

The conservation ecology of the European nightjar
(*Caprimulgus europaeus*) in a complex heathland-plantation
landscape.

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Abstract

The conservation ecology of the European nightjar (*Caprimulgus europaeus*) was investigated in a complex heathland-plantation landscape in eastern England. Using radio telemetry, 31 nightjars were tracked in 2009 and 2010. The breeding behaviour of males was found to have potential implications for nightjar survey methods. While surveyors should be aware of the possibility of song territory overlap between male birds, results suggest that the occurrence of roaming unpaired males would not lead to an over-estimate in population. Home range 95% kernels for females, paired and unpaired males were an order of magnitude larger than song territories, highlighting the importance of foraging habitat in the broader landscape. Compositional analysis showed that foraging nightjars selected open canopy plantation forest (aged 5-10 years) and newly planted coupes (aged 0-4 years), with grazed grass-heath also used when available within 2km of the territory centre. Open ungrazed and un-planted habitat within the forest was avoided by birds, relative to availability. Moth trapping indicated that birds may choose foraging habitat based on the ease of prey capture rather than prey abundance. Dissection of nightjar faecal pellets demonstrated that moths and beetles were key components of the diet and that variation in diet during the breeding season may be due to changes in resource abundance and varying chick requirements. Comparison of the diets of birds nesting or roosting at varying distances from grass-heath suggested that forest and heathland habitats provide similar foraging resources for the nightjar. Behavioural data from nest camera footage indicated that the factors influencing the duration and frequency of adult non-attendance at the nest were incubation stage, temperature and chick requirements. This thesis combines investigations of nightjar breeding behaviour, home range, habitat use and diet, which can be used as an evidence base to inform conservation management.

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Introduction

The importance of applied ecology for conservation management

In the field of applied ecology, a detailed understanding of the ecology of a species, for example, habitat use, key prey species and behavioural processes can be used to address conservation management questions. Indeed, the importance of evidence based interventions in conservation is becoming widely recognised, with increased emphasis on management practices being based on robust, detailed data collection and analysis rather than anecdotal evidence (Sutherland et al. 2004, Pullin et al. 2004).

The study of habitat use can provide information on whether a species uses available habitats in the landscape at random; if habitat use differs between sexes or adults and juveniles; the effects of factors such as temperature and prey abundance on habitat choice; the ranking of habitats in terms of preference and how habitat availability affects home range size and animal movements (Aebischer et al. 1993). This information can then be used to provide habitat management recommendations. For example, Carvell (2002) investigated the habitat preferences of bumblebees (*Bombus* spp.) on unimproved chalk grassland in Salisbury, UK, in order to provide guidance on the suitability of several grassland management regimes for bumblebee conservation, while Gray et al. (2009) found sex-specific habitat use in the critically endangered Bengal florican (*Houbaropsis bengalensis*) in Cambodia, with annual grassland burning by villagers providing crucial habitat heterogeneity in the landscape.

Having a comprehensive knowledge of the dietary requirements of a species is also essential, particularly if the species is of conservation concern. For threatened species dependent on supplementary feeding, this knowledge is crucial and can assist in increasing population distribution (Jones 2004) and breeding success (González 2006). Dietary studies can also reveal competition amongst species for prey and the capacity of a particular site to sustain a population (Sutherland 2004). If the key elements of the diet are known, habitat managers can monitor prey abundance to ensure that prey is readily available. Lastly, dietary studies can provide additional information on optimal foraging habitats and contribute further to the evidence base on the requirements of a species; studies often combine habitat use and dietary analysis, (e.g. Green et al. 2000, Donald et al. 2001).

Information collected on the behaviour of a species can also be used to provide knowledge required for conservation management (Sutherland 1998). Predation of a threatened species may be reduced by examining predator behaviour and acting to ensure that predation is made more

difficult, for example by increasing cover next to food sources (Hinsley et al. 1995). The potential effects of environmental change, including habitat fragmentation or habitat loss, can be examined using models based on the behavioural decisions made by a species (Goss-Custard and Sutherland 1997). In addition to collecting data on animal behaviour, an understanding of the factors driving behaviours is also useful. The choices organisms make during particular life stages can be understood in terms of an economic analysis of costs and benefits (Krebs & Davies 1981). For example, during foraging, an organism must balance prey handling time with the energy return from the prey (Krebs et al. 1977). The idea of trade-offs – a beneficial change in one life history trait leads to a detrimental change to another - is central to life history theory (Charnov and Krebs 1974). Trade-offs can occur during reproduction, which is an energetically costly period, for example, between brooding eggs (offspring survival) and adult foraging for self-maintenance (adult survival) (Vleck 1981) and between the frequency and duration of periods off the nest to provision chicks (Kerry 1995). Time spent off the nest can also be influenced by external factors such as temperature or risk of predation (Conway and Martin 2000). An examination of behaviour at the nest by an adult bird can therefore provide information on the level of predation, with parents increasing the rate of feeding nestlings when predation risk is low (Fontaine and Martin 2006) or the availability of prey (Hamer et al. 1993, Naef-Daenzer et al. 2000) in the breeding grounds. Thus behavioural data can be a very useful additional source of information when planning conservation management.

Integrating biodiversity into forest management

The world's forests have a wide variety of economic and ecological functions. As the importance of preserving biodiversity in forests has become recognised, there is an emphasis on managed forests serving other purposes in addition to or as an alternative to timber production (Lähde et al. 1999), including watershed protection (Asquith et al. 2008) carbon sequestration, and recreational and landscape amenity (Willis et al. 2003). The Forest Stewardship Council (FSC), a non-governmental, independent forest certification scheme, which requires ten principles and criteria to be adhered to before certification is awarded, was set up in 1993. Principles include forest managers ensuring that environmental and social benefits are gained from the forest's multiple products and reducing environmental impact by conserving biodiversity within the forest and maintaining the forest's ecological integrity (FSC 1996). There are currently 1.6 billion hectares of FSC certified forest in the world, in a total of 80 countries (FSC 2012). There is therefore incentive for forests to be managed sustainably and for biodiversity. The Helsinki

Process (1995) provided guidelines for the sustainable management of such multi-use forestry, balancing timber production and biodiversity conservation.

Forest management practices for biodiversity should be considered at a landscape scale as home range size, dispersal abilities and complex habitat requirements of species inhabiting the forest must all be accounted for (Ratcliffe and Peterken, 1995). Managed forests comprise a heterogeneous landscape, with the configuration of patches of differing growth stage being important landscape suitability for, and the population dynamics of, species within the forest (Dolman et al. 2007). For example, in North America, both the Northern Spotted Owl (*Strix occidentalis caurina*) and the Bachmann's Sparrow (*Aimophila aestivalis*), have specific forest habitat requirements and there is evidence that the population viability of these species is dependent on forest design and management (Carey et al. 1990, Dunning et al. 1995, Liu et al. 1995).

