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Effects of habitat on breeding success in a declining migrant songbird: the Pied Flycatcher *Ficedula hypoleuca*

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Abstract. Habitat is a key determinant of breeding success in hole-nesting birds. Identifying the factors that influence breeding success is important in understanding nest-site selection behaviour and devising appropriate conservation strategies. This is especially true for declining species like the migratory Pied Flycatcher *Ficedula hypoleuca*. Here, I analyse the effect of 24 habitat variables on clutch size, hatching success and fledging success for 137 Pied Flycatcher nests in Gloucestershire, UK, using volunteer-collected data from a 5-year period. More successful nests tended to be located in areas with a lower density of mature trees but abundant saplings. Tree and sapling species richness was also important. Success was positively related to abundance of Oak *Quercus robur* and Silver Birch *Betula pendula* and negatively related to Beech *Fagus sylvatica*, Sycamore *Acer pseudoplatanus* and Bracken *Pteridium aquilinum*. Success was lower in boxes facing south-southwest and higher in boxes located on sorter trees. Despite Pied Flycatchers often being regarded as birds of grazed (open) woodland, success was not related directly to grazing. Close proximity to footpaths was associated with significantly lower clutch size, numbers of young to fledge, and percentage success, while close proximity to water was associated with increased success at all stages of breeding. This is a single-site study and the generality of these findings at other sites cannot be assumed without empirical testing. However, the results provide useful additional insight into success-habitat interactions in this species that, to some extent, challenge the general view of Pied Flycatchers, in the UK at least, as grazed woodland specialists.

Keywords: Reproductive success, *Ficedula hypoleuca*, Pied Flycatcher, grazing, nestboxes, breeding, nest site selection, , volunteer-collected data, citizen science

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INTRODUCTION

Avian reproductive success depends on a range of interacting factors. These factors can relate to the birds themselves (e.g. parental fitness and experience) or external environment (e.g. weather, predation risk, food supply). External environment factors often relate to the location of a nest in relation to habitat, which means that there are generally complex spatial patterns in reproductive success (e.g. Nilsson 1984, Pogue & Schnell 1994, Jones 2001). Understanding the factors that influence breeding success is important for all species to establish the adaptive nature, or otherwise, of nest-site selection behaviour (Mänd et al. 2005). Moreover, from an applied perspective, knowledge of species-habitat interactions is vital to understand how habitat change may affect populations and to devise effective conservation strategies.

For some species, there is comprehensive quantitative information on how habitat influences breeding success through single holistic studies (e.g. Gutzwiller & Anderson 1987, Saab 1999, Luck 2002). In other cases, there are multiple studies on the same species, which, between them, provide a comprehensive overview of species-habitat relationships. For example, for Blue Tits *Cyanistes caeruleus*, the effect of cavity parameters has been studied (e.g. van Balen 1984), the correlation between breeding success and surrounding vegetation has been analysed (Lambrechts et al. 2004) and effects of landscape processes such as edge effects has been documented (e.g. Hinsley et al. 1995). However, for other species, even some that are well studied, there are important gaps in knowledge. Some of these gaps in knowledge could potentially be filled by scientific analysis of data collected by volunteers through specific schemes or as part of citizen science initiatives (Greenwood 2007, Hart et al. 2012).

The Pied Flycatcher *Ficedula hypoleuca* is a migratory passerine that winters in sub-Saharan Africa and breeds in woodlands throughout Europe. The species is a secondary cavity nester, which uses natural cavities, woodpecker-excavated holes, or artificial nestboxes and generally has one brood per year. Pied Flycatcher populations are declining rapidly in several European countries, including the UK and Poland (Amar et al. 2006, Baillie et al. 2010, Pan-European Common Bird Monitoring Scheme 2010). The reasons for decline are not particularly well understood, but recent and ongoing climatic change could be an important factor (Sanz et al. 2003, Both et al. 2006). A detailed understanding of habitat-productivity relationships is

currently lacking and would be extremely useful to inform conservation and management initiatives.

Nest-site choice in Pied Flycatchers is not always possible (Goodenough et al. 2009a), even when boxes are provided in abundance, and when choice does occur is usually fairly simplified (e.g. choosing upright boxes rather than tilted nestboxes: Slagsvold 1987). Once a potential nest site and territory is located by each male, he then sings to attract a female. Males are time-limited when finding a nest site on their return from migration and potential sites have often already been claimed by resident species, reducing options available. Each female must select her partner and the nesting situation that he offers — the nest cavity and the territory that surrounds it – as one unit (Lundberg & Alatalo 1992, Potti & Montavlo 1991). Both nest site quality and male quality are considered by the female, but relative importance seems to differ between populations (Slagsvold 1986, Sirkkiä & Laaksonen 2009). This probably reflects the magnitude of the variability in these parameters at a given site (e.g. if male quality is fairly consistent, the environment would become the main choice determinate, and vice versa). Population dynamics could also have an effect, with females bet-hedging and settling for a sub-optimal breeding situation when female-female competition is high (risk of losing the opportunity to breed) or at low population densities (high search-cost). When nestboxes are placed in very close proximity to one another to allow a male to monopolise several boxes, females show a preference for high boxes with small entrance holes (Lundberg & Alatalo 1992).

Even when Pied Flycatchers do not, apparently, choose boxes based on habitat, habitat parameters can still be important correlates of breeding success. For example, cavity and entrance size influence success (Karlsson & Nilsson 1977, Slagsvold 1986, Czeszczewik & Walankiewicz 2003, Alatalo et al. 1988), as does cavity orientation (Goodenough et al. 2008). At a broader scale, birds have higher reproductive success in deciduous rather than coniferous woodland (Lundberg et al. 1981, Alatalo et al. 1985, Huhta et al. 1998). Siikamäki (1995) also showed experimentally that females translocated from deciduous to coniferous woodland laid fewer eggs than those remaining in the deciduous areas, suggesting clutch sizes can be adjusted in relation to habitat quality. In general, Pied Flycatchers are regarded, in the UK and several other European studies, as a bird of grazed or open Oak *Quercus* sp. woodland. This perception of the species' habitat requirements is largely based on qualitative information (Simms 1971, Lundberg & Alatalo 1992). In a rare quantitative study, Amar et al. (2006) found UK Pied Flycatcher populations declined more steeply at sites with high canopy coverage, smaller trees (low canopy, small tree girth and basal area) and low horizontal visibility. However, this study examined population density (and change therein) not reproductive success and it is not clear

how habitat variables, such as vegetation structure and species, affect breeding success. The location of nestboxes relative to landscape features such as water sources and roads could also have an effect (low success in boxes near roads in Scandinavia (Kuitunen et al. 2003) and near forest edges in Finland (Huhta et al. 1999)) but further research is needed.

