Using citizen science to assess drivers of Common House Martin *Delichon urbicum* breeding performance

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Many hirundine (swallows and martins) species are declining throughout their ranges. The Common House Martin *Delichon urbicum* is a migratory hirundine that breeds throughout Europe but has shown recent declines in some parts of the UK, particularly in the south. We conducted a large-scale citizen science survey to assess how the breeding performance of House Martins, measured by the number of attempted broods and nest success, is influenced by nest-specific, landscape and weather factors. Pairs in eastern parts of the UK started breeding earlier than those in the west, and breeding performance was higher in eastern regions. There was no effect of latitude on either aspect of breeding performance, so our measures of breeding performance alone do not help to explain differences in population trends across the UK. The probability of attempting multiple broods and producing successful nests was higher in previously used nests than in newly built nests, and in artificial nests than in natural nests. Nests built on plastic soffits of buildings were less likely to be multi-brooded and less likely to be successful compared with other materials. Suggested conservation measures therefore include discouraging the removal of old nests and encouraging the installation of artificial nests, particularly on buildings with plastic soffits. This study provides comprehensive insight into the breeding biology of House Martins, and although our findings do not show conclusively that breeding performance is the sole driver of population trends, they go some way to explain declines in House Martins and ultimately provide information that may help conserve this species.

Keywords: aerial insectivore, breeding success, hirundine, productivity.

Many species of aerial-feeding insectivorous birds, including those in the hirundine family (swallows and martins), have shown declines in many parts of the world (Grüebler *et al.* 2010, Paquette *et al.* 2014, Woodward *et al.* 2018). Mechanisms underlying hirundine population declines remain largely speculative, although they are probably related to a decrease in insect food availability (Evans *et al.* 2007, Nebel *et al.* 2010, Piersma 2016). Factors affecting breeding performance – a major driver of population trends (Newton 2013) – are likely to be important in some hirundine species (Imlay *et al.* 2018). In addition to individual effects (e.g.

condition and experience of adults), the key factors affecting breeding performance can be characterised as nest-specific, landscape or weather variables, which often interact.

Many hirundine species use human-made buildings to nest, including those in farmland and residential areas. Hence, hirundines tend to be closely associated with human landscapes. Many people welcome nesting birds by installing artificial nest-boxes, which may improve breeding performance of some hirundine species because it is thought that they are less prone to predation than those in natural nests and/or competition for nest-sites is reduced (Norris *et al.* 2018, Teglhøj 2018). Conversely, predation rates are sometimes higher in artificial nests, adversely affecting breeding

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performance of other aerial insectivores (Miller 2002). Some hirundines also construct natural nests on buildings, typically made from mud and other organic materials. Historically, mud-nest-building hirundines nest on cliff and rock faces, but those nesting on buildings have to construct nests on modern materials such as plastic or concrete. Although the importance of different geo-materials used for nest construction has been investigated (Papoulis et al. 2018), there appear to be no studies on how the surface material of the building might affect breeding performance.

The land-use surrounding colonies is also important to consider when assessing breeding performance. Agricultural landscapes may provide good prey availability for some hirundine species, which can have a positive impact on breeding performance such as nestling survival (Grüebler et al. 2010). However, agricultural intensification may reduce the availability of aerial invertebrates through changes in plant structure and diversity and use of pesticides (Benton et al. 2002, Grüebler et al. 2010), negatively affecting breeding performance (Stanton et al. 2016). Agricultural landscapes associated with higher availability of prey, such as farms with livestock, are likely to be better for hirundines than arable landscapes (Evans et al. 2007). The strong association with buildings means hirundine species are often closely associated with urban environments. Although urban environments may provide sufficient nest-sites, as for other urban-living wildlife, these novel landscapes may present other challenges such as human disturbance (Schlesinger et al. 2008), predation from non-native predators (Loss et al. 2013) and reduced food availability (Marzluff & Ewing 2001). Assessing the influence of different land-uses on breeding performance should aid our understanding of what is driving population trends in some species.

Climate change and weather patterns are also likely to influence hirundine breeding performance. Widespread seasonal advancement of aerial invertebrate activity (Forrest 2016) and a northern expansion of some aerial invertebrate populations (Parmesan et al. 1999, Hickling et al. 2005) are associated with responses to earlier springs and higher temperatures. Shifts in aerial invertebrate populations alter interactions at other trophic levels (Posledovich et al. 2017). Moreover, warm conditions reduce energetic demands of laying females and may trigger the onset of breeding (Dunn 2004). Indeed, the egg-laying date of some hirundine species has advanced by 8–11 days in recent decades in North America and Europe (Dunn & Winkler 1999, Rubolini et al. 2007, Woodward et al. 2018, Imlay et al. 2018). Although changes in breeding phenology may not always affect the success of breeding attempts (Morrison et al. 2015), earlier breeding may allow time for replacement clutches (Morrison et al. 2019).