Open habitat in a forested landscape is also important for biodiversity; for example, large bats (Patriquin et al. 2003) and butterflies such as the ringlet butterfly (*Aphantopus hyperantus*) (Sutcliffe & Thomas 1996) require open habitats to forage and breed. In the UK, the Open Habitat Policy of the Forestry Commission has been developed to create diverse landscapes of forest and open habitat, replacing forest areas (publicly and privately owned, planted on soil considered poor for timber production) with important open habitats such as heathland, moor and marshland (Driver 2010). This will benefit species of conservation concern requiring open forest habitats such as the European nightjar (*Caprimulgus europaeus*), woodlark (*Lullula arborea*) and tree pipit (*Anthus trivialis*).

In the UK, the percentage cover of woodland has more than doubled since the end of the 19th century, increasing from 5% (Smith & Gilbert 2001), to 13% in 2011 (Forestry Commission, 2011). This is due to re-planting schemes of plantation and broadleaf forest, however this is still a small area compared to mainland Europe, with an average of 37% woodland cover (FAO 2010). The Forestry Commission (FC) was set up by the UK government in 1919 to manage woodland across the UK. The largest land manager in the UK, the FC is committed to sustainable use forestry and conserving biodiversity. The current UK government aimed to privatise forest management in the UK, however after widespread protest by members of the public, this has been averted for the time being, with an independent panel concluding that England's forests should remain in public ownership (DEFRA 2012).

The nightjars (Family Caprimulgidae, sub-family Caprimulginae)

The sub-family Caprimulginae consists of 69 species in c. 15 genera, with the majority being nocturnal, aerial insect feeders (Cramp 1985). The nightjars can be found across the world from Africa to Argentina and are associated with dry, sandy habitats, including scrub land with scattered trees, and also forest (Cleere and Nurney 2000). Some species, for example, the Nubian nightjar (*Caprimulgus nubicus*) can be found in bare desert. Due to their secretive, nocturnal habitats, the nightjars can be difficult to study and there are gaps in the ecological knowledge for many species (Cramp 1985).

The European nightjar (*Caprimulgus europaeus*) (hereafter referred to as 'nightjar') is a crepuscular, ground-nesting species. The nightjar is insectivorous, feeding primarily on moths and beetles and the male has a "churring" call, which is used both to attract females and in territorial defence (Cramp 1985). Males can call from a variety of perches, including tree tops, branches, the tops of wooden pylons, low tree stumps and the ground (Cleere and Nurney 2000). This species has the most northerly distribution of the Caprimulgidae, stretching across Europe as far north as Finland and with birds breeding as far as Siberia to the east. The nightjar migrates from temperate breeding grounds to overwinter in west Africa (Cleere and Nurney 2000). Around 50% of the breeding nightjar population is in Europe with this population being estimated at 295,000 to 809,000 breeding pairs (Hagemeijer & Blair 1997). Primarily due to habitat loss, there has been a historical population decline in Britain and across Europe and subsequently the nightjar is a Species of European Conservation Concern (SPEC 2) (Burfield and Van Bommel 2004) and is protected under the EC Habitat and Species directive (EC 1992). In the UK, the nightjar population is thought to have halved between 1972 and 1981 (Gribble 1983) and is a Red- Listed species due to a decline in excess of 50% in breeding range between 1972 and 1992 (Gregory et al. 2002). In recent years however, despite continuing declines in northern Europe, nightjar numbers have been rising in the UK (Conway et al. 2007). Whereas the preferred breeding habitat of nightjars has previously been heathland, studies have shown that nightjars in the UK are increasingly relying on clear-felled and young forest plantations (Morris et al. 1994). Population increases are therefore thought to be a response to increases in suitable habitat as a result of changes in forest management and also heathland improvement/restoration projects (Conway et al. 2007). However, despite an overall increase in population, localised population declines have occurred in some areas of the country and nightjar range in the UK has not recovered and (Conway et al. 2007). As range is not expanding despite suitable nesting habitat being available, it has been suggested that there may be other limiting factors to nightjar colonisation, such as availability of prey and foraging habitat (Langston et al. 2007b). A further possible explanation for lack of

population recovery is recreational disturbance. Liley & Clarke (2003) found that nightjar breeding densities on heathland decreased in areas with high levels of urban development and nightjar breeding success was found to be lower the closer the nest was to recreational footpaths (Langston et al. 2007a). This is thought to be due to a higher level of diurnal avian predation when adults are flushed from the nest due to recreational disturbance.

Thesis outline

The ecology of the nightjar remains poorly understood. A more complete knowledge of the habitat use, dietary requirements and the factors that influence behavioural decisions at the nest (for example, the trade-off between nest attendance and foraging) of the European nightjar is essential in order to understand the reasons behind population declines and also to use conservation evidence to facilitate a much needed range expansion (Conway et al. 2007), which is a national objective for nightjar conservation in the UK Biodiversity Action Plan (UKBAP) for the species.

Thetford Forest, the largest lowland coniferous plantation forest in the UK (185 km²) contained 10% of the nightjar population during the last national survey in 2004 (349 churring males) (Conway et al. 2007), but has shown recent declines in the number of churring males, from 420 in 1998 (Evans 2002) to 240 in a Breckland survey of churring male nightjars in 2010 (Conway & Henderson 2010). Thetford Forest is itself a heterogeneous landscape, containing a mosaic of growth stages with varying canopy cover and open habitats such as unplanted grassland and is surrounded by a variety of habitats including heathland and arable land. The wide variety of habitats in the study site therefore provides an ideal location in which to conduct investigations into nightjar foraging habitat preferences and to determine if birds are feeding within the forest or leaving the forest to forage on exterior habitats such as heathland. There is also the opportunity to examine how the abundance of nightjar prey and nightjar diet varies between different habitats.

Aims

By studying the ecology of a nightjar population within a complex heathland-plantation landscape, we aimed to investigate:

- 1) Unpaired male behaviour and the potential effect on census results
- 2) Nightjar home range size and structure

- 3) Foraging habitat preferences of the nightjar, using radio telemetry and compositional analysis
- 4) Variation in nightjar prey abundance between habitat types in order to explain foraging habitat preferences
- 5) Factors influencing the varied generalist diet of the nightjar during the breeding season
- 6) Differences between heathland and forest habitat in terms of foraging resources
- 7) Factors influencing parental non-attendance at the nest, including temperature, necessity for egg brooding and chick requirements.

