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Evaluating the population-level impact of an invasive species, Ring-necked Parakeet *Psittacula krameri*, on native avifauna

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The introduction of exotic species to ecosystems can have severe consequences for populations of native organisms, but logistical limitations and shortage of historical data often hinder attempts to quantify the ecological implications of such relationships. The establishment and rapid expansion of Ring-necked Parakeets *Psittacula krameri* in England therefore presents a rare opportunity to apply novel analytical methods to existing extensive national bird monitoring data from the UK Breeding Bird Survey for an invasive species. A previous study from Belgium suggests that Ring-necked Parakeets have the potential to reduce the abundance of Eurasian Nuthatch *Sitta europaea* through competition for nesting cavities. Our analysis provides no evidence for a significant impact through competition on Nuthatch populations or those of any other cavity-nesting species within the Parakeet's current range in the UK. However, we cannot exclude the possibility that competitive exclusion could be occurring at a minority of sites at which availability of nest cavities is limiting. This may yet have significant implications for future conflict if Parakeets continue to increase in numbers and range.

Keywords: cavity-nesting bird, competition, invasive species, rates of population change, Ring-necked Parakeet.

When novel organisms are introduced to an ecosystem, consequences for native species can be severe (Gurevitch & Padilla 2004, Clavero *et al.* 2009). Impacts may be direct, through predation, competition or hybridization, or indirect, via the introduction of new parasites and pathogens. Once an exotic species becomes established, it is necessary that any impacts are quantified as quickly as possible in order to implement effective mitigation. However, efforts to quantify impacts may be compromised by a lack of data on native species prior to the establishment of the invasive species and by the logistical restrictions of carrying out monitoring at large spatial scales (Wittenberg & Cock 2001). In North America, for example, the non-native European Starling *Sturnus vulgaris* and House Sparrow *Passer domesticus* may compete for nesting sites with native cavity-nesting birds (Ingold 1998), but because the populations of these species became established in the 19th century, the patterns and processes occurring at their initial colonization are poorly understood and the influence of these species on native species remains a subject of debate (Koenig 2003). Studies of the relationship between invasive species and indigenous birds in the UK are facilitated by the existence of long-term monitoring programmes such as the British Trust for Ornithology (BTO)/RSPB/Joint Nature Conservation Committee (JNCC) Breeding Bird Survey (BBS), which records changes in avian abundance at a national scale (e.g. Newson *et al.* 2008).

The focus of this study is to examine the evidence for a population-level impact of Ring-necked Parakeets *Psittacula krameri* on native cavity-nesting bird species in the UK. The Ring-necked Parakeet is the most widely introduced parrot in the world, with breeding populations established in 35 countries in five continents (Butler 2003). Ring-necked Parakeets became established in the wild in the UK in the 1970s after captive birds

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escaped or were released (Butler 2003). The majority of the UK population is located in the southeast of England, centred on the Greater London area. In 1996, a census by simultaneous roost counts estimated the population to be approximately 1500 birds (Pithon & Dytham 1999), and BBS data suggest that the population grew by as much as 600% between 1995 and 2007 (Baillie *et al.* 2009). Butler (2003) noted that Parakeets are increasingly being seen in rural areas rather than the previously typical urban and semi-urban areas, and suggested that they may soon spread into the wider UK countryside.

Ring-necked Parakeets are secondary cavity nesters and are therefore dependent on holes excavated by other species, such as Great Spotted Woodpecker *Dendrocopos major* and Green Woodpecker *Picus viridis* (Butler 2003). This behaviour has the potential to bring them into conflict with a number of native species that use similar sites to nest, including Eurasian Nuthatch *Sitta europaea*, Blue Tit *Cyanistes caeruleus*, Great Tit *Parus major*, Stock Dove *Columba oenas* and European Starling, particularly as cavity availability in England is thought to be decreasing as a result of changing woodland management (Newton 1998). As a guide to natural hole use by the smaller native species considered here, Blue Tit and Great Tit, minimum entrance hole diameters recommended for nest-boxes (25 and 28 mm, respectively; Du Feu 2003) would exclude Parakeets, which cannot enter holes smaller than 40 mm (Strubbe & Matthysen 2009). However, these native species also make use of larger cavities of 40–60 mm created by Great Spotted and Green Woodpeckers (Nilsson 1984, Wesolowski & Rowiński 2004). In two recent studies of Ring-necked Parakeets in the UK, the majority of nest cavities were between 40 and 80 mm in diameter (54%: Butler 2003; 77%: D. Parrott, C. Rhodes, S. Brown, P. Cropper, unpubl. data), so we retain these two smaller native species here as potential competitors. Competition may be exacerbated by the early onset and relatively prolonged duration of breeding of Parakeets. In England, Parakeets start breeding at the end of February (median date 23 March; Butler 2003) and nests remain active until the chicks fledge towards the end of May, long after the majority of native species have initiated their first breeding attempts. The relatively large size and aggressive nature of the Parakeets makes it unlikely that they are usurped during the breeding cycle.

