Long-term occupancy of nest boxes as a measure of territory quality for Pied Flycatchers

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ABSTRACT. The rate of occupation of territories or nest locations has been proposed as a suitable surrogate of breeding territory/habitat quality when more precise, but costly, measures are not available. However, whether the frequency of breeding territory occupancy actually reflects its quality regardless of the habitat type is unclear. We address this issue using 22 yr of data on Pied Flycatchers (*Ficedula hypoleuca*) breeding in nest boxes in two contrasting habitats in central Spain: a mature, structurally complex oakwood, and a homogeneous pine plantation. Favored nest boxes in the oak forest were the earliest ones occupied, whereas the opposite was true in the pine plantation. In addition, the most frequently used nest boxes in the latter habitat were occupied by older and darker males, and also produced more offspring and recruits. These relationships were not observed in the deciduous forest. Long-term patterns of nest box occupancy may be a reliable surrogate for territory quality, but, as suggested by our results, its accuracy will depend on the heterogeneity of the habitats where nest boxes are located.

RESUMEN. **La ocupación de cajas-nido a largo plazo como medida de la calidad del territorio en el Papamoscas cerrojillo**
La tasa de ocupación de los nidos o territorios se ha propuesto como un buen sustituto de la calidad del hábitat/territorio de reproducción cuando no se dispone de medidas más precisas, generalmente difíciles de obtener. Sin embargo, no está claro si la precisión de la tasa de ocupación, usada como un indicador de la calidad del territorio, depende de las características del hábitat. Abordamos esta cuestión utilizando veintidós años de datos reproductores de Papamoscas cerrojillo (*Ficedula hypoleuca*) criando en cajas-nido de dos bosques con diferentes características del centro de España, un robledal maduro y estructuralmente complejo y un monocultivo manejado de pinos. En el robledal, los papamoscas criaron antes en los nidales utilizados más frecuentemente, aunque la tendencia fue la inversa en el pinar. Además, los nidales usados más frecuentemente en el pinar produjeron un mayor número de pollos y de reclutamientos a la población y fueron ocupados por los machos de plumaje más oscuro y mayor edad, presumiblemente de mayor calidad. La tasa de ocupación de cajas nido a largo plazo puede ser un sustituto fiable de la calidad del hábitat a escalas espaciales reducidas aunque esto podría depender de la heterogeneidad de los hábitats donde se instalan los nidales.

Key words: breeding, habitat selection, hole–nesters, long–term monitoring, occupation

Habitat selection by birds has been studied at several levels, from coarse to fine-grained (Cody 1985, Orians and Wittenberger 1991, Jones 2001, Razgour et al. 2011, Maícas et al. 2012, Eichholz and Elmberg 2014, Camacho et al. 2016, Kumar et al. 2017). At the micro-habitat scale, habitat quality is a key factor for reproductive success for many avian species (Johnson 2007) and its variation is therefore an important factor to consider in ecological studies. However, because environmental quality is difficult to measure, especially over long periods, ornithologists have attempted to find surrogates based on indirect measures of habitat quality. In this category, occupancy of either territories (Sergio and Newton 2003) or nests (Askenmo 1984, Potti and Montalvo 1991a, Janiszewski et al. 2013) has been proposed as a measure of site attractiveness under the assumption that the places most favored by different individuals of a species or population should reflect improved conditions for breeding (Penteriani et al. 2002, Ferrer and Bisson 2003).

Sergio and Newton (2003: 857) reviewed 22 studies and concluded that "occupancy

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always deviated from a random pattern in species in which it was tested and was always correlated with productivity and/or with some other measure of territory quality." However, the extent to which these findings are repeatable or generalizable across spatial scales in a range of locations, species, or populations is, to our knowledge, still unknown, which is understandable given the logistical constraints imposed on such an assessment. For example, in highly homogeneous habitats, differences in territory quality may remain undetected without using more direct and accurate measures of environmental quality such as food availability. Here, we took advantage of a two-patch system to ask if the rate of occupancy can be universally used as a reliable proxy for territory quality regardless of habitat type.

