



## THE ROLE OF THE EURASIAN SPARROWHAWK (*ACCIPITER NISUS*) IN THE DECLINE OF THE HOUSE SPARROW (*PASSER DOMESTICUS*) IN BRITAIN

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**ABSTRACT.**—We compared the pronounced geographic pattern in the recolonization of Britain by the Eurasian Sparrowhawk (*Accipiter nisus*) from 1970 onward with the spatiotemporal pattern among House Sparrow (*Passer domesticus*) populations over the same period, using data on the occurrence of both species at garden feeding stations. Using a simulation of House Sparrow population trends based on a logistic model that incorporated a predation index derived from Eurasian Sparrowhawk incidence functions, we generated a close approximation to the unique trajectories among House Sparrow populations in rural and urban sites in different regions of Britain. We carried out further comparisons using two contrasting methods that focused solely on temporal patterns. We used estimates of the varying date of Eurasian Sparrowhawk recolonization at different sites to derive time variables in relation to recolonization date. One such relative time variable proved to be a better predictor of House Sparrow numbers than chronological time; it indicated that House Sparrow numbers were generally stable or increasing prior to recolonization by Eurasian Sparrowhawks but declined continuously afterward. We also detected a significantly greater decrease in House Sparrow numbers when Eurasian Sparrowhawks were present using a method that compared annual changes in the abundance of prey species in the presence or absence of a predator. On the basis of these results, we argue that predation by Eurasian Sparrowhawks may be a sufficient explanation for the decline in House Sparrows in Britain. We also argue that urban House Sparrow populations' long-term release from predator pressure made them especially vulnerable when urban habitats were colonized by Eurasian Sparrowhawks. Received 3 April 2009, accepted 31 October 2009.

**Key words:** *Accipiter nisus*, blitzkrieg hypothesis, Eurasian Sparrowhawk, House Sparrow, *Passer domesticus*, population limitation, predator–prey interaction, songbird declines, urban ecology.

### Le rôle d'*Accipiter nisus* dans le déclin de *Passer domesticus* en Grande-Bretagne

**RÉSUMÉ.**—Nous avons comparé le patron géographique de la recolonisation de la Grande-Bretagne par *Accipiter nisus* depuis 1970 et le patron spatiotemporel des populations de *Passer domesticus* au cours de la même période, à partir de données sur la présence des deux espèces à des mangeoires. À l'aide d'une simulation des tendances des populations de *P. domesticus* basée sur un modèle logistique incorporant un indice de prédation dérivé de fonctions d'incidence de *A. nisus*, nous avons généré une bonne approximation des trajectoires uniques des populations de *P. domesticus* dans des sites ruraux et urbains de différentes régions de Grande-Bretagne. Nous avons effectué des comparaisons plus poussées à l'aide de deux méthodes opposées qui portaient uniquement sur les patrons temporels. Nous avons utilisé des estimations de la date de recolonisation d'*A. nisus* à différents sites pour dériver des variables temporelles. L'une de ces variables s'est avérée être un meilleur indice de l'abondance de *P. domesticus* que le temps chronologique; elle a indiqué que le nombre de *P. domesticus* était généralement stable ou augmentait avant la recolonisation par *A. nisus* mais diminuait régulièrement par la suite. Nous avons aussi détecté une baisse significativement plus importante du nombre de *P. domesticus* lorsque *A. nisus* était présent, en utilisant une méthode qui comparait les variations annuelles de l'abondance de l'espèce-proie en présence ou en l'absence d'un prédateur. Sur la base de ces résultats, nous croyons que la prédation par *A. nisus* peut expliquer le déclin de *P. domesticus* en Grande-Bretagne. Nous soutenons également que le relâchement à long terme de la pression de prédation sur les populations urbaines de *P. domesticus* les a rendues particulièrement vulnérables lorsque les habitats urbains étaient colonisés par *A. nisus*.

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THE HOUSE SPARROW (*Passer domesticus*; hereafter “sparrow”) has undergone a marked population decline in many parts of its range over the past 30 years. The decline is particularly well documented in Britain, where the population has shrunk by almost half (Robinson et al. 2005), but reduced numbers have also been noted more widely in Europe (De Laet and Summers-Smith 2007), North America (Anderson 2006), and Australia (Olsen et al. 2003). In Britain, the decline among rural sparrow populations has been attributed to changes in agricultural practice (Hole et al. 2002), but even steeper declines have occurred among urban populations, which generally exist at much higher densities (Robinson et al. 2005) and are therefore unlikely to be sink populations whose decline is caused by reduced immigration from rural areas. A range of alternative explanations has been put forward to explain urban sparrow declines (Summers-Smith 2003), but there is a lack of critical evidence to support any of these ideas.

A role for predation as a causal factor in sparrow declines has generally been dismissed as unlikely, despite a recent increase in the Eurasian Sparrowhawk (*Accipiter nisus*; hereafter “sparrowhawk”) population in Europe (Lensink 1997). Studies of the possible effects of resurgent sparrowhawk populations on songbirds in general have detected no significant relationship between predator incidence and prey numbers (Newton et al. 1997, Thomson et al. 1998), which has led to the conclusion that increased predation-related mortality must be compensatory, accounting only for an already “doomed surplus” among songbird populations (Tucker and Galbraith 2000, Newton 2004, Gibbons et al. 2007). However, a more recent study analyzed data from the British Trust for Ornithology’s Garden Bird Feeding Survey (GBFS) and found some evidence of local declines among certain prey species following the appearance of sparrowhawks, although the sparrow was not among them (Chamberlain et al. 2009).

The approach used by both Thomson et al. (1998) and Chamberlain et al. (2009) involved analyzing whether an index of sparrowhawk presence explained a significant degree of variation in year-to-year changes in prey numbers. Neither analysis included a spatial component, however, and in both sparrowhawks and sparrows there is pronounced geographic variation in population trends (Newton and Haas 1984, Robinson et al. 2005), which provides an opportunity to test whether such patterns of variation are linked. The resurgence of sparrowhawk populations in Europe represents a recovery following collapse in the 1950s caused by the toxic effects of chlorinated hydrocarbon pesticides (Newton and Wyllie 1992). In Britain, the most intensive use of such pesticides occurred in predominantly arable eastern England, which consequently experienced the greatest decline in sparrowhawk numbers. Populations in the mainly pastoral areas of the north and west were much less affected, forming effective “refugia” from which populations gradually spread southward and eastward in the second half of the 20th century to recolonize areas from which they had disappeared (Newton and Haas 1984).

