Evidence that population increase and range expansion by Eurasian Sparrowhawks has impacted avian prey populations

Christopher Paul Bell

Abstract

The role of increased predator numbers in the general decline of bird populations in the late 20th century remains controversial, particularly in the case of the Eurasian Sparrowhawk, for which there are contradictory results concerning its effect on the abundance of potential prey species. Previous studies of breeding season census data for Sparrowhawks and prey species in Britain have measured predator abundance either as raw presence-absence data or as an estimate derived from spatially explicit modelling, and have found little evidence of association between predator and prey populations. Here, a predator index derived from site-level binary logistic modelling was used in a regression analysis of breeding census data on 42 prey species, with significant effects emerging in 27 species (16 positive, 11 negative). The frequency of significant positive associations may indicate the tracking of prey abundance by Sparrowhawks, which would tend to cancel out any negative predation effect on prey populations, rendering it difficult to detect using census data. If so, the negative effects that have emerged for some species may underestimate the impact of increased Sparrowhawk numbers on the prey populations concerned. Nevertheless, estimates of the effect on national populations of prey species, obtained by combining effect sizes with a measure of the increase in site occupancy by the predator, suggest the possibility of a substantial impact. It cannot, therefore, be ruled out that the increase in abundance and range expansion of Sparrowhawks made a significant contribution to contemporaneous declines in the populations of many of its prey species.

Introduction

The marked population decline that occurred across a wide range of bird species in the British Isles during the late 20th Century is an event of major conservation concern that remains imperfectly understood. Consequently, it is still liable to generate controversy, particularly over the possibility that increased predator populations may have played a role (Gibbons et al. 2007, Roos et al. 2018). Declines occurred chiefly among songbirds, of which the major predator in western Europe is the Eurasian Sparrowhawk *Accipiter nisus* (henceforth ‘Sparrowhawk’), a species that increased rapidly in range and abundance during the same period, following a pesticide-related crash in the 1940s and 50s (Newton 1986).

The main source of evidence for population declines in Britain is the Common Birds Census (CBC), which ran from 1962 to 2000, and involved intensive field survey designed to estimate the number of breeding territories in a census plot (Marchant 1983). Previous analyses of CBC data have concluded that there is little evidence for any connection between increased Sparrowhawk numbers and songbird population declines (Thomson et al. 1998, Newson et al. 2010), but analyses of data from another census scheme, the Garden Bird Feeding Survey (GBFS), have consistently found evidence of a negative association between Sparrowhawks and House Sparrows (Bell et al. 2010, Swallow et al. 2015, 2016, Jones-Todd 2018).

GBFS data is derived from weekly maximum counts made at bird feeding stations over the winter months (Chamberlain et al. 2005), which can be averaged to derive an annually varying index of species abundance, with that for Sparrowhawk being effectively the proportion of weeks during which attacks on a feeding station were observed. The GBFS-derived Sparrowhawk index may thus be taken to be a continuous measure of predation pressure at a point location, resulting in commensurate declines in the use of the feeder at that location by potential prey species. CBC data are recorded during the breeding season, and refer to a much wider area, typically 20-150 ha depending on the habitat, and can therefore be more reliably used to infer population effects of a predator. However, they provide a much less precise measure of predator activity, effectively devolving to presence or absence in any given year.

Newson et al. (2010) addressed this problem by using smoothed relative abundance surfaces to produce year-specific predator indices for each CBC site within their focal area (England), effectively using broad-scale spatio-temporal trends to estimate variation in local abundance. However, this approach may fail to capture variation in predator activity at the narrower scale represented by the area of a typical CBC census plot, accurate representation of which requires modelling at the individual site level. Here, therefore, I reprise the approach used by Newson et al. (2010) for a wider range of potential prey species, using indices of Sparrowhawk activity derived from site-level modelling.

Materials and Methods

Model structure

The approach used retains the basic structure of the model used by Newson et al. (2010) (see appendix), and implements a regression of change in log prey population against change in a log predator index:

$$\ln\left(\frac{\mu_{i,t}}{\mu_{i,1}}\right) = \sum_{j=1}^{t-1} r_j + \alpha.\ln\left(\frac{P_{i,t}+1}{P_{i,1}+1}\right) \qquad \text{Equation 1}$$

where $\mu_{i,t}$ is estimated prey population and $P_{i,t}$ an estimate of predator activity in site *i* and year *t*, r_j is the instantaneous rate of change in global prey population caused by all factors other than predator activity in year *j*, and α is the effect of the change in the log predator index ($\ln(P_{i,t} + 1)$) between the first year with site data (t=1) and year *t*. Change in the log predator index underestimates change in log predator activity due to the need to accommodate instances of zero activity by adding one, but remains highly correlated with it.