Heterogeneity in habitat quality sets the stage for potential competition among individuals for the best breeding locations. Under this scenario, it can be predicted that (i) more attractive territories will be monopolized by high-quality individuals in what has been referred to as the despotic distribution (Fretwell 1972), and (ii) this will be observable from studying the aggregated phenotypic composition of individuals using those territories (Janiszewski et al. 2013).

Pied Flycatchers (*Ficedula hypoleuca*) are long-distance migratory songbirds that breed in a wide variety of temperate forests across Europe, ranging from pure deciduous to pure coniferous habitats (Lundberg and Alatalo 1992). Males arrive in breeding areas between late April and early May, search for and defend suitable cavities, and sing to attract females. Although predominantly socially monogamous, some males occupy a second nest cavity, attract a second female and become socially bigamous (Lundberg and Alatalo 1992). Unlike other coexisting hole-nesting species, e.g., tits (Perrins 1979, Stenning 2018), that establish all-purpose territories (sensu Hinde 1956) more or less centered around nests, flycatchers only defend their nest cavities (von Haartman 1956, Lundberg and Alatalo 1992).

We examined the relationships between territory and individual quality in Pied Flycatchers in two different habitats: a mature oakwood and a pine monoculture. We focus on the territories (i.e., nest boxes) as the subjects of enquiry by asking if their identities/locations relate to intrinsic (e.g., body size) or mainly extrinsic (e.g., breeding phenology) traits of the Pied Flycatchers that occupy them. Even if all nest boxes have the same structural attributes (e.g., material, dimensions, and entrance-hole diameter), nest boxes at different locations may differ in degree of exposure to predation (Finch 1989, Beck 2013), proximity to the best foraging sites (Huhta et al. 1999, Aitken et al. 2002, Janiszewski et al. 2013), and the density of surrounding competing conspecifics and heterospecifics with a preference for the same or similar sites (Avarguès-Weber et al. 2013). For Pied Flycatchers, singing conspecifics, as well as the presence of other species that compete for nest holes, attract individuals searching for forest patches holding suitable nesting cavities (Samplonius et al. 2017). For species like Pied Flycatchers that only defend nest sites, this may result in exceptionally high densities (Newton 1998) that may limit breeding success by negative density-dependent effects on breeding performance (Alatalo and Lundberg 1984, Stenning et al. 1988) and mask the utility of any surrogate of territory quality. Otherwise, highly heterogeneous forests could provide Pied Flycatchers with multiple microhabitat and foraging opportunities (Lundberg et al. 1981, Mäntylä et al. 2015), so that the breeding success of all males might be similar regardless of their morphology (Camacho et al. 2015).

In contrast, habitat simplicity could provide advantages for particular phenotypes through access to food resources or competitive advantages, e.g., large individuals may forage more efficiently than smaller individuals in habitats where large prey are more abundant or are easier to capture than small prey (Gaston 1974, Korner-Nievergelt and Leisler 2004). On the basis of earlier evidence (Sergio and Newton 2003), we predicted that the most frequently used nest boxes would be occupied, on average, earlier in the breeding season than those used less frequently. This is because individuals arriving earlier at the breeding grounds, and usually regarded as being of higher quality than later-settled individuals, are more likely to occupy the best territories (Slagsvold and Lifjeld 1988, Aebischer et al. 1996, Hasselquist 1998, Siefferman and Hill 2005, Beck 2013). This would yield,

on average, increased fecundity by way of the number of fledged young and recruits. Our null hypothesis was that the relationship between nest-box attractiveness and bird phenology and "quality" would not differ between habitats.