In this study, I analyse the influence of 24 habitat variables on breeding success for Pied Flycatchers in a UK woodland over a five-year period. Historically, the study population has been large in a UK context (>100 pairs), such that it has been listed as being of national importance (Proctor and Pollard 2005). However, numbers have declined by 73.3% during the last two decades, and the population is now of immediate conservation concern (Goodenough et al. 2009b). Previous research undertaken at the same site suggests that Pied Flycatchers occupy nestboxes randomly, with the frequency distribution of occupied nestboxes not differing from random, both in relation to the overall nestbox resource, and boxes available to Pied Flycatchers post-migration (Goodenough et al. 2009a). This contrasts with co-occurring Blue and Great Tits *Cyanistes caeruleus* and *Parus major*, which choose nest-sites actively, and is despite boxes being provided in super-abundance (Petit and Petit 1996). Reproductive success is already known to link to nestbox orientation at this site (Goodenough et al. 2008). This means that lack of active choice is not due to success being unaffected by nest site characteristics, and suggests that Pied Flycatchers are either constrained in their choice (see above) or that lack of choice is an ecological trap (Mänd et al. 2005). Three main predications are tested in this study. Firstly, it is predicted that vegetation structure and species assemblage will influence Pied Flycatcher reproductive success. Pied Flycatchers are typically regarded as birds of grazed Oak woodland. The reason that grazing is thought to be important is that it creates a more open woodland structure with sufficient space between the field layer and canopy to allow birds to catch prey on the wing. It is thus hypothesised that success will be higher in grazed areas (and thus might also be linked to a reduced shrub layer and areas with fewer saplings), together with high abundance of Oak (which might also be linked to lower abundance of other common tree species). Secondly, it is predicted that the location of nestboxes relative to landscape features will be a key determinant of breeding success, with an anticipated negative relationship between success and footpaths. The rationale is that personal observation that nests near paths often attract large numbers of bird watchers and seem, anecdotally, more prone to failure. A further negative relationship between success and proximity to roads is predicted, based on previous research in Scandinavia (Kuitunen et al. 2003). Thirdly, it is anticipated that nestbox orientation affects success, with success being lower in boxes facing south-southwest as previously found through univariate analysis (Goodenough et al. 2008). Adding orientation into the current study of multiple habitat parameters is important, both to allow for its likely effect, and ensure that previous findings were not confounded by previously-unknown autocorrelation between orientation and other habitat variables.

Overall, this study aims to provide a comprehensive description of local spatial variability in Pied Flycatcher success relative to multiple environmental and habitat factors to inform conservation efforts for this declining migrant. Such insight is especially necessary given that individuals seem to be constrained in their ability to optimize breeding through adaptive nest-site choice. Although this study is based at just one site, albeit over a number of years, the findings will hopefully provide insights that can be tested at other sites so that management can be optimised on a case-by-case basis. It is also hoped that this study will provide insights into species-habitat interactions, and the problems of constrained nest choice, that can be applied to other avian species.

METHODS

Study site

This study was conducted at Nagshead Nature Reserve (Gloucestershire, UK). This 308 ha reserve, centered on 2°34'0"W, 51°47'0"N, is managed by the Royal Society for the Protection of Birds (RSPB) and is home to the longest-running UK nestbox scheme. Nestboxes are located within an area of pre-1841 Pedunculate Oak *Quercus robur* plantation, now classified as ancient semi-natural deciduous woodland (Tickner & Evans 1990). Indeed, despite its anthropogenic origins, the site has a varied vegetative community, with frequent Silver Birch *Betula pendula*, Rowan *Sorbus aucuparia*, Beech *Fagus sylvatica*, and Sycamore *Acer pseudoplatanus*. Holly *Ilex aquifolium*, Bramble *Rubus fruticosus* agg., Hawthorn *Crataegus monogyna* and Hazel *Corylus avellana* dominate the shrub layer, while Bracken *Pteridium aquilinum* dominates the field layer.

Until 2001, about one third of the site was sheep-grazed by free-roaming animals belonging to local commoners. There is essentially one grazed section of the reserve and one non-grazed section, with historical grazing obvious by stock-proof fence lines. In spring 2001, all sheep were culled due to an outbreak of Foot and Mouth disease, such that the reserve was sheep grazed for about one year of the current five year study. Although sheep were reintroduced in 2003, the distribution was very different and sheep were not seen on the reserve for the rest of the study period. The historically-grazed area is more open with a reduced shrub layer and fewer saplings compared to the ungrazed area.

There are a few well-used public footpaths bisecting the site, mostly running north-south, as well as a few vehicular tracks (used by reserve vehicles and forestry staff). Boxes occur within 1 to 320 m from the nearest footpath (mean = 105 m). The site is bordered on one side by a moderately busy public road and there are three small ponds within, or adjacent to, the area.

Volunteer-collected bird data

Breeding data were obtained from the RSPB for all Pied Flycatcher breeding attempts from each Nagshead nestbox during 2000–2004. These data were collected during weekly nestbox visits throughout the breeding season by experienced volunteer nestbox recorders co-ordinated by the RSPB Reserve manager. Records from each visit were submitted to the RSPB local office and data from all visits were summarised by another volunteer to provide breeding biology data: (1) clutch size (number of eggs); (2) hatching success (number of young to hatch); (3) fledging success (number of young to fledge). For this study, a percentage success variable was also calculated with the number of young to fledge expressed as a percentage of eggs laid (e.g. 50% when 6 eggs were laid and 3 birds fledged). In addition, as a measure of phenology, the first egg date (FED) of each breeding attempt was calculated. This was achieved by using the number of eggs recorded in an incomplete clutch and counting back the days to establish the day on which the first egg had been laid (on the basis that one egg was laid each day early in the morning; Perrins & McCleery 1989). All nests were found during the nest building stage or extremely soon thereafter (within two days as a maximum). Because of this, and the fact that the nests were monitored throughout the breeding season by dedicated volunteers, actual data were collected at all stages of breeding. This meant that there was no need to calculate daily nest survival rates using the Mayfield method (Mayfield 1975; Hensler and Nichols 1981), such that the simplifying assumptions therein (e.g. spatial consistency in nest vulnerability, which is unlikely to be true especially when predation, food availability or disease risk interact with landscape or habitat features: Green 1977) did not confound analyses. Predation levels are extremely low in these boxes as the box entrances are surrounded by metal protection plates to prevent entrance enlargement by predatory Grey Squirrels *Sciurus carolinensis*. There is occasional predation by rodents and small Mustelids *Mustela* spp. that use nestbox entrance itself, and by Great Spotted Woodpeckers *Dendrocopos major* that drill their way in. This affects < 5% of nests and has only been recorded after the onset of incubation when all nests have been found and recorded.

In total, there were 137 breeding attempts over the 5-year study period in 101 different nestboxes (with each nestbox being used one, two or three times over this 5-year period; mean = 1.37). Data were analysed at the level of each individual nest, with year included in models as a covariate, as detailed below. This prevented analysis being confounded by the fact that there were multiple nests in some nestboxes (there were never multiple nests in one breeding season). The nests included were all in wooden rectangular boxes with a sloping roof (approximate internal measurements: 110 mm width, 170 mm depth, 210 mm mid-point height) accessible through a 32 mm hole in the front panel. All boxes were affixed to mature Oaks, approximately 3 m above the ground (mean = 3.1 m \pm 0.20 se) and nesting material was removed from each

box between seasons to minimise pre-breeding ectoparasite load. The 101 nestboxes that were used were part of a nestbox resource of 295 regularly-monitoring boxes of broadly the same specification. About 80 non-typical boxes, which were not routinely monitored by volunteers, were excluded due to very incomplete data. Due to the data gaps, it is not clear how many Pied Flycatchers might have nested in these boxes, but this resource included triangular boxes designed for other species and never known to house Pied Flycatchers. Nestboxes were provided in abundance, with around 28% remaining unoccupied each year (Goodenough et al. 2009c). These were largely in unoccupied territories since inter-box spacing meant each individual territory usually only included one box.

