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EDITOR'S COMMENT

This paper reviews the literature in relation to the accepted decline in the House Sparrow population in both urban and rural environments in the UK over the past 40 years. It is timely in its evaluation which critically appraises the accepted hypotheses with respect to distribution, abundance and demographical aspects of sparrow populations deemed responsible for the observed declines.

What is in evidence from the review is that predator/prey interactions are currently only receiving scant attention by the scientific community. The possibility that Sparrowhawks are significant contributors to House Sparrow (and other passerine) fluctuations in both urban and rural habitats appears to be out of vogue. Birds of prey in particular are above rebuke and today hypotheses are designed to verify their innocence rather than test the extent of their contribution to prey population regulation.

This paper dares to question the scientific evidence being used to drive rural agri-environmental schemes and urban environmental enhancement projects and even National Biodiversity Action Plans. It hints at the negative impact of the competing forces of politics and business on scientific rigour and objectivity, reminding us that indirect evidence and correlation are a poor substitute for direct cause and effect relationships.

Note: The opinions expressed in this paper are not necessarily the view upheld by the ISS journal.

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MISAPPLIED ECOLOGY: INVESTIGATIONS OF POPULATION DECLINE IN THE HOUSE SPARROW

Ecology aims to explain the distribution and abundance of organisms, and to this end has generated a vast array of theory, empirical data and models. However it has been unable to offer a robust explanation of the rapid decline of a common and conspicuous species, the House Sparrow *Passer domesticus*, which lives in close proximity to human populations. This is despite intensive analysis of long-term datasets on the species' distribution, abundance and demography, and the implementation of a range of field investigations. Nevertheless, a tacit consensus among researchers has coalesced around the hypothesis that population decline is related to deteriorating food availability, though with different ultimate causes in urban and rural populations. Recently, however, evidence has emerged that the decline of sparrow populations in Britain can be simply explained as a consequence of a build up in the population of its major predator, the Eurasian Sparrowhawk *Accipiter nisus*.

This review of research on the decline of the House Sparrow is divided into two parts. In the first part I summarize the investigations that have been undertaken and their major findings. In the second part I examine the evidential base of the consensus, and argue that despite the extensive research effort, there is little or no critical evidence to support the consensus view. I also argue that the emergence of compelling evidence in favour of predation as a cause of sparrow decline undermines the rationale both of continuing research, and of emerging conservation recommendations. I finally consider the implications of these conclusions for the wider issue of bird population declines on farmland and the implementation of agri-environment schemes aimed at reversing such declines.

REVIEW OF RESEARCH ON HOUSE SPARROW DECLINES

Coverage in this review section is confined to studies carried out or supervised by professional ecologists, and supported by recognised public or private research funding bodies. It does not, therefore, brave the wilder frontiers of speculation that have been generated by widespread public awareness of this issue.

HOUSE SPARROWS AND FARMLAND BIRD DECLINES

Intensive monitoring of bird populations in Britain from the 1960s onwards revealed declines in populations of many birds on farmland, particularly from the mid-1970s (Marchant et al.1990). In a review of these declines, Fuller et al. (1995) considered a range of possible causes, including climate, disease, predation, and changes in agricultural practice. They recommended that research should focus particularly on agriculture but also on predation, citing the possible effect of an increase in numbers of corvids and Sparrowhawks. Clues to the demographic nature of the declines were sought by Siriwardena et al. (1999), who analysed ringing data for a range of farmland granivores. For the House Sparrow it was found that the decline coincided with a period in which survival estimates were generally lower than in the previous decade, suggesting that reduction in survival may have been the cause. However, the credibility of predation as a possible agent was undermined by the findings of Thomson et al. (1998), who found a negative effect of Sparrowhawk and Magpie presence no more often than expected by chance in an analysis of long-term bird census data on a wide range of British songbirds. From this point onwards, attention focused on the possible role of food availability and its relation to changes in agricultural practices as a cause of farmland bird declines.