The overall aim of this thesis was to provide an evidence base on the ecology of nightjar in a forested landscape in order to provide conservation management recommendations for the species.

Chapter outline

The first chapter after the introduction describes the General Methodology of the thesis, outlining the fieldwork carried out and discussing the techniques used for data collection and analysis.

The initial data chapter (Chapter three) explores the song territory size of paired and (assumed) unpaired nightjars and investigates the level of territory overlap between male birds. The movements of radio-tagged unpaired males were used to determine if the presence of 'floating males' could lead to an overestimate in nightjar population. Results can be used to provide recommendations for nightjar surveyors and interpretation of survey results.

Chapter four investigates size differences between home ranges for radio-tagged female, paired and unpaired male nightjars and compares home range size and structure between males and females. Within the mosaic landscape, nightjar habitat preferences were determined, in order to explore the relative importance of forest, heathland and other open habitats. Moth trapping was used to investigate if preferred nightjar foraging habitats have the greatest prey abundance.

In Chapter five, nightjar faecal pellet dissection is used to examine the factors influencing the varied diet of the insectivorous nightjar during the breeding season. Using a measure of moth biomass (based on a non-linear indicator of moth scale abundance) and beetle abundance (an index of beetle fragments), we aimed to determine if nightjar diet varied at different times in the breeding season or when adults were feeding chicks compared to incubating and roosting adults. The variation in moth biomass from moth trapping throughout the breeding season was also

compared to changes in the biomass of moths in the diet. Lastly, diet was compared between faecal pellets collected from birds nesting/roosting at varying distances from heathland and restock stage forest (0-4 years since planting).

Chapter six investigates factors influencing behavioural decisions made by nesting nightjars. Nest camera footage and radio telemetry were combined to compare the duration and frequency of nightjar parental non-attendance at the nest among nesting stages (incubating, chicks ≤ 3 days, chicks > 3 days). The presence of the male at the nest was also compared between nightjar nesting stages. The effects of temperature on parental non-attendance at the nest were explored. Differences between the nesting behaviour of the nocturnal nightjar and diurnal species, which are more influenced by the risk of nest predation are considered. Finally, the use of this behavioural study as a source of information for conservation management is discussed.

The final chapter summarises the results of the data chapters and discusses how information gained in one chapter can be used to inform that from another. The strengths and weaknesses of techniques used during the thesis are reviewed. Finally, conservation recommendations for habitat managers of a forested landscape and possibilities for future research are discussed.

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General methodology

Nightjar fieldwork

A combination of practical methods was used to investigate the conservation ecology of the European nightjar. Birds were caught and radio-tagged, then tracked between May and September in 2009 and 2010 to record male churring positions and foraging habitat use. Moth trapping in five habitats (grass-heath, ungrazed grassland and three forest growth stages aged between 0-80 years since planting) available to foraging nightjars was also carried out between the start of June and the end of August during the summers of 2009 and 2010. In a collaborative study between the British Trust for Ornithology and the University of East Anglia, nest cameras were placed at nightjar nests to monitor predation between May and August 2008 and 2009 (Dolman 2010). During this camera study, nightjar faecal samples were collected from nest and roost sites between May and August 2008 and 2009 on nest finding days, when nest cameras were being installed and when chicks (if present) were ringed. In addition, faecal samples were collected from nest and roost sites between June and August 2010 on nest finding days and during regular nest monitoring (every 5 days where possible).

Investigating habitat use

Habitat use in birds can be investigated using a number of methods, with two of the most common being territory mapping and radio-telemetry. Territory mapping involves the plotting of the locations of singing males on a map to delineate song territory (Bibby 2000), whereas radio telemetry allows a tagged animal to be tracked continuously or in sampling “bursts” (Kenward 2001). Each method has advantages and limitations. While the main skill required for territory mapping is knowledge of bird song and there is no need for expensive equipment, this method can only be used in the breeding season and can be very time consuming (Emlen 1977). In addition, it can be difficult to distinguish between calling males, with territory overlap occurring in some species (Bibby 2000) and there have also been studies describing the presence of ‘floating unpaired males,’ (Stutchbury 1991, Brown et al. 2000), leading to the potential of recording the habitat use of the same male twice. Radio telemetry can be particularly useful for species that are cryptic or nocturnal, can provide continuous information on the habitat use and allows individuals to be distinguished (Kenward 2001). The key limitations of this technique are the need for catching and tagging the animal, (which can be time consuming and lead to the animal becoming stressed), the need for a large sample size (Aebischer et al. 1993) and the expense of equipment.

Anich et al. (2009) emphasise that the results of territory mapping and radio telemetry can provide differing measures of habitat use, with the former providing the habitats within the song territory and the latter all habitats that the animal is using, including those exterior to the territory. The most appropriate method depends on the study species; while some birds, for example, many songbirds, hold small territories (Fuller 1992), many others, for example, the twite (*Carduelis flavirostris*) (McLoughlin et al. 2010) and the chaffinch (*Fringilla coelebs*) (Hanski and Haila 1988) forage long distances outside the song territory, therefore while territory mapping is useful for providing information on breeding habitat, in many cases, this technique does not provide adequate information on foraging habitat. As the nightjar is nocturnal and can be difficult to study, radio telemetry was used to investigate the movements and habitat use of this species.

Radio telemetry methodology

During the summers of 2009 and 2010, nightjars were captured in three distinct study areas (that covered six of the main management units within Thetford Forest) based on location of suitable nesting habitat and accessibility. All fieldworkers involved in nightjar capture and tagging possessed endorsements on their standard ringing license, which included “authorisation to use CD/tape lures in the breeding season for nightjar” and “authorisation to use traps, decoys and radio transmitters (tail) on adult nightjars.” Nightjars were located through initial surveys conducted one hour before sunset during May 2009 and 2010. Where birds were present, capture was attempted using taped lures (consisting of nightjar contact calls and male churring) at the base of a 9 or 12m mist net. Radio-telemetry tags (Biotrack Pip Ag-392) were attached to the central tail feather following Bowden and Green (1991). Tags weighed 1.5g, within the recommended 2% (Kenward, 2001) of adult body weight (mean=73g \pm 7.5 sd, range=63-88, n=363; BTO data). While males responded well to the lure, females were more difficult to catch. Further attempts were made to mist net females in the vicinity of active nests, located by nest searching using volunteers.