Vegetation structure and species assemblage

The approach adopted here was a territory-level analysis that focussed on detailed study of the habitat immediately surrounding the nestbox, rather than at a landscape scale. The rationale was that Pied Flycatchers defend a very small nesting territory — just the nest cavity and its immediate surroundings (Lundberg & Alatalo 1992) — where all nesting and breeding activity plus the majority of foraging activity occurs (Pettingill 1985). It should be noted that the home range of breeding Pied Flycatchers can be larger than the territory due to extra-territory foraging activity (Pettingill 1985, Huhta et al. 1999). Extra-territory foraging does not always happen and, when it does, foraging distances vary substantially on a per-site, per-year, and per-bird basis. A home range analysis would require radio tagging data for all birds to establish the precise foraging range of each individual at each individual nest (e.g. Holt et al. 2010). Such an analysis was outside the remit of the current study and is, arguably, of less importance than focussing on the territory where all breeding activity and most foraging occurs.

Vegetation data comprised details of: (1) species richness; (2) abundance of specific species; and (3) density in different vertical strata (see Table 1). To quantify these parameters, a circular plot was established around each nestbox that was 11.3 m in diameter (survey area of 100 m²; 0.01 ha) centered on the nestbox tree. This is the standard recommended protocol (James & Shugart 1970, Bibby et al. 2000) and use here retains consistency with major nest record schemes, such as the North American BBIRD program (Martin et al. 1997). There were three plant species richness variables. Tree and sapling species richness variables were simple counts of the number of different tree and sapling species in the circular plot, respectively (saplings were classified as having a diameter at breast height of < 60 mm and/or < 50% of the height of mature trees of the same species in the immediate surrounding area). Field-layer species richness quantified the number of different non-woody vascular plants in the field layer. Vegetation density variables included the number of trees, the number of samplings, and the

number of shrubs in the 100 m² plot - shrubs were classified as woody plant species that were not saplings or trees and that formed part of the understory. The density of specific species was quantified in the same way. Percentage cover was used to quantify density of the ground layer and the canopy. Ground cover (both overall and for specific field-layer species) were visual estimates to the nearest 5% as per Sutherland (2006). In the case of canopy closure, digital canopy photographs were taken vertically upwards from the forest floor during the bird breeding season in May. These were analysed using CanopyDigi, a computer package that uses the ratio of “canopy” to “sky” pixels to calculate coverage (Goodenough & Goodenough 2012). This method has significantly lower variability and error levels compared to conventional methods.

Vegetation data were collected in one year (2003) and used across all years (2000–2004). This was justified by: (1) the mature nature of the woodland; (2) consistent management throughout the time period; and (3) the relatively short study period (bird data were held for 1990–2004, but analysis was restricted to 2000–2004 because backdating the 2003 habitat data to 1990 was not considered appropriate). Moreover, vegetation plots laid out and surveyed by Asamoah (2005) were re-surveyed in 2004, using identical techniques. The surveyed parameters (number of trees, shrub cover, field-layer cover, and canopy cover) did not differ statistically (paired samples t-test: $p > 0.654$ in all cases). Details of all vegetation variables can be found in Table 1.

Proximity to landscape features

The location of each box was mapped using a handheld GPS unit (Garmin eTrex®, Southampton, U.K.) and location was noted ($n = 56$ boxes in ungrazed woodland; $n = 45$ in grazed woodland). All footpaths, vehicular tracks and public roads within, or immediately adjacent to, the site were mapped (c. 5000 datapoints); as were permanent water sources (c. 1200 datapoints). The straight line distance from each nestbox to the nearest footpath, road/track, and water source was calculated from GPS data.

Consideration was given the whether some measure of land coverage of these landscape features within a certain (arbitrary) distance from each nestbox would be useful in addition to nearest distance measurements. This was discounted as the few paths present mainly run parallel to one another at well-spaced intervals. Moreover, to avoid numerous zero records (i.e. nestboxes where there was no path/track within the set distance) the distance itself would have to be so substantial ($> 250\text{m}$) as to be of limited biological impact. In the case of water, there were three permanent ponds on site, which were approximately equal size (25m^2) and were again well-spaced (minimum distance between ponds = 538m).

Nestbox placement

Data were collected on (1) size of the nestbox tree, quantified using diameter at breast height; (2) height of the nestbox tree, established using a clinometer and trigonometry; and (3) orientation the box faced. Orientation was already known to influence breeding success of Pied Flycatchers, with boxes facing south-southwest (180–269°) being associated with reduced success relative to other directions (Goodenough et al. 2008). Orientation was added as a binary coding variable (boxes facing S-SW or not). Adding orientation into the current study was important, both to allow for its likely effect, and to ensure that previous findings were not confounded by previously-unknown autocorrelation between orientation and other habitat variables.

Data analysis

To achieve normality in the dependant variables, the count variables describing clutch size, number of young to hatch and number of young to fledge variables were $\ln+1$ transformed, while the percentage success variable (birds to fledge per egg laid) was arcsine square root transformed (Fowler & Cohen 1996). To provide a measure of when each breeding attempt was started, FEDs were converted to a scale whereby 1=1st April; this index was normally distributed and thus did not require transformation. Sample sizes in subsequent analyses differed depending on the dependent variable under consideration since analysis excluded failed nests (i.e. those abandoned or depredated). Sample sizes were as follows: analyses of clutch size (and FED) included nests where at least one egg was laid ($n = 137$), analyses of number of young to hatch and fledge only included nests where at least one young hatched ($n = 131$) or fledged ($n = 120$), respectively. Analyses of percentage success also had $n = 120$. Given the small sample sizes of failed nests, and the fact that the cause of failure was only determined in a very few cases so it was not possible to sub-divide “failure” into biologically-meaningful categories such as abandoned or depredated, no further analysis was undertaken to assess any pattern in overall failure rate.

One approach to analysing this complex dataset was Multiple Linear Regression, possibly with as stepwise procedure to identify individual factors related statistically to the dependent variable and establish the optimal subset of predictors. The disadvantages of this technique are, however, increasingly highlighted (e.g. Olden & Jackson 2000, Whittingham et al. 2006). Briefly, these are: (1) inconsistencies in selection algorithms; (2) type II errors because removal of less significant predictors artificially inflates the significance of remaining predictors; (3) lack of model robustness if there is high multicollinearity; (4) only testing a small number of possible models; and (5) missing the optimal model because of the one-at-a-time nature of adding/dropping variables (Olden & Jackson 2000, Faraway 2002, Crawley 2005, Whittingham

et al. 2006). Accordingly, an Information Theoretic approach has become popular whereby numerous models are created and compared using a measure such as Akaike's Information Criterion (AIC) (Burnham & Anderson, 2002). The best individual model, or all models that are well-supported, are then reported. In this way, use of an arbitrary significance value to demarcate "important" and "unimportant" variables – and models – is avoided. However, with increasing numbers of predictors, the number of models generated increases exponentially (e.g. 1,073,741,823 models for 30 predictors: Goodenough et al. 2012). Although it is possible to compare all possible models (e.g. through `bestglm` in R: McLeod & Xu, 2010), it is not necessarily desirable when there are numerous predictors since there is usually support (AIC or equivalent) for a considerable number of competing models. While this is not a problem statistically, it becomes increasingly hard to understand the biological meaning of the models, especially when competing models contain a large number of different variables (as opposed to minor differences or different combinations of similar variables). This was exhibited by work by on bird-habitat associations, when 42 highly-supported competing models, with many different variable combinations, were generated (Whittingham et al. 2006).