Assessment of the role of productivity in population declines using nest record data is less straightforward than analysis of survival, owing to a lack of information on number of repeat broods (Crick & Baillie 1996). However an opportunity arose to study this aspect of the problem in the House Sparrow in the form of an intensive breeding

study of a rural population that had been undertaken in the 1960s, since when the population had declined. A repeat study was undertaken on the same population in the late 1990s, but no significant differences in breeding parameters or overall productivity were found compared to the pre-decline period (Hole et al. 2002b). Supplementary feeding appeared to improve over-winter survival, however, and it was therefore concluded that the most likely explanation for decline in sparrows on farmland was a reduction in survival, proximately caused by lower food availability related to decline of over-winter stubbles and improved harvesting and storage of grain (Hole et al. 2002a).

PATTERNS IN ABUNDANCE AND DEMOGRAPHY

House Sparrows are unique among the species declining on British farmland, in that their major population centres occur in urban habitats. By the year 2000 it had become apparent that the species' urban populations had also undergone a substantial decline (Summers-Smith 1999), and following widespread media interest, the British government sponsored a more in-depth analysis of abundance and demographic data held by the British Trust for Ornithology (Crick et al. 2002a). This revealed that House Sparrow population trends varied among the British regions, with relative stability in the north and west, but severe declines in the south and east. It also showed that in rural areas the decline began in the 1970s followed by stabilization in the 1990s, while in urban areas the decline was delayed until the 1980s and was continuing in the south and east, but with evidence of recovery in the north and west (Siriwardena et al. 2002, Robinson et al. 2005). Small scale variations in population trends also occurred among urban sparrows, with the most severe declines in areas of high socio-economic status, but relative stability in low income areas (Siriwardena et al. 2002).

The fact that rural House Sparrows declined earlier than urban populations ruled out the possibility that the latter were sink populations declining in response to decreased immigration from the countryside, which was in any case unlikely because of the much higher density of urban populations (Heij & Moeliker 1990). If the theory linking rural declines to farming practices was correct, therefore, and urban declines could not be an indirect result of rural decline, there must logically be a quite separate reason for the decline of urban House Sparrow populations. Clues to the nature of this difference were therefore sought in detailed analyses of demographic datasets.

A model incorporating survival and productivity estimates indicated that reduced survival of 1st year birds in particular was behind the population decline overall, and that improved breeding performance may have stabilized the population at a lower level (Freeman & Crick 2002), perhaps indicating a density-dependent response of breeding output. This idea was supported by Crick & Siriwardena (2002) who presented evidence that breeding performance was positively correlated with population trends in rural sparrow populations but not in urban populations. They therefore deduced that some unknown factor was blocking density dependent improvement in urban

breeding performance, so preventing stabilization in urban areas. Crick & Siriwardena (2002) also conducted a regional comparison of breeding performance, and concluded that populations in the north and west were recovering because breeding performance was improving most rapidly there, and least rapidly in the south-east where populations were still declining. Based on these findings Crick et al. (2002b) made numerous recommendations for further research, including supplementary feeding experiments to test whether breeding output was being limited by food shortage in declining populations, and comparative studies of breeding performance and habitat use in areas of contrasting population trajectory, particularly in urban areas.

REPRODUCTION AND HABITAT USE IN URBAN POPULATIONS

The challenge was taken up by Vincent (2005), who undertook a 3 year study of breeding performance and habitat utilization by House Sparrows along an urban-rural gradient. Results revealed that nestling condition and survival correlated with a range of parameters, including density of aphids around the nest, proportion of vegetable matter in nestling diet, a habitat gradient measuring the relative area of vegetation and concrete, and the concentration of NO_2 in the atmosphere. This led to the conclusion that low breeding success caused by a shortage of insect food for nestlings was a 'plausible mechanism for demographic decline', and to speculation on possible reasons for insect decline in urban environments, including increased traffic volume and decreased urban greenery (Peach et al. 2008).

The recommendations of Crick et al. (2002b) were further implemented in the form of a volunteer survey of over 1,000 randomly chosen 1 km squares in built up areas across Britain. House Sparrow densities were estimated for 13 habitat categories, and then modelled as a function of relative habitat area, with the model predicting a steep decline in sparrow density from 60 per hectare where 100% of buildings have gardens to around 7 per hectare where half the buildings in an area are without gardens (Chamberlain et al. 2007). From this it was concluded that sparrow populations are likely to decline rapidly if a small proportion of gardens are converted for other use.