METHODS

Data used in our study were collected from a population of Pied Flycatchers in central Spain (~41°N, 3°W, 1200–1300 m a.s.l.) breeding in two different habitats: an old deciduous oak forest and a managed coniferous forest (see characteristics below). Since 1995, 156 (oakwood) and 80 (pinewood) wooden nest boxes (of the same model; details in Appendix I in Lambrechts et al. 2010) placed 2–4 m above ground and separated by a mean distance of 30 ± 14 (SD) m have remained on the same trees except for three that were removed after tree falls, giving a total of 233 nest boxes. Songbird reproduction has been monitored in the two habitats over 22 yr (1995–2017), except for 2003 when sampling was limited (e.g., Camacho et al. 2013, 2015, 2016, 2018).

The two forest areas differ in vegetation structure and composition. Forest structure is complex in the oakwood, dominated by Pyrenean oak (*Quercus pyrenaica*) and more sparse Montpellier maples (*Acer monspessulanus*), with trees of different ages coexisting with fully developed shrub (*Erica arborea*, *Cistus laurifolius*, and *Crataegus monogyna*) and herbaceous layers. The pinewood consists primarily of a monoculture of Scots pine (*Pinus sulvestris*), where canopy closing and management operations have removed or hindered development of the herbaceous and bush layers, and pine trees of approximately the same age are growing at regular distances apart, with some sparse thickets in borders and clearings (Fig. 1). Besides habitat heterogeneity (e.g., structural complexity and composition), the two areas differed in size (oakwood = 9.3 ha; pinewood = 4.8 ha), density of natural holes (almost nonexistent in the managed pinewood, and abundant, but little used by flycatchers, in the oakwood), spatial arrangement of nest boxes (oakwood = a mix of subplots and linear paths with nest boxes; pinewood = a more regular plot; Fig. 1), and breeding densities,

determined by quantifying yearly nest-box occupancies either by flycatchers or other hole-nesting species (see below). For further details about the two study sites, see Camacho (2018).

Sampling from 1995 to 2017 at both study sites resulted in 5170 "nest-box years" of breeding records by tits, treecreepers, nuthatches, and Pied Flycatchers. Each year, nest boxes were inspected at 1–3-d intervals to determine the occupant species. Nest boxes occupied by Pied Flycatchers continued to be monitored at regular intervals to determine laying and hatching dates, clutch sizes, and numbers of hatchlings and fledglings on day 13. Nest boxes were cleaned after each breeding attempt to assess infestation by nest ectoparasites (Merino and Potti 1996) and again before breeding started the following spring to remove debris and feces from roosting bats, tits, and nuthatches. In the case of Pied Flycatchers, we trapped both adults when nestlings were 8–10 d old (Camacho et al. 2017) and aged them by plumage characteristics as yearlings or older ((Karlsson et al. 1986, Potti and Montalvo 1991b). Based on the patterns of age at first breeding for birds of known age (Potti and Montalvo 1991a), immigrant (previously unbanded) birds were ascribed as either 1 or 2 yr old, respectively, and 1 yr was added each season if they survived. We knew the exact age of many birds due to high levels of natal philopatry (Camacho et al. 2016).

