe groot en zwaar de jongen waren. Bovendien werd nagegaan in hoeverre er van concurrentie sprake was met soortgenoten of andere vogels. De Draaihalzen vestigden zich bij voorkeur op plekken met de speciale kast voor Draaihalzen. In de meeste gevallen werden die ook gebuikt om te broeden. Het aantal uitgevlogen jongen verschilde niet tussen de nestkasttypes, maar de jongen waren iets zwaarder in de kleinere nestkast, vermoedelijk doordat in deze kasten minder last van Hoppen werd ondervonden. Dit onderzoek laat zien dat de aantrekkelijkheid van een gebied verhoogd kan worden door geschikte nestkasten op te hangen. Het ophangen van nestkasten is een geschikte manier om een soort als de Draaihals te beschermen, mits voldoende aandacht aan het ontwerp wordt besteed. (DH)

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