Previous studies have identified nest-holes as a limiting resource for cavity-nesting species (Nilsson 1984, Newton 1998). Recent evidence from Belgium indicates that European Nuthatch abundance in the Brussels area is negatively correlated with abundance of Parakeets (Strubbe & Matthysen 2007) and subsequent experimental studies carried out on the same population provides some further support that this relationship is driven by competitive exclusion from nest-sites (Strubbe & Matthysen 2009). The aim of this study was therefore to assess the evidence for a similar relationship between Parakeet abundance and that of eight secondary cavity nesters in England that occur within the current distribution of Ring-necked Parakeet, using national monitoring data that cover the main period of Ring-necked Parakeet population expansion.

METHODS

Survey methods

We use survey data from the BBS (Newson *et al.* 2008), which was introduced in 1994 and provides a rigorous approach to the monitoring of widespread bird species. The BBS is based on a formal sampling framework in which 1-km squares are randomly selected from those in the National Grid according to a stratified random sampling design, and approximately 2500 1-km squares are surveyed each year. Fieldwork involves two visits to squares to count birds along two non-overlapping 1-km transects across each square. In these analyses we use only data from the early visit between early April and mid-May to reduce the possibility of including juvenile birds in the analyses. As this study focuses on impacts of Ring-necked Parakeets, which currently have a relatively restricted range centred on the London area in southern England, analyses were restricted to 180 sites at which Parakeets were recorded in at least one of the survey years between 1994 and 2008. This period coincided with a period of major population growth and expansion of the Parakeet population.

Native cavity-nesting species which occur within the current distribution of Ring-necked Parakeet and which may therefore potentially compete for nesting holes include Green Woodpecker, Great Spotted Woodpecker, Nuthatch, Great Tit, Blue Tit, Jackdaw *Corvus monedula*, Stock Dove and European Starling. Another potential competitor, Lesser Spotted Woodpecker *Dendrocopos minor*, was only recorded on 11 BBS squares and considered too scarce to include in these analyses.

Analytical methods

The first analysis presented here explores the relationship between the number of Ring-necked Parakeets and potential nest-site competitors on surveyed sites. This approach is broadly comparable with Strubbe and Matthysen (2007), who identified a negative correlation between Ring-necked Parakeet and Eurasian Nuthatch abundance across 44 sites in their Belgian study area. We used a repeated-measures generalized linear model with Poisson errors and log link, applied using the GENMOD procedure in SAS (SAS Institute 2001), to examine the relationship between Ring-necked Parakeets and each potential competitor in turn. Non-independence of successive counts in the same 1-km squares was taken into account by applying a repeated statement using the 1-km square as subject. Important to the interpretation of these results are species–habitat associations, which may result in significant correlations unrelated to species interactions. We used the Centre for Ecology and Hydrology (CEH) Landcover dataset (Haines-Young *et al.* 2000) to determine the proportion of each BBS square that could be assigned to 'human habitation', one of three aggregate habitat classifications that can be derived from these data (the others being woodland and agricultural land). Where a significant association between species was identified, we repeated the analyses incorporating a term for 'human habitation' in the model.

A second set of analyses used a recent approach developed by Freeman and Newson (2008) to relate change in the abundance of cavity-nesting species (referred to here as the focal species) to the abundance of potential competitors at individual sites. The range and mean count of each species on surveyed sites are shown in Table 1. Although the main interest here is the impact of Parakeets, for a balanced view we consider the importance of each species as a potential competitor, controlling for all other species present. Details of the full model are as follows.