A comparatively new approach called REVS (Regression with Empirical Variable Selection) combines the rigour of all-subsets regression, the intuitiveness of stepwise procedures, and the transparency of post-hoc multiple model consideration. This analytical approach, which is run in R, uses sophisticated branch-and-bound all-subsets regression to quantify empirical support for each independent variable. A series of models is created (n = the number of predictors); the first containing the variable with most empirical support, the second containing that and the next most-supported, and so on. The resultant models are compared post-hoc using Akaike's Information Criterion (AIC). Delta (Δ) AIC values are calculated for each model as $AIC_i - AIC_{\min}$; where AIC_{\min} is the AIC value of the model that has the lowest AIC score. All models with strong support ($\Delta AIC < 2$; Burnham & Anderson 2002) can be compared. This is easier than in general all-subsets regression since: (1) the number of models that need to be compared is lower (same as the number of predictors not many times that number) and (2) all competing models will have many variables in common (i.e. the main "core" is the same and there are just minor differences in presence/absence of additional variables): this makes interpretation much easier. REVS has been shown to be superior to stepwise and all-subsets regression (Goodenough et al. 2012) and used previously to investigate species-habitat interactions for several species (e.g. Black Howler Monkeys *Alouatta pigra*: Arroyo-Rodríguez et al. 2013). See Goodenough et al. (2012) for full statistical details.

Here, the REVS process was run five times, once for each of the dependent variables (FED, clutch size, number of young to hatch, number of young to fledge, and percentage

success). As there were 24 independent variables, 24 models were created for each dependent variable (model 1 contained only the variable with most empirical support, model 2 added the variable with the next most empirical support and so on until the final model contained all independent variables). Because of the potential influence of year and FED on breeding success, a hierarchical framework was used to add these two covariates into all models via forced entry before any independent variables. This also controlled for the temporal pseudoreplication that would otherwise have resulted from having multiple samples (breeding attempts) per experimental unit (nestbox) (Hurlbert 1984). For FED analysis, year was the only independent variable added through forced entry (FED having been entered as the dependent variable). Models were compared post-hoc using AIC based on $\Delta\text{AIC} < 2$, while R^2 was used to assess the biological significance of models. Although P values are arguably not important in AIC-driven analyses, p values were given at model-level so overall statistical significance could also be assessed. For each dependent variable under consideration, four models were reported: (1) Covariate model — contained only covariates of year and lay date; (2) Minimum model — the most parsimonious model (i.e. the model that had fewest predictors whilst still attaining $\Delta\text{AIC} < 2$; covariates included); (3) Optimal model — the model that best balanced the number of variables and explanatory power (i.e. $\Delta\text{AIC} = 0$; covariates included); and (4) Maximum model — the model that increased R^2 to the maximum possible within the $\Delta\text{AIC} < 2$ limit, covariates included. The minimum models were useful not only for highlighting which variables are particularly strongly related to breeding success, but also guarded against the risk of over-parameterisation – no minimum model had > 5 predictors relative to a minimum of 120 cases. (On this topic of potential over-parameterisation, it should also be noted that as the basic premise of AIC is that a model is penalised each time a new variable is added so models should not, de facto, become over-parameterised.) It should be noted that a significant relationship between a specific habitat factor and success during more than one stage of breeding does not necessarily provide independent support for the importance of this variable. This is because breeding stages are intrinsically linked, such that carry-over effects can occur (i.e. a variable that affects clutch size or number of young to hatch might be carried over to show as an effect on number of young to fledge). The original dataset met, and indeed exceeded, the minimum case:variable ratio of 3:1 as recommended by Tabachnick & Fidel (1989), such that analysing a relatively large number of independent variables in one analysis was valid. The assumptions of normality and homoscedasticity were assessed by examining residual plots (Berry & Feldman 1985, Fox 1991) and were met. The assumption of orthogonality was tested using the variance inflation factor (VIF) according to suggested criteria: VIF of all variables < 10 (Myers 1990). In general, these criteria were met, such that although there was multicollinearity within the predictor variables (Fig. 1), it

was not high enough to confound the model. In order to aid interpretation of the results, however, relationships between independent variables were visualised using a graphical correlation matrix (Fig. 1). This was generated using the Ellipses command in R (Murdoch & Chow 2013), with the strength and direction of each correlation displayed using an ellipse after eccentricity had been parametrically scaled to the correlation value (Murdoch & Chow 1996). This approach is superior to scatterplot correlation matrices for large numbers of variables (Friendly 2002) and allows understanding of how different individual habitat features interact.

To establish if there was any difference in breeding success according to historical grazing, as was predicted, independent t-tests were conducted. These compared clutch size, number of young to hatch, number of young to fledge, and percentage success in grazed and ungrazed areas.

RESULTS

Vegetation, proximity to landscape features and nestbox placement variables

Numerous vegetation variables were related to breeding success (Table 2). In terms of vegetation structure, nests located in areas with abundant saplings had higher clutch sizes, while a higher number of young fledged from boxes with a low density of mature trees. Vegetation species richness was also important, with the most successful nests being located in areas with numerous different floral species. Tree species richness was positively associated with clutch size and number of young to fledge, while sapling species richness was associated with both number of young to hatch and number of young to fledge. The number of species in the field layer was important for both clutch size and number of young to fledge (success again being greater when richness was high). With regard to specific vegetation species, highly successful nests were generally located in areas with high abundance of Oak and Silver Birch, but low abundance (or absence) of Beech, Sycamore and Bracken.

Proximity to landscape features was also important (Table 2). As predicted, close proximity to footpaths had a significant detrimental effect on success in terms of clutch size, number of young to fledge, and percentage success. Nests near footpaths were also associated with later laying. However, contrary to prediction, the number of young to fledge and percentage success were both positively associated with vehicular forest tracks and roads, with nests near these features being more successful than those further away. Nests close to water were more successful than those further away throughout all stages of the nesting process.

In terms of precise placement of the nestbox, orientation was included as a significant factor in all models created for number of young to hatch, number of young to fledge, and

percentage success, with boxes facing south-southwest being associated with lower success in all cases (Table 2). This was predicted and expected given previous findings on the same dataset (Goodenough et al. 2008). Nestbox tree height was also important, with nests on taller trees being associated with smaller clutches compared to nests in boxes affixed to shorter trees. Overall, the most important factors (i.e. those factors that were repeatedly included in the minimum model – the type of model that contained only the most influential variables) were: sapling species richness, number of Oak, amount of Bracken, proximity to footpaths and water, and nestbox orientation.