Analyses. Following the rationale of Askenmo (1984), Sergio and Newton (2003), and Janiszewski et al. (2013), among others, we considered nest boxes occupied in a given year when they contained a clutch of eggs where incubation started. We characterized the quality or attractiveness (henceforth treated as synonymous terms; but see Robertson and Hutto 2006) of nest boxes to Pied Flycatchers as the proportion of years they were occupied relative to the years they were available for use, i.e., not occupied by other species. Thus, nest-box attractiveness ranged from 0 (never occupied by Pied Flycatchers) to 1.0 (occupied all years when available), with its distribution not differing from a normal distribution (Kolmogorov–Smirnov $d = 0.056$, $P > 0.20$). To determine if particular nest boxes were preferentially occupied by Pied Flycatchers, patterns of nest-box
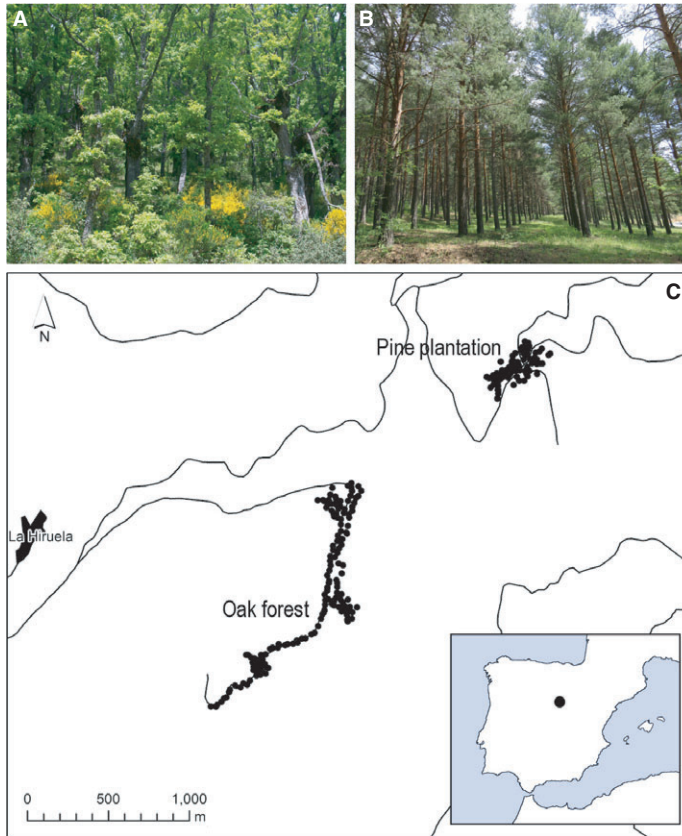
Fig. 1. Study sites near the village La Hiruela in central Spain. (A) Oakwood, (B) pinewood, and (C) map of the two study areas; each black dot denotes a nest box monitored for 22 yr. Black lines indicate roads. The inset shows the location of our study area in the Iberian Peninsula (photo credits: Carlos Camacho).

occupancy were tested against a Poisson distribution, which is expected if selection of nests is random. We also scored nest boxes each year as either predated (1) or not (0), and used across-year averages of those within-nest box scores as proxies of exposure to predation risk, mainly by Great Spotted Woodpeckers (*Dendrocopos major*), pine martens (*Martes foina*), and least weasels (*Mustela nivalis*) (Potti and Merino 1994).

Nest-box availability for Pied Flycatchers (i.e., empty nest boxes not occupied by other species) decreased during the study period due to increases in populations in both forest patches (Camacho et al. 2013). However, population growth was greater in the pinewood, where saturation of nest box occupation by Pied Flycatchers and other species is already manifest. Therefore, we considered

the possible influence and variation along the years of population density on the settlement decisions of flycatchers, which might be conditioned by the abundance of hole-nesters (Samplonius et al. 2017) and affect the possible use of nest-box occupancy as a proxy of nest-box quality. To assess this, we looked separately at correlations between occupancy rates and bird traits in two contrasting periods, namely the first (1995–2001) and last (2012–2017) 6-yr periods when density of flycatchers was relatively low (51% and 31% of the nest boxes in pinewood and oakwood, respectively) and high (63% and 70% of the nest boxes in pinewood and oakwood, respectively), especially in the pinewood. Nest-box attractiveness during these two periods was recalculated for both habitats by considering only rates of occupancy in the above-specified

periods. In these analyses, the same qualitative trends as in the entire period, or lack thereof, were observed in each forest patch for the two 6-yr periods (results not shown), indicating that population density did not seem to affect correlates of nest-box occupancy. On the other hand, the intrinsic quality of each nest box in both areas should have remained approximately constant throughout the years —except for nest-box aging—because old nest boxes were repaired or replaced by new ones when necessary.