Suppose that $\mu_{i,t}$ is the expected count of the focal species at site i in year t, $P_{k,i,t}$ is the count of the competitor k, R_t is the instantaneous rate of change of the focal species population during the period $t-1$ to t in the absence of any covariate effect, α_k is the effect on that rate of change of competitor k, and K is the total number of competing species. We assume that $\mu_{i,t}$ has a Poisson distribution, and account for large-scale annual changes and the local effect of each competitor. The effect of each competing species is introduced using parameter α_k, such that the change of the focal species population at a site where competing

Table 1. Information relevant to the analyses of BBS data and results of a correlation between Ring-necked Parakeets and focal species counts with and without controlling for habitat (% woodland and human habitation).

Focal species	No. of sites recorded as present	Mean count/ site (range)	Trend[1]	Relationship with Ring-necked Parakeet counts: Without controlling for human habitat	Relationship with Ring-necked Parakeet counts: Controlling for human habitat
Blue Tit *Cyanistes caeruleus*	171	12.6 (0–42)	−1	**1.291** (0.004)***	0.003 (0.001)
Green Woodpecker *Picus viridis*	145	1.2 (0–7)	117 ↑	**0.007** (0.003)**	**0.009** (**0.004**)*
Great Spotted Woodpecker *Dendrocopos major*	155	1.3 (0–6)	97 ↑	0.003 (0.005)	0.003 (0.006)
Great Tit *Parus major*	172	6.9 (0–21)	25 ↑	**0.012** (0.004)**	**0.007** (0.001)***
Western Jackdaw *Corvus monedula*	110	5.1 (0–82)	200 ↑	**0.012** (0.006)*	0.011 (0.005)
Eurasian Nuthatch *Sitta europaea*	83	0.4 (0–5)	17	−**0.078** (0.038)*	0.006 (0.011)
Ring-necked Parakeet *Psittacula krameri*	180	3.7 (0–39)	534 ↑	NA	NA
Stock Dove *Columba oenas*	88	0.7 (0–7)	31	−0.008 (0.013)	0.007 (0.006)
European Starling *Sturnus vulgaris*	171	30.3 (0–154)	−42 ↓	**0.031** (0.002)***	0.001 (0.003)

*P < 0.05, **P < 0.01, ***P < 0.001. Significant results are further highlighted in bold. Columns are estimated coefficients for the predictors, and their standard errors in parentheses.

[1]Trends (percentage change in relative abundance between 1994 and 2008) on BBS squares recording Parakeets in one or more years. An arrow denotes significant (at the P < 0.05 level) net change in population size.

species abundance is r_t, the annual rate of change in focal species abundance is modified by a factor $\exp(r_t/\alpha_k)$.

$$\ln \mu_{i,T} = \sum_{t=1}^{T-1} R_t + \sum_{k=1}^{K} \left(\alpha_k \sum_{t=1}^{T-1} P_{k,i,t} \right) + \ln(\mu_{i,1})$$

Models were implemented by fitting generalized linear models using the GENMOD procedure in SAS with Poisson errors and a log link function. Because the Pearson chi-squared divided by the degrees of freedom was > 3 for several species, we formally account for overdispersion in these analyses. To reduce the degree of multiple testing, we fitted a single model for each focal species that included all potential competitor terms and the overall effect of those competitor terms was assessed using a likelihood ratio (LR) test. Further investigation of the individual coefficients was only undertaken if a significant result was found at this stage. Examination of the residuals suggested that model fits were good.

RESULTS

In agreement with Strubbe and Matthysen (2007), our initial analyses identified a significant, though weak, negative association between numbers of Ring-necked Parakeets and Eurasian Nuthatches (GLM coefficient = −0.078, se = 0.038, $z = -2.04$, $P = 0.041$) on surveyed sites (Table 1). However, once we control for human habitation in the analyses, which we demonstrate is positively associated with numbers of Ring-necked Parakeets (GLM coefficient = 0.015, se = 0.002, $z = 6.84$, $P \leq 0.0001$) and negatively associated with Nuthatches (GLM coefficient = −0.023, se = 0.003, $z = -7.35$, $P \leq 0.0001$), the relationship between Parakeets and Nuthatches was removed (GLM coefficient = 0.006, se = 0.011, $z = 0.57$, $P = 0.57$). A number of significant positive associations between Ring-necked Parakeets and other cavity-nesting species were similarly removed once human habitation was included in the model (Table 1).