The model was implemented in R version 3.1.2 (R core team 2014) with prey population as the response variable, using Poisson errors and a $\log_e$ link:

$$\mu_{i,t} = \exp\left[\sum_{j=1}^{t-1} r_j + \alpha . \ln\left(\frac{P_{i,t}+1}{P_{i,1}+1}\right) + \ln \mu_{i,1}\right] \qquad \text{Equation 2}$$

Estimates of r_j emerge as year effects with each data year represented in the linear model as a binary variable with the value 1 corresponding to all higher values of *t* at site level (i.e. the effect of previous years is ‘present’) and otherwise as 0, while $\ln \mu_{i,1}$ is estimated as a site effect, with each site represented as a level within a categorical variable (cf. Freeman & Newson 2008), or in some cases as more than one level to take account of changes in the size of the area censused. Variance in change in prey population between the first and any subsequent year with site data is therefore partitioned between the effect of change in predator activity over the same period, and the effect of conditions in each of the intervening years. The implementation of Newson et al. (2010) included a number of additional covariates, which are excluded here for reasons set out in the appendix.

Derivation of predator indices

CBC data were supplied by volunteer surveyors as part of a national scheme covering around 250 plots each year. There was relatively high turnover and a policy of replacing a lapsed plot with another of similar character, so the number of years surveyed at individual sites varied considerably. Plots were generally <150 ha, which provides little resolution for Sparrowhawks as the density of breeding territories is rarely as high as 1 per km^2 (Newton 1986). For practical purposes, therefore, the data for the species emerges as annual presence or absence at any given CBC site.

Such binary data can be viewed as a probabilistic manifestation of continuously varying Sparrowhawk activity within a census plot, and because any resulting effect on prey populations will also be continuous, it is appropriate to use the binary predator data to derive a model of the continuous variation that underlies it. Annual presence and absence data for Sparrowhawk were therefore modelled at site level using binary logistic regression, and since this cannot provide meaningful estimates for short runs of data, modelling was confined to sites in which census data were recorded for at least 5 years. The estimates of predator activity derived for each site and year were then used as the explanatory variable ($P_{i,t}$ in equations 1 and 2) in the analysis of change in prey populations.

Both Thomson et al. (1998) and Newson et al. (2010) performed analyses that treat the Collared Dove *Streptopelia decaocto* as a ‘dummy predator’ in order to test whether the methodology used is liable to indicate association where no possibility of predation exists. Like the Sparrowhawk, the Collared Dove increased rapidly in abundance and expanded its range during late 20th century, during which it newly settled many CBC sites. A further analysis was therefore performed, using indices derived in analogous fashion from Collared Dove presence and absence data as the explanatory variable in the regression model.

Comparison of predator effects with population change

The analysis follows Newson et al. (2010) in using data from the period 1967-2000, facilitating comparison of results with change in national population estimates, which for most prey species are available from 1966 onwards (Woodward et al. 2018). Change in national prey population associated with increased Sparrowhawk numbers was estimated using prey-specific effect values (α_{prey}) in combination with a measure of increase in site occupation by the predator, calculated as difference between annual means of the log predator index. The predicted effect on national prey populations (R_{prey}) of change in Sparrowhawk occupation across all sites between 1967 and 2000 is then:

$$R_{prey} = \exp\left(\alpha_{prey}\left(\frac{\sum_i \ln(P_{i,2000}+1)}{n_{2000}} - \frac{\sum_i \ln(P_{i,1967}+1)}{n_{1967}}\right)\right) \qquad \text{Equation 3}$$

where n_t = the number of sites (i) contributing predator activity estimates ($P_{i,t}$) in year t.

Results

Effect sizes and their significance are presented in Table 1, and (following Newson et al. 2010) plots of residuals against values of the explanatory variable are shown in supplementary Figure S1 for prey species with significant effects. Of the 42 species analysed in relation to Sparrowhawk, 27 showed a significant association, of which 11 were negative

Table 1. Estimated effects (α) of change in log indices for Sparrowhawk and Collared Dove on log population change among prey species, with bold coloured type representing significant positive (blue) or negative (red) effects. Standard errors were estimated using quasipoisson errors where the model dispersion (Disp) was >1.4 (indicated by bold type). Following Newson et al. (2010) no adjustment is made to significance levels for repeat analyses.