The Common House Martin Delichon urbicum (hereafter 'House Martin') is a migratory hirundine that breeds in Europe and north and west Africa. Its population declined by 20% between 1995 and 2018 in the UK, with a decline of 21% in the most recent decade (2008 and 2018; Harris et al. 2020). There are interesting geographical patterns in population trends, declines being most pronounced in England and Wales, where the species has declined by 28 and 17%, respectively, over the 10-year period. Conversely, populations have increased by 33% in Northern Ireland, and have remained stable in Scotland during this period (Harris et al. 2020). These patterns are similar to other hirundine species in the UK, suggesting that any drivers of population change may be local to the UK (Piersma 2016). The House Martin is a colonial-nesting species, often building mud-pellet cup nests on human-made buildings. Historically the House Martin lays its first brood towards the end of May, producing up to two broods in the UK (Bryant 1975, 1979). The breeding performance of the House Martin has been relatively well studied in the UK (Bryant 1975, 1979, Bryant & Westerterp 1983). However, there are no detailed studies on breeding performance at a national level. Moreover, much of our knowledge is based on studies carried out before pronounced declines, so our understanding of House Martin demography is outdated.

House Martin nests are fragile and difficult to access without causing damage, making it challenging to obtain detailed demographic data. However, the House Martin's strong association with humans and the high visibility of nests means that observational surveys can be made by members of the public. Here, we conducted a large-scale citizen science survey over 2 years to measure aspects of breeding performance and factors influencing breeding performance, at a national scale. Using comprehensive observational data, we estimated breeding initiation date, estimated the number of

broods attempted and looked for evidence of success or failure of nesting attempts as measures of breeding performance. To understand the mechanisms influencing breeding performance of this declining species, we investigated the effect of (1) nest-specific factors (e.g. building material and type of nest), (2) landscape (e.g. local land-use and regional differences) and (3) weather variables and breeding initiation date. This information, considered in the context of pressures from other drivers, should help direct appropriate conservation efforts.

METHODS

National House Martin nest survey

During April–October of 2016 and 2017, volunteers across the UK were asked to locate a House Martin colony and record nesting activity once a week (although not all volunteers recorded this often). Multiple nests in the same colony could be observed. For each nest, observers used standardized forms to provide information on the nest-site, including the height of nest on the building, the wall surface that the nest was built on, the soffit material on which the nest was built, the location of the nest on the building and whether the nest was located within either 500 or 500–1000 m of any livestock (see Table S1 for categories within each variable). Observers also noted whether the nest was used in previous years or if the nest was newly built in the year of observation.

For each visit to the nest, observers provided information about the nest, the activity observed at the nest and incidents that occurred where there was a suspected nest failure (see Table S1 for categories within each variable). Location (six-figure grid reference), times and dates of visits were noted.

Landscape and weather data

To obtain information on weather and landscape variables, we analysed data at a 1-km square grid scale. The easting and northing coordinates were determined for each surveyed nest. The percentage of land-use in each 1-km square where the nest was located was calculated using the broad habitats from the Land Cover Map 2015 (LCM; Rowland *et al.* 2017) in ARCGIS version 10.5.1. We selected land-uses from the LCM for subsequent

analyses that were likely to influence House Martin breeding performance either negatively or positively: arable and horticultural, improved grassland, freshwater, suburban (areas where there is a mix of urban and vegetation signatures) and urban (dense urban areas, such as town and city centres, where there is typically little vegetation). Early analysis showed that arable and improved grassland were significantly correlated ($r = 0.25$, df = 4448, $P < 0.001$), so arable land-use was not included in subsequent analyses (described below) to avoid multicollinearity. Improved grassland is defined as being typically 'managed as pasture or mown regularly for silage production' (Rowland *et al.* 2017). Although we expect House Martins to be found in both arable and improved grassland habitats, we chose improved grassland over arable habitats due to the demonstrated association between livestock farming and the breeding performance of other aerial insectivores (Grüebler *et al.* 2010).

Weather has been shown to affect the foraging conditions for House Martins (Bryant 1975, Frampton *et al.* 2001). To test the effect of weather, we used the HadUK-Grid weather dataset, which produces weather data on a 1×1-km grid resolution for each year (Met Office 2018). We extracted the total rainfall (mm) and daily mean air temperature (°C) for each 1-km House Martin survey square during the spring months (April, May, June) matching each year of survey.

Extracting nesting metrics from survey data

Individual House Martins were not marked, and observers did not access nests in this study. We therefore made several assumptions about nesting metrics based on the sequence of behavioural observations.

Firstly, we took the date when an adult was first observed entering a complete nest as the start of breeding activity (hereafter referred to as 'breeding initiation date'). Not all observers witnessed this behaviour (i.e. birds were not recorded entering the nest before any obvious signs that there were young in the nest), so those nests were removed from subsequent analyses on breeding initiation date. All calendar dates were transformed to Julian dates (i.e. 1 January = 1).

Secondly, breeding attempts were determined by looking at the sequence of activities per nest. It is

important to note here that we are assuming that the number of breeding attempts at a particular nest reflects breeding attempts by the same pair, but we do not know for certain whether these are the same individuals. A breeding attempt was assumed if the activity at the nest included audible young in the nest, visible young observed at the entrance, adult(s) feeding young at the nest or if flying young were seen still using the nest. If no activity had been observed previously at the nest, then the breeding attempt was defined as the first brood. If there was at least 25 days between the same activity (e.g. adults were observed feeding young 25 days after adults were feeding young at the same nest) then this was assumed to be another breeding attempt because it is implausible they would be feeding the same brood for that length of time. Sometimes observers were unable to make observations from the beginning of the nesting season, so it was difficult to determine how many breeding attempts were made at the nest. Nest observations were removed from the brood analyses if the sequence of activities, and thus brood number, was unclear. However, if the observer did not make observations late in the season but there was evidence of a nesting attempt in May, June or July, then this was assumed to be the first brood.