If the decline in sparrow populations has been caused by increased predation by sparrowhawks, it should be possible to identify differences in population trends of both sparrowhawks and sparrows in different regions of Britain, and to also show that within such regions the trajectory of sparrow decline can be explained by the trajectory of sparrowhawk increase. A further aspect of the resurgence of sparrowhawk populations has been their

increased colonization of urban habitats during the last two decades of the 20th century, which corresponds with the period of rapid decline in urban sparrow populations. In the present study, therefore, we used GBFS data to seek evidence for spatiotemporal matching of population trends in sparrows and sparrowhawks, both regionally and along the rural–urban gradient. We also follow Thomson et al. (1998) and Chamberlain et al. (2009) in developing analyses of variation in sparrow trends in relation to sparrowhawk presence without an explicit spatial variable.

The GBFS data, which begin in 1970, cover the winter period only, but annual trends derived from the survey are nevertheless very closely related to trends in breeding populations (Chamberlain et al. 2005). The survey data therefore provide a good index of wider sparrow abundance. The survey is particularly useful for an investigation of a commensal species such as the sparrow and is designed to maintain consistent coverage across the whole of Britain and across a range of habitats, particularly along the rural–urban gradient.

## METHODS

### Data Preparation

The GBFS data for sparrows take the form of weekly peak counts of birds attending feeding stations for up to 26 weeks between October and March each winter, and the data for sparrowhawks comprise presence–absence data, referring to whether the species is observed hunting birds at a feeding station in a given week. For the purpose of this analysis, sparrow data were reduced to an annual mean of weekly peak counts (hereafter “sparrow count”), and sparrowhawk data were reduced to annual presence or absence (i.e., counted as present where recorded in one or more weeks). Peak counts of species using garden feeders vary over the course of the winter period (Chamberlain et al. 2005), but there is no interannual trend in within-season timing of observations, so this should not introduce any bias. Data were analyzed from 264 sites across Britain where sparrows were recorded and for which continuous records were available for  $\geq 10$  years between 1970 and 2004. Statistical analyses were conducted in R (Crawley 2007, R Development Core Team 2008), with most analyses performed using the generalized linear mixed-models program (Bates 2007).

### Regional and Rural–Urban Patterns

We determined the variation in temporal patterns of occurrence of the two species according to two location criteria, using grid references that were available for 201 of the sites (Fig. 1). First, we classified sites according to the sparrowhawk “recovery zone” in which they were located. Newton and Haas (1984) characterized the recovery of the sparrowhawk by mapping four such zones across mainland Britain and adjacent islands (Fig. 1). Second, we classified sites according to their degree of rurality. We entered grid reference locations on the Ordnance Survey website (see Acknowledgments) to produce a  $4 \times 4$  km map centered on the site and then determined the proportion of 1-km squares with  $>50\%$  cover of buildings and associated roads to score the site on a rurality scale from 0 (totally rural) to 16 (totally urban). This score is likely to have increased at some sites between 1970 and 2004

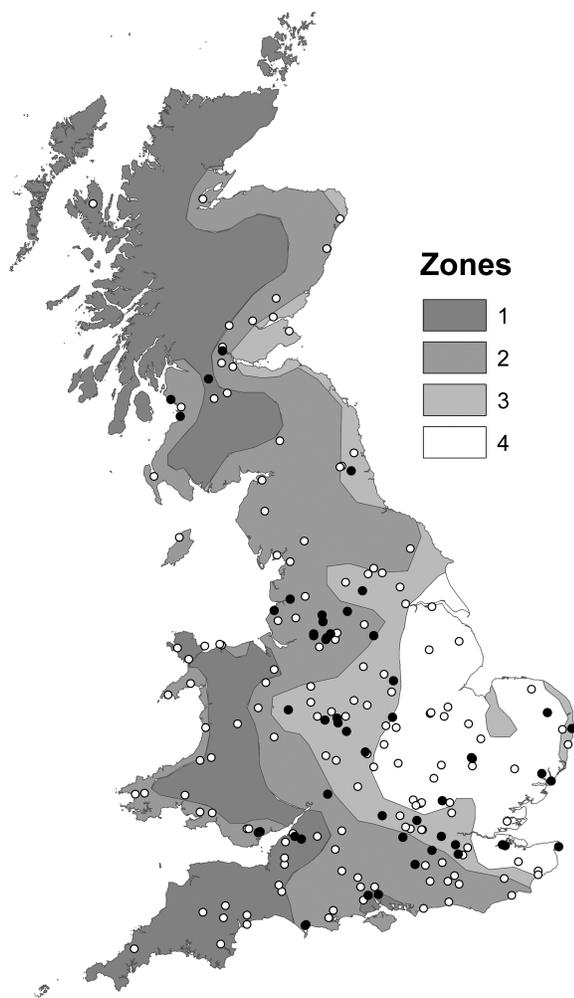


FIG. 1. Garden Bird Feeding Survey sites and Eurasian Sparrowhawk recolonization zones. White dots represent rural sites and black dots urban sites. Zone 1: <50% organochlorine-related decline and full recovery before 1970. Zone 2: >50% population decline but recovered to >50% before 1970. Zone 3: recovered to >50% before 1980. Zone 4: almost extinct in 1960 and little recovery by 1980. Adapted from Newton and Haas (1984).

as a result of urbanization, although no measures of change are available for the period in question. For this reason, we adopted a broad definition and reduced the categorization to a two-level factor (0–8 = rural, 9–16 = urban) to minimize the likelihood that change in land cover within sites over time could bias the results (Fig. 1).

Evidence was sought for significant differences in the temporal trends in sparrowhawk incidence and sparrow numbers between adjacent sparrowhawk recovery zones and between rural and urban sites, using generalized linear mixed models with GBFS site as a random effect and recovery zone and rurality as categorical fixed effects. Incidence functions for the sparrowhawk were fitted by binary logistic regression, and estimates of mean sparrow count were fitted by log-linear modeling. The general trajectory of

variation in sparrow numbers was more complex, so for this analysis, time was treated as a seven-level categorical variable based on 5-year intervals. Zone or rurality was entered as a two-level categorical variable in separate analyses for data within each of the levels of the other variable (i.e., zone 1 vs. 2, 2 vs. 3, 3 vs. 4 for rural and urban sites, respectively, and rural vs. urban sites for zones 1, 2, 3, and 4, respectively), and log likelihood ratios were obtained for sequential step-down removal of interaction and intercept terms.