		Sparrowhawk						Collared Dove					
		N	Sites	Disp	Effect	*SE*	*P*	*N*	Sites	Disp	Effect	*SE*	*P*
Grey Partridge	*Perdix perdix*	3139	263	0.89	0.218	0.128	0.088	2984	255	0.89	0.075	0.116	0.517
Lapwing	*Vanellus vanellus*	2839	235	**1.67**	0.199	0.153	0.193	2725	227	**1.65**	-0.104	0.127	0.413
Collared Dove	*Streptopelia decaocto*	3866	285	1.22	0.005	0.098	0.956						
Turtle Dove	*Streptopelia turtur*	3162	245	1.11	**-0.352**	**0.121**	**0.004**	3051	239	1.11	-0.008	0.114	0.942
Great Spotted Woodpecker	*Dendrocopos major*	4780	368	0.54	**0.535**	**0.111**	**0.000**	4630	365	0.54	0.139	0.129	0.279
Blue Tit	*Cyanistes caeruleus*	7353	640	1.02	**0.190**	**0.026**	**0.000**	7099	629	1.03	**0.114**	**0.029**	**0.000**
Great Tit	*Parus major*	7313	634	0.87	**0.277**	**0.034**	**0.000**	7054	621	0.87	**0.113**	**0.038**	**0.003**
Coal Tit	*Periparus ater*	4853	404	0.95	-0.060	0.070	0.389	4692	398	0.95	0.020	0.081	0.801
Willow Tit	*Poecile montana*	2144	155	0.84	-0.057	0.218	0.793	2076	151	0.83	-0.251	0.201	0.211
Marsh Tit	*Poecile palustris*	2951	245	0.80	**0.520**	**0.120**	**0.000**	2837	240	0.81	-0.046	0.129	0.724
Skylark	*Alauda arvensis*	4694	409	1.23	**-0.104**	**0.040**	**0.009**	4521	399	1.23	0.027	0.041	0.516
Long-tailed Tit	*Aegithalos caudatus*	6112	491	0.73	**0.717**	**0.085**	**0.000**	5888	480	0.74	0.107	0.094	0.255
Wood Warbler	*Phylloscopus sibilatrix*	995	77	1.17	**-0.533**	**0.244**	**0.029**	948	75	1.14	0.005	0.342	0.987
Chiffchaff	*Phylloscopus collybita*	5755	472	1.00	**0.328**	**0.052**	**0.000**	5548	463	1.00	**0.148**	**0.059**	**0.012**
Willow Warbler	*Phylloscopus trochilus*	7093	605	**1.43**	**0.103**	**0.039**	**0.009**	6847	594	**1.41**	-0.104	0.127	0.413
Whitethroat	*Sylvia communis*	5614	481	1.25	**0.187**	**0.056**	**0.001**	5343	466	1.24	0.065	0.068	0.339
Nuthatch	*Sitta europeaea*	3133	246	0.72	-0.071	0.105	0.499	3027	241	0.73	**0.272**	**0.118**	**0.022**
Treecreeper	*Certhia familiaris*	4926	399	0.69	**0.285**	**0.098**	**0.004**	4755	391	0.69	-0.103	0.114	0.367
Wren	*Troglodytes troglodytes*	7454	650	**1.63**	**0.210**	**0.028**	**0.000**	7194	638	**1.65**	**0.163**	**0.031**	**0.000**
Starling	*Sturnus vulgaris*	3877	416	**1.66**	**0.496**	**0.089**	**0.000**	3728	405	**1.66**	**0.384**	**0.084**	**0.000**
Blackbird	*Turdus merula*	7528	658	1.10	0.016	0.022	0.480	7264	646	1.08	0.042	0.023	0.070

Song Thrush	*Turdus philomelus*	7311	632	0.96	**-0.316**	**0.041**	**0.000**	7053	620	0.96	**0.132**	**0.040**	**0.001**
Mistle Thrush	*Turdus viscivorus*	6479	532	0.59	**0.324**	**0.088**	**0.000**	6262	524	0.59	**0.206**	**0.088**	**0.019**
Spotted Flycatcher	*Muscicapa striata*	4461	355	0.94	**-0.264**	**0.128**	**0.039**	4255	348	0.93	0.220	0.124	0.077
Robin	*Erithacus rubecula*	7401	644	1.33	**0.057**	**0.023**	**0.014**	7143	632	1.33	**0.132**	**0.025**	**0.000**
Dunnock	*Prunella modularis*	7287	634	1.24	0.057	0.032	0.069	7002	619	1.23	**0.212**	**0.032**	**0.000**
House Sparrow	*Passer domesticus*	1869	187	**1.84**	**-0.393**	**0.114**	**0.001**	1824	182	**1.83**	**0.706**	**0.166**	**0.000**
Tree Sparrow	*Passer modularis*	3148	274	**2.22**	**-0.769**	**0.157**	**0.000**	3012	265	**2.14**	**0.351**	**0.110**	**0.001**
Yellow Wagtail	*Motacilla flava*	1327	104	1.06	**-0.741**	**0.155**	**0.000**	1256	99	1.07	-0.241	0.164	0.142
Grey Wagtail	*Motacilla cinerea*	1190	95	0.70	**0.702**	**0.305**	**0.021**	1133	93	0.71	-0.302	0.309	0.329
Pied Wagtail	*Motacilla alba*	4186	336	0.67	-0.012	0.117	0.916	4055	334	0.66	**0.316**	**0.112**	**0.005**
Tree Pipit	*Anthus trivialis*	1767	144	0.98	**0.528**	**0.201**	**0.009**	1725	144	0.99	0.229	0.173	0.187
Meadow Pipit	*Anthus pratensis*	2099	165	**1.51**	0.096	0.122	0.433	2038	164	**1.46**	**-0.423**	**0.139**	**0.002**
Chaffinch	*Fringilla coelebs*	7328	634	1.10	**0.186**	**0.024**	**0.000**	7070	621	1.10	0.045	0.026	0.087
Bullfinch	*Pyrrhula pyrrhula*	6179	496	0.73	**-0.151**	**0.076**	**0.046**	5955	484	0.73	**0.150**	**0.076**	**0.049**
Greenfinch	*Chloris chloris*	6069	511	1.17	**-0.244**	**0.055**	**0.000**	5802	494	1.16	**0.290**	**0.054**	**0.000**
Linnet	*Linaria cannabina*	5298	447	**1.47**	-0.028	0.069	0.687	5120	439	**1.46**	**0.208**	**0.071**	**0.003**
Redpoll	*Acanthis cabaret*	2669	208	1.23	**-1.243**	**0.176**	**0.000**	2597	206	1.27	0.260	0.140	0.063
Goldfinch	*Carduelis carduelis*	4941	398	1.05	0.005	0.087	0.955	4755	390	1.04	**0.386**	**0.090**	**0.000**
Corn Bunting	*Emberiza calandra*	1404	112	1.22	-0.105	0.152	0.491	1356	108	1.23	-0.178	0.126	0.156
Yellowhammer	*Emberiza citrinella*	5231	438	1.18	0.083	0.043	0.055	5022	427	1.17	**0.203**	**0.049**	**0.000**
Reed Bunting	*Emberiza schoeniclus*	3671	310	1.20	0.004	0.071	0.953	3528	305	1.19	**0.217**	**0.065**	**0.001**