Tagged nightjars were tracked from dusk until dawn between May and August in 2009 and 2010 using a Biotrack Sika receiver and 3-element Yagi antenna. One primary bird was tracked each night, with information recorded on other birds present in the area where possible. Birds were tracked using the “burst sampling” method following Barg et al. (2005), with successive observations, separated by short and regular intervals, taken within a burst of sampling, while the interval between bursts was longer. During this study, “bursts” lasted approximately seven hours per day; beginning just before individuals became active at dusk (c. 22.00) until dawn (c.05.00)

with the last fix taken after the bird was roosting and inactive. Where possible, birds were tracked on foot to reduce disturbance however when flying, birds were tracked by vehicle. Fixes were taken every ten minutes, reduced to every 30 minutes between sunset and sunrise, when the birds were generally stationary (with the exception of females actively provisioning chicks throughout the night, which were sampled at a fixed rate of every ten minutes). The interval of ten minutes was sufficient for a nightjar to cross its home range, ensuring independence of each fix (following Kenward 2001).

For each bird, fixes were triangulated sequentially by one person using bearings (measured by compass) from each of three locations (recorded using hand-held GPS); in as open a position as possible (avoiding areas surrounded by tall conifers and dips in the ground) to reduce problems of signal reflectance (Kenward 2001). Antenna elements were held horizontally to provide a more accurate reading in woodland areas (Kenward, 2001). Movement of tagged birds could be detected by a change in frequency and volume of “bleeps” coming from the telemetry receiver as the bird moved either closer or further away from the observer (Kenward 2001). Thus for each set of three bearings, activity could be classed as: (1) Stationary, if the bird was not moving when all bearings were taken; (2) Churring, if a male bird was churring whilst at least one bearing was taken; (3) Active, if the bird was moving whilst at least two bearings were taken, this included foraging, flying between churring posts and flying around the territory; (4) Interactive, if the bird was flying in a group, pursuing another bird or wing clapping whilst at least one bearing was taken. For each bearing, the time, individual’s activity, signal strength and additional clues to the bird’s location were noted.

Wherever possible, bird locations were determined using tri (45% of fixes) or bi-angulation (35% of fixes). The average time span between two consecutive bearings was four minutes (± 2 sd), (stationary: 66%, active: 22%, churring: 11%, interactive: 1% of bearings). A one-way ANOVA ($F_{3, 3861}=21.8$, $p<0.001$) with post-hoc Tukey tests showed that the mean time span between two consecutive bearings differed between stationary ($\bar{x}=4.49$ mins, ± 2.23 sd), active ($\bar{x}=3.75$ mins, ± 2.07 sd) and churring ($\bar{x}=4.16$ mins, ± 2.31 sd) bearings ($p<0.05$ for each comparison), while there was no difference between interactive bearings ($\bar{x}=4.03$ mins, ± 2.48 sd) and all other categories ($p>0.05$ for all comparisons). Active fixes had the lowest difference between consecutive bearings because points were often driven to using the fieldwork vehicle rather than walking between GPS locations. This method was found to be the most efficient for tracking moving birds, however an average time cost of 3.75 minutes between bearings was still incurred while the observer got in the vehicle, drove to the next location and got out to take the next reading. While this does

represent a possible source of error, these active birds tended to be moving within the same habitat/forest coupe. If the bird changed location, then either the bird would be lost and no active fix taken or a new set of bearings would be started. It should be noted however that if the bird was flying quickly back and forth between two habitats, these movements may have been missed.

On some occasions, it was only possible to take one bearing before the bird left the coupe or multiple bearings were taken but as the bird was active, they did not line up to produce a fix (20% of all positional fixes). In these cases, locations were only retained if there was clear evidence of the bird's position either because the bird was sighted or heard calling in the habitat or from the gain and signal movements. Visual bearings only comprised 0.8% of all positional fixes, therefore they should not introduce high levels bias to the data set. For bearings where the bird could have been in two possible habitats, these locations were included in the home range analysis but not the compositional analysis. Uncertain fixes with no evidence of the bird's location were excluded from analysis. If the bird visited several locations within the 10 minute observation period then the location (often a forestry coupe) where the bird spent the most time and/or the location with the strongest evidence was included in the dataset. If a bird disappeared from a territory for a period of nights, attempts were made to relocate the bird by driving around the forest with the receiver set to the bird's frequency.

The mean distance between the observer and the estimated position of the bird was calculated for a sub-set of the data ($n=174$ fixes). The mean distance for one fix (i.e. the mean distance between the n bearings taken and the bird's estimated location) was calculated, and this was repeated six times (three stationary and three active points) for each bird. The overall mean for the subset of data was 205m, ± 144 sd, range =37-1136m, with an independent t -test ($t_{(172)}=2.4$, $p=0.017$) indicating a greater mean distance for active points ($\bar{x}=231$ m, ± 187 , range=44-1136m) than for stationary points ($\bar{x}=179$ m, ± 36 , range=37-409m). This difference was due to the difficulties involved in getting closer to moving birds.

The breeding status of each male bird (paired or unpaired) was predicted during radio-tracking, based on behavioural observations (Table 1). Apparently unpaired males, with differing behavioural characteristics to known paired males, though circumstantial, allowed an assumption of their breeding status to be made. Classification of male breeding status using these methods has been carried out in many studies, for example, Van Horn et al. 1995, Guillemain et al. 2003, however it must be noted that the behaviour of paired and unpaired males may sometimes overlap, therefore some males may have been misclassified and there is the possibility that a male bird could change breeding status during the breeding season.

Fix locations were determined using the program Locate, Version III (Pacer Computing, Tatamagouche, Nova Scotia). Telemetry error was measured by comparing locations estimated from triangulation (using either two or three bearings) to the known location of stationary tags in forest coupes of varying growth stage (restock, n=8; pre-thicket, n=8; thicket, n=8; mature, n=8) held by a colleague at ground level. Mean telemetry error was 26m (± 20 m sd, range=2-99m) and did not differ with bearing number ($F_{1,56}=0.317$, $p=0.576$) or among forest growth stages ($F_{3,56}=1.237$, $p=0.305$). Moving tags were not tested as it was felt that it would be difficult to realistically create similar movements to an active nightjar. While it is possible that the error for moving tags may have differed from stationary tags, triangulation positions for active birds were always chosen with the aim of determining the bird's location as accurately as possible, for example, if there was the possibility that the bird was in two habitats, attempts were made to take a bearing on the boundary of these habitats.