It is worth noting that some were important at specific stages only (e.g. sapling species richness only affected number of young to hatch) while others were important throughout (e.g. proximity to water was positively related to success at all stages of breeding). When a specific factor was important at multiple stages, the direction of the relationship remained consistent, such that a factor was never related positively to success at one stage but negatively at another (Table 2). Relationships between habitat factors and number of young to fledge (the most important breeding success measure from an applied perspective) are shown graphically (Fig. 2).

Grazing

By contrast, grazing (historically sheep grazed or not) was not entered as a parameter in any model. Moreover, there was no difference in any success parameter between grazed (open) and ungrazed (closed) woodland (t-tests $p > 0.132$ in all cases: grazed vs ungrazed mean \pm standard error — FED 13th May ± 0.57 days vs 15th May ± 1.08 days; clutch size 6.89 ± 0.13 vs 6.76 ± 0.23 ; number of young to hatch 5.94 ± 0.21 vs 5.55 ± 0.28 ; number of young to fledge 4.05 ± 0.30 vs 4.24 ± 0.36 ; proportional success $59.36\% \pm 4.25\%$ vs $60.26\% \pm 5.15\%$). Indeed, the (non-significant) trends were actually largely the opposite of those predicted: breeding attempts in ungrazed areas were started earlier compared with those in grazed areas (rather than later, as predicted), and were more successful, having larger clutch sizes and higher numbers of young to hatch, compared with those in grazed areas (rather than less successful, as predicted). To explore this further, each vegetation parameter found to be significantly related to breeding success in previous analyses (see above; Table 2) was analysed in relation to historical grazing. This revealed that eight out of the ten vegetation variables influencing breeding success were themselves related significantly to grazing (Table 3). The pattern, however, was far from straightforward, with success being higher in areas of fewer trees, and a lower abundance of Beech and Sycamore (all associated with grazed areas) but also higher in areas with more saplings, higher plant species richness (in trees, saplings and field layer vegetation), more Oak, more Silver Birch and less Bracken coverage (all associated with ungrazed areas) (Table 3).

DISCUSSION

Vegetation density and species composition

Although Pied Flycatchers are often considered to be grazed Oak woodland specialists (based on largely qualitative information: Simms 1971, Lundberg & Alatalo 1992), the results of the current study do not fully support this preconception. There are several reasons for this. Firstly, grazing, despite being a key influence on vegetation (Table 3), is not a significant predictor of reproductive success at any stage. Indeed, the (non-significant) tendency is for FEDs to be earlier, and clutch sizes and number of young to hatch to be higher, in ungrazed woodland; the opposite of what might be expected. Secondly, success is related to vegetation parameters that are associated with grazed areas (fewer trees), but also with vegetation parameters that are associated with ungrazed areas (more saplings and less Bracken coverage). As noted in the introduction, the main reason that Pied Flycatchers are typically regarded as birds of grazed woodland is that grazing promotes open woodland with sufficient space between the field layer and canopy to allow birds to catch prey on the wing. This view accords with work by Amar et al. (2006), which found a positive relationship between Pied Flycatcher population sizes and horizontal visibility. However, although aerial foraging is an important foraging technique, Flycatchers also undertake a high proportion of ground foraging - up to 50% or even 65% of food captures are made this way at some sites (Silverin & Andersson 1984 and von Haartman 1954; respectively). This might be why Pied Flycatchers avoid areas with high Bracken coverage (Stowe 1987) and why such areas are associated with less successful nests (this study). Food shortages can reduce offspring quality and even reduce the number of young to fledge due to starvation-related mortality. It could also affect FED, since there is a strong selection to nest in areas with good food supplies early in the breeding season. Taken together, the evidence here suggests that extremely closed, dense, shrub-rich, woodland is not ideal for Pied Flycatchers, it also suggests that very open woodland with a lot of light and resultant abundant understory is not ideal either, possibly because of limitations on ground foraging. Accordingly, although grazing might affect vegetation species and community structure, which in turn affects suitability for Pied Flycatchers, there is not a straightforward direct relationship between grazing and breeding success. This demonstrates the dangers inherent in making assumptions about habitat requirements, for any species, without undertaking detailed research.

Pied Flycatcher reproductive success is higher in areas of high species richness in tree, sapling and field strata. A potential explanation is that plant species richness is typically related to invertebrate abundance. This is especially true for Lepidoptera larvae, which account for 42% of

the nestling diet of Pied Flycatchers (Cholewa & Wesolowski 2011) and that are often associated with specific host plants. It is especially interesting that sapling species richness seems relatively more important than richness in other woodland strata. This may be because, in early summer when Pied Flycatchers are provisioning for their young, saplings have a higher caterpillar abundance per unit area than mature trees (Murakami et al. 2005). Similar relationships might occur for other insectivorous species, although obviously this would have to be tested empirically. Success is also linked to the abundance of certain vegetative species. Successful nests are generally those in nestboxes surrounded by a high abundance of Oak and Birch, and low abundance (or absence) of Beech and Sycamore. It is noteworthy that the two vegetative species that are positively related to breeding success support unusually high Lepidoptera larvae species richness (Oak = 126 larval species; Birch = 94 larval species), while those that are negatively associated with success support unusually few Lepidoptera larval species (Beech = 24 larval species; Sycamore = 5 larval species) (Southwood 1961). There is also the possibility that the abundance of calcium-rich food items, such as land snails Gastropoda could differ according to woodland vegetation sub-type. If so, this might influence the date by which the female has sufficient calcium reserves to begin laying and the number of eggs she is able to lay, as has been recorded previously for Great Tits (Mänd et al. 2000).

It is important to remember that all the vegetation parameters discussed here are interlinked, as is evident in Fig. 1. This adds to the importance of testing the relationships between reproductive success and habitat factors highlighted in this study empirically at other sites, as missing of even one particular component from an ecosystem (e.g. presence of Beech or Sycamore) may alter relative importance and mutual relationships of the rest of components. This is particularly true when populations are distanced geographically, since both bird breeding biology and response to environmental factors can differ even in the same species. For example, in the case of the Pied Flycatcher, eggshell parameters and adaptation (versus inertia) to climate-induced changes in food supply both differ geographically and sometimes also co-vary with habitat (Burger et al. 2012, Morales et al. 2013).

Proximity to landscape features

Breeding success is generally lower for Pied Flycatchers in this study that nest near footpaths; indeed this factor is repeatedly included in the minimum models as one of the most influential variables. This raises the possibility that Pied Flycatchers are affected negatively by human disturbance. Because this is a correlative study, it is important not to infer causality when interpreting results. However, the footpaths at the study site are extremely well-used especially during the breeding season: around 25% of the estimated 18,000 reserve visitors per annum

visit in May when Pied Flycatchers are breeding (Proctor & Pollard 2005). The possibility that this pattern is due to something other than disturbance, for example, changes in canopy cover around footpaths, seems unlikely as no such variables were significant in any models. Therefore, although it is speculation to conclude the causal mechanism, disturbance does seem most likely. Further research, ideally manipulative experiments, would be necessary to disentangle these possibilities.

