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STUDYING NUTRITION AND REPRODUCTION OF NESTBOX-BREEDING BIRDS WITHIN LOCH LOMOND NATIONAL PARK

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ABSTRACT

There are 260 nestboxes deployed in the oak-dominated woodland around the Glasgow University Field Station, Rowardennan. These nestboxes are used by four species of breeding passerine and were home to over 150 clutches of eggs in 2005 alone. These boxes and birds provide a valuable resource for ecological research and have been used in several studies. This paper presents a) some information on these nestboxes and birds that use them and b) outlines four research projects, investigating topics of current scientific interest and environmental concern, which have utilised this resource.

INTRODUCTION

Over the last several years I have been involved in a number of research projects concerning the influence of environmental nutrition on reproduction and fitness. Much of this research has utilised populations of small passerines that breed in nestboxes within Loch Lomond and the Trossachs NP and, in particular, around the Glasgow University Field Station (UFS), Rowardennan.

One of my current research projects, part funded by GNHS, uses blue tits breeding in nestboxes around UFS and I present here an outline of this project and its current status. In order to further highlight the value of the Loch Lomond NP for research, and in view of the exciting development of new research facilities at UFS, I also present some information regarding the nestboxes around UFS and a brief summary of some previous research projects which have utilised them.

NESTBOXES AROUND GLASGOW UNIVERSITY FIELD STATION

The University Field Station is surrounded by ancient semi-natural oak woodland recognised as being of national conservation importance and designated as a Site of Special Scientific Interest and a Special Area for Conservation. As a result of its managed history the tree species diversity is relatively low with a very high proportion of oak. A further consequence of management history, as with most woodlands of Western Europe, is that there are few old, dead and dying trees and, consequently, relatively few natural nesting holes.

Nestboxes

In the early 1990s 195 nestboxes were deployed in the woodland around UFS. These boxes were all of weather-resistant 'woodcrete' construction (manufactured by the 'Schwegler' company of Germany) and are ideal for research as they can be lifted down to the ground and the fronts removed for easy access to nest contents. At the end of 1993, an additional 76 nestboxes were deployed: 26 of these being 'woodcrete' and the remaining 50 being timber. In January 2004, all timber boxes were removed and replaced with woodcrete ones, giving a current total of 260 nestboxes.

Species using nestboxes

Four bird species have been observed to breed in these nestboxes: blue tit (*Parus caeruleus*), great tit (*Parus major*), pied flycatcher (*Ficedula hypoleuca*), and redstart (*Phoenicurus phoenicurus*). Blue tit are by far the most numerous species: in the mid 1990s there were 55-65 breeding pairs, rising to 93 pairs in 2004 and an impressive 120 breeding pairs in 2005. Breeding great tits generally number around 15 pairs, with less variation between years than blue tit. Numbers of pied flycatcher breeding in the area have fluctuated markedly over the last decade but for the last two years have remained at 13-14 pairs. Finally, in each year for which records are available, there has been a single pair of breeding redstart. Pipistrelle bat (*Pipistrellus pipistrellus*) and Brown long-eared bat (*Plecotus auritus*) have also frequently been observed to roost in these nestboxes during spring and summer.

ENVIRONMENTAL NUTRITION AND AVIAN REPRODUCTION

Adequate nutrition is vital to a successful breeding attempt and in many species the breeding season is timed to coincide with a particular peak in food supply. Research which examines the relationship between diet and reproduction is, therefore, a key component in understanding the interaction between species and their environment. Only armed with such knowledge can we attempt to both understand and predict the impact of environmental change. Such understanding is vital for the effective conservation of both individual species and entire ecosystems.
Summarised below are four research projects which have utilised nestboxes in Loch Lomond NP to study the interaction between nutrition and reproduction in passerine birds and to investigate issues of environmental concern.

Acid rain and calcium for eggshells (Ramsay and Houston, 1999)

The normal diet of most small passerines contains insufficient calcium for effective eggshell formation and birds must often forage specifically for calcium-rich items in the environment (Jones 1976; Repasky *et al.*, 1991). The most important natural source for temperate passerines such as tits appears to be snail shells (Ankney and Scott, 1980). It has been demonstrated that anthropogenic acid precipitation can significantly reduce levels of available calcium in soil and the abundance of calcareous items such as snail shells (Scheuhammer, 1991; Graveland and van der Wal, 1996; Graveland *et al.*, 1994). Research in areas adversely affected by acid precipitation on Continental Europe had suggested that reduced calcium availability had resulted in an

increased incidence of eggshell defects in small birds (Graveland and van der Wal, 1996; Graveland *et al.*, 1994).