Table 1. Criteria for determining breeding status of the male nightjar

Paired male nightjars:	Unpaired male nightjars:
<p>Were regularly seen flying with a female in their song territory.</p> <p>Had a daytime roost located near (5-10m) to known nest.</p> <p>Exhibited behaviours that indicated nest incubation, for example as the female left the nest area, the male moved towards the nest and was stationary until the female returned.</p> <p>Churred only at the beginning and end of the night or in response to rival males in the territory and were often silent during the middle of the night.</p> <p>Went on long feeds at dusk and dawn.</p> <p>Carried out active bouts of wing-clapping display, butterfly flight and gave a regular 'winding down'/bubbling call after churring (Cramp 1985).</p>	<p>Often churred from earlier in the evening than paired males, in brighter light conditions and continued throughout the night.</p> <p>Rarely had a clear feeding time.</p> <p>Were only seen interacting with a female as part of a group with other males or chasing a female.</p> <p>Did not have a female seen in their song territory regularly.</p>

On collection of radio telemetry data to investigate habitat use, there are a number of ways it can be analysed, including home range analysis. An animal's home range is defined as "that area traversed by the individual in its normal activities of food gathering, mating, and caring for young" (Burt 1947).

The Minimum Convex Polygon (MCP) method connects uses the peripheral points of an animal's locations to create the smallest convex polygon (with internal angles not exceeding 180 degrees) that contains all animal positions (Mohr 1947). While simple to create, the MCP does not describe the usage of space within the home range and can also under or over-estimate a home range depending on sample size (Worton 1987). However, this method has been widely used and is considered to be broadly comparable between studies (Kenward 2001). The Kernel Density Estimate, adapted for use in home range analysis by Worton (1989), is now widely accepted as a more accurate technique for analysing the home range (Seaman and Powell 1996). Kernels can be fixed (the same smoothing parameter is used for all data points) or adaptive (the level of smoothing is varied to adjust for outlying points) (Worton 1989). If the range includes outer points of a low density, the use of fixed kernels can lead to an over-estimate of the core range in order to include these points, while adaptive kernels can produce an over-estimate of the outer isopleth as low density points are given more smoothing (Rodgers and Kie 2011). A number of studies have concluded that fixed kernels provide the most accurate results (Worton 1995, Seaman and Powell 1996, Seaman et al. 1999) however adaptive kernels can be more suitable in some cases, depending on the structure of the dataset (Silverman 1986, Worton 1989). It is recommended that the choice of smoothing method is based on an investigation of which is the most appropriate for the collected dataset (Rodgers and Kie 2011).

When using kernel density estimates, the choice of fixed and adaptive kernels is not as important as choosing the correct value of smoothing factor (h) (Worton 1995, Seaman and Powell, 1996). The reference bandwidth (h_{ref}) can lead to over-smoothing and an over-estimate of the home range if points are highly clustered (Kie et al. 2010). Alternatively, Least Squares Cross Validation (LSCV) can be useful if the dataset is multi-modal, however it can produce a less accurate home range with small sample sizes ($n < 50$) (Seaman et al. 1999, Blundell et al. 2001) and can lead to "under-smoothing" if there are duplicates or clusters of points in the data (Seaman and Powell 1996, Hemson et al. 2005, Rodgers and Kie 2011). Both methods have shortcomings and there is no single, correct option that covers all data types. A further alternative is the ad hoc smoothing

parameter, incrementally decreasing the reference bandwidth (h_{ref}) to the minimum at which the 95% isopleth's contour remains entire (Berger and Gese 2007, Jacques et al. 2009, Kie et al. 2010) so that the home range kernel is continuous. This is designed to minimise both under and over-smoothing (Berger and Gese, 2007), but may misrepresent habitat use, especially of multi-modal home ranges in a patchy landscape, with areas that are not used included in the range (Mitchell and Powell 2008). A final option is to use a fixed proportion of the h_{ref} value for all individuals (Bertrand et al. 1996, Kie and Boroski 1996, Kie et al. 2002, 2010). The proportion of h_{ref} that best fits the distribution of the data is chosen for each home range and the mean value then used for all individuals.

Compositional analysis

Compositional analysis (Aebischer et al. 1993) also allows data from radio telemetry to be used to investigate habitat use, with the use versus availability of a set of key habitats compared. Habitat types are ranked, independently of availability, based on the number of positive differences between pairs of habitats, with significant differences determined using paired t-tests. This technique reduces some of the sources of error previously involved in analysis of habitat use: each tagged animal is considered a sample unit, rather than each positional fix, (which removes non-independence of the data) (Kenward 2001) and the proportions of each habitat type do not sum to one (this can lead to avoidance of one habitat being interpreted as apparent preference for another, which may not be the case) (Aebischer et al. 1993). It is recommended that an investigation into habitat preferences and the following compositional analysis of results is carried out on different spatial scales, for example, Johnson (1980) describes how habitat use is the result of choices at different levels, with "first order selection" defined as the selection of the geographical range by a species, "second order selection," the choice of home range within that range for an individual or group of animals and "third order selection," the use of habitats within the home range.

There are limitations to using compositional analysis; an adequate sample of tagged animals is required for statistical analysis (recommended as >10, but preferably >30 (Aebischer et al. 1993)). However, this is the case for many methods of analysing habitat use. Also, as proportional habitat use is compared to proportional availability, rare habitats can be mistakenly represented as very strongly selected or avoided because small differences between use and availability in absolute terms are proportionately larger than similar absolute differences between habitats that are more common (Marzluff et al. 1997). However, overall, compositional analysis is a widely used, flexible

technique for investigating habitat preference, which does not violate any of the key assumptions as some of the other more simple methods can do (Aebischer et al. 1993).

Dietary analysis

There are a number of methods for studying the diet of birds. Firstly, direct observations of the birds consuming prey or provisioning chicks at the nest can be made. This is commonly used for studies of raptor diet for example, both nest cameras and field observers with telescopes were used to investigate the diet of nestling Bearded Vultures (*Gypaetus barbatus*) (Margalida et al. 2005). As watching birds directly with a telescope can be time consuming, the additional use of nest cameras allows time to be used more efficiently and also reduces disturbance to the birds (Margalida et al. 2002). However, diet estimation using direct observation can lead to bias towards conspicuously coloured or shaped prey and depending on the distance observations are made, smaller prey can be missed (González-Solís et al. 1997).