It is interesting that proximity to paths is inversely related clutch size and that clutches in nestboxes near paths are also started later given that lay date and clutch size are themselves inversely related. Generally, late-laying females have smaller clutch sizes relative to earlier-laying females (e.g. Klomp 1970, Crick et al. 1993); this is true in this Pied Flycatcher population (Goodenough et al. 2009c). This could indicate either that: (1) individuals are selecting boxes near footpaths relatively late compared to other boxes and thus have smaller clutches or (2) that females nesting in footpath-adjacent boxes are manipulating their clutch size. As regards the first possibility, there is no pattern in overall nestbox choice (Goodenough et al. 2009a), but settlement time has not been studied (i.e. the time when a box is “adopted” by a male and chosen by a female). It is possible that the best boxes are chosen first and less suitable ones are chosen later (Lundberg et al. 1981) and are thus associated with small clutches. When considering this, it should be noted that although FED is likely to be related to settlement time, it might not be a very reliable proxy as individuals can delay laying after nest-building (pers. obs.). To take the second possibility, manipulation of clutch sizes is a commonly-cited, although often poorly evidenced, avian phenomenon that dates back to the offspring number optimization hypothesis (Lack 1947). Unusually, there is experimental evidence this occurs in Pied Flycatchers, with clutch size reduction in females moved from optimal to sub-optimal habitat (Siikamäki 1995).

Proximity to footpaths also affects number of young to fledge. This might be, in part, a carry-over effect from smaller clutch sizes (i.e. a factor that affects clutch size might, de facto, affect number of young to fledge because of the smaller numbers of eggs laid). However, as footpath proximity also influences percentage success, there is also an additive effect here (i.e. proximity to footpaths affects success more than can be explained by its effect on clutch size). Indeed, regressing percentage success against proximity to footpaths using a simple bivariate regression shows the importance of this single variable ($R^2 = 0.154$; Fig. 2). This could be a result of human disturbance reducing adult provisioning the chicks in the nest with food (feeding rates decrease with people-based disturbance as the adults seem wary of flying to the nest; pers. obs), which could affect nutritional status and growth.

The fact that both number of young to fledge and percentage success was higher near to vehicular forest tracks and public roads is contrary to research by Kuitunen et al. (2003) where

roads had a detrimental effect on number of young to fledge. Again this highlights how the effect of the same environmental factor might differ very substantially between study sites, even for the same avian species. The decrease in fledging success in Kuitunen's case was due to parental mortality during foraging along busy roads. This is likely to be site-specific as previously Pied Flycatchers had only been found to be frequent road casualties in France (Erritzoe et al. 2003). At the current study site, the road is relatively minor and the forest tracks are rarely used. These sites thus provide good foraging opportunities without substantive mortality risk, which could explain the positive relationship. A similar result has been found for a mixed-species nesting guild in New Hampshire, with higher nest survival rates close to unmaintained roads (King & DeGraaf 2002). Nests near water also tended to be more successful, possibly because insects associated with open water are a good food source for adult flycatchers (Lundberg & Alatalo 1992).

Proximity to water is also important — again, this factor is repeatedly included in the minimum models as one of the most influential variables. It is interesting that success is positively related to proximity to water but negatively with proximity to footpaths because these two factors are themselves correlated (paths often lead to hides, which tend to overlook water holes). This correlation is non-significant and not particularly strong (Pearson $r^2 = 0.124$; Fig. 1) so entering both variables in a single model is valid. However, this is indicative of the tradeoffs that could occur between multiple factors that influence breeding success, in the same way as there are for nest site selection cues in Northern Flickers *Colaptes auratus* (Fisher and Wiebe 2006).

Nestbox placement

Shorter nestbox trees are associated with higher reproductive success. This disagrees with work by Amar et al. (2006), which found a positive correlation between Pied Flycatcher population and a PCA variable with high positive weightings for canopy height (and also tree girth and basal area). However, as all nestbox trees in at the current study site are mature (around 200 years old), the height of the tree often correlates with its state of decay, with trees progressively losing height as they become over-mature. It is possible that shorter (more decayed) trees might have better invertebrate communities, but again that is speculative. The fact that nestbox tree height is related to FED, as well as clutch size, can be interpreted as above — late-laying females using sub-optimal habitat and laying fewer eggs because they are late laying, or late laying females adjusting clutch size to cope with sub-optimal habitat. This study has also reinforced the importance of nestbox orientation, with boxes facing south-southwest being associated with lower numbers of young to hatch and fledge (see Goodenough et al. (2008) for a further discussion).

Standardising the nestbox design in this study made interactions between other environmental and habitat parameters (discussed above) and breeding success clearer by reducing potentially confounding factors. It should, however, be noted that nestbox factors might have an effect and that average breeding performance in this study population may somehow be linked to the average box design in interaction with external factors (see Slagsvold 1987).

Conclusions, implications and recommendations

The work documented here builds on previous studies on species-habitat relationships and breeding success using volunteer-collected or citizen science data (e.g. Crick et al. 2003, Cooper et al. 2005, Greenwood 2007, Hart et al. 2012). The results suggest habitat is an important influence on breeding success in Pied Flycatchers at this study site, despite the fact that individuals do not appear to exhibit active nest choice. This suggests that analysing habitat-success patterns is important for avian species even when habitat-choice patterns are lacking.

In the case of Pied Flycatchers, it is important that boxes are positioned carefully to maximise the reproductive success of nestbox-breeding populations. Boxes should be placed away from footpaths but near to water sources. Placement in areas with a rich and abundant sapling layer, in addition to mature trees, is recommended, as is placement in areas of high Oak and Silver Birch abundance and a sparse understory. Boxes should be affixed to tall trees and oriented away from the south-southwest compass quarter. Once again, it is important to reemphasise that this is, undeniably, a study on one bird species at one study site, and it is always dangerous to speculate on findings being applicable outside of this. However, the findings here do provide a starting point for future analyses of Pied Flycatcher habitat associations in other regions and at other study sites, as well as for other woodland passerines.

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Table 1. Habitat characteristics quantified in this study. All vegetation characteristics were measured within a circular plot (diameter = 11.3m) centred on the nestbox tree. * — see methods for definitions.

Habitat feature	Variable
Vegetation	
Density	Number of trees Number of saplings* Number of shrubs* Ground cover (%) Canopy cover (%)
Richness	Tree species richness Sapling species richness Field-layer species richness (non-woody vascular plants) Total species richness
Abundance	Number <i>Quercus robur</i> Number <i>Betula pendula</i> Number <i>Fagus sylvatica</i> Number <i>Sorbus aucuparia</i> Number <i>Acer pseudoplatanus</i> Cover <i>Ilex aquifolium</i> (%) Cover <i>Rubus fruticosus</i> (%) Cover <i>Pteridium aquilinum</i> (%) Cover <i>Crataegus monogyna</i> (%)
Proximity to landscape features	Proximity to footpath (m) Proximity to forest track or public road (m) Proximity to water source (m) Grazing (historically grazed or ungrazed)
Nestbox placement	Orientation category (S-SW or not) Nestbox tree height (m) Nestbox tree DBH (cm)

Table 2. Habitat variables that influence Pied Flycatcher breeding success. Models were generated using REVS, which is based on Akaike's Information Criterion (AIC). Four model types were generated for each reproductive success parameter. The delta value (Δ AIC), significance and effect size (R^2) is given for each model. The independent variables in each model are shown with their respective unstandardized parameter estimate \pm standard error. The direction of the relationship with breeding success variables is also shown (+ positive; - negative). Covariate Model — contained only covariates of year and lay date (except lay date model when only year entered), Minimum model — The most parsimonious model (i.e. the model that had fewest predictors whilst still attaining Δ AIC < 2), containing only covariates and the independent variables indicated by ***. Optimal model — the model that best balanced the number of variables and explanatory power (i.e. Δ AIC = 0), containing covariates, independent variables included in the MAM, and all other independent variables indicated by **, Maximum model — the model that increased R^2 to the maximum possible within the Δ AIC < 2 limit, containing covariates, all independent variables entered in the optimal model, plus those shown with *. In this way, the number of asterisks indicates the relative importance of the variable (more = higher importance). SSW = South-Southwest.