*Sparrowhawk presence as a predictor of sparrow decline.*—The detection of significant variation in trends in sparrow count among the four sparrowhawk recovery zones is a prerequisite for establishing a link between the spatial patterns of sparrowhawk resurgence and sparrow decline. However, the existence of such variation does not amount to critical evidence for such a link. Sparrowhawk recovery zones are highly correlated with an east-to-west geographic gradient, so differences among the zones would result from variation in the temporal trend in sparrow numbers along this axis, whatever the underlying cause. However, if it were possible to show that variation in sparrow trends is explicable in terms of variation in the trajectory of sparrowhawk incidence, the inference of a causal link between the two would be greatly strengthened. We therefore modeled variation in the trajectory of sparrow count among the contingencies of sparrowhawk recovery zone and rurality to determine whether sparrow count is predicted by variation in the trajectory of sparrowhawk incidence. Annual changes in sparrow numbers were simulated using a logistic model:

$$N_{t+1} = P_t(N_t + 0.3N_t(1 - N_t/K)) \quad (1)$$

where  $N_t$  = sparrow count in year  $t$ ,  $P_t$  = the effect of predation by sparrowhawks in year  $t$ , and  $K$  = mean sparrow carrying capacity for sites within a particular category of recovery zone–rurality. The coefficient 0.3 determines the intrinsic rate of increase in the absence of predation and density dependence and is similar to the value of 0.279 estimated for a presumed “source” population of sparrows in North America (Anderson 2006).  $P_t$  defaults to unity when sparrowhawks are absent, or to a value  $0 < P_t < 1$  when they are present. Sparrowhawk presence or absence was determined by a probability derived from the fitted value from the statistical model of sparrowhawk incidence for year  $t$  in a given zone–rurality. This was multiplied by a quantity,  $m$ , that takes account of the possibility of unrecorded sparrowhawk presence in the vicinity of a site, because GBFS sparrowhawk records are related only to hunting behavior at garden feeding stations. Predation on local sparrow populations may therefore not be recorded if a feeding station is not a viable hunting site because of its location and surroundings.

During the modeling process, values of  $P^*$ ,  $K$ , and  $m$  were varied, and the simulated population trends were compared with those described by the statistical model of sparrow count. Goodness-of-fit was calculated by comparing the values derived for the mid-point years of each of the 5-year periods with the corresponding fitted value from the statistical model. The final model is that with  $P^*$ ,  $K$ , and  $m$  values that provided the closest fit to the empirical trends. The modeling process is explained in greater detail in the Appendix.

### Effects of Sparrowhawk Recolonization

In addition to evidence of correspondence in spatial patterns of variation between the two species, we sought evidence of a general correspondence between sparrowhawk reappearance and sparrow decline at all 264 sites. Following Thomson et al. (1998) and Chamberlain et al. (2009), we classified sparrowhawks as present or absent at each site in a particular year. The analysis of Thomson et al. (1998) used recorded presence or absence for each individual year, which may be confounded by nonrecording of sparrowhawks in some years when they were actually present or by records of transient sparrowhawks that had little effect on local prey populations. Chamberlain et al. (2009) attempted to resolve this problem by assuming that sparrowhawks were ever present at a site after the first year in which they were recorded, on the basis of the marked rebound in sparrowhawk populations and the resulting reestablishment of the species across wide areas of Britain.

Here, we look at sparrow population trends in relation to sparrowhawk presence using two alternative methods of dating sparrowhawk reestablishment at a site and examine general trends before and after these dates. The first method of estimating the date of sparrowhawk establishment at a site simply used the first year of sparrowhawk presence to define a transition between absence and presence (absent–present or AP transition), and the second used the first year from which sparrowhawks were consistently present year after year (present–constant or PC transition). For many sites, therefore, the recording period is divided into three discrete subperiods defined as successive stages in which the species was absent (start of recording period to AP transition), intermittently present (AP to PC transition), and constantly present (PC transition to end of recording period).

A minimum requirement for identification of an AP transition was a period of  $\geq 4$  years of absence from the beginning of the recording period followed by  $\geq 2$  subsequent years of presence, and for a PC transition a period of  $\geq 4$  years of constant presence at the end of the recording period. A single year of absence that occurred  $\geq 10$  years after the start of a period of constant presence that otherwise lasted until the end of the recording period was not considered to have broken the sequence for the purpose of defining a PC transition.

*Sparrow trend before and after AP and PC transitions.*—The effect of the AP and PC transitions on sparrow numbers was tested by defining two new predictor variables in the form of AP- and PC-centered time, in which the date of the transition was set to zero for each site. In this form, the sign of the year variable is negative before the AP or PC transition and positive after the transition. As in the log-linear analyses in relation to chronological date, AP- and PC-centered time were treated as categorical variables, but with levels defined as 3-year periods.

*Annual change in sparrow numbers.*—The approach of Thomson et al. (1998) involved modeling annual change in songbird territories on census plots as a function of the presence or absence of predators. We applied the same log-linear modeling method to our data set but restricted it to sites with a PC transition, and we used quasi-likelihoods to account for overdispersion (Crawley 2007). The structure of the GLM was as follows:

$$N_{t+1,i} = Y_t + S_{t,i} + H_{t,i} + \text{offset}(\log_e(N_{t,i})) \quad (2)$$

where  $N_{t,i}$  is sparrow count in year  $t$  and site  $i$ ,  $Y_t$  represents separate intercepts for each year  $t$  (i.e., change in  $N$  when  $S$  and  $H$  both equal zero),  $S$  is an index of relative sparrow abundance, and  $H$  represents sparrowhawk presence or absence.  $S_{t,i}$  is calculated as sparrow count for site  $i$  in year  $t$  divided by the mean sparrow count for the site over the whole period of data recording and multiplied by a universal mean index for the same period, calculated from the entire data set ( $n = 264$  sites). The latter is simply the mean of fitted values for individual years over the relevant period from a generalized mixed model of sparrow count, with year defined as a categorical variable and site as a random effect. The standardization process for  $S$  takes account of intersite differences in sparrow abundance by dividing by the site mean, and of intersite variation of the recording period in relation to overall population trends by multiplying by the universal mean.  $Y$  is included to factor out the effect of possibly spurious temporal correlation, and  $S$  to remove the possible masking of a predation effect by density dependence.