An alternative method, particularly for species that present a food bolus to chicks, is to collect and dissect faecal samples or regurgitated pellets. This technique is widespread and there are numerous examples in the literature (Green 1978, Ralph et al. 1985, González-Solís et al. 1997). While this method allows minimal disturbance to the bird and is inexpensive to carry out, it can be very time consuming. Neck ligatures, which prevent chicks from swallowing prey, have the advantage that prey is undigested and can therefore be easily identified (Sutherland 2004), however there are flaws with this method, particularly related to the welfare of the chicks. Rosenberg and Cooper (1990) describe increased chick mortality, adult birds removing prey from the neck collars and the possibility of smaller prey items still being consumed. In addition, as neck collars can only be used for a short period of time, sample size can be smaller than other methods (Moreby and Stoate 2000). In a comparison between faecal dissection and neck ligatures, Poulsen and Aebischer (1995) found no difference between these sampling methods for skylark chicks (*Alauda arvensis*) fed an insectivorous diet (including Coleoptera, Hymenoptera and Diptera), possibly due to the speed of insects passing through the chicks' gut. Moreby and Stoate (2000) compared the diet of three species, which fed nestlings an invertebrate diet (common whitethroat, *Sylvia communis*; hedge accentor, *Prunella modularis*; yellowhammer *Emberiza citrinella*) using faecal dissection and neck ligatures. Dietary composition inferred from faecal dissection differed from the composition of prey fed to chicks as determined by neck ligatures for both the hedge accentor and common whitethroat, with more Coleoptera in faecal samples of both species and for the hedge accentor, a greater proportion of soft bodied Collembola in neck

ligatures than faecal samples. Inconsistent bias was found for dietary insect diversity, which was higher in faecal samples for common whitethroat and in neck ligatures for the hedge accentor. Yellowhammer diet was similar for both methods. The authors suggest that both differential digestion and the number of meals per sample (faecal samples may represent foraging over a period of days while neck ligatures generally contain one food parcel) may be responsible for differences between methods. Therefore, it is possible that diet as determined by faecal dissection may over-represent hard-bodied insects (e.g. Coleoptera) and that some soft-bodied insects (e.g. Diptera, Trichoptera) may not be detected as they may be either highly fragmented or completely digested. While moths (Lepidoptera) are soft-bodied, the persistence of scales in dissected faecal pellets means their presence in the diet can be detected (Whitaker et al. 1996).

Molecular approaches, such as the investigation of stable isotopes in blood, feathers or eggs, can provide information on the habitats birds have been feeding in during particular stages in the season, for example, Klaassen et al. (2001) found that for ten wader species, eggs were produced from nutrients collected in the breeding tundra habitats rather than in the estuarine wintering habitats. Prey DNA can also be collected from faecal samples and compared with prey DNA primers to provide an extremely detailed record of diet. This non-invasive technique can be particularly useful if diet is unable to be determined using other means and reduces the possibility of any bias due to differential digestion or misidentification of prey fragments in the faeces (Jarman et al. 2002). This novel technique has not been used widely in studies of bird diet, however has been tested to investigate the diet of marine mammals (e.g. Deagle et al. 2005) and bats (Clare et al. 2009). The main limitations of this method are the expertise required to choose and extract the correct prey DNA primers and also the expense involved in carrying out the laboratory techniques. Faecal samples also have to be fresh and/or well preserved in order to preserve DNA integrity (Deagle et al. 2005). Overall, the methods used to investigate diet are varied and the optimal choice depends on the study species and its feeding style. In some cases, a combination of methods can be the best option, reducing the chance of any possible bias (Redpath et al. 2001).

Behaviour at the nest

Many studies on the behaviour of adults at the nest have been carried out, using a variety of methods. The nest can be observed directly, from behind a hide/blind (e.g. Neudorf & Sealy 1994), however this can be time consuming and can also potentially lead to the disturbance of the nesting birds, for example, on arrival of the observers or (if the bird is nocturnal), when a light is flashed on the nest to determine if the adult is present. Temperature changes at the nest caused

by parental non-attendance can be monitored using temperature sensors such as thermistors (Purdue 1976), data loggers (Manlove & Hep 2000) or a device that measures both non-attendance and temperature, containing a microswitch and data logger (Flint & MacCluskie 1995). The most detailed information can be provided by placing cameras at the nest, allowing all parental absences from the nest to be recorded and timed (e.g. Cartar & Montgomerie 1987, Matysiokova & Remes 2010).

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Chapter 3: Song territory overlap and size variation among breeders and non-breeders: implications for censusing nightjars

Abstract

Territory mapping using bird song is a common census technique however the possibility of territory overlap and roaming behaviour of unpaired males may lead to under or over-estimates of a breeding population. The behaviour of radio-tagged male European nightjars (*Caprimulgus europaeus*) was used as a case study to provide recommendations for census techniques and the interpretation of survey results, based on song territory size and overlap. Radio telemetry was used to track the movements of paired and unpaired male nightjars during the breeding season in a complex plantation forest in Eastern England. Individual song territories were mapped using Minimum Convex Polygons (MCPs) based on male churring points during a four week period. The level of territory overlap for tagged males was calculated using the percentage of MCP overlap and also with Bhattacharyya's Affinity (BA). The area and dimensions of each song territory were calculated. There was a high level of territory overlap, with fifteen out of nineteen tagged males having an overlapping territory with that of another male nightjar. Both paired and unpaired males defended a single territory at a time. Mean song territory size did not differ between paired ($\bar{x}=8.54$ ha, range=3-23ha, se=1.69, n=11) and unpaired ($\bar{x}= 6.78$ ha, range=3-17ha, se=1.66, n=8) male nightjars ($t_{(17)} = 0.818$, $p=0.425$). The mean longest dimension for all male song territories was 533m (± 220 m sd). Two of the 19 males were recorded churring in temporary locations more than 1km from their main churring territory. However, each bird was only recorded doing this once throughout the season. Surveyors must be aware of the potential for territory overlap, as this could lead to an under-estimate of nightjar numbers. The likelihood of over-estimating the number of nightjar territories due to behavioural differences of unpaired males is low. However, as unpaired males hold a clear territory, this should be accounted for when estimating the UK population of nightjar, as the number of males counted does not necessarily equate to the same number of female birds. It is recommended that observers take time to record behavioural observations, particularly on male breeding status, at each potential territory during national surveys.

Introduction

Bird census techniques allow monitoring of populations in relation to habitat loss, climate change and to track the progress of conservation management practices (Bibby 2000). One common method is territory mapping. During surveys, typical emphasis is placed on the locations of singing

males. Individual song territories are mapped based on such locations, yet a number of possible limitations exist when using this method to calculate species abundance, such as overlap of territory boundaries and roaming non-breeding males (Emlen 1971, Bibby 2000). The European nightjar (*Caprimulgus europaeus*), is a nocturnal species which is regularly surveyed to monitor population abundance and trends in the UK. There is some anecdotal evidence to suggest that male 'song' and population abundance may not correlate precisely, because of the potential for inaccuracies due to the presence of unpaired males (pers. comm. Ian Henderson, BTO). Also, considerable overlap in male territories could lead to potential underestimates of populations if based on male song alone.