Finally, we determined apparent nest success (hereafter referred to as 'nest success'). A nesting attempt was defined as likely to be successful if flying young were observed still using the nest, or if adults were seen feeding them or there were visible young in the nest for at least 22 days. Twenty-two days was chosen, as this is the typical minimum number of days it takes between hatching and fledging (Cramp 1988, Turner & Rose 1989). A nesting attempt was assumed to have failed if any of the failure signs (Table S1) were noted with no subsequent evidence of young fledging. Although nest success by these criteria could not be determined for half of monitored nesting attempts, this information nonetheless provides a relative measure that can be used to test for the influence of weather and other factors. Nest success was determined where possible for each breeding attempt; in some cases, the brood number was determined using the method described above, and in other cases the brood number was not known but still included in analyses; i.e. all records were included in nest success (where nest success could be determined) whether the brood number was known or not.

Statistical analyses

To ascertain which factors influenced breeding initiation date, we ran a general linear model relating nest initiation date to nest-specific and landscape variables. Using one model with Gaussian error structures and an identity link function, the breeding initiation date was fitted as the response variable. Fixed variables included BROOD NUMBER, EASTING, NORTHING, whether the nest was ARTIFICIAL OR NATURAL and whether the NEST WAS USED PREVIOUSLY.

Separate generalised linear models (GLMs) with binomial error structures and a logit link function were fitted to test the effects of various factors on (1) the probability of having two broods (i.e. a response variable of one or two broods) and (2) the probability of nest success (i.e. a response variable of successful or not successful). First, we were interested in nest-specific variables, so fitted NEST HEIGHT, NEST LOCATION on the building, WALL SURFACE of the building, SOFFIT MATERIAL, whether the nest was ARTIFICIAL OR NATURAL, whether the NEST WAS USED PREVIOUSLY or not (for natural nests only), EASTING and NORTHING (to account for non-independence of nests in the same colony) as fixed effects in a first model.

Secondly, to ascertain which landscape variables affect breeding performance, we fitted the percentage of IMPROVED GRASSLAND, percentage of URBAN land-use, percentage of SUBURBAN land-use, percentage of FRESHWATER, presence of LIVESTOCK (none, within 500 m, between 500 and 1000 m, and both within 500 m and within 500–1000 m), EASTING and NORTHING in a second model.

Finally, we were interested in whether weather and/or breeding initiation date affects breeding performance, so fitted total SPRING RAINFALL, mean SPRING TEMPERATURE and BREEDING INITIATION DATE as fixed effects in a third model. The YEAR of survey was fitted as a fixed effect in all models, as this variable might affect the likelihood of significance, but we were not explicitly testing for differences between years.

Although there is an argument for non-independence of nests from the same colony, we did not include unique colony ID in the final models. Earlier analysis attempted to include colony as a random term in the GLMs, but due to the small number of nests monitored per colony (2016

mean ± se number of nests per colony: 5.20 ± 0.20; 2017 mean: 4.35 ± 0.21), models failed to fit. Instead, we chose to include easting and northing in the models to account for this non-independence. Nests on a wall surface of metal, PVC or unknown, nests on a soffit type of metal or unknown, nests located within a doorway, and nests in Northern Ireland or the Republic of Ireland were removed from analyses testing these variables due to low sample sizes ($n < 10$). Sample sizes for the variables used are shown in Table S2.

We calculated the variance inflation factor (VIF) for the variables within each model. No variables had a VIF of > 2 so there was no collinearity in the models. All statistical analyses were performed using R version 3.4.4 (R Core Team, 2019), using the lme4 package for GLMs (Bates *et al.* 2015).

RESULTS

The total number of nests (i.e. nest-sites) surveyed was 4779 from 944 colonies in 2016 and 4510 from 872 colonies in 2017; 2514 of these nests were surveyed in both years. Most nests were located in England (79.5%), followed by Wales (10.1%), Scotland (8.8%) and Northern Ireland (1.5%). We also received data for six nests in the Republic of Ireland (Fig. 1). A total of 996 volunteers participated in the study.

Number of broods and breeding initiation date

Number of broods, inferred from the number of breeding attempts at a particular nest or nest location, was determined for 2561 of 4779 nests (54%) in 2016 and 2294 of 4510 nests (51%) in 2017. Over half of nests where brood numbers were determined showed evidence of only one brood, and just under half of nests showed evidence of two broods in 2016 and 2017. There was evidence of triple-brooding on only four occasions over the 2 years (Table 1).

The mean first breeding initiation date across both years was 28 May. Breeding activity started significantly earlier in nests that were used previously than in those that were not (estimate ± se = −10.591 ± 0.818, $z = 19.426$, $P < 0.001$) and in artificial nests compared to natural nests (−5.710 ± 0.953, $z = -5.991$, $P < 0.001$). Breeding activity started significantly earlier the further east (−6.715$_{e-06}$ ± 3.091$_{e-06}$,

Figure 1. Distribution of surveyed House Martin nests in 2016 and 2017 across the UK and Republic of Ireland.

Table 1. The number and percentage of House Martin nests known to attempt one, two or three broods in 2016 and 2017 in the UK.