Because Pied Flycatchers are relatively short-lived (medians = 2 and 3 yr for females and males, respectively; authors' unpubl. data), nest-box occupancy should largely be independent of individual identities because most surviving birds do not renest where they bred the previous year (Montalvo and Potti 1992). Nest-box reuse by the same individuals accounted for only 7.9% of all breeding events ($N = 157$ and 82 cases of male- and female-nest box between-year repetitions, respectively). In addition, few males ($N = 112$) acquired two nest boxes in a year and became bigamous, so our results should not be severely affected by pseudoreplication.

We used Linear Models (LM) in R statistical software (http://www.R-project.org). The dependent variable in all models was the occupancy rate of each nest box over the study period (used as a proxy of nest box attractiveness; see above). As explanatory terms of individual quality, we used a set of variables that, averaged across all breeding events in a particular nest box, were likely indicators of the quality of the Pied Flycatcher occupants. Variables selected to measure associations between nest-box and individual qualities were: (i) the age of males and females in years, (ii) attractiveness, as scored by the percent of black feathers in the mantle plumage of males (Camacho et al. 2018) and the size of the forehead patch for both sexes (Potti and Canal 2011), (iii) overall body size, as ascertained by the first axis of a Principal Component analyses of tarsus length, wing length, and mass (standardized for hourly variation; Potti and Montalvo 1991b) that explained 48% and 47% of the variance in body size in males and females, respectively, (iv) mating dates (dates of initiation of nest construction; Potti 1999, Both et al. 2017), (v) breeding dates (dates of laying of first egg in each clutch, standardized within years as deviations from the within-habitat annual medians), (vi) clutch sizes; (vii) number of hatchlings, (viii) number of fledglings on day 13 post-hatching, and (ix) number of recruits resulting from breeding attempts in a nest box. For more details, see Potti (1999), Potti and Merino (1994), Canal et al. (2011), and Potti et al. (2014). We ran all models separately for each explanatory term and selected the most parsimonious models using the Akaike Information Criteria for small samples (AIC). Models were split by habitat to avoid comparing competing models that differed in sample size due to habitat differences in the number of nest boxes (see above). Models that differed by more than two units in relation to the smallest AIC were not considered further (Burnham and Anderson 2002).

RESULTS

Overall, there were 3039 nests of Pied Flycatchers (1991 and 1048 in the oakwood and pinewood, respectively) and 695 of other species over the 22 yr of our study, plus 1394 cases where nest boxes remained unused in some years (27% of "nest box-year" events). Only one nest box was occupied by Pied Flycatchers during all years, but six additional nest boxes were always occupied when available. In both forest plots, nest boxes were used during an average of 13 breeding seasons (Fig. 2).

In the oakwood forest, the distribution of nest boxes occupied by Pied Flycatchers deviated significantly from a Poisson distribution ($\chi_9^2 = 85.6$, $P < 0.0001$), indicating that some nest boxes were occupied more (and fewer) times than expected (Fig. 2). However, occupation of nest boxes by Pied Flycatchers in the pinewood conformed to a Poisson distribution, suggesting a random distribution of independent events ($\chi_9^2 = 8.4$, $P = 0.49$; Fig. 2).