Due to long term habitat loss throughout the 20th century, the nightjar is a Species of European Conservation Concern (SPEC 2) (Birdlife International 2004) and is protected under Annex 1 of the EU 'Birds' Directive (Directive on the conservation of wild birds 79/409/EEC). In the UK, the nightjar is a Red-Listed species, following a decline in breeding range of over 50% between 1972 and 1992 (Gregory et al. 2002). There have been several national nightjar population surveys in the UK (1981, 1992 and 2004) in order to monitor changes in number and distribution (Gribble 1983, Morris et al. 1994, Conway et al. 2007).

During previous national nightjar surveys, precautions were taken to reduce the effect of overlapping territories by recording males that were "churring" simultaneously separately by assuming that clusters of registration less than 350m apart over more than one visit to a site identified a breeding territory and by assuming that calls not given simultaneously but located greater than 350m apart were most likely two different males (Conway et al. 2007). This threshold value of 350m was based on expert opinion that known breeding territories can be as close as 350m and that simultaneously calling males are known to occur at this distance apart and beyond. However, the threshold is not based on accurate measurements of birds moving around at night or the possibility that in variable habitats such as plantations and heathland, the proximity between neighbouring pairs could be greater than 350m. Using territory mapping of nightjar song, Cadbury (1981) found no evidence of territory overlap for nine nightjar territories over a 3.5km transect, over a period of eleven visits. However, territory mapping can lead to uncertainty over individual bird identities. An investigation into the level of nightjar song territory overlap using radio-telemetry would allow individuals to be distinguished and has the potential to add greater precision to our assumptions about the dispersion of breeding or territorial birds.

A number of studies have described the size and habitat characteristics of the nightjar song territory (Berry 1979, Ravenscroft 1989, Bult 2002, Wichmann 2004, Verstraeten et al. 2011) based on territory mapping using male calls. However, these studies did not distinguish between the song territories of paired and unpaired male nightjars. While unpaired nightjars have been recorded patrolling and holding a territory (Cramp 1985) unpaired birds may behave differently from those in a pair. In other species, there are examples of 'floating' birds; non-breeding birds that can apparently range widely across a site (Stutchbury 1991, Brown et al. 2000, Bayne and Hobson 2001). Some unpaired birds can also defend multiple territories (Amrhein et al. 2007), meaning that due to their presence and mobility, they could potentially create both over and under-estimates respectively, of true breeding population size.

A clearer understanding of nightjar song territories will provide guidance on the interpretation of the results of territory surveys and additionally allow survey methods to be based on the ecology of the birds. In turn, this will ensure that conservationists and habitat managers are able to monitor the effects of strategies implemented to increase the number and range of this species.

Methods

Study Site

The study was carried out in Thetford Forest (0°40'E, 52°27'N), in Breckland, Eastern England. The largest lowland conifer forest in the UK (185km²), Thetford is divided into distinct blocks and consists of a mosaic of growth stages. Trees are arranged in even-aged stands (mean coupe area 9.0 ha ±8.6 sd), which are felled at economic maturity (60-80 years) and replanted. The exterior forest landscape contains a variety of habitats including semi-natural grass-heath, improved grassland and arable land.

Thetford Forest and surrounding farmland were designated a Special Protection Area (SPA) in 2000 due to internationally important populations of breeding nightjar. During the last national survey, Thetford Forest contained c. 10% of the UK nightjar population (349 churring males) (Conway et al. 2007), however there has been a decline to 240 males (Conway and Henderson 2010).

Nightjar radio-telemetry

See the general methods chapter (Chapter 2) for details of procedures carried out during nightjar radio-tagging and telemetry.

A total of 36 birds were radio-tagged; 20 in 2009 (13 male and 7 female) and 16 in 2010 (12 male and 4 female). In 2009, two birds shed their tags and three were lost, leaving a total of 31 (21 male and ten female) for analysis.

Nightjar breeding status

The breeding status of each male bird (paired or unpaired) was predicted during radio-tracking, based on behavioural observations (See Chapter 2, Table 1). Apparently unpaired males, with differing behavioural characteristics to known paired males, though circumstantial, allowed an assumption of their breeding status to be made. Classification of male breeding status using these methods has been carried out in many studies, for example, Van Horn et al. (1995), Guillemain et al. (2003), however it must be noted that the behaviour of paired and unpaired males may sometimes overlap, therefore some males may have been misclassified and there is the possibility that a male bird could change breeding status during the breeding season.

Of the tagged males, 11 birds were paired and the ten remaining were considered to be unpaired, with three of the paired males becoming unpaired during the season. Therefore 47% of the tagged male birds in this study were considered to be unpaired.

Nightjar song territories

Minimum Convex Polygons (MCPs) were created for nightjar song territories (n=19) using Hawth's Tools with ArcGIS 9.2, with points in the MCP representing a churring position (\bar{x} churring registrations=19, ± 6 sd, range = 9-32). Two males were not included in the analysis as there was an insufficient number of churring positions to create song territory MCPs.

As some males changed breeding status (n=4) and/or changed churring positions during the season, MCPs drawn for each bird represent churring within a four week period in order to represent the size of the churring territory within a snapshot of time. The four week time period was judged appropriate in order to provide indication of the churring posts that male birds used

regularly and also to investigate any incidences of roaming males. MCPs were deemed more suitable than the Kernel Density Estimate (kde), as the aim was to use the churring points around the perimeter to delineate the nightjar song territory. This is the equivalent of the territory mapping that occurs during national nightjar surveys. It should be taken into consideration that the accuracy of MCPs can increase with increasing sample size (Swihart and Slade 1997), however sample sizes were thought to be appropriate for the purposes of this study as male birds tended to be faithful to churring sites.

For radio-tagged males with overlapping song territories, the area of the overlap between the two MCPs is presented. However, this can be misleading as two birds could have a small overlap that was used frequently by both, or a large overlap that was rarely used by one or both animals (Powell, 2000). A more accurate method of quantifying song territory overlap is to investigate the relative probability of use (the Utilisation Distributions (UDs) of the two animals) (Fieberg and Kochanny 2005). There are a number of indices of overlap; Bhattacharyya's affinity (BA; Bhattacharyya, 1943) provides a measure of affinity between two populations, with the value ranging from zero (no UD overlap) and one (100% UD overlap) (Fieberg and Kochanny 2005). For each pair of tagged birds with overlapping song territories, the function 'kerneloverlap' in the package 'adehabitat' (Calenge, 2006) for R (R Core Development Team, 2012) was used to create the UD for churring locations and then calculate the BA. As with home range kernels, the use of the UD becomes more accurate as sample sizes increase (Fieberg and Kochanny 2005) therefore some of the results presented should be interpreted with caution.

Song territory size was not related to number of churring fixes ($r=0.11$, $p=0.650$) therefore territory size was compared between paired and unpaired males using an Independent *t*-test. Birds that changed status during the tracking season were only included in the analysis once.