Analyses were performed using both the approach of Thomson et al. (1998), in using recorded presence or absence in each individual year, and the approach described above that makes use of the PC transition, with sparrowhawks assumed to be absent before the transition and ever present afterward. Both approaches were also subject to model criticism via removal of a small number of data points identified as influential by the default residual plot option in R.

## RESULTS

### Regional and Rural/Urban Patterns

*Sparrowhawk.*—Among rural sparrowhawks, a significant difference ( $P < 0.05$ ) existed between zones 2 and 3, with a more rapid increase in the latter, so that starting from a lower base in 1970, sparrowhawks became more frequent in zone 3 than in zone 2 around the mid-1980s. The increase in sparrowhawk frequency also occurred later in zone 4 than in zone 3 (Fig. 2A and Table 1). There was a similar difference between zones 2 and 3 among urban sparrowhawks. However, contrary to expectations, there was a suggestion that the increase occurred later in zone 1 than in zone 2. Within recovery zones, sparrowhawks increased significantly later in urban than in rural sites in zone 1, and significantly less quickly in urban than in rural sites in zone 3 (Fig. 2A, B and Table 1).

*Sparrow.*—There were significant differences among sparrows in temporal trends in all comparisons (Fig. 2C, D and Table 1). In rural sites, sparrow numbers were generally higher in zone 4 than in zone 3 and were perhaps higher in zone 2 than in zone 1. In zone 4, rural sites generally held higher numbers than urban sites. Numbers were essentially stable in rural zones 1–3 up to the mid-1980s but started to decrease from the late 1980s, with some indication of leveling out in the late 1990s, in zone 1 at least. In rural zone 4, numbers increased during the 1970s and were stable through the 1980s, before starting to decrease in the early 1990s (Fig. 2C). Among urban sparrows, numbers appeared to be stable across all zones until the mid-1980s, after which a decrease occurred in zones 1–3. The apparent late-1980s decrease in zone 4 was nonsignificant, and significant decrease was delayed until the early 1990s (Fig. 2D).

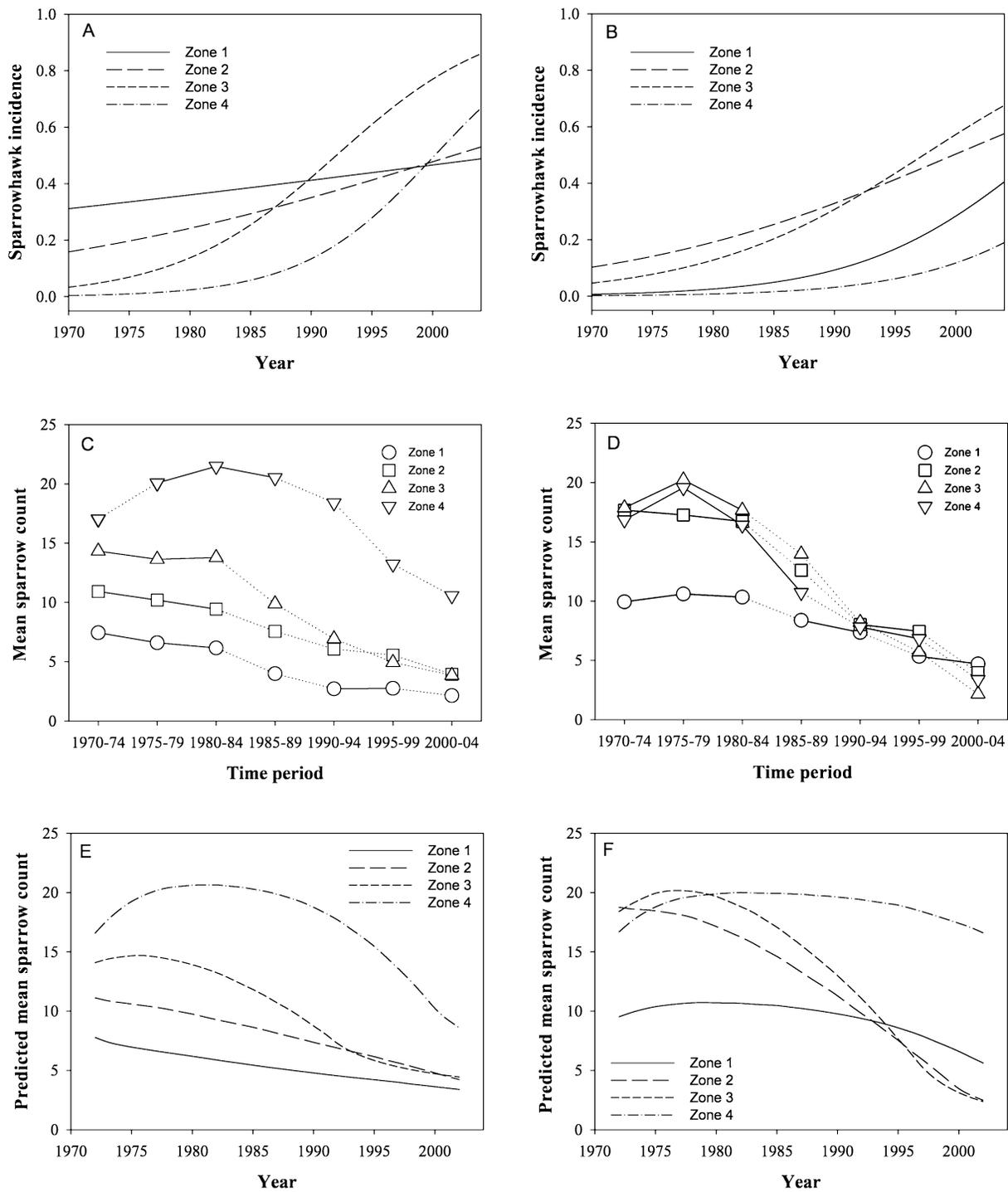


FIG. 2. Best-fit lines for Eurasian Sparrowhawk incidence (A = rural sites, B = urban sites), fitted values for mean House Sparrow count (C = rural, D = urban), and mean House Sparrow count predicted by Eurasian Sparrowhawk incidence (E = rural, F = urban), in relation to year. For each contingency of zone–rurality, significance of differences between time categories for the House Sparrow data was assessed by progressive aggregation of adjacent categories until the resulting log likelihood ratio exceeds  $\chi^2$  with  $df = 1$  at  $P = 0.01$ . The resulting aggregated groupings are connected by solid lines, whereas groups that are significantly different at  $P < 0.01$  are joined by dotted lines in C and D.