In the oakwood, based on AIC values, the most parsimonious models suggested that the attractiveness of nest boxes to Pied Flycatchers was best explained by breeding time, indexed as laying date (Table 1). Examination of the slope and directionality of this association revealed a significant negative relationship between nest-box attractiveness and laying date
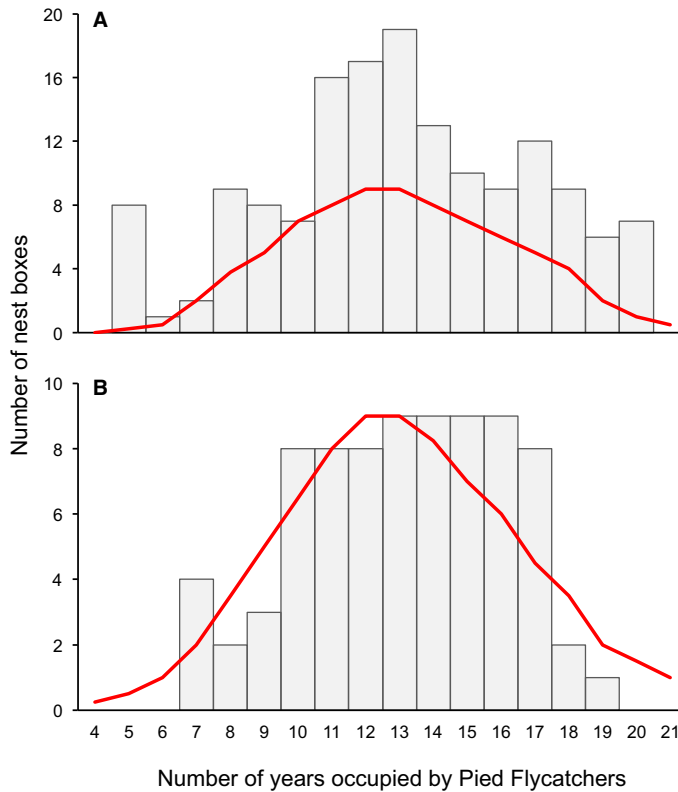
Fig. 2. Distribution of the use of nest boxes by Pied Flycatchers in (A) the oakwood and (B) the pinewood; black lines depict the expected Poisson distributions. Note the difference in the y-axes for the two forests.

Table 1. Results of the model selection procedure split by habitat for the relationships between nest-box occupancy rate and individual traits used as proxies of their quality.

Oak forest			Coniferous forest		
Variable	AIC_c	ΔAIC_c	Variable	AIC_c	ΔAIC_c
Standard laying dates	**−90.828**	**0.000**	**Male age**	**−83.263**	**0.000**
Mating date	−88.655	2.173	**Standard laying dates**	**−81.979**	**1.285**
Male size (PC1)	−77.889	12.938	**Number of fledglings**	**−81.606**	**1.657**
Nest box predation exposure index	−77.863	12.964	**Number of recruits**	**−81.562**	**1.702**
Number of fledglings	−76.741	14.087	**Male plumage blackness**	**−81.382**	**1.882**
Male plumage blackness	−72.803	18.025	Male size (PC1)	−80.967	2.297
Number of hatchlings	−72.558	18.269	Male forehead patch size	−80.946	2.318
Male forehead patch size	−72.147	18.680	Female forehead patch size	−80.863	2.401
Male age	−70.280	20.548	Clutch size	−80.451	2.812
Clutch size	−69.902	20.926	Female age	−80.287	2.977
Female size (PC1)	−69.084	21.744	Mating date	−80.203	3.060
Number of recruits	−68.495	22.333	Number of hatchlings	−80.176	3.088
Female forehead patch size	−68.184	22.644	Nest box predation exposure index	−79.963	3.300
Female age	−67.521	23.306	Female size (PC1)	−79.923	3.341

Models are ranked in relation to their AIC value (AIC). Differences in AIC values in relation to the model with the smallest AIC (ΔAIC) are also shown, the models with ΔAIC < 2 being highlighted in bold.

(estimate: -0.031 ± 0.006, $F_{1,146} = 25.0$, $P < 0.001$), indicating that nest boxes most frequently occupied by Pied Flycatchers were those where breeding occurred earliest in the season (Table 1). Models exploring the association between the average size of male forehead ornaments and plumage coloration had AICs with a difference > 2 in relation to the best model. Similarly, models assessing the association between nest-box attractiveness and phenotypic traits of males and females had AICs > 2 (Table 1).