In 1994 Prof. David Houston and I decided to investigate this in nestbox breeding tits around Loch Lomond (Ramsay and Houston, 1999). The basal rocks of the Scottish Highlands are poorly buffered, having among the lowest calcium levels in Europe. At the time of the study, however, West-central Scotland also experienced the highest levels of acid rain in Britain. Consequently, snail abundance (0.36 snails per m^2) and exchangeable soil calcium levels (0.02 mg g^{-1}) at our study sites (Rowardennan, Tarbet & Inversnaid) were extremely low: lower than values at sites in the Netherlands where severe eggshell defects occurred. The provision of supplementary calcium and the examination of eggshells, however, provided no evidence that blue tits were constrained in their ability to form effective eggshells as a result of calcium deficiency. We were therefore able to suggest that other factors besides low calcium availability, such as industrial pollutants, may have been contributory to the high incidence of eggshell defects seen in other areas.

Climate change and phenology of bird breeding
Pan-European Pied Flycatcher study (Both *et al.*, 2004):
In recent years, many studies have reported advances in the phenology of organisms and this has usually been attributed to climate change. However, such studies are usually uncontrolled and observed advances could be caused by other factors, unrelated to climate change. In addition, there is likely to be a publication bias towards studies of populations that show advances.

In order to address this, Both *et al.* published a study in 2004 which drew on breeding date data from 25 long-term studied populations of *Ficedula* flycatchers across Europe. This data set included the population breeding in nestboxes around UFS. Trends in spring temperature were found to vary markedly between study sites, and across populations. The advancement of laying date was much stronger in areas where the spring temperatures increased more, giving much stronger support to the theory that climate change causally affects breeding date advancement.

Phenology of Parid breeding: In 2004 and 2005 average laying dates for blue tits breeding in nestboxes around UFS were over one week earlier than in mid 1990s. In a pan European study of great tit and blue tit (Visser *et al.*, 2003), however, laying dates were found to have advanced in only 5/13 great tit populations and 3/11 blue tit populations. The observed differences between populations are, in part, due to differences in local temperature change, as with pied flycatchers, above. However, there are additional factors involved.

There are populations of tits where many pairs are traditionally double-brooded and, in some of these, birds have responded by reducing the incidence of second broods (Visser *et al,.* 2003): an advancement of the invertebrate availability window and accelerated larval development means that many pairs now have insufficient time to rear two broods. If parents are no longer trying to fit two broods into the breeding season they may start their first brood slightly later. As a consequence, it may be that no advancement of average laying date is seen in response to increased spring temperatures.

Blue tits occupy a range of habitats and their breeding interacts closely with conditions in that ecosystem. Different ecosystems respond to increased temperatures in different ways, and consequently this influences the birds breeding there. For example, in the evergreen oaks of Corsica, caterpillars appear much later in the year and blue tits breed later. Consequently, their breeding is unaffected by changes in spring temperatures. Rather, as climate is hot at the time young are in the nest, breeding is limited by water supply for evaporative cooling, rather than food availability (Blondel, 1985; Blondel *et al.*, 1993). It is important, therefore, to try and understand the nature of interactions between breeding, food supply and ecosystem if one is to be able to understand or predict the outcome of perturbations to that ecosystem.

Nutritional constraints on egg production in the blue tit (Ramsay and Houston, 1999; Ramsay and Houston, 1998; Ramsay and Houston, 2003)
This was the topic of my PhD research from 1993-1997 and field work was carried out using blue tits breeding in nestboxes around UFS. Research methods included the provision of different food supplements to breeding pairs, monitoring of breeding attempts, observation of foraging and determination of invertebrate availability and nutritional value.

Our research showed that increasing natural food supply (irrespective of actual composition of food) influenced timing of breeding, by advancing laying date. Many other studies investigating parid breeding and food supply have also reported similar advancements of laying date. Tits appear to use the timing of food availability early in season to anticipate food availability for chick rearing and adjust timing of breeding in response.

Within our study population, egg production was increased by the provision of high quality protein, whilst lower quality protein and energy supplementation had no effect, suggesting that natural availability of specific amino acids could be limiting. Evidence for a nutritional constraint on egg production from other studies, however, was limited and mixed.

Analyses of nutrients in arthropod prey (Ramsay and Houston, 2003) and comparison with the dietary requirements of laying blue tits indicated that birds on a predominantly arthropod diet would be unlikely to face such a constraint: eating enough arthropods to simply satisfy energy needs should provide more than enough good protein. Supplementary feeding studies by other researchers, using both blue and great tits, in a variety of other habitats, had produced mixed results with some reporting increases in egg production and others not.

Using further observational data and additional diet information from literature, we argue that blue tits living in oak woodland face a particular problem. Different tree species come into leaf at different times and bud burst in oak trees is relatively late. Crucially, the appearance of arboreal

invertebrates in significant quantity is closely related to bud burst.