Number of broods	Number and percentage of nests	
	2016	2017
1	1382 (53.96%)	1394 (60.77%)
2	1177 (45.94%)	898 (39.14%)
3	2 (0.08%)	2 (0.09%)

$z = -2.172$, $P < 0.05$) and later the further north (9.055$_{e-06}$ ± 2.110$_{e-06}$, $z = 4.292$, $P < 0.001$) the nest was.

Types of nest failure

Of 4617 nesting attempts where the outcome was assessed as either failed or succeeded (50% of total

nests monitored), 875 (19%) failed (or at least partially failed, where some chicks may have fallen but not all) and therefore 81% were assessed as succeeding (i.e. where there was observational evidence of success). Collapse of nests (32%) and eggs or young being usurped from the nest by another species (26%) were the most common reasons for failure. Sixty-five volunteers stated that the House Martins were usurped by House Sparrows *Passer domesticus* and one stated that a Wren *Troglodytes troglodyte* had taken over the nest. Unknown damage to the nest (15%), eggs or chicks predated (11%), chicks or eggs thrown or fallen from the nest (10%), unintentional or intentional damage by humans (4%) and wind damage (2%) were also reported as causes of nest failure.

Factors affecting breeding performance

House Martins were significantly more likely to attempt two broods (Table 2a) and to succeed in nesting attempts (Table 3a) in artificial nests compared with natural nests. Of the natural nests, the probability of attempting two broods (Table 2a) and the probability of success (Table 3a) were significantly higher in nests that were used in previous years than in those that

Table 2. Results from models testing the effects of various (a) nest-specific factors, (b) landscape and (c) weather and breeding initiation date variables on the probability of House Martins attempting two broods in the UK.

	Estimate	$\pm$ 1 se of estimate	*z*-value	*P*-value
(a) Nest-specific variables				
Year	−0.138	−0.074	−1.856	0.063
Artificial nest	0.601	0.103	5.835	< 0.001***
Used in previous year	0.559	0.086	6.474	< 0.001***
Soffit type (wood)	0.357	0.109	3.270	< 0.01**
Soffit type (other)	0.440	0.168	5.065	< 0.01**
Wall surface of building (pebbledash)	0.163	0.102	1.608	0.108
Wall surface of building (render)	0.270	0.133	2.032	< 0.05*
Wall surface of building (stone)	0.201	0.118	1.711	0.087
Wall surface of building (wood)	0.150	0.175	0.855	0.392
Wall surface of building (other)	0.815	0.161	5.065	< 0.001***
Nest location (under a gable)	0.043	0.127	0.338	0.735
Nest location (top of gable)	−0.002	0.106	−0.017	0.986
Nest location (attached to window)	−0.078	0.229	−0.339	0.734
Nest location (other)	−0.139	0.211	−0.661	0.508
Nest height (1st storey)	0.119	0.197	0.061	0.952
Nest height (2nd storey or above)	0.115	0.197	0.058	0.953
Easting	8.993_{e-07}	3.533_{e-07}	2.545	< 0.01**
Northing	3.653_{e-07}	2.302_{e-07}	1.587	0.113
(b) Landscape variables				
Year	−0.106	0.0628	−1.690	0.091
Percent improved grassland	−0.000	0.001	−0.301	0.763
Percent urban land-use	0.001	0.004	0.194	0.846
Percent suburban land-use	−0.003	0.002	−1.474	0.140
Percent freshwater	0.002	0.007	0.220	0.826
Presence of livestock (within 500 m)	−0.120	0.106	−1.130	0.258
Presence of livestock (within 500 m & 1000 m)	−0.116	0.094	−1.226	0.220
Presence of livestock (none)	−0.050	0.102	−0.566	0.571
Easting	1.172_{e-06}	3.066_{e-07}	3.822	< 0.001***
Northing	2.973_{e-07}	1.824_{e-07}	1.630	0.103
(c) Weather and breeding initiation				
Year	−0.158	0.065	−2.430	< 0.05*
Breeding initiation date	−0.016	0.002	−10.088	< 0.001***
Spring rainfall	0.001	0.001	1.420	0.155
Mean spring temperature	−0.049	0.046	−1.062	0.288

Samples sizes for each category within each variable are shown in Table S2. *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

Table 3. Results from models testing the effects of various (a) nest-specific, (b) landscape and (c) weather and breeding initiation date variables on the probability of House Martins producing a successful nesting attempt in the UK.