In the pinewood, however, several models had an AIC < 2 relative to the best model, suggesting equally parsimonious fits (Table 1). Specifically, male age, laying date, number of fledglings, number of recruits, and male plumage darkness were the variables most related with nest-box occupancy in the pinewood. Further examination of these associations suggested that the frequency of nest box occupancy was weakly and positively associated with male age (estimate: 0.058 ± 0.031, $F_{1,76} = 3.3$, $P = 0.071$), laying date (estimate: 0.010 ± 0.007, $F_{1,76} = 2.0$, $P = 0.16$), number of fledglings (estimate: 0.042 ± 0.032, $F_{1,76} = 1.7$, $P = 0.20$), number of recruits (estimate: 0.071 ± 0.055, $F_{1,76} = 1.6$, $P = 0.21$), and male blackness (estimate: 0.002 ± 0.002, $F_{1,76} = 1.4$, $P = 0.23$).

DISCUSSION

Associations between Pied Flycatcher phenotypes and territory quality in our study were rather modest, as expected given the high signal noise due to the large stochasticity in both the identities and trait expression of birds that occupied particular nest boxes. Furthermore, these associations depended on where nest boxes were located. In the structurally heterogeneous oak forest, birds occupied nest boxes in a nonrandom fashion, and the most frequently used nest boxes were also those occupied earliest in the season. By contrast, in the homogeneous environment of the artificial pine forest, nest boxes were occupied randomly, with weak associations between occupancy rates and phenotypic and fitness traits of their occupants.

The long-term pattern of nest-box occupancy by Pied Flycatchers in the oakwood showed clear preferences for particular nest

boxes. Birds occupying the most attractive nest boxes in the oakwood also started to breed on average earlier than those using less-preferred ones, a pattern reversed in the pine plantation. The association of increased nest attractiveness with early breeding phenology, also reported in Eurasian Magpies (*Pica pica*, Matthysen 1990), Black Kites (*Milvus migrans*, Sergio and Newton 2003), and White Storks (*Ciconia ciconia*, Janiszewski et al. 2013), means that the most preferred nest boxes were those first claimed and then signaled to conspecifics by male Pied Flycatchers after arrival in the spring. Previous studies have shown that early arrival of male Pied Flycatchers in breeding areas enhances their chances of mating and becoming socially polygynous because early settlement allows them to acquire several, usually neighboring cavities (Potti and Montalvo 1991b, 1993, Canal et al. 2012), a prerequisite for attracting more than one female (Lundberg and Alatalo 1992).

In contrast to the oak forest, nest boxes were occupied randomly in the pinewood. To our knowledge, this may constitute the first report of territory occupancy not deviating from a random pattern, as reviewed by Sergio and Newton (2003) for 23 bird populations representing 17 species (including our Pied Flycatcher population studied over a 5-yr period in other section of the oakwood). These results suggest that particular nest boxes in the pinewood were not preferred (or avoided) over others, and were occupied only on the basis of availability. The finding of random occupancy in the pinewood hints to homogeneity of environmental conditions for Pied Flycatchers in this artificial plantation, in contrast to the highly heterogeneous nest-box surroundings in the natural, old oakwood.

Even if nest-box occupation in the pine plantation seemed random, once occupied by the species, subtle differences between nest boxes in the phenology and phenotype of their occupants seemed to arise, indicating possible links between nest-box and individual (male) quality. However, except for the influence of male age, most statistical models for the pinewood had similar, low explanatory power so their relative importance (Table 1) is difficult to evaluate. The weak relationship between rate of nest-box occupancy and delayed breeding phenology in the

homogeneous pinewood is also difficult to explain because breeding early is advantageous in both forest types in terms of breeding success and recruitment (Potti et al. 2002, authors' unpubl. data). We note, however, that the peak of food abundance occurs later and is more sustained in coniferous than deciduous forests, somewhat negating the overriding importance of the early breeding schedule typical of deciduous oak forests (Burger et al. 2012).