and 16 positive. Of the 41 species analysed in relation to Collared Dove, 20 showed a significant association, of which 1 was negative and 19 positive. The trend in site occupation by Sparrowhawks is shown in Figure 1, with best-fit values for 1967 and 2000 of 0.067 and 0.438, respectively, denoting an increase of 0.371. The predicted change in national populations of prey species as a result of this increase and prey-specific predator effects is shown in Figure 2, alongside actual population change.

Figure 1. Trend in the annual mean of ln($P_{i,t}$+1) based on values of $P_{i,t}$ derived from site-level models of Sparrowhawk activity within CBC census sites. The trend line ± 2 standard errors was fitted using the loess smoother of the GAM package in R using a span of 0.2.

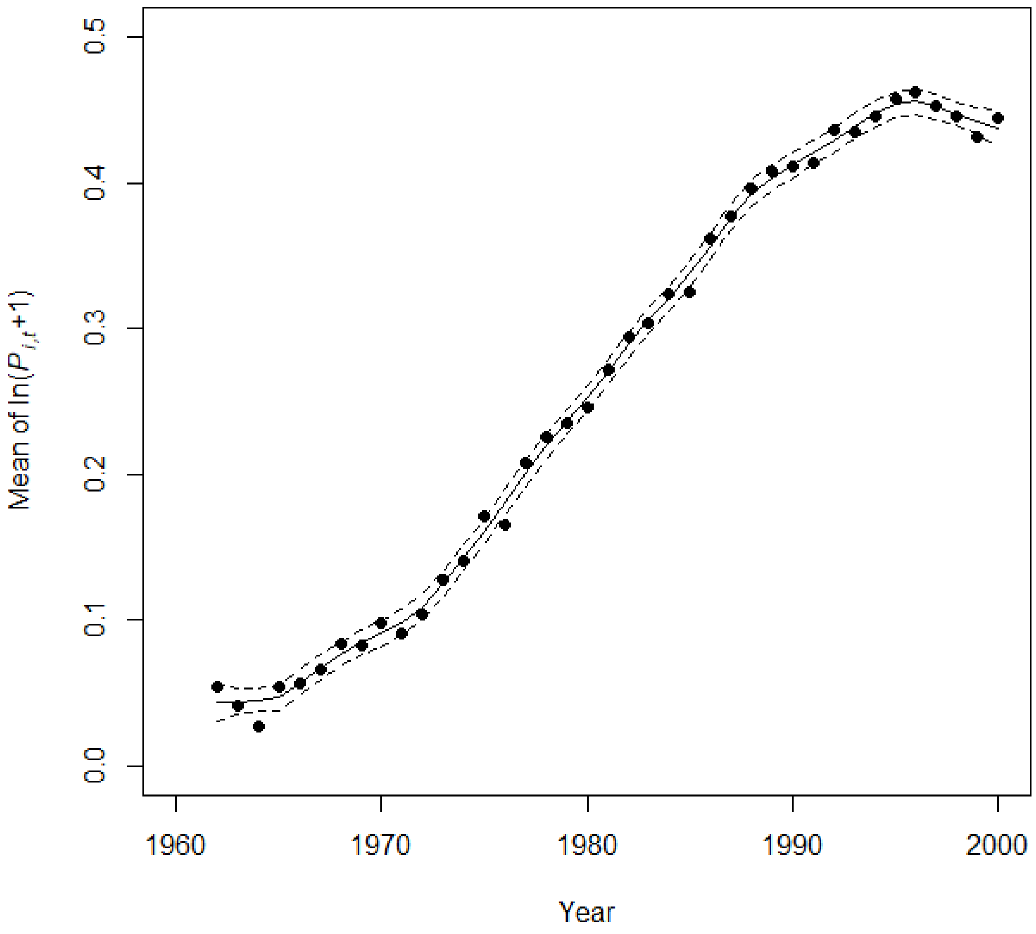
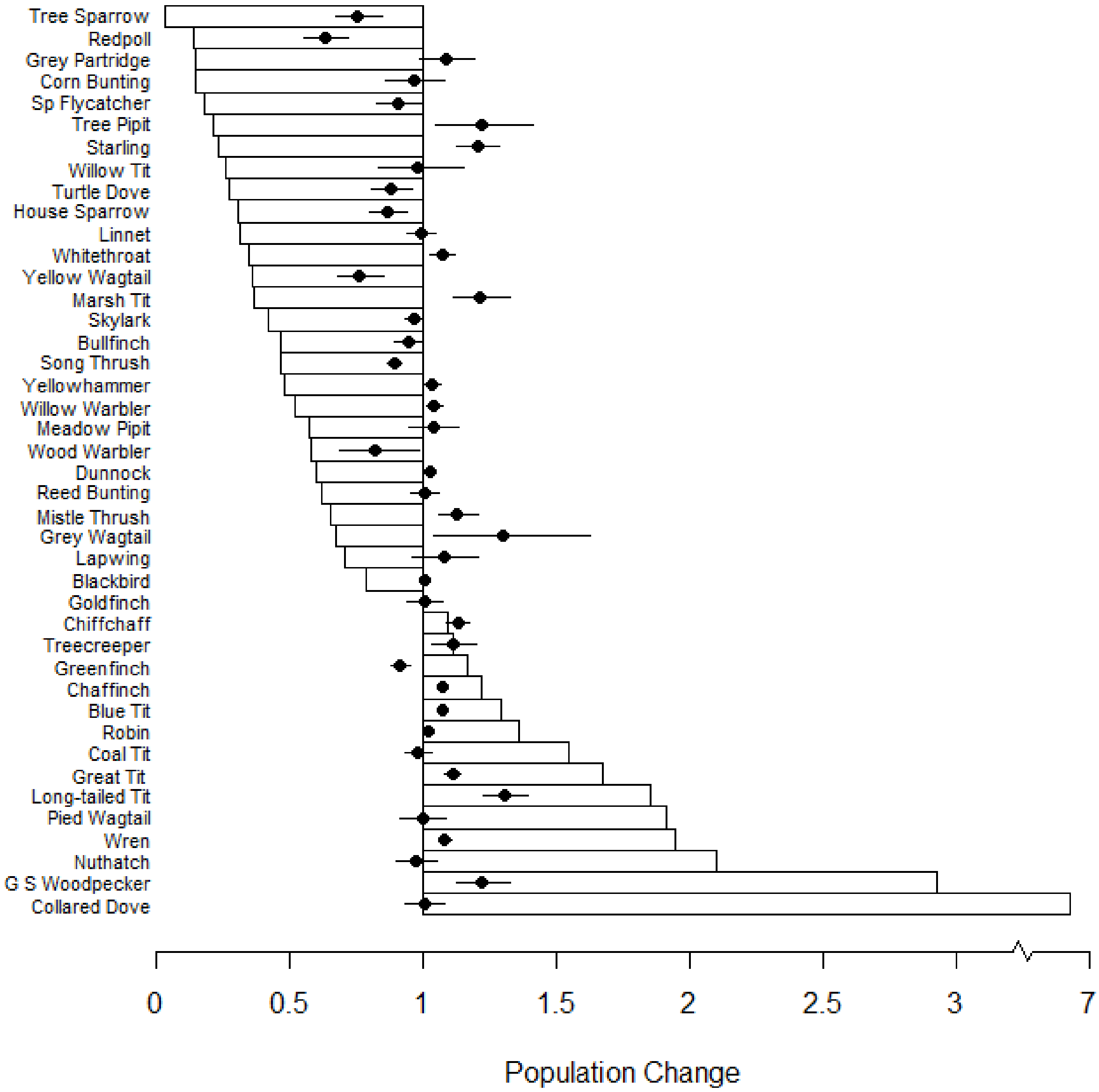


Figure 2. Species population change compared with that predicted on the basis of prey specific effects and change in site occupation by Sparrowhawks. Bars represent actual population change (Woodward et al. 2018), and dots show predicted population change ± 2 standard errors. The time interval for actual population change is 1967-2000 except for species for which population estimates start later than 1967, i.e. Collared Dove (1971), House Sparrow (1976) Wood Warbler (1994), and Grey Wagtail (1974). There is a significant positive association between predicted and actual change (Kendall's τ = 0.238, P=0.026).