	Estimate	± 1 se of estimate	*z*-value	*P*-value
(a) Nest-specific variables				
Year	−0.012	0.091	−0.216	0.829
Artificial nest	0.635	0.142	4.477	< 0.001***
Used in previous year	0.201	0.098	2.055	< 0.05*
Soffit type (wood)	0.618	0.122	5.068	< 0.001***
Soffit type (other)	0.322	0.196	1.649	0.099
Wall surface of building (pebbledash)	0.216	0.128	1.684	0.092
Wall surface of building (render)	−0.079	0.168	−0.473	0.636
Wall surface of building (stone)	−0.109	0.140	−0.776	0.437
Wall surface of building (wood)	−0.304	0.203	−1.501	0.133
Wall surface of building (other)	0.122	0.204	0.597	0.55
Nest location (under a gable)	−0.012	0.151	−0.074	0.941
Nest location (top of gable)	−0.120	0.122	−1.635	0.102
Nest location (attached to window)	−0.415	0.236	−1.757	0.078
Nest location (other)	0.025	0.239	0.103	0.918
Nest height (1st storey)	0.108	0.325	−0.033	0.974
Nest height (2nd storey or above)	0.107	0.325	−0.036	0.971
Easting	2.214_{e-06}	4.330_{e-07}	5.113	< 0.001***
Northing	1.501_{e-07}	2.702_{e-07}	0.556	0.578
(b) Landscape variables				
Year	−0.090	0.078	−1.158	0.246
Percent improved grassland	0.001	0.001	0.467	0.640
Percent urban land-use	0.001	0.006	0.104	0.917
Percent suburban land-use	0.011	0.003	4.276	< 0.001***
Percent freshwater	0.039	0.013	3.053	< 0.01**
Presence of livestock (within 500 m)	0.282	0.132	2.141	< 0.05*
Presence of livestock (within 500 m & 1000 m)	0.285	0.117	2.441	< 0.05*
Presence of livestock (none)	−0.13	0.128	−1.011	0.312
Easting	2.219_{e-06}	3.539_{e-07}	6.270	< 0.001***
Northing	-1.845_{e-07}	2.100_{e-07}	−0.879	0.379
(c) Weather and breeding initiation				
Year	−0.179	0.124	−1.434	0.151
Breeding initiation date	0.012	0.002	4.713	< 0.001***
Spring rainfall	−0.004	0.001	−3.174	< 0.01**
Mean spring temperature	−0.003	0.085	−0.038	0.969

Samples sizes for each category within each variable are shown in Table S2. *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

were newly built in the survey year. Nests built on plastic soffits were less likely to attempt two broods and to be successful compared with those built on soffits made from wood or another material (Tables 2a and 3a). Nests built on a render surface or 'other' surface were more likely to attempt two broods than were those built on brick (Table 2a) but the wall surface had no effect on the success of nests (Table 3a). About 5% of wall surfaces were classified as 'other' and not specified by the observers. Nest height had no effect on either parameter of breeding performance (Tables 2a and 3a).

Four landscape variables appeared to influence House Martin breeding performance. Both the probability of producing two broods (Table 2b) and the probability of nest success (Table 3b) increased the further east the nest was in the UK (Fig. 2), whereas northing had no effect.

The probability of nest success increased with freshwater and suburban land-use (Fig. 2) and was positively affected by the presence of livestock within 500 m of the nest (Table 3b).

Nests that started later in the year were significantly less likely to attempt two broods but were more likely to be successful (Tables 2c and 3c; Fig. 3).

Finally, there was a negative effect of total spring rainfall on the probability of nest success (Table 3c; Fig. 3), but no effect of temperature on

either breeding performance parameter (Tables 2c and 3c).

DISCUSSION

We undertook a large-scale citizen science survey to better understand the drivers of breeding performance of a nationally declining population of