TABLE 1. Statistical significance of differences in temporal trends in Eurasian Sparrowhawk incidence and House Sparrow count data between adjacent recovery zones, and between rural and urban sites within recovery zones, in Britain, 1970–2004.

| Data            |         |                     | Eurasian Sparrowhawk |    |            | House Sparrow |    |            |
|-----------------|---------|---------------------|----------------------|----|------------|---------------|----|------------|
| Rurality        | Zone    | Effect <sup>a</sup> | $\chi^2$             | df | <i>P</i>   | $\chi^2$      | df | <i>P</i>   |
| Rural           | 1 vs. 2 | Year * zone         | 1.40                 | 1  | 0.2371     | 26.09         | 6  | 0.0002***  |
|                 |         | Intercept           | 0.11                 | 1  | 0.7418     | 3.66          | 1  | 0.0558     |
|                 | 2 vs. 3 | Year * zone         | 34.10                | 1  | <0.0001*** | 59.45         | 6  | <0.0001*** |
|                 |         | Intercept           | 14.42                | 1  | 0.0001***  | 0.15          | 1  | 0.6975     |
|                 | 3 vs. 4 | Year * zone         | 1.23                 | 1  | 0.2660     | 172.83        | 6  | <0.0001*** |
|                 |         | Intercept           | 7.23                 | 1  | 0.0072**   | 9.94          | 1  | 0.0016**   |
| Urban           | 1 vs. 2 | Year * zone         | 1.87                 | 1  | 0.1712     | 22.22         | 6  | 0.0011**   |
|                 |         | Intercept           | 3.69                 | 1  | 0.0547     | 0.77          | 1  | 0.3802     |
|                 | 2 vs. 3 | Year * zone         | 3.95                 | 1  | 0.0469*    | 45.82         | 6  | <0.0001*** |
|                 |         | Intercept           | 0.01                 | 1  | 0.9263     | 0.09          | 1  | 0.7658     |
|                 | 3 vs. 4 | Year * zone         | 0.16                 | 1  | 0.6873     | 30.37         | 6  | <0.0001*** |
|                 |         | Intercept           | 2.64                 | 1  | 0.1039     | 0.01          | 1  | 0.9283     |
| Rural vs. urban | 1       | Year * rurality     | 1.19                 | 1  | 0.2762     | 19.73         | 6  | 0.0031**   |
|                 |         | Intercept           | 4.38                 | 1  | 0.0364*    | 1.22          | 1  | 0.2687     |
|                 | 2       | Year * rurality     | 1.43                 | 1  | 0.2306     | 32.70         | 6  | <0.0001*** |
|                 |         | Intercept           | 0.03                 | 1  | 0.8601     | 0.88          | 1  | 0.3490     |
|                 | 3       | Year * rurality     | 4.64                 | 1  | 0.0312*    | 109.17        | 6  | <0.0001*** |
|                 |         | Intercept           | 11.68                | 1  | 0.0006***  | 0.2781        | 1  | 0.5980     |
|                 | 4       | Year * rurality     | 1.30                 | 1  | 0.2544     | 30.78         | 6  | <0.0001*** |
|                 |         | Intercept           | 2.05                 | 1  | 0.1524     | 6.29          | 1  | 0.0121*    |

<sup>a</sup>2 × log likelihood ratio is shown for generalized linear mixed models with interaction + intercept versus intercept only, and with and without intercept. Site is included as a random effect in all cases. Separate analyses were conducted for all 10 dichotomous comparisons for each species. Significance levels: \**P* < 0.05, \*\**P* < 0.01, \*\*\**P* < 0.001.

*Sparrowhawk presence as a predictor of sparrow decline.*— Simulated trends generated by the model of sparrow population as a function of sparrowhawk presence are shown in Figure 2E, F. The model proved to be predictive of sparrow decline in all cases except urban sites in zone 4, among which the estimated trend for sparrowhawks was not significantly different from that for zone 3 (Table 1). The *P*\* value that gave the best approximation to empirical trends was 0.7 in urban sites and 0.8 in rural sites (see Appendix), which indicates that the observed trends may be partly explicable in terms of a greater effect of sparrowhawk presence in urban than in rural sites. The best-fitting value of *m* was 2, which suggests that sparrowhawks may be present in up to twice as many sites as indicated by the model of sparrowhawk incidence.

**Effects of Sparrowhawk Recolonization**

*Sparrow trend before and after AP and PC transitions.*— Analysis of sparrow numbers in relation to AP-centered time explained less variation in sparrow numbers than an equivalent analysis in relation to chronological time (Table 2), and values fitted to the levels of AP-centered time showed no indication of any effect of the AP transition, with numbers undergoing a general steady decline (Fig. 3). By contrast, PC-centered time explained more variance than chronological time (Table 2). The trend in relation to PC transition revealed evidence of a slight increase in sparrow numbers before the transition, with the first significant decrease in numbers occurring immediately afterward, beginning a decline that continued for >15 years (Fig. 3).