Model	Lay Date	Clutch size	Number young to hatch	Number young to fledge	Overall % success
A. Covariate-only model	$R^2 = 0.023$ $p = 0.077$	$R^2 = 0.151$ $p < 0.001$	$R^2 = 0.018$ $p = 0.113$	$R^2 = 0.092$ $p = 0.001$	$R^2 = 0.077$ $p = 0.002$
B. Minimum model	$R^2 = 0.087$ Δ AIC = 0.987 $p = 0.034$	$R^2 = 0.218$ Δ AIC = 1.239 $p < 0.001$	$R^2 = 0.188$ Δ AIC = 1.278 $p < 0.001$	$R^2 = 0.218$ Δ AIC = 1.987 $p < 0.001$	$R^2 = 0.206$ Δ AIC = 1.529 $p < 0.001$
C. Optimal model	$R^2 = 0.096$ Δ AIC = 0.000 $p = 0.010$	$R^2 = 0.237$ Δ AIC = 0.000 $p < 0.001$	$R^2 = 0.208$ Δ AIC = 0.000 $p < 0.001$	$R^2 = 0.233$ Δ AIC = 0.000 $p < 0.001$	$R^2 = 0.226$ Δ AIC = 0.000 $p < 0.001$
D. Maximum model (where generated)		$R^2 = 0.259$ Δ AIC = 0.026 $p < 0.001$		$R^2 = 0.258$ Δ AIC = 1.860 $p < 0.001$	$R^2 = 0.256$ Δ AIC = 1.023 $p < 0.001$
Independent variables included in model					
Vegetation	Number of trees			-0.700 \pm 0.016**	-2.466 \pm 0.042**
	Number of saplings	+0.829 \pm 0.032***			
	Tree species richness	+0.309 \pm 0.105**		+0.225 \pm 0.057*	

Landscape	Sapling species richness			+0.246 ± 0.050***	+0.050 ± 0.017***	
	Field-layer species richness		+0.140 ± 0.013**		+0.105 ± 0.005**	
	Number <i>Quercus robur</i>	-0.325 ± 0.141***	+0.104 ± 0.023*		+0.265 ± 0.094***	+7.616 ± 0.779***
	Number <i>Fagus sylvatica</i>	+0.093 ± 0.088**		-0.022 ± 0.017**		
	Number <i>Acer pseudoplatanus</i>		-0.087 ± 0.050**	-0.126 ± 0.048**		-2.575 ± 1.444*
	Number <i>Betula pendula</i>		+0.043 ± 0.007**			+4.797 ± 2.349**
	Cover <i>Pteridium aquilinum</i> (%)	+0.002 ± 0.001***	-0.005 ± 0.003***		-0.013 ± 0.006*	-0.198 ± 0.085***
	Proximity to footpath (m)	+0.007 ± 0.001***	-0.002 ± 0.001***		-0.007 ± 0.002***	-0.097 ± 0.035***
	Proximity to track/road (m)				+0.007 ± 0.004**	+0.330 ± 0.018*
	Proximity to water source (m)		+0.003 ± 0.001***	+0.002 ± 0.001***	+0.002 ± 0.001***	+0.100 ± 0.051***
Position	Orientation (SSW or other)			Not SSW***	Not SSW***	Not SSW***
	Nestbox tree height (m)	+0.025 ± 0.018***	-0.032 ± 0.017***			

Table 3. Differences in habitat variables significantly associated with breeding parameters (Table 2) in relation to historical grazing (mean \pm standard error). Significance was quantified using an independent samples t-test with Bonferroni corrections applied to allow for family-wise error (* = significant at $\alpha = 0.05$; *** = significant at $\alpha = 0.001$; NS = not significant). Direction of relationship shows how the variable links to breeding success (which, taken together mean values in ungrazed and grazed woodland, shows where conditions are better).

Variable	Ungrazed (mean \pm S.E.)	Grazed (mean \pm S.E.)	Significance of difference	Direction of relationship with success
Number of trees	2.620 \pm 0.193	1.180 \pm 0.061	NS	-
Number of saplings	4.080 \pm 0.459	0.040 \pm 0.027	***	+
Tree species richness	1.700 \pm 0.074	1.080 \pm 0.038	***	+
Sapling species richness	1.140 \pm 0.091	0.040 \pm 0.027	***	+
Field-layer species richness	1.650 \pm 0.092	1.140 \pm 0.101	***	+
Number <i>Quercus robur</i>	1.210 \pm 0.053	1.080 \pm 0.038	NS	+
Number <i>Betula pendula</i>	1.220 \pm 0.197	0.140 \pm 0.063	***	+
Number <i>Fagus sylvatica</i>	0.700 \pm 0.142	0	***	-
Number <i>Acer pseudoplatanus</i>	0.880 \pm 0.291	0	*	-
Cover <i>Pteridium aquilinum</i> (%)	23.660 \pm 3.501	69.800 \pm 5.339	***	-