House Martins with pronounced regional differences in population trajectories. Using data collected by a large network of volunteers meant that we had to make several assumptions about breeding performance. First, we defined breeding attempts using audible young, visible young or adults feeding at the nest. This method misses out the breeding attempts that failed at the egg stage,
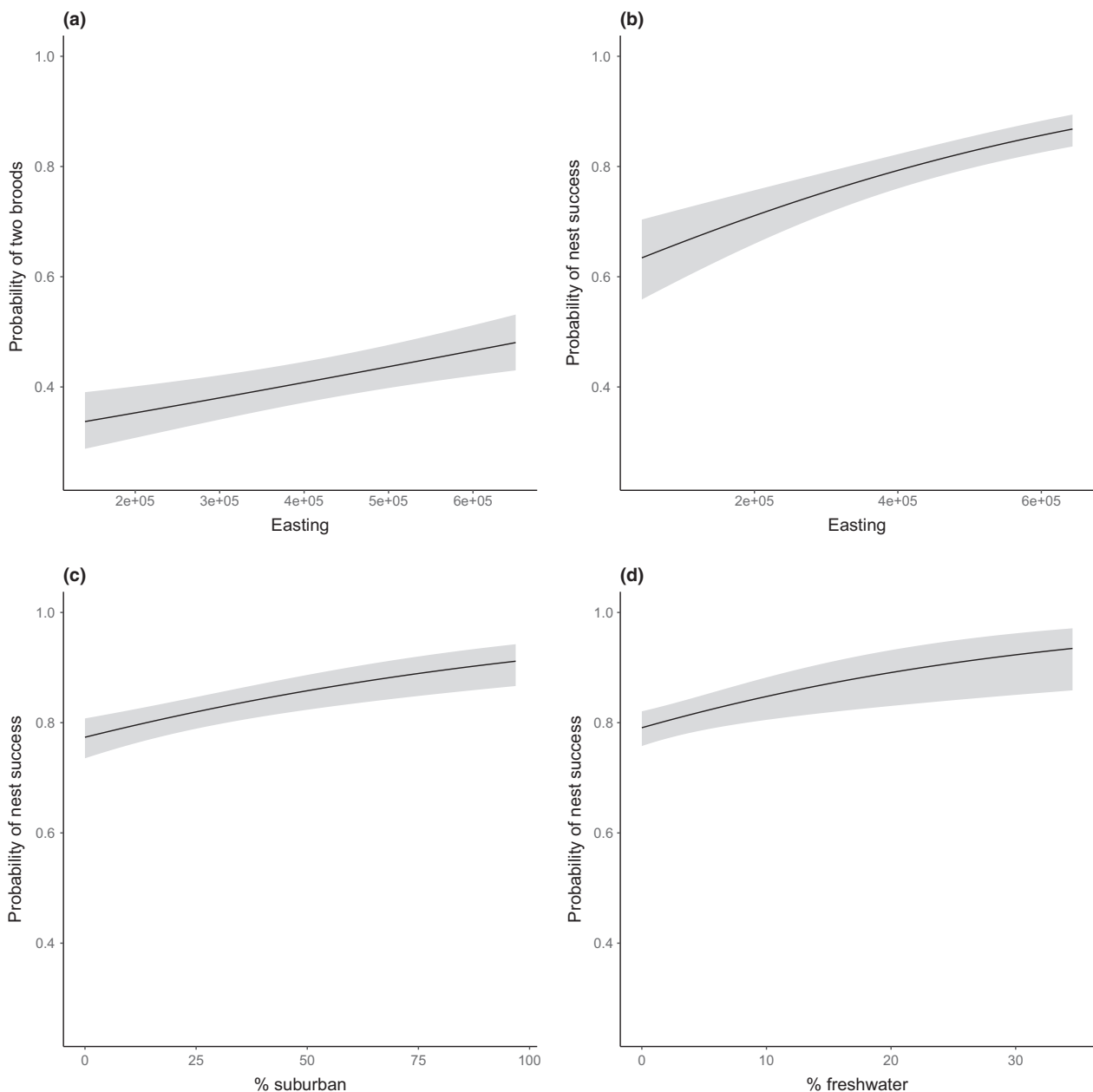
Figure 2. Probability of House Martins producing two broods (fitted value ± 95% CI) (a) and a successful nesting attempt (b) in relation to easting, and the probability of breeding successfully in relation to the percentage of suburban (c) and freshwater (d) land-use.
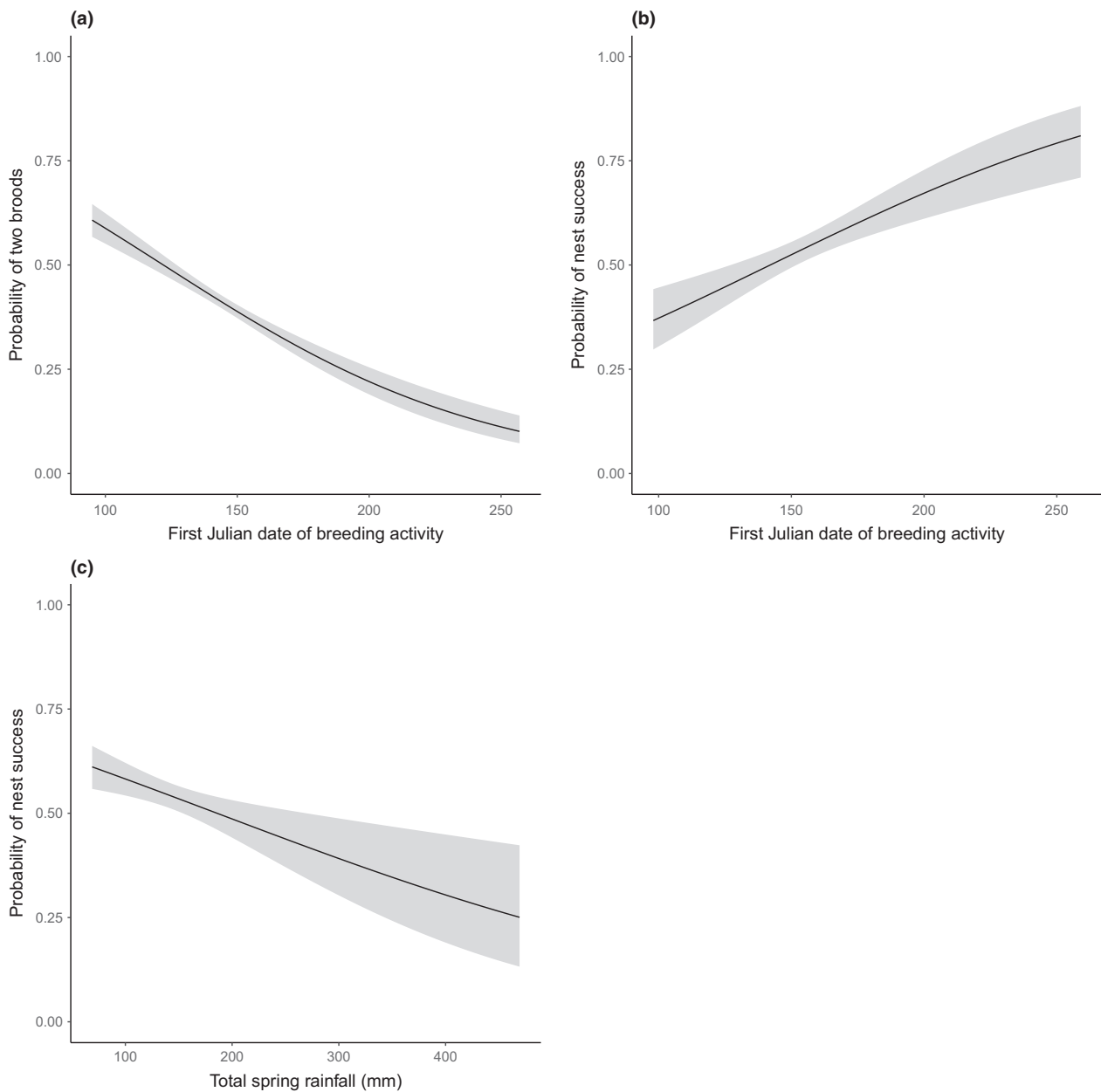
Figure 3. Probability of House Martins producing two broods (fitted value ± 95% CI) (a) and a successful nesting attempt, (b) in relation to breeding initiation date (in Julian dates), and the probability breeding successfully in this attempt in relation to total spring rainfall (c).

and so some breeding attempts may have been overlooked, i.e. our methods may be biased against early failures.