The consensus emerging from these studies on the cause of urban sparrow declines was summarised by Shaw et al. (2008), who reasoned that variation in the development and maintenance of urban landscapes explains the evidence that sparrows have declined less in areas with lower socio-economic status. Thus, 'deprived' areas are said to provide more nest sites in ill-maintained buildings, and more feeding opportunities in gardens with mainly native shrubs, while sparrows in affluent areas are deprived of nesting opportunities through home improvements and modern building techniques and of feeding opportunities by development of brown-field sites and conversion of gardens for off-road parking.

THE SIGNIFICANCE OF PREDATION BY SPARROWHAWKS

The authors of all of these works are unanimous in their rejection of Sparrowhawk predation as a possible agent of House Sparrow decline, despite a four-fold increase in Sparrowhawk numbers over the same period accompanied by widespread colonisation of urban areas (Newton 1993, Baillie et al. 2002). Crick et al. (2002b) recommended that the irrelevance of predation should be verified by extending Thomson et al.'s (1998) approach to the House Sparrow, perhaps using data gathered from observations at garden feeding stations, and this was taken up by Chamberlain et al. (2009) who found no association between Sparrow numbers and presence of Sparrowhawks. Such conclusive evidence would appear to have finally excluded predation by Sparrowhawks as a possible cause of House Sparrow declines. However an independent re-analysis of the same data produced a contrasting result.

Bell et al. (2010) used an index of Sparrowhawk incidence designed to reflect the species' re-establishment in localities during its population increase, in which the predator was registered as present at a site only during years of continuous occurrence lasting until the end of the recording period. This showed a significant negative effect on Sparrow abundance, indicating that the index captures the effect of continuous predation pressure on local sparrow populations. This result was reinforced by a further analysis indicating that timing of the first year of continuous Sparrowhawk presence explained much of the variation in Sparrow trends among sites, with stable Sparrow populations before and continuous decline beginning immediately after Sparrowhawk establishment. A modelling exercise also showed that variation in Sparrow population trends by region and between rural and urban sites could be explained by parallel variation in Sparrowhawk incidence.

CRITICISM OF RESEARCH ON HOUSE SPARROW DECLINES

The finding that Sparrow populations in gardens are generally stable prior to the beginning of Sparrowhawk predation suggests that the latter may be the sole factor behind Sparrow declines. However this has to be weighed against the evidence that the major factor is a reduction in the availability of food in both rural and urban environments. Breeding in the Sparrowhawk is timed to ensure that nestlings emerge at peak availability of fledgling songbirds, which means that mortality among prey species is skewed towards 1st year birds (Newton 1986). This corresponds with Freeman & Crick's (2002) finding that 1st year mortality is the main demographic driver of sparrow decline, though this conclusion derives mainly from data for the period 1980-83, during which a downturn in the national Sparrow population index coincides with a run of low estimated 1st year survival values. Given the wide confidence intervals for survival

estimates derived from House Sparrow ringing returns (Freeman & Crick 2002) it is far from clear that the low estimated values for the period 1980-83 are not simply caused by random noise, so any inference derived from this is necessarily weak.

THE ROLE OF DENSITY DEPENDENCE

The improvement in breeding performance with declining population, and the suggestion that this may be a density dependent response, is more compatible with food shortage as a driver of population decline, and this is supported by the inference of a positive correlation between population change and breeding performance in rural populations (Crick & Siriwardena 2002). The fact that population change appears to be negatively correlated with breeding output in urban populations supports the idea that the latter have not responded in a density dependent manner. Such conclusions are highly questionable, however, since the pattern of improved breeding output shown by Crick & Siriwardena (2002, Fig. 9.4.2.1.1) is remarkably similar to that emerging from a model devised by Peach et al. (2008, Fig. 5), which derives an index of breeding success as a function of annual fluctuations in climate. Improved breeding performance may therefore simply reflect a trend towards more favourable summer weather rather than a response to reduced food competition. Moreover, the inference of an urban/rural contrast in relationships between population change and breeding output is unsafe, since it relies on a series of non-significant correlation coefficients between sets of estimates averaged over year blocks (section 9.4.2., Crick & Siriwardena 2002). It may be, therefore, that the only reliable evidence suggesting that urban and rural population declines have different causes is the difference in timing between the two. However this is parsimoniously explained by the fact that Sparrowhawks generally colonised urban areas in the 1990s, after re-colonising the countryside during the 1970s and 80s (Bell et al. 2010).