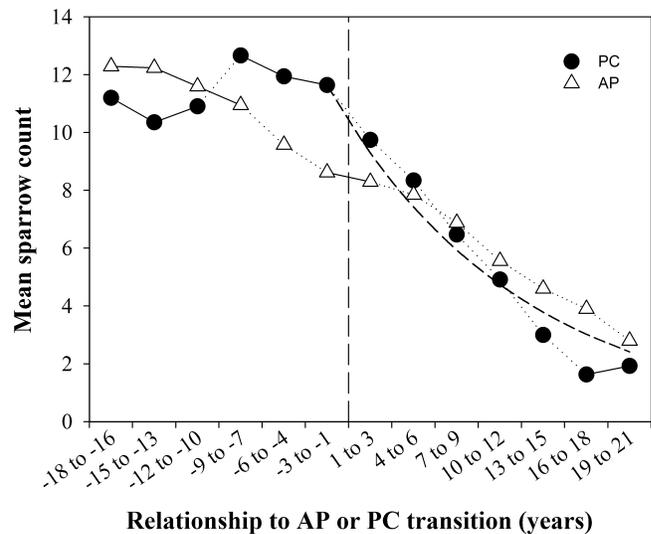


FIG. 3. Fitted estimates of mean House Sparrow count in relation to absent–present (AP) or present–constant (PC) centered time. Otherwise, the convention is the same as in Figure 2C, D. The dashed vertical line indicates the position of the AP or PC transition, and the dashed curve indicates a trend equal to  $n = 11.64 \exp(-0.075t)$  where 11.64 = fitted value for the period -3 to -1 years in relation to the PC transition. The value of -0.075 is close to the mean of the four estimates of relative decline with Eurasian Sparrowhawk presence from the analysis of annual changes in House Sparrow numbers (Table 4) and gives a reasonable approximation to the estimated post-PC decline.

TABLE 2. Residual deviance in generalized linear mixed models of sparrow count in sites with absent–present (AP) and present–constant (PC) transition data.

| Transition | <i>n</i> | Sites | Site only <sup>a</sup> |          | Site + chronological time |          | Site + transition – centered time |          |
|------------|----------|-------|------------------------|----------|---------------------------|----------|-----------------------------------|----------|
|            |          |       | df                     | Deviance | df                        | Deviance | df                                | Deviance |
| AP         | 2,254    | 132   | 2                      | 8,467    | 14                        | 6,078    | 19                                | 6,199    |
| PC         | 912      | 54    | 2                      | 4,069    | 13                        | 2,917    | 19                                | 2,655    |

<sup>a</sup>Site is a random effect in all three versions of the model, and the table compares deviance in a model with site only, with that in models also including chronological time and transition (AP or PC) centered time, both defined as categorical variables with 3-year intervals as levels.

TABLE 3. Values of Akaike’s information criterion (AIC), Aikake weights (*w<sub>i</sub>*), and evidence ratios (*w<sub>i</sub>/w<sub>j</sub>*) for generalized mixed models of variation in House Sparrow numbers in Britain (1970–2004) for sites with a present–constant (PC) transition.

|                                |                                    | All                     | Zone 1            | Zone 2            | Zone 3                  | Zone 4                  |
|--------------------------------|------------------------------------|-------------------------|-------------------|-------------------|-------------------------|-------------------------|
|                                |                                    | ( <i>n</i> = 912)       | ( <i>n</i> = 121) | ( <i>n</i> = 161) | ( <i>n</i> = 386)       | ( <i>n</i> = 181)       |
| Sites <sup>a</sup>             |                                    | 54                      | 7                 | 12                | 22                      | 8                       |
| PC-centered (3-year periods)   | AIC                                | 2,693                   | 250               | 405               | 968                     | 583                     |
|                                | <i>w<sub>1</sub></i>               | 0.999                   | 0.817             | 0.999             | 0.999                   | 0.999                   |
| Chronological (3-year periods) | AIC                                | 2,943                   | 268               | 428               | 1,057                   | 653                     |
|                                | <i>w<sub>2</sub></i>               | 0.000                   | 0.000             | 0.000             | 0.000                   | 0.000                   |
| Chronological (2-year periods) | AIC                                | 2,935                   | 253               | 430               | 1,078                   | 651                     |
|                                | <i>w<sub>3</sub></i>               | 0.000                   | 0.182             | 0.000             | 0.000                   | 0.000                   |
| Evidence ratios                | <i>w<sub>1</sub>/w<sub>2</sub></i> | 1.92 × 10 <sup>54</sup> | 8,103             | 98,715            | 2.12 × 10 <sup>19</sup> | 1.59 × 10 <sup>15</sup> |
|                                | <i>w<sub>1</sub>/w<sub>3</sub></i> | 3.54 × 10 <sup>52</sup> | 4.48              | 268,337           | 7.69 × 10 <sup>23</sup> | 5.83 × 10 <sup>14</sup> |

<sup>a</sup>Grid references were available for only 49 of the 54 sites, so 5 sites were not assignable to zone.

The greater variance explained by PC-centered than by chronological time suggested that the trend in relation to PC date was not simply an artifact of the overall temporal trend of accelerating decline in sparrow numbers. This conclusion is reinforced by comparisons of Akaike’s information criterion (AIC) for models that used PC-centered time and those that used two versions of the model based on chronological time (Table 3). Akaike weights and evidence ratios (Burnham and Anderson 2002) strongly supported the former as the best model (Table 3), and this held within recovery zones, so the overall result was not simply attributable to the zonal patterns described above.

*Annual changes in sparrow numbers.*—Results of the analysis of year-to-year changes in sparrow numbers are presented in Table 4. The analysis that followed the original methodology of Thomson et al. in using recorded presence or absence of sparrowhawks in individual years as the predictor variable yielded no

significant effect, but the analysis that defined sparrowhawks as present after the PC transition yielded a significant negative effect of sparrowhawk presence on sparrow numbers. When the data were reanalyzed after model criticism that involved deletion of a small number (5–6, where *n* = 797) of data with a large influence on the model parameter estimates, a significant negative effect of sparrowhawk presence was detected by both approaches.

DISCUSSION

The trends in sparrowhawk incidence in rural areas among the four sparrowhawk recovery zones support their original definition in Newton and Haas (1984), with a progressively lower starting point and later increase from zones 1 through 4, reflecting the more severe decline that occurred in areas with a higher proportion of arable land. The trends also suggested that the increase

TABLE 4. Year-to-year change in House Sparrow count in Britain (1970–2004) as a function of Eurasian Sparrowhawk presence for sites with a present–constant (PC) transition.

| Sparrowhawk index | Model criticism | <i>n</i> | Coefficient <sup>a</sup> | ΔDeviance <sup>b</sup> | Dispersion <sup>c</sup> | <i>F</i> | <i>P</i> |
|-------------------|-----------------|----------|--------------------------|------------------------|-------------------------|----------|----------|
| Recorded presence | All data        | 797      | −0.0656 ± 0.0414         | 7.56                   | 3.017                   | 2.505    | 0.114    |
|                   | Censored data   | 791      | −0.0686 ± 0.0294         | 8.23                   | 1.517                   | 5.425    | 0.020*   |
| Present after PC  | All data        | 797      | −0.0903 ± 0.0454         | 11.84                  | 3.004                   | 3.941    | 0.047*   |
|                   | Censored data   | 792      | −0.0827 ± 0.0324         | 9.88                   | 1.521                   | 6.498    | 0.011*   |

<sup>a</sup>Estimated coefficient of Eurasian Sparrowhawk presence parameter ± SE.