Secondly, some failures may be only *partial* failures (e.g. where some chicks have fallen but some remain in the nest). The proportion of failures attributed to different causes may differ slightly in reality; the rate of failures attributed to human damage is likely to be higher than the rate reported here, as the nests are self-selected by observers who are conservationists and/or have an interest in wildlife and hence unlikely to cause intentional damage.

Finally, although we obtained data from across the UK, participants and their homes are unlikely to be representative of the general UK population.

Despite the caveats of the study, using a citizen science approach allowed for a large-scale and cost-efficient assessment of aspects of breeding performance that could be used to test for the influence of potential drivers. Citizen science can be a useful way of engaging the general public with science and wildlife (Dickinson *et al.* 2012) and we show that a citizen science approach can be used to obtain demographic data even on species that can be easily observed but whose nest contents (eggs and chicks) are difficult to view and monitor. There is a long history and global use of the citizen science approach in monitoring bird populations and breeding parameters. Schmeller *et al.* (2012) provide an overview of volunteer-based bird monitoring schemes across Europe, most run by national institutions and employing structured protocols aimed at producing population trends. The BTO/JNCC/RSPB Breeding Bird Survey, from which annual population trends for *c.* 120 species are produced, is a good example of this in the UK (Harris *et al.* 2020). Horns *et al.* (2018) address the use of opportunistic bird recording schemes, in use globally, to calculate population trends for North American birds. Citizen science schemes are also widely used to collect demographic information (reviewed in Bailey *et al.* 2015), including the calculation of temporal and spatial trends in parameters such as nest success, number of breeding attempts, clutch size and phenology. Results of such studies have helped to understand the impact of land management practices such as changes in cropping regimens on Skylark *Alauda arvensis* (Chamberlain & Crick 1999) or the impact of climate change (Dunn & Møller 2014).

We found that under half of nests attempted a second brood, which is lower than historically reported by Bryant (1979) in Scotland (76%) and south-east England (87%). This may be due to the difficulty detecting a second brood from the methods used and the data available from volunteer observers. Although triple-brooding has been reported in studies elsewhere in Europe (Pajuelo *et al.* 1992, Piersma 2013), we believe this is the first study to provide evidence of triple brooding attempts for House Martins breeding in the UK. Using the probability of attempting two broods and the probability of nest success as measures of breeding performance, we show that the breeding performance of House Martins is driven by a combination of nest-specific, landscape and weather variables.

Nest-specific impacts on House Martin breeding performance

Nest-specific factors have a large influence on House Martin breeding performance, given that most of our nest-specific variables had an effect on either the probability of attempting two broods or the probability of nest success. House Martins nesting in previously used nests was more likely to be multi-brooded and successful. One explanation for this might be that older birds are the first to occupy existing nests (Piersma 2013) and are more experienced at building nests and rearing broods, and thus more likely to have high reproductive success (Forslund & Pärt 1995). The findings that birds nesting in previously used nests have an increased breeding performance are in line with work carried out on House Martins elsewhere (Bryant 1979, Piersma 2013) and on other hirundines (Safran 2006, Teglhøj 2018), where old nests are generally taken up early and produce multiple broods with more nestlings. There might be a trade-off, as old bird nests generally have more parasites (Tomás *et al.* 2007) but constructing new nests could be energetically costly and more time-consuming, reducing time invested in brooding and feeding young, as suggested for other species (Wiebe *et al.* 2007). This is in line with our finding that breeding activity started significantly earlier in previously used nests than in newly built nests. House Martin breeding performance was also better in artificial nests than in natural nests and artificial nests were taken up significantly earlier than natural nests. Breeding performance has been shown to be better in artificial nests in other hirundine species because of reduced predation and competition (Norris *et al.* 2018, Teglhøj 2018). As well as a reduced nest construction time, pairs nesting in artificial nests are unlikely to face some of the challenges associated with nest failure in natural nests, such as nest collapse (the most common case of nest failure) and wind damage.

The probability of attempting multiple broods and producing successful nests was lower when nests were built on soffits made of PVC or other plastics than those made of wood or another material. Sample sizes for each failure category against each soffit type were small and so were not tested here, but it might be that nests built on smooth materials such as PVC are more prone to collapse

or may prove a more difficult substrate on which to construct nests.