In the second set of analyses we assessed whether there is evidence that rates of change in native cavity-nesting birds have been depressed by Parakeets. Here the only significant negative relationship identified between Parakeets and a potential competitor was for Blue Tits (Table 2). However, a coefficient value for α of −0.001 corresponds to an approximate 0.1% decrease in growth rate of Blue Tits on a BBS square for each additional Parakeet, which is negligible. Therefore there is little evidence from these analyses that Ring-necked Parakeets have had a biologically important impact on the populations of any native cavity-nesting bird in England during the period 1994–2008. Although not the principal focus of this paper, there was better evidence in the above analyses for interactions between some of the native species considered than for interactions between Parakeets and native species (Table 2).

DISCUSSION

Although a negative correlation between Parakeet numbers and those of Nuthatches was detected initially, this relationship did not persist when the degree of urbanization of the study site was taken into account. The association detected is therefore unlikely to stem from the competitive exclusion of Nuthatches from nest-cavities. Instead, it is most likely to reflect the differential habitat preferences of the two species, with Parakeets favouring built-up habitats that Nuthatches either avoid or are unable to colonize due to their relatively poor dispersal ability (Bellamy *et al.* 1998).

Our analyses of extensive national bird monitoring data from England therefore provide no statistical evidence that Nuthatch populations are either smaller or that growth rates are depressed at sites where Ring-necked Parakeet numbers are higher. These findings do not agree with those of Strubbe and Matthysen (2007), who identified a negative association between Parakeet and Nuthatch numbers across a number of study sites in Brussels and interpreted this as most likely to represent a causal relationship of one species on the other. While their models did not incorporate the proportion of each site that could be classified as urban, they did account for broad-scale habitat type by including a term specifying the amount of woodland, which is likely to display a strong negative correlation with urban land cover. Furthermore, experimental work undertaken by the same authors has provided some further support for the idea that Parakeets outcompete Nuthatches for nesting sites in their study area (Strubbe & Matthysen 2009). At two sites, a proportion of cavities were blocked, leading to a significant decline in Nuthatch numbers the

Table 2. Change in the abundance of cavity-nesting species in relation to the abundance of potential competitors as indicated by Breeding Bird Survey data 1994–2008. Here we focus on sites where Ring-necked Parakeets were recorded during the survey period.

Focal Species	Potential competitor: Blue Tit	Green Woodpecker	Great Spotted Woodpecker	Great Tit	Jackdaw	Nuthatch	Ring-necked Parakeet	Stock Dove	Starling
Blue Tit	–	−0.003 (0.004)	−0.001 (0.004)	−0.001 (0.001)	−**0.001** (0.000)**	−0.003 (0.006)	−**0.001** (0.000)*	−0.003 (0.002)	−0.000 (0.000)
Green Woodpecker	*0.003 (0.001)*	–	*−0.005 (0.007)*	*−0.003 (0.003)*	*0.000 (0.001)*	*−0.013 (0.009)*	*−0.002 (0.001)*	*0.003 (0.004)*	***0.001 (0.000)****
Great Spotted Woodpecker	*0.000 (0.001)*	*−0.007 (0.007)*	–	*0.003 (0.003)*	*−**0.002** (0.001)**	*−0.004 (0.009)*	*0.000 (0.001)*	*−0.006 (0.004)*	*−0.000 (0.000)*
Great Tit	0.000 (0.001)	−0.006 (0.005)	−**0.010** (0.005)*	–	−**0.001** (0.001)*	0.012 (0.007)	−0.001 (0.001)	−0.001 (0.002)	−0.000 (0.001)
Western Jackdaw	**0.005** (0.001)***	**0.031** (0.007)***	−0.004 (0.006)	−**0.007** (0.003)*	–	−**0.030** (0.010)**	−0.001 (0.001)	−0.005 (0.003)	0.000 (0.000)
Eurasian Nuthatch	**0.003** (0.002)*	−0.006 (0.007)	0.006 (0.007)	−0.004 (0.003)	−**0.003** (0.000) **	–	−0.002 (0.001)	−**0.019** (0.006)**	−0.000 (0.000)
Ring-necked Parakeet	−**0.010** (0.002)***	0.016 (0.013)	−**0.035** (0.016)*	0.002 (0.005)	−**0.003** (0.000) ***	0.048 (0.025)	-	−**0.032** (0.009)***	−0.000 (0.000)
Stock Dove	−0.004 (0.003)	0.002 (0.012)	**0.029** (0.013)*	**0.010** (0.005)*	0.000 (0.002)	−0.001 (0.020)	0.000 (0.003)	–	0.001 (0.001)
European Starling	0.001 (0.001)	−0.005 (0.006)	0.001 (0.007)	−**0.004** (0.002)*	−**0.002** (0.001)*	−0.022 (0.011)	−0.001 (0.001)	−0.005 (0.003)	–