The most frequently used nest boxes in the pine forest were associated with an older average age and darker dorsal plumage of their male occupants. Moreover, they rendered an increased reproductive success. Male-male competition for nest boxes among *Ficedula* flycatchers can be fierce and even result in injuries and death (Merilä and Wiggins 1995, authors' unpubl. data). With intense competition, older, more experienced males with better knowledge of the breeding area may enjoy a competitive advantage over younger males (Maynard Smith and Parker 1976). Presumably, such advantages can translate into occupying better foraging areas, or having foraging areas located closer to their nests for older males, resulting in a higher proportion of young and recruits than males in less attractive nest boxes, as our results support. The blackness of male dorsal plumage, also an influential factor involved in nest-box occupancy in the pinewood in our study, may be explained by similar arguments because male color has been shown to be important in male-male agonistic interactions in contests for nest sites, with blacker males being dominant over lighter ones (Slagsvold and Lifjeld 1988).

No significant link was found between nest-box attractiveness and female phenotype (e.g., age and morphology); these associations were restricted to males. This makes sense because male Pied Flycatchers are responsible for competing for and defending nest-sites from rival males (Lundberg and Alatalo 1992). Females, on the contrary, compete for access to already established males (Dale et al. 1990, Dale and Slagsvold 1996). Therefore, the associations of combined phenotypic traits with nest-box characteristics are likely to be more evident for males than females, except for those traits potentially leading to assortative mating, such as age (Potti 2000, Potti and Canal 2011). Because the intrinsic quality of nest boxes remained approximately constant throughout our study period, we hypothesize that the availability of foraging sites and/or food items in the nearby surroundings of nest boxes should be a key factor underlying these associations (Janiszewski et al. 2013). However, Mäntylä et al. (2015) attempted to address this question in a northern population of Pied Flycatchers and found no food-related benefits of breeding in particular territories/nest boxes, suggesting the absence of cues early in the season allowing Pied Flycatchers to make optimal decisions concerning where to breed (Mäntylä et al. 2015).

Due to the descriptive nature of our study, we can only speculate about why nest-box attractiveness is explained by different factors depending on habitat type. Perhaps, in a structurally heterogeneous forest like the oakwood, early arrival might give males a competitive advantage to hold the best territories, regardless of their body condition or sexual attractiveness, thus partially explaining the non-random selection of nest boxes in this habitat. Conversely, in a structurally homogeneous forest, the choice of a breeding territory might be more related to male experience and quality as determined by age and plumage ornaments (Slagsvold and Lifjeld 1988, Potti 1998, Beck 2013). Because of habitat simplicity, food resources may be limited in the less productive pine plantation so that older, more experienced males might be better able to compete for nest-sites and/or to exploit a variety of food resources near nest boxes. This idea might support random selection of nest boxes in the pinewood because the nest-box environment per se might not determine the future breeding success of its occupants, but, rather, be shaped by individual experience where variance in reproduction/heterogeneity in breeding success might be better explained by individual quality (i.e., experience and sexual attractiveness) rather than territory quality (i.e., nest-box environment). Certainly, more studies are needed to tease apart the relative influence of individual vs. territory quality on nest-box selection patterns.

To conclude, our results support the notion suggested by Sergio and Newton (2003) that, in the absence of detailed data on prey availability and abundance in the neighborhoods of nests, the occupancy rate of nest boxes over

medium to long-term periods can be used as a reliable measure of their quality and/or attractiveness to Pied Flycatchers. Nonetheless, as shown here, the factors explaining the frequency of nest-box occupancy may vary depending on habitat characteristics. Caution is therefore required when using rates of nest box use as a proxy for territory quality, at least at the local scale where nest-box population studies are usually conducted. Differences in size and configuration (e.g., plots vs. linear arrangements) of nest-box areas, as in our study system, may also influence habitat quality, but, in the absence of additional replicated studies, this remains conjecture. Further studies are needed to assess the generality of the variation in the long-term links between territory and bird quality among hole-nesting songbirds. Foreseeably, the widespread monitoring of nest boxes in educational and popular (e.g., citizen science, Brossard et al. 2005, Bonney et al. 2009) as well as scientific (Cooper et al. 2005) realms will provide the answers in the near future.

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