<sup>b</sup>Increase in residual deviance when *H* (Eurasian Sparrowhawk presence–absence) is deleted from the model.

<sup>c</sup>This value is greatly reduced by deleting a small number of influential data.

proceeded more rapidly the later it occurred, eventually resulting in higher overall incidence, which may reflect an increased proportion of intrinsically suitable lowland habitat in the east of Britain. Where differences in the trend of sparrowhawk increase were detectable along the rural–urban gradient, these showed a slower or later increase in urban areas than in rural areas within the same recovery zone, which suggests that during the spread back across the country from northwestern refuge areas, sparrowhawks may have built up numbers in rural habitats before they penetrated urban areas in the same district.

The contrasts in the pattern of sparrowhawk increase between rural and urban areas corresponds to published evidence of a difference in the trajectory of sparrow declines along the rural–urban gradient, because farmland sparrows declined earlier than those in gardens (Robinson et al. 2005). Variation in the timing of sparrowhawk recovery can also explain previously detected patterns of variation in the extent of sparrow decline on farmland, where steep declines have occurred since the mid-1970s in the English midlands, East Anglia, southeast England, but no declines in Scotland and southwest and northern England (Robinson et al. 2005). The areas where sparrows are stable are mainly in sparrowhawk recovery zones 1 and 2, where reestablishment of sparrowhawks in rural areas was essentially complete before the mid-1970s. Thus, predator and prey may have already returned to equilibrium in those zones. The areas of decline correspond largely with zones 3 and 4, where continued build-up of sparrowhawk numbers may have caused sparrow numbers to diminish on farmland until well into the 1980s.

Such broad-scale correlations between the timing of sparrowhawk increase and sparrow decline are no more than suggestive of a link between the two. However, the degree to which variation in the trends among sparrow populations can be reproduced by addition to a logistic population model of a multiplier derived from a statistical model of sparrowhawk incidence provides considerably stronger grounds to infer that the varying patterns of sparrow decline have been caused by increased predation. In the one instance in which it proved impossible to derive a close approximation of sparrow population trajectory from sparrowhawk incidence, that for urban sites in zone 4, the estimated trends for both species were based on data from only eight sites and so may not provide an accurate summary of the underlying trends.

The correspondence between broad-scale geographic patterns in the two species suggests that it should also be possible to detect such correspondence on an even finer scale. Because predation can only begin to affect sparrow populations once sparrowhawks have reappeared at a site, intersite variation in the beginning of downward trends in sparrow numbers should be explicable in terms of the varying date of sparrowhawk reappearance. However, when this was estimated using the first year in which sparrowhawks were recorded at a site, no effect was apparent, which indicated that this may not provide a good estimate of the date of sparrowhawk reestablishment. Frequently the first year of recording was followed by a period in which sparrowhawks were recorded in some years and not in others, which may reflect the presence of transient birds in the area that have little effect on local sparrow populations. The relatively weak evidence for an effect of predation by sparrowhawks on prey species that Chamberlain et al. (2009) found could conceivably be related to their use

of a similar approach, in which sparrowhawks were assumed to be present every year after that in which they were first recorded at a site.

By contrast, when sparrowhawk reappearance was estimated as the first year of consistent yearly presence at a site, sparrow numbers appeared to decline only after the transition and were stable beforehand. Time in relation to this estimate of sparrowhawk establishment also provided a better explanation of variance in sparrow numbers than simple chronological time. The start of constant presence, therefore, may have provided a much better estimate of the date of permanent establishment of sparrowhawks in the vicinity of a site, and of the beginning of significant predation pressure on local sparrow populations. Use of this proxy estimate of predation by sparrowhawks in the context of the approach adopted by Thomson et al. (1998) also indicated that it may be a more useful measure than raw presence and absence data, since it explained a greater proportion of variance in the rate of year-to-year sparrow population change than if presence and absence data were used. The greater explanatory power of both measures when influential data points were censored also emphasizes the importance of carrying out a thorough model criticism before reaching a conclusion that no relationship exists between two variables.

The correspondence between the beginning of consistent sparrowhawk presence at individual locations and the start of the decline in sparrow abundance suggests that the main effect on sparrow populations occurs when sparrowhawks become newly established as breeders in areas from which they were formerly absent. This may have been particularly severe in urban areas, as suggested by the fact that urban trends are best defined in relation to rural trends by lower survival when sparrowhawks are present. Sparrowhawks have until very recently been absent from urban areas (Newton 1993), which therefore represented predator-free islands for small birds. Such predator release can lead to selection for the loss of behavioral strategies to avoid predation (Blumstein and Daniel 2005), a process that may have been especially strong for a species such as the sparrow, which forages on human detritus in open areas and appears to be at particularly high risk of predation by sparrowhawks (Götmark and Post 1996).

The sudden appearance of sparrowhawks in urban areas may therefore have had an effect analogous to that of predators introduced to oceanic islands. The extinctions that follow such introductions are thought to result from the inability of naïve populations of prey species to adjust behavior quickly, an idea dubbed the “blitzkrieg hypothesis” (Steadman 2006). This could also apply to recent colonizations of urban habitats by other small-bird specialist species, which have coincided with declines in sparrow populations. These include the Merlin (*Falco columbarius*) and Sharp-shinned Hawk (*Accipiter striatus*) in North America (Sohdi et al. 1992, Coleman et al. 2002), and the Collared Sparrowhawk (*A. cirrhocephalus*) in Australia (Veerman 2003). Both of these regions have much in common with Europe in their history of human activities affecting birds of prey, including the severe effects of organochlorine pesticides on populations that recovered and ultimately colonized urban habitats after the chemicals were withdrawn (Bednarz et al. 1990, Olsen 1995).