Crick & Siriwardena (2002) attempted to generalize the relationship between breeding performance and population trajectory by inferring that populations in the north and west were recovering because breeding performance was improving most rapidly there, and least rapidly in the south-east where populations were still declining. However, the results presented indicate that breeding performance (qua nest failure rate) was increasing most rapidly in the east, where populations were also still decreasing, and that the other regions cluster together with widely overlapping standard errors at a much lower rate of increase (table 9.4.4.2, Crick & Siriwardena 2002). Again, the regional difference in Sparrow population trends is parsimoniously explained by the pattern of Sparrowhawk recolonisation, which started in the species' strongholds in the north and west, before spreading south and east across the country into areas from which it had been almost totally wiped out by heavy use of organochlorines (Newton & Haas 1984).

CORRELATES OF AGRICULTURAL INTENSIFICATION

Crick & Siriwardena's (2002) analysis of breeding performance in relation to agricultural practice illustrates the pitfalls inherent in such investigations. A finding of poorer breeding performance where spring sowing is more prevalent was opposite that expected on the hypothesis that declines are caused by reduced availability of fallen seed following a general switch from spring to autumn sowing (Hole et al. 2002a). Similarly, a finding of lower reproductive parameters in areas with greater livestock densities proved contrary to the expectation that declines would be less severe in pastoral areas because of feeding opportunities on livestock forage. Instead of causing the rejection of the underlying hypothesis, however, these results are explained away as evidence of 'probable reduction of fallen seed around farmyards because of more efficient harvest and storage standards' in arable areas, and 'more careful control of livestock provisioning' in areas of high stock density (Crick & Siriwardena 2002). This shows clearly the difficulty of any critical interrogation of the idea that bird declines are caused by agricultural intensification, since the multiplicity of variables involved always provides a fallback position, should a predicted relationship fail to emerge.

PATTERNS OF URBAN DECLINE

The contrived nature of the food availability narrative is illustrated by the discussion in Peach et al. (2008), which appears to vacillate between arguing that urban declines may be caused by decreased insect availability in urban areas, perhaps related to increased traffic pollution, and support for the scenario favoured by Crick & Siriwardena (2002) in which urban declines are continuing because generically low insect availability prevents density dependent improvement in breeding output. The former position is undermined by evidence that reduced survival is the proximate mechanism of population decline in urban as well as rural populations (Crick et al. 2002b). The latter position implies that insect availability is greater in urban areas where sparrow populations are stable, but again, no evidence is provided for such a pattern. Peach et al. (2008) attempt to bolster their argument by citing references showing a correlation between NO_2 and insect density, but the studies referred to actually show increased insect density in areas of high NO_2 concentration, caused by the effects of nitrogen enrichment.

Chamberlain et al.'s (2007) attempt to model urban sparrow distribution predicts a drop in density by an order of magnitude with a small decline in garden area. However this is difficult to reconcile with reported densities of around 2 per hectare for residential areas with gardens and between 1 and 2 per hectare for residential areas lacking gardens altogether. Meanwhile Shaw et al. (2008) argue that stability of Sparrow populations in low status districts of cities can be explained by greater prevalence of native shrubs supporting higher densities of insects. All such explanations may be redundant however, since a simple explanation of variation in urban Sparrow declines

is provided by the settling pattern of Sparrowhawks in cities, where only well-to-do districts provide safe nesting opportunities for the predators in the form of private grounds and large gardens with trees.