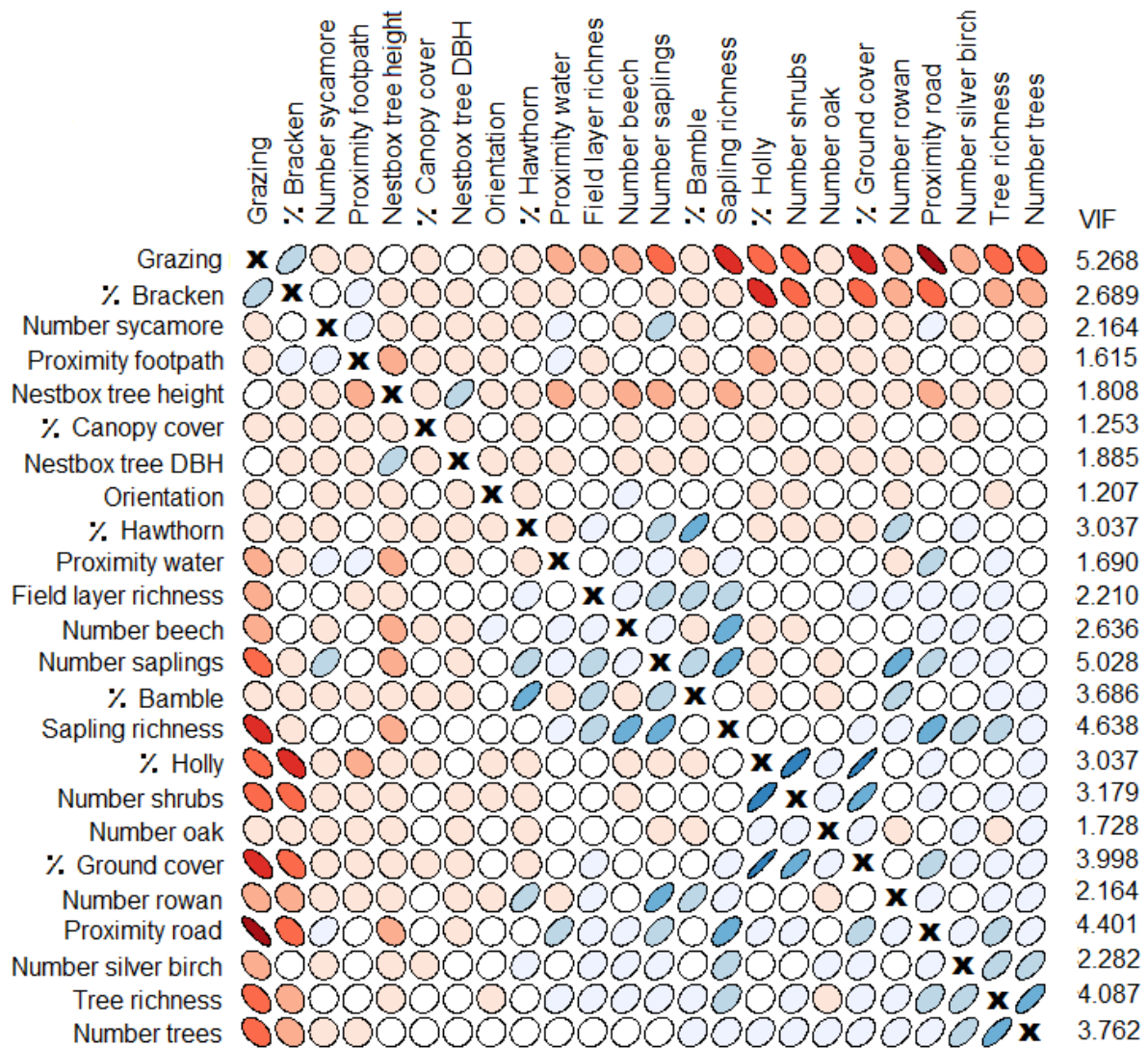


Fig. 1. Graphical correlation matrix for different habitat variables. Direction of correlation matches direction of ellipse, correlation strength shown by the shape (more elliptical = stronger, more round = weaker). Positive correlations are shaded blue and negative correlations are shaded red with the shading intensity relating to correlation strength (more intense shading for strong correlations). Also shown is the Variance Inflation Factor (VIF) as a measure of multicollinearity in the overall dataset – this is given for each variable and shows the extent to which that one variable is correlated with the overall dataset (i.e. all other variables in total). Lower values = lower correlation; all factors are under the VIF critical threshold of 10 (see methods).

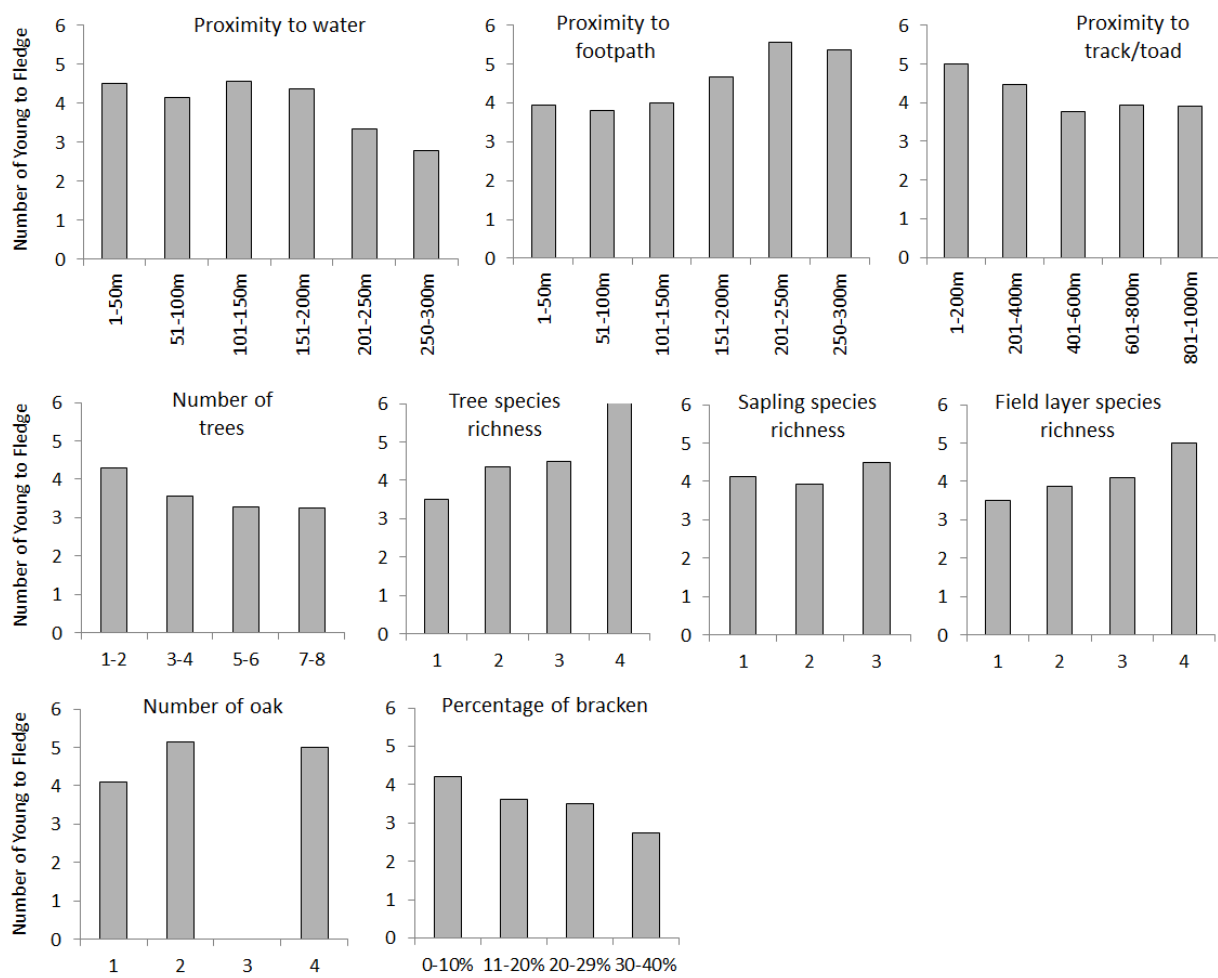


Fig. 2. Univariate relationships between the number of young to fledge and habitat parameters. Graphs shown for all habitat parameters that were significantly related to fledging in statistical models as detailed in Table 2.