Landscape and weather impacts of House Martin breeding performance

Breeding performance was higher in eastern parts of the UK. Studies show that an earlier onset of breeding is linked to an increased breeding performance in birds (Dunn 2004). In our study, House Martins started breeding earlier in the east. This supports the suggestion that early breeding allows time for replacement clutches if needed (Morrison *et al.* 2019) and may help to explain why the probability of attempting two broods was higher in eastern parts of the UK. The drier climate of eastern parts of England may help to explain an increased breeding performance, given that we found a negative effect of spring rainfall on nest success. Population monitoring studies show that House Martins have declined in southern parts of the UK but have increased in the north in recent years (Woodward *et al.* 2018, Harris *et al.* 2020). Historical studies suggest breeding performance decreases with latitude in hirundines (Bryant 1979, Møller 1984), but we found no effect of northing. Our findings do not explain the decreases in England, but the lack of difference in breeding performance latitudinally may indicate wider environmental changes since previous studies on House Martin breeding ecology were carried out. Other Afro-Palaearctic insectivorous passerines also show declines in England but increases in Scotland, and it is thought that this variation is strongly linked to breeding processes (Morrison *et al.* 2013) as potentially are differences in wintering areas or migration routes. Flying invertebrates, including Lepidoptera and Odonata species, have shifted northward in recent decades in the UK (Hickling *et al.* 2005, Conrad *et al.*, 2006), which may have reduced any latitudinal effects.

Hirundine breeding performance is negatively associated with agricultural intensity (Ghilain & Bélisle 2008, Stanton *et al.* 2016) and population declines of some species are more prominent in intensively cultivated areas (Ambrosini *et al.* 2012). Although we found no effect of the amount of improved grassland, we did show a positive effect of the presence of livestock within 500 m of the nest, which might be associated with high abundance of aerial invertebrates and thus might benefit House Martin as well as other hirundines that feed on aerial invertebrates closer to the ground (Grüebler *et al.* 2010). We found that the amount of freshwater and suburban land-use were also of importance. Freshwater habitats presumably support large numbers of good quality invertebrate prey (Imlay *et al.* 2017). Wetlands are thought to provide important feeding sites for swallows and martins and are exploited before pairs arrive in the surrounding areas, including urbanized landscapes, to nest (Arena *et al.* 2011). Residential houses provide important nest-sites, and areas on the edge of urban areas support a high abundance of aerial invertebrates (Teglhøj, 2018), which is presumably why we found a positive effect of suburban land-use on the probability of House Martin nest success. We only used a crude measure of urban land-use here, and urban environments present many novel challenges for wildlife (Marzluff & Ewing 2001). For instance, Barn Swallows *Hirundo rustica* nesting in more central urban areas produced nestlings with lower body mass and fewer fledglings than those on the periphery of urban areas because of the lower abundance of prey in urban centres (Teglhøj, 2018). Future studies should attempt to use other indicators of House Martin breeding performance, and other measures such as adult survival and health, before strong conclusions on the importance of suburban and urban landscapes are reached.

Conclusions and management recommendations

Given the findings presented here, it is suggested that to maximize breeding performance in subsequent years by reducing nest-building effort, previously used natural nests should not be removed from buildings. Artificial nests are likely to improve breeding performance and should be installed where possible, especially on modern buildings with PVC soffits, as these might be less suitable for natural nests. Given our finding that suburban areas can have a positive effect on House Martin breeding performance, artificial nests are likely to provide valuable nesting opportunities in both suburban and rural areas where there is suitable prey. Designing buildings with wildlife in mind may not only have positive ecological consequences but will also probably benefit the well-being of residents (Goddard *et al.* 2012).

The majority of House Martin nests (81%) were successful, at least by our definition based on no definite signs of failure. We do not have any historical UK data to compare this success rate against; however, it is similar to other studies on hirundines (Nooker *et al.* 2005, Imlay *et al.* 2018), although lower than the 91% nest success rate for House Martins observed by Piersma (2013). Our data suggest that the proportion of second broods may have declined. This may be due to methodological difficulties in detecting second broods but merits further investigation as a possible mechanism behind the observed declines in England. The generally high success rate of nests suggests that survival rates may be a parameter in driving patterns of population change, as in other passerines (Peach *et al.* 1999, Robinson *et al.* 2004, Freeman *et al.* 2007), rather than (or in addition to) breeding performance. We therefore suggest future work should also assess survival rates of both adult and fledgling House Martins. Although we do not provide direct links between breeding performance and population trends of House Martin here, we show that nest-specific, landscape and weather variables can affect breeding performance, and a combination of changes in agricultural practices, increasing urbanisation with modern constructions and changes in weather patterns may be drivers of regional and hence national population trends, as well as changes on wintering grounds or pressures during migration not explored here.

AUTHOR CONTRIBUTION

Esther Kettel: Formal analysis (lead); Methodology (equal); Visualization (lead); Writing-original draft (lead); Writing-review & editing (lead). **Ian Woodward:** Conceptualization (equal); Data curation (equal); Formal analysis (supporting); Methodology (equal); Project administration (equal); Writing-review & editing (equal). **Dawn Balmer:** Conceptualization (equal); Funding acquisition (equal); Methodology (equal); Project administration (equal); Writing-review & editing (equal). **David Noble:** Conceptualization (equal); Funding acquisition (equal); Methodology (equal); Project administration (equal); Writing-review & editing (equal).

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. Variables and categories within each variable regarding information on the location and nest condition and activity of observed House Martin nests.

Table S2. Sample sizes of each of the variables used in the GLMs testing the effects on the probability of House Martin producing two broods and the probability of nest success in the UK.