*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$. Significant results are further highlighted in bold and results where the likelihood ratio test is not significant are highlighted in italics. Columns are estimated coefficients for the predictors, and their standard errors in parentheses.

following year, but not in Parakeet abundance (although Parakeet abundance was reduced by a third at one of the two study areas).

If Parakeets do competitively exclude Nuthatches in Belgium, leading to a reduction in abundance, why do we not observe similar impacts in England? It is possible that our ability to detect such an effect may have been confounded by spatial variation in environmental variables across the study area. However, this is unlikely as several positive relationships between Parakeet numbers and those of other cavity nesters were detected, as discussed below. The statistical power to detect a relationship using the Freeman and Newson (2008) model is relatively high, as indicated by the small, but significant, effects presented in Table 2. In addition, a power analysis was carried out to quantify the magnitude of decline that would be detectable should Ring-necked Parakeets be driving declines in native cavity-nesting species. We focus here on Nuthatches, although we expect that the power to detect a relationship would be equivalent or higher for other cavity-nesting species, which were recorded on a greater number of sites (Table 1).

The analytical approach used in the power analyses was the Freeman and Newson (2008) recursive log-linear model, where simulated populations were analysed in the same way. Simulated populations were established with the same number of sites on which Nuthatches were seen. For each simulated population, the site effects and year effects were each drawn from a normal distribution with mean and variance the same as the real data. The number of years with site counts was also taken from the real data, so that the occurrence of missing values and site turnover was realistic. As in the main Freeman and Newson analyses, the cumulated numbers of Parakeets at the different sites from the real data were used. Sixteen different effect sizes of Parakeet/Nuthatch interactions were considered, ranging from zero to −0.030, at intervals of 0.002, where an effect size of −0.030 is equal to about a 3% decline in the annual rate of change of the Nuthatch population for each additional Parakeet. For each effect size, 1000 populations were simulated, and for each of these a model was run on the simulated data, and the coefficient and significance of the effect of Parakeets on Nuthatches were recorded. The proportion of the 1000 simulations that recorded a significant ($P < 0.05$) negative effect of Parakeets

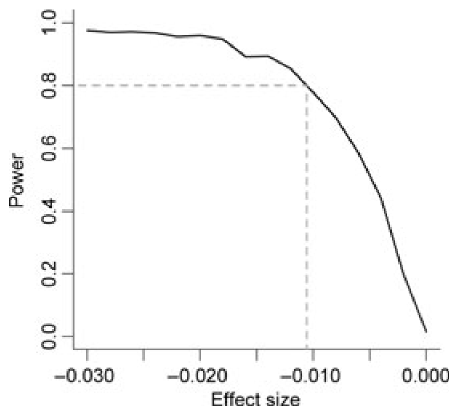

Figure 1. The power to detect different levels of negative effects through competition of Ring-necked Parakeets on another cavity-nesting species based on 1000 simulations. The effect size that can be detected with 80% power is shown with a dotted line. Number of individuals and sites are based on Eurasian Nuthatch data, although power should be equivalent or higher for other cavity-nesting species considered here which were recorded on a larger number of sites.

was recorded as the power of detecting an effect of that size. The relationship between effect size and power is shown in Fig. 1. This shows that it would be possible to detect an effect size of −0.0106 with 80% power, which is equivalent to about a 1% decline in annual growth rate of the Nuthatch population for each additional Parakeet. Should this power to detect a relationship exist, we feel that the absence of an association here supports the interpretation that there is currently no strong evidence for a significant impact through competition of Ring-necked Parakeets on cavity-nesting species within the Parakeet's current range in the UK.