Discussion

The resurgence of the population of Sparrowhawks in Britain, following the pesticide-related mid-20th century population crash, has the character of a quasi-experiment in which a major predator of adult songbirds re-settled a wide area from which it had been removed. This occurred in a place and period with a well-established system of songbird population monitoring, which also provided some data on the expanding distribution of the predator. The data available for Sparrowhawk are very limited, however, and may be misleading if taken at face value, as in the analysis of Thomson et al. (1998), who regressed territory counts of a number of potential prey species against a binary measure of Sparrowhawk presence and absence. This was recognised by Newson et al. (2010), who instead used a modelling approach to derive year-specific site estimates of relative Sparrowhawk activity from interpolated annual abundance surfaces. Again, however, there is reason to doubt whether such estimates reflect the true situation on the ground.

The level of predation experienced by a local bird community is directly related to the breeding status of Sparrowhawks within the locality, since the heaviest predation pressure occurs during the breeding season, when over 20 prey deliveries can be made to a nest per day (Newton 1986). The level of predator activity will generally decline at greater distances from the nest (Newton 1986), so predation within a census site will vary with its distance to local nest sites. The predator may then be recorded as present on the basis of anything from an occasional foray to a census site on the periphery of a hunting range, to a consistently high level of hunting pressure from a pair with a nest within or adjacent to the plot. Equally, given the elusive nature of the species, it may be that quite a high level of activity is required to guarantee observation of the species at a site, in which case it may be recorded as absent even when significant predation is taking place.

Regressing prey population data against raw predator presence-absence data therefore has obvious potential to produce misleading results. However, this also applies to spatial modelling based on presence/absence within census sites that are typically tens of kilometres apart, as although this provides a picture of varying density at a commensurate scale, it cannot represent variation in activity at the sub-kilometre scale of a typical census plot. To do so requires independent modelling of data from individual sites, though confidence in model estimates can only be achieved for sites with a reasonable sequence of data. The benefits of site-level modelling therefore trade off against loss of data from short-lived sites, all of which can be utilised by spatial modelling. However, the results strongly suggest that this is worthwhile, since the predictive power of the predator indices so derived is vastly improved over those of previous studies.

The frequency of significant positive associations with both Sparrowhawk and Collared Dove suggests that, despite the rapid increase and spread of both species, much of the variance in recorded presence within sites is still related to temporal variation in habitat quality. Collared Dove may therefore be responding to habitat changes in parallel with other species, while Sparrowhawk may also be responding directly to changes in prey species abundance. For Collared Dove especially, therefore, a significant degree of overlap in habitat requirements is a prerequisite for a positive association to emerge, and this may explain the single instance of a negative association with Meadow Pipit. This is a species that concentrates in rough grass and heathland in upland and coastal areas, contrasting with Collared Dove’s preference for the environs of human habitation, so overlap between the two species will often be in habitats that are marginal to both. A negative association may therefore arise as the declining Meadow Pipit population withdraws from mutually marginal habitats while the growing Collared Dove population expands into them.

It is impossible to rule out a similar explanation for the 11 negative associations that emerged for Sparrowhawk. However, given the frequency and in many cases the strength of these associations, an inference of direct interaction in the form of a predation effect may be more parsimonious, especially given the lack of obvious contrasts in habitat between Sparrowhawk and many of the negatively associated species. Such direct interaction does not preclude the occurrence of positive covariance caused by temporal variation in habitat quality, and the net association that emerges may therefore depend on the relative importance of the two opposing sources of covariance. Positive associations may emerge for species that are less affected by predation, and negative associations only where the impact of predation is sufficiently high to outweigh the effect of prey abundance tracking by the predator. This may in turn explain why the magnitude of actual population change is generally much larger than that predicted on the basis of increased site occupation by the predator despite the cross-species correlation between the two.

The effects reported here may therefore underestimate the negative impact of increased Sparrowhawk numbers on the abundance of prey species. Even so they indicate that increased Sparrowhawk numbers are often associated with a more negative prey population trajectory, predicting declines of almost a quarter in Tree Sparrow and Yellow Wagtail, and of more than a third in Redpoll. They also predict a decline in the Greenfinch, which increased in abundance over the relevant period, suggesting that its increase might have been substantially greater without the effect of increased Sparrowhawk abundance.

Whether or not the negative associations indicate a predation effect it is clear, contrary to the conclusions of previous studies such as those of Thomson et al. (1998) and Newson et al. (2010), that association between population change in Sparrowhawk and potential prey species was the rule in late 20th century Britain rather than the exception. This has wider implications owing to the influence of Newson et al. (2010) on the conclusions of recent reviews such as Madden et al. (2015) and Roos et al. (2018), since the very large number of predator-prey cases covered by Newson et al. tends to overpower the influence of other studies. Furthermore, if negative outcomes of increased predation are indeed being cancelled out by correlated changes in abundance caused by a common response across species to environmental variation, this may severely limit the utility of census data for investigation of ecological interactions between species, including competition. Nevertheless, the negative associations with Sparrowhawk that have emerged from this study are most readily interpreted, given their strength and frequency, as evidence of depression of prey populations as a result of the predator's increased abundance and ubiquity, and establish at the very least that such an effect cannot be dismissed as unlikely.