Early in a mixed wood, tits can feed on arthropods from other tree species and switch to oak later in the season when arthropod abundance has increased. In an oak-dominated wood, however, blue tits' ability to switch trees early in the season is severely restricted and they may thus be expected to experience an extremely low availability of invertebrates. The scarcity of invertebrates at the start of the laying season was confirmed by invertebrate sampling (Ramsay, 1997). Consequently, tits may also have to feed on other, non-invertebrate, food items early in the season. A study by Betts (Betts, 1955) showed that early in the breeding season, the gizzards of most blue tits in oak woodland contained over 75% plant tissue (mostly oak bud tissue) and they may consume significant quantities of other plant material such as birch sap.

This study highlights the significance of studying specific species-habitat interactions and the potential problems of generalising between populations in different habitats or between related species. The high proportion of oak trees in historically managed woodland such as that around UFS creates a very different nutritional environment early in the season than that in a mixed woodland. Similarly, whilst blue tits primarily forage in twigs and leaves, great tits will also forage to an extent on the trunks of trees and the ground litter, where arthropods tend to occur year round. As a result, great tits in oak woodland do not face the same nutritional constraints that blue tits do.

Do spiders in the diet make tit chicks fitter?
(Current research project in collaboration with Dr Kate Arnold, University of Glasgow)

Background In Blue tits (*Parus caeruleus*) and other Parids, an intriguing pattern of parental provisioning has been observed. Caterpillars generally form the majority of the chicks' diet (Perrins, 1979) with strong selection pressure for brood rearing to coincide with the seasonal peak in caterpillar abundance (Perrins, 1991). However, several studies have recorded a particularly high proportion of spiders in the diet during early stages of chick development Royama, 1970; Tinbergen, 1960; Balen, 1973; Cowie and Hinsley, 1988; Woodburn, 1997; Grundel and Dahlsten, 1991). This trend, while strongly correlated with the age of the nestlings, occurs irrespective of season or habitat, indicating that it is not related to variations in natural spider abundance. During chick rearing, spiders are much less abundant than caterpillars (Ramsay 1997; Woodburn, 1997), yet spiders are still preferentially collected in relation to their relative density (Naef-Daenzer *et al.*, 2000). So, are Parids preferentially provisioning their chicks with spiders to provide a specific nutrient vital for neonatal development?

Spiders and caterpillars have broadly similar nutritional composition, except that spiders contain 40 – 100 times the level of taurine (a free sulphur amino acid) found in caterpillars (Ramsay and Houston, 2003). In mammals, taurine cannot be made by neonates, is found in high concentrations in placenta and milk and is vital for neonatal development (Aerts and Assche, 2002). Taurine is essential for normal fat digestion and has significant effects on growth. A recent profusion of research into taurine has demonstrated that it also has antioxidant properties Wu *et al., 2003;* Aerts and Assche, 2002). Further, there is also a suggestion that it may promote the uptake of important fat-soluble antioxidants, such as carotenoids and vitamins A and E, by making them water soluble (Petrosian and Haroutounian, 2000). Antioxidants protect the body against damage caused by free radicals and can thus enhance immune function and protect against many diseases whilst carotenoids provide the yellow colouration of blue tit plumage which plays an important role in signalling. Finally, one of the best studied roles of taurine is in mammalian brain and eye development, where adequate taurine is essential for optimal development.

Our project aims to investigate the role of taurine in parid chick development and whether it is limiting, thus explaining the selective provisioning of spiders in Parids.

Methodology
Diet supplementation
Throughout early development, individual nestlings were fed once a day with either taurine supplement or control treatment. Within each nest, roughly half the nestlings were randomly assigned to the taurine-group, with the remainder as controls.

Morphological development, plumage colouration and antioxidant levels
Prior to fledging size and mass recorded; feather colouration measured using spectrophotometer; blood sample taken for analysis of antioxidant levels and health status.

Cognitive and visual performance of offspring
One taurine chick and one control chick, from each of several nests, brought into aviaries at the University of Glasgow. After hand rearing to independence, birds studied in a range of behavioural trials to examine their visual and learning abilities as well as their reactions to novelty and conspecifics. After completion, birds released at capture site.

Natural prey delivery
The frequency and relative abundance of prey types brought to broods was monitored using infrared in-nestbox video cameras. From analysis of recordings we were able to determine provisioning level of spiders to each brood and examine relationship between chick fitness and spider delivery. Further, by manipulating natural brood sizes at some nests, we could examine effect on relative spider delivery rates. Do parents respond to lower demands of reduced brood by increasing provisioning of harder to find spiders?

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Results
Data from this project are currently under analysis, but we hope to be publishing some exciting results soon.

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