Due to differences in the survey methodology used to calculate abundance in our study (line transects across randomly selected 1-km squares) and those of Strubbe and Matthysen (point counts in suitable habitat only), we are unable to compare absolute densities of either Parakeets or native cavity-nesters in Brussels with those in England, and cannot exclude the possibility that the intensity of competition in England is low because the number of competing individuals is lower. A similar discrepancy might be predicted if the number of suitable cavities per unit area was lower in Belgium than in England. The availability of nest-sites has been shown to be important in the USA, where European Starlings have been introduced and are known to evict several native species such as flickers *Colaptes* spp. and bluebirds *Sialia* spp. from potential nest-sites (Davies *et al.* 1986, Ingold 1998). However, in the presence of Starlings, bluebirds shift to breed in smaller and deeper cavities not preferred by Starlings (Pinkowski 1976, Peterson & Gauthier 1985), thus allowing coexistence. Comparative studies would be valuable in assessing whether the Belgian Parakeet population has reached a threshold level with respect to potential nest-sites that the English population has yet to attain, thus informing predictions of impacts on native species if numbers continue to increase.

Although we found no evidence of a population-level effect, we cannot exclude the possibility that this threshold could have been exceeded at a minority of sites in England. Models used by Strubbe and Matthysen (2007) controlled for tree species composition and cavity availability that were identified as important in determining Nuthatch abundance, but do not report whether the relationship with Parakeet abundance remained significant if these terms were removed. Equivalent data are not currently available for the English sites used in our analyses, although it should be noted that the deviance (Pearson chi-squared divided by the degrees of freedom) of a model exploring the relationship between Nuthatch numbers and Parakeet abundance was close to 1, providing little evidence for over-dispersion in our analyses, and suggesting that the amount of unexplained variance in the dependent variable was low. Intensive fieldwork studies will be important in determining the strength of interactions between cavity availability and competition.

There was perhaps stronger evidence for significant relationships between Parakeets and the other native cavity nesters included in the analysis. Butler (2003) located 108 Parakeet nests in the London area and observed that the majority were using holes originally excavated by Green Woodpeckers. We observed a weak significant correlation between numbers of these two species in our study, providing some support for the hypothesis that Parakeet abundance could be limited by the availability of cavities created by woodpeckers. The positive relationship between Great Tit numbers and those of Parakeets is more difficult to interpret, and may be driven by shared associations with fine-scale habitat features.

The only evidence for a negative effect of Parakeets on the populations of any native species is the observation that Blue Tit population growth rates were lower at sites where there were more Parakeets. However, it should be noted that the magnitude of this relationship is small, approximately equivalent to a 1% decline in the annual rate of change for each additional competitor. In addition, the relationship may not be driven by competition, but could be due to differential habitat selection, with Parakeets favouring those areas that were less suitable for Blue Tits. This might also explain the significant negative correlations observed between Parakeet population growth rates and the abundance of Blue Tit, Great Spotted Woodpecker, Jackdaw and Stock Dove, the native species potentially being less abundant in the more urban areas apparently preferred by Parakeets (Strubbe & Matthysen 2007).

In conclusion, this study found no strong evidence that, within their current geographical range and at current densities in England, Ring-necked Parakeets are negatively influencing the abundance of Nuthatches or any other common native cavity-nesting species. It should be noted here that the overlap between core areas of Parakeet and Nuthatch populations at a national scale is, at present, minimal (BTO Bird Atlas 2007–2011 unpubl. data). However, neither of these observations excludes the possibility of conflict in the future, particularly as Ring-necked Parakeet populations are continuing to grow (Baillie *et al.* 2009). The studies of Strubbe and Matthysen (2007, 2009) suggest that, in situations where nest-cavities are a limiting resource, Ring-necked Parakeets may have the ability to out-compete Nuthatches, resulting in population declines of the latter, and it is possible that at higher Parakeet densities, other native species might be affected in similar ways. Further intensive field studies, focusing on known Parakeet hotspots in England, are therefore required to determine whether there are any sites at which such negative impacts are already occurring, and if so, how population densities and habitat types interact to mediate competition. This approach, coupled with predictive modelling of the Parakeet population expansion, will enable us to assess the potential for impacts of Ring-necked Parakeets on native species in future.

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REFERENCES

Baillie, S.R., Marchant, J.H., Leech, D.I., Joys, A.C., Noble, D.G., Barimore, C., Grantham, M.J., Risely, K. & Robinson, R.A. 2009. *Breeding Birds in the Wider Countryside: Their Conservation Status 2008*. BTO Research Report No. 516. BTO, Thetford. (http://www.bto.org/birdtrends).