PSEUDOSCIENCE INTO POLICY

The questionable scientific basis of the consensus explanation of urban Sparrow declines has proved to be no disincentive to action based on their premises, particularly when set against the benefits derived in terms of marketing to urban communities that are normally beyond the reach of conservation bodies. Thus, Crick et al.'s (2002b) recommendation for supplementary feeding experiments has recently been implemented in London under the auspices of the RSPB. The RSPB is also implementing the recommendations of Peach et al. (2008) that urban spaces be managed to increase invertebrate densities through planting of native species and restricting mowing in sites away from roads under the banner of the 'London House Sparrow Parks Project'. Elsewhere Shaw et al. (2008) urge the development of mitigation measures for regeneration and the planning of new settlements to create an urban landscape "sympathetic to the needs of the house sparrow", and there is widespread implementation of conservation recommendations emerging from these studies, via their incorporation in 'Biodiversity Action Plans' devised by local authorities.

FARMLAND BIRDS AND AGRI-ENVIRONMENT SCHEMES

Such issues are trivial, however, compared to some of the wider implications of the failure of the food availability narrative. The House Sparrow is just one of a group of granivorous farmland songbirds that has undergone population decline over recent years. The diagnosis of the cause of this collective decline as an outcome of agricultural intensification has been a critical factor in the implementation of agri-environment schemes intended to reverse such population declines, and to benefit the wider biodiversity thought to be indexed by healthy bird populations (Wilson et al. 2009). The fact that House Sparrows have also declined in cities appears to be at odds with this diagnosis, since this clearly cannot be attributed to agricultural intensification, and this has led to pressure to find a separate cause. The possibility that a third, unknown factor may be causing both urban and rural sparrow declines inevitably raises questions over whether agricultural intensification really is responsible for farmland bird declines in general, especially since significant aspects of population trends in House Sparrows are shared by a range of declining farmland species.

The House Sparrow is one of a large group of species in which the population trend on British farmland displays a striking turning point in the mid-1970s, from increase or stability to consistent decline through the 1980s followed by return to stability at a lower level (Marchant et al. 1990). The mid-1970s turning point happens to coincide

with the period of most rapid increase in Sparrowhawk incidence, which more than doubled when measured using the same criteria over the period 1972-76 (Marchant 1980). The return to stability of many farmland songbird species also coincides with the levelling out of Sparrowhawk populations at a new high, suggesting a return to predator-prey equilibrium. As with the House Sparrow there is evidence among other species, particularly thrushes and finches, for stability or increase in the north and west of Britain, but continued decline in the south and east (Risely et al. 2008). Such patterns are generally cited as evidence for especially severe consequences of agricultural intensification in the arable-dominated landscape of southern and eastern England. However these are the very areas from which Sparrowhawks were most completely extirpated by heavy organochlorine use. Loss of predator averse behaviour among the songbird populations of these areas, followed by a sudden and relatively late return of the Sparrowhawk, can economically account for the continued declines among such populations.

It has been apparent for some time that the evidence for benefits to biodiversity of agri-environment schemes is weak (Kleijn & Sutherland 2003), and despite the fact that a majority of English farmland is now managed under such schemes (Natural England 2009) the measure chosen by the British government to measure their success, the Farmland Bird Indicator, continues to flatline (DEFRA 2009). Such results are generally explained away in the conservation literature as a result of difficulty in monitoring the impact of agri-environment schemes, of time lags in the response of bird populations, or as evidence of a need for better implementation and more research (Wilson et al. 2009, Davey et al. 2010). However, the fact that schemes implemented in the UK are designed around the results of studies of the relationship of agriculture to biodiversity (Grice et al. 2004) raises the possibility that the causes of bird declines in particular have been wrongly deduced from such studies. This is almost certainly the case for the House Sparrow, and evidence relating to other declining species has on the whole been gathered and analysed by the same agencies and analysed using similar approaches to that used in the House Sparrow research reviewed here.

The contrast between the huge investment in research on the effects of agricultural intensification on bird populations contrasts starkly with the handful of studies carried out on the effects of predation. This is partly because a negative result obtained from a predation study tends to be viewed as conclusive, while absence of an effect of agricultural practice is explained away. However, given the increasing doubts over the cost-effectiveness of the conservation policy derived from such research, there is an urgent need to revisit the role of predation in the widespread declines of farmland birds, not least because of the potential implications for the future of agricultural policy in the UK and elsewhere.

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