Predation by sparrowhawks provides a parsimonious explanation for the general decline in sparrow abundance that occurred

in Britain from the mid-1980s onward and, unlike other explanations, can equally account for declines in both rural and urban populations. Predation by sparrowhawks may account for such declines without the need for any additional factors, because the PC-centered analysis presented here indicated that no declines occurred where sparrowhawks remained absent, and regional variations in sparrow decline mirrored the trajectory of reestablishment by breeding sparrowhawk populations. The role of sparrowhawks in urban sparrow declines can be further investigated by seeking evidence of negative spatial and temporal correlations between the two species, both on the small scale, within individual cities, and at a larger scale, among a sample of cities across Europe and elsewhere. Of particular current interest are cities such as Berlin (Witt 1996, 2005) and Paris (Anonymous 2008), where sparrows are still common and sparrowhawks have yet to reach high densities, because any future influx of sparrowhawks should lead to a collapse in sparrow abundance. In light of our results, the same methodologies might be used to revisit the issue of predation with regard to wider declines in songbirds.

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## APPENDIX

The first stage of simulation involves assigning sparrowhawks as either present or absent in year  $t$  in each of 100 simulated sites. The probability of presence in year  $t$  is calculated as the product of the corresponding fitted value ( $F_t$ ) from the sparrowhawk incidence model (Fig. 2A, B), and a correction factor ( $m = 1.0, 1.5, 2.0, 2.5$ ) that accounts for the possibility of unrecorded sparrowhawk presence. Each simulated site is assigned an index  $i = 0.01, 0.02 \dots 1.0$ , and sparrowhawks are considered present in year  $t$  only when  $mF_t$  exceeds  $i$ . Thus, if  $m = 1.0$  and  $F_t = 0.25$ , sparrowhawks are considered present in 25% of sites (0.01–0.25). However, if  $m = 2.0$  it is considered present in 50% of sites (0.01–0.50) where  $F_t = 0.25$ , and at all sites where  $F_t \geq 0.50$ .

The second stage involves determining the optimal  $K$  value for each of the eight contingencies of recovery zone and rurality. Population trends are generated for each of the 100 simulated sites using Equation 1, beginning with values of  $N_0$  generated at random from a Poisson distribution with a mean equal to the fitted values for the period 1970–1974 from the sparrow statistical model (Fig. 2C, D) and assigned to the midpoint year of 1972. Where sparrowhawks are absent  $P_t = 1$ , and where they are present  $P_t = P^*$  (values = 0.5, 0.6 . . . 0.9), which is the proportion of the sparrow population that avoids predation in any one year.  $K$  values are also generated from a Poisson distribution and assigned to sites in the same rank order as  $N_0$  values (this is to avoid instances where  $N_0 > K$ ). To determine the set of optimal  $K$  values, the mean of the distribution generating  $K$  values is varied between 4 and 30 to determine that which results in the closest fit to each of the eight observed mean population trends. The fit is calculated on the basis of an error term estimated as the sum of the absolute difference between the fitted values of the sparrow statistical model (Fig. 2C, D) and the simulated mean for the corresponding midpoint years.

The third stage involves repeating stage 2 for all combinations of  $m$  and  $P^*$  values, generating a varying set of optimal  $K$  values and goodness-of-fit estimates for each combination. Figure A1 shows minimum error estimates, summed across recovery zones for rural and urban sites respectively, as generated by each combination of  $m$  and  $P^*$  values. In most cases, a reasonable fit was achieved except for urban sites in zone 4, which was excluded from the summations since its error estimate was in most cases substantially higher than for any of the other contingencies. The best fit to the data is achieved when  $m = 2$ , with  $P^* = 0.8$  for rural sites and 0.7 for urban sites.

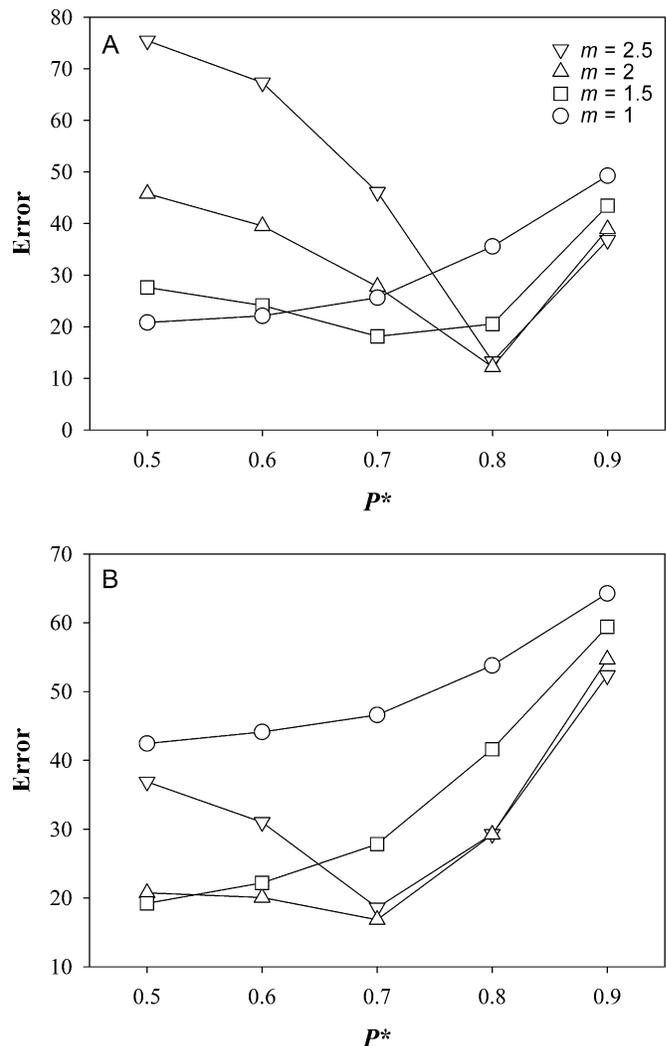


FIG. A1. Error values, generated by simulation model and summed across Eurasian Sparrowhawk recovery zones, plotted against  $P^*$  for each value of  $m$ . Values are the sums of the error terms for (A) zones 1–4 for rural sites and (B) zones 1–3 for urban sites. The method of calculating error values is set out in the text.