Bellamy, P.E., Brown, N.J., Enoksson, B., Firbank, L.G., Fuller, R.J., Hinsley, S.A. & Schotman, A.G.M. 1998. The influences of habitat, landscape structure and climate on local distribution patterns of the Nuthatch (*Sitta europaea* L.). *Oecologia* **115**: 127–136.

Butler, C.J. 2003. *Population biology of the introduced Rose-ringed Parakeet* Psittacula krameri *in the UK*. PhD thesis, Department of Zoology, Edward Grey Institute of Field Ornithology, University of Oxford.

Clavero, M., Brotons, L., Pons, P. & Sol, D. 2009. Prominent role of invasive species in avian biodiversity loss. *Biol. Conserv.* **142**: 2043–2049.

Davies, W.H., McComb, W.C. & Allaire, P.N. 1986. Nest box use by starlings: does it inhibit bluebird production? *J. Ky. Acad. Sci.* **47**: 133–136.

Du Feu, C. 2003. *The BTO Nestbox Guide*. Thetford: British Trust for Ornithology.

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

Gurevitch, J. & Padilla, D.K. 2004. Are invasions a major cause of extinctions? *Trends Ecol. Evol.* **19**: 470–474.

Haines-Young, R.H., Barr, C.J., Black, H.I.J., Briggs, D.J., Bunce, R.G.H., Clarke, R.T., Cooper, A., Dawson, F.H., Firbank, L.G., Fuller, R.M., Furse, M.T., Gillespie, M.K., Hill, R., Hornung, M., Howard, D.C., McCann, T., Morecroft, M.D., Petit, S., Sier, A.R.J., Smart, S.M., Smith, G.M., Stott, A.P., Stuart, R. & Watkins, J.W. 2000. *Accounting for Nature: Assessing Habitats in the UK Countryside*. London: DETR.

Ingold, D.J. 1998. The influence of Starlings on Flicker reproduction when both naturally excavated cavities and artificial nest boxes are present. *Wilson Bull.* **110**: 218–225.

Koenig, W.D. 2003. European Starlings and their effect on native cavity-nesting birds. *Conserv. Biol.*, **17**: 1134–1140.

Newson, S.E., Evans, K.L., Noble, D.G., Greenwood, J.J.D. & Gaston, K.J. 2008. Use of distance sampling to improve estimates of national population sizes for common and widespread breeding birds in the UK. *J. Appl. Ecol.* **45**: 1330–1338.

Newton, I. 1998. *Population Limitation in Birds*. London: Academic press.

Nilsson, S.G. 1984. The evolution of nest site selection on hole-nesting birds: the importance of nest predation and competition. *Ornis Scand.* **15**: 167–175.

Peterson, B. & Gauthier, G. 1985. Nest site use by cavity-nesting birds of the Cariboo Parkland, British Columbia. *Wilson Bull.* **97**: 319–331.

Pinkowski, B.C. 1976. Use of tree cavities by nesting Eastern Bluebirds. *J. Wildl. Manage.* **40**: 556–563.

Pithon, J.A. & Dytham, C. 1999. Breeding performance of Ring-necked Parakeets *Psittacula krameri* in small introduced populations in southeast England. *Bird Study* **46**: 342–347.

SAS Institute. 2001. *SAS/STAT User's Guide Version, 8.02*. Cary, NC: SAS.

Strubbe, D. & Matthysen, E. 2007. Invasive Ring-necked Parakeets *Psittacula krameri* in Belgium: habitat selection and impact on native birds. *Ecography* **30**: 578–588.

Strubbe, D. & Matthysen, E. 2009. Experimental evidence for nest-site competition between invasive Ring-necked Parakeets (*Psittacula krameri*) and native Nuthatches (*Sitta europaea*). *Biol. Conserv.* **142**: 1588–1594.

Wesolowski, T. & Rowiński, P. 2004. Breeding behaviour of Nuthatch in relation to natural hole attributes in a primeval forest. *Bird Study* **51**: 143–155.

Wittenberg, R. & Cock, M.J.W. 2001. *Invasive Alien Species: A Toolkit of Best Prevention and Management Practices*. Wallingford: CAB International.

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