Supplementary Information

Figure S1. Plots of residuals against change in log predator indices for prey species with significant predator effects.

Data Accessibility

Access to Common Birds Census data was purchased under licence from the British Trust for Ornithology on condition of no disclosure to third parties.

Acknowledgements

Funding and moral support were provided by SongBird Survival, with special thanks to Keith Cowieson and Nick Forde.

References

Bell, C.P., Baker, S.W., Parkes, N.G., Brooke M. de L., and Chamberlain, D.E 2010. The role of the Eurasian Sparrowhawk (*Accipiter nisus*) in the decline of the House Sparrow (Passer domesticus) in Britain. The Auk 127: 411-420.

Chamberlain, D.E., Vickery, J.A., Glue, D.E., Robinson, R.A., Conway, G.J., Woodburn, R.J.W. and Cannon, A.R. 2005. Annual and seasonal trends in the use of garden feeders by birds in winter. Ibis 147: 563-575.

Chamberlain, D. E., Glue, D.E. and Toms, M.P. 2009. Sparrowhawk Accipiter nisus presence and winter bird abundance. Journal of Ornithology 150:247-254.

Freeman, S.N. & Newson, S.E. 2008. On a log-linear approach to detecting ecological interactions in monitored populations. Ibis 150: 250-258.

Gibbons, D.W., Amar, A., Anderson G.Q.M, Bolton, B., Bradbury, R., Eaton, M.A., Evans, A.D., Grant, M.C., Gregory, R.D., Hilton, G.M., Hirons G.J.M., Hughes, J., Johnstone, I., Newbery, P., Peach, W.J., Ratcliffe, N., Smith, K.W., Summers R.W., Walton, P. & Wilson J.D. (2007) *The predation of wild birds in the UK: a review of its conservation impact and management.* Research Report no 23, RSPB, Sandy.

Jones-Todd, C. M., Swallow, B., Illian. J.B., and Toms, M. 2017. A spatiotemporal multispecies model of a semicontinuous response. Journal of the Royal Statistical Society, Series C 67: 705-722.

Madden, C. F., Arroyo, B. & Amar, A. 2015. A review of the impacts of corvids on bird productivity and abundance. Ibis 157: 1–16.

Marchant, J.H. 1983. BTO Common Birds Census Instructions. British Trust for Ornithology.

Newton, I. 1986. The Sparrowhawk. Poyser.

Newson, S.E., Rextad, E.A, Baillie, S.R., Buckland, S.T & Aebischer, N.J. 2010. Population change of avian predators and grey squirrels in England: is there any evidence for an impact on avian prey populations? Journal of Applied Ecology 47: 244-252.

R Core Team. 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.

Roos, S., Smart, J., Gibbons, D.W. & Wilson, J.D. 2018. A review of predation as a limiting factor for bird populations in mesopredator-rich landscapes: a case study of the UK. Biological Reviews 93: 1915-1937

Swallow, B., Buckland, S.T., King, R., and Toms, M.P. 2015. Bayesian hierarchical modelling of continuous non-negative longitudinal data with a spike at zero: An application to a study of birds visiting gardens in winter. Biometrical Journal 58: 357-371.

Swallow, B., King, R., Buckland, S.T. & Toms, M.P. 2016. Identifying multispecies synchrony in response to environmental covariates. Ecology and Evolution 6: 8515-8525

Thomson, D. L., Green, R.E., Gregory, R.D., and Baillie, S.R. 1998. The widespread declines of songbirds in rural Britain do not correlate with the spread of their avian predators. Proceedings of the Royal Society, Series B 265: 2057-2062.

Woodward, I.D., Massimino, D., Hammond, M.J., Harris, S.J., Leech, D.I., Noble, D.G., Walker, R.H., Barimore, C., Dadam, D., Eglington, S.M., Marchant, J.H., Sullivan, M.J.P., Baillie, S.R. & Robinson, R.A. 2018. BirdTrends 2018: trends in numbers, breeding success and survival for UK breeding birds. Research Report 708. BTO, Thetford. www.bto.org/birdtrends

Appendix

The linear model used in Newson et al. (2010) included covariates in the form of measures of change in a number of additional predator indices, and in overall prey biomass, annual climatic averages, and bird detectability, viz.:

$$
\begin{aligned}
E[N_{i,t}] = \exp\Bigg[& \sum_{j=1}^{t-1} r_j + \alpha_{Squirrel}.\ln\left(\frac{P_{Squirrel,i,t} + 1}{P_{Squirrel,i,1} + 1}\right) + \alpha_{Crow}.\ln\left(\frac{P_{Crow,i,t} + 1}{P_{Crow,i,1} + 1}\right) \\
& + \alpha_{Magpie}.\ln\left(\frac{P_{Magpie,i,t} + 1}{P_{Magpie,i,1} + 1}\right) + \alpha_{Jay}.\ln\left(\frac{P_{Jay,i,t} + 1}{P_{Jay,i,1} + 1}\right) \\
& + \alpha_{Woodpecker}.\ln\left(\frac{P_{Woodpecker,i,t} + 1}{P_{Woodpecker,i,1} + 1}\right) + \alpha_{Hawk}.\ln\left(\frac{P_{Hawk,i,t} + 1}{P_{Hawk,i,1} + 1}\right) \\
& + \alpha_{Kestrel}.\ln\left(\frac{P_{Kestrel,i,t} + 1}{P_{Kestrel,i,1} + 1}\right) + \alpha_{Buzzard}.\ln\left(\frac{P_{Buzzard,i,t} + 1}{P_{Buzzard,i,1} + 1}\right) \\
& + \alpha_{Dove}.\ln\left(\frac{P_{Dove,i,t} + 1}{P_{Dove,i,1} + 1}\right) + \beta.\ln\left(\frac{Biomass_{i,t}}{Biomass_{i,1}}\right) \\
& + \gamma_{STemp}.\ln\left(\frac{W_{STemp,i,t}}{W_{STemp,i,1}}\right) + \gamma_{SRain}.\ln\left(\frac{W_{SRain,i,t}}{W_{SRain,i,1}}\right) \\
& + \gamma_{WTemp}.\ln\left(\frac{W_{WTemp,i,t}}{W_{WTemp,i,1}}\right) + \gamma_{WRain}.\ln\left(\frac{W_{WRain,i,t}}{W_{WRain,i,1}}\right) + \ln(N_{i,1}) \\
& + \ln\left(\frac{\widehat{P}_t}{\widehat{P}_1}\right)\Bigg]
\end{aligned}
$$

where *STemp* = mean daily minimum summer temperature, *WTemp* = mean daily minimum winter temperature, *SRain* = number of summer days with rainfall, *WRain* = number of winter days with rainfall, and $\widehat{P}$ = prey species detection probability. The detectability variable was used only in their analysis of Breeding Bird Survey data, and will not be considered further.

The rationale for using indices of change in predator activity as explanatory variables rather than simple measures of predator activity in any given year, as in Thomson et al. (1998) and Chamberlain et al. (2009), is that the response of prey populations is likely to be density-dependent. If there is an episodic increase in predator presence at a site, an affected prey population will decrease, but then re-establish stability at a lower level. Consequently, zero change in prey populations will correspond with both low and high levels of the predator, and the regression will indicate no association (Newson et al. 2010). By contrast, change in predator activity returns to zero after the increase and therefore has a linear negative relationship with prey population change.

It may be safe to assume that this applies to all monotonic changes in predator activity (including declines) to a reasonable approximation, even if the prey population shows a lagged response, since the effect of each annual change will tend to reinforce that of the last. If lags do occur it may not be so safe in the case of fluctuating predator populations, especially if the fluctuations are abrupt, but this is not an issue with the present application since reversals in the trend of Sparrowhawk activity are rare to non-existent, and in any case the logistic model used to derive the predator index assumes a monotonic trend.

The same does not apply to some of the other change indices included in the linear model of Newson et al. (2010), particularly those relating to weather, as seasonal means in temperature and rainfall fluctuate more or less randomly about their long-term average. In addition, prey populations are unlikely to respond symmetrically to changes of equivalent magnitude in the opposite direction, e.g. a decline caused by severe winter may not be immediately reversed by an average winter or even by a mild one. Consequently, $\ln\left(\frac{W_{WTemp,i,t}}{W_{WTemp,i,1}}\right)$ may bear little relation to the aggregate effect of weather between years 1 and t, and the same applies to change indices derived from the other weather variables.

Even if this were not so, the weather variables would be largely redundant, since variance in prey populations related to annual variation in weather conditions is explained by the $\sum r_j$ term in the model. The various weather terms could therefore account only for variance among sites related to differences from national average weather conditions over any given period. Given the geographic scale of the study, such differences will be minor, and will converge rapidly on the long-term average over lengthening time intervals, so are unlikely to have any additive explanatory power in relation to spatio-temporal variation in prey populations.

The rationale for including measures of change in a range of predatory species is that all of the predators included have increased their abundance, and therefore change in predator abundance within census sites may be correlated. Independently-measured covariance between an individual predator and a prey species may therefore be partially attributable to the impact of the correlated predators. However, Newson et al. (2010) report low variance inflation factors for the predator variables in their analysis, indicating low multicollinearity, and it is therefore unlikely that the effect sizes reported here have been amplified by the absence of covariates representing the abundance of other predators.

The reason given for including measures of change in overall prey biomass is that it ‘may buffer against impact on the prey species of interest’. This assumes that the change in focal species abundance caused by a change in predation is likely to be inversely related to the simultaneous change in alternative prey abundance, which may be true if the two are coupled solely through the action of the predator. However, change in environmental factors such as weather, habitat and predation are likely to have similar effects across species, in which case change in overall prey biomass will be correlated with change in focal prey abundance. Inclusion of the former as a predictive variable will therefore partition out much of the variance in the latter, including that attributable to predation, and its inclusion in the linear model is therefore problematic.