The longest dimension (distance between the two most distant churring points) was measured for each song territory.

In order to calculate the chance of double counting due to roaming males, the number of nights each bird was found to be churring in temporary locations >1km from their main churring territory was counted and divided by the overall number of nights each male was monitored, and an average taken for all male birds. The resulting percentage was then multiplied by the percentage of males recorded as roaming. As each nightjar site is visited two to three times during the national survey, the final percentage was multiplied by three to calculate the overall chance of over-counting due to roaming males.

Results

Song territory overlap

Of the 19 radio-tagged male nightjars (11 paired and eight unpaired), 15 male song territories overlapped with that of at least one other male. Of these, eight overlapped with another radio-tagged male (Table 1), with a mean overlap of 29% (± 25.6 sd) of the territory. Three out of four of these sets of birds overlapped simultaneously (during the same four week period), while for one pair of overlapping males (295 and 323) there was one month between the overlapping song territories.

Table 1: The percentage overlap of song territory MCPs and Bhattacharyya's affinity (BA; a measure of overlap of the Utilisation Distributions, 0=no overlap, 1=100% overlap) for male nightjars with overlapping song territories.

Bird ID	No. churring Points	MCP Overlap (%)	BA
757	9	55.70	0.57
822	17	17.80	
235	16	31.00	0.34
259	23	29.40	
295	19	3.15	0.24
323	28	13.30	
314	26	6.21	0.52
836	8	77.04	

Song territory size

Song territory size did not differ between paired (\bar{x} =8.54 ha, range=3-23 ha se=1.69, n=11) and unpaired (\bar{x} = 6.78 ha, range=3-17 ha, se=1.66, n=8) male nightjars ($t_{(17)} = 0.818$, $p=0.425$) (Figure 1). The mean longest dimension of the male song territories was 533m (± 220 m sd, range= 295-1204m).



Figure 1: An example of Minimum Convex Polygons for the 4-week song territories of a sub-set of paired male nightjars (black) (n=3) and unpaired male nightjars (dark grey) (n=4) in Thetford Forest in 2009/10. Each territory is for a different individual. Note the overlapping song territories for both groups of birds.

There were no cases of unpaired males defending multiple territories. One unpaired male moved the position of the churring territory after the first four week period, with the longest distance between two churring points in the different territories for this bird being 701m. Another unpaired male was only recorded on the territory for one week before the signal was lost; the bird could have moved to a new area of the forest or the tag could have been shed. Two of the 19 males were recorded churring in temporary locations more than 1km from their main churring territory. However, each bird was only recorded doing this once throughout the season. Overall, 11% of birds were found roaming the forest for 3.5% of the time monitored, thus the chance of a surveyor erroneously double-counting a roaming male per survey, based on this study, is only 0.4%. Therefore in the national survey, the chance of double counting due to roaming males is 1.2%.

Discussion

Using radio-telemetry, this study has investigated two of the potential pitfalls of territory mapping and results can be used to form guidelines for future nightjar surveys. In Thetford Forest, the level of territory overlap between birds over a four week period was high. The results in this study show that the overlap of MCPs and the probability of use should both be calculated in order to understand territory overlap fully. For example, for birds 314 and 836 (Table 1), only 6% of the

song territory of 314 is overlapped by that of 836 but there is a high BA value of 0.52, as this small area of overlap is used frequently by both birds. There is also asymmetry in territory overlap, with some birds' territories overlapping into their neighbour's territory more than others. Surveyors must be aware of the possibility of overlap when carrying out nightjar territory mapping as this could otherwise lead to under-estimates of the population. However, it should be noted that while the results of this study provide information on the utilisation of space within the territories over a four week period, they do not provide an estimate of the probability that an observer would encounter the two birds in the same territory on the same night. This would require further analysis and a larger data set. Nevertheless, based on the results of this study, it can be recommended that care is taken to provide detailed behavioural observations (for example, interactions between males, including defensive behaviour, at the territory) on each visit in order to try and tease apart possible overlaps.

Although unpaired nightjars can show behavioural differences from paired males, birds in both groups established a single territory, with no size difference, and then defended it. While some shifting in unpaired male territory position was recorded, only two unpaired males were confirmed roaming considerable distances through the forest on two occasions. Therefore the results of this study suggest that the chances of over-estimates during surveys due to 'floating' males are low. There was no evidence of unpaired males defending multiple territories at a time (although one male out of the 19 did move territory altogether during the season). This result is important for interpreting national survey data. The churring males in an established territory may not be paired birds therefore the total number of churring males for a site does not equate to the number of female birds present.

When the Avian Sex Ratio (ASR) is highly skewed towards males, this can indicate that a population is under threat (Donald 2007). In a meta-analysis into the risks of extinction due to female dispersal, Dale (2001) found higher levels of unpaired males in threatened, small, isolated populations (median 0.4) than in core populations (median 0.13). In this study, 47% of the radio-tagged males were considered to be unpaired, suggesting that the population of nightjars in Thetford Forest may have a highly skewed ASR and may be at risk. However, this could also be because unpaired males were easier to catch and tag, for example, they may be younger, inexperienced birds or come more readily to the taped lures. As this potentially high percentage of unpaired males would not be recorded as such using the current methods of the national survey, it may be that survey data should be analysed and presented differently. Using observations and notes on the predicted breeding status of the churring males made by surveyors

on multiple visits, an estimate for both paired and unpaired males could be presented, providing a more informative and accurate view of the total number of nightjars in the UK.

As it can be difficult to determine the breeding status of male birds and birds can change status during the season, care would need to be taken when designing survey methodology. As with the potential overlap of song territories, this would require behavioural observations to be recorded by surveyors. There is currently no set guideline on the time that should be spent monitoring the male nightjars on each potential territory. Bult (2002) recommended that study areas in plantation forest in the SW Netherlands should be divided into plots of <35ha and then surveyed slowly (15-30 ha/h). In the most recent UK national nightjar survey, surveyors were instructed not to cover more than 80 ha per survey (Conway et al. 2007). If surveyors were provided with a recommended time to spend at each site, this would ensure that behavioural observations could be recorded and also provide a more accurate figure for the number of males present in the area. Although not possible in this current study, it would be very useful if the optimum time for observers to spend at each territory was investigated.

The mean song territory size of 8 ha for paired males and 7 ha for unpaired males in Thetford Forest obtained using radio telemetry can be compared to studies of mapped territories. Using territory mapping in heathland adjoining a mature conifer plantation in Suffolk, Cadbury (1981) found a mean song territory size of 8.16 ha ($n=8$, range=1.5-19.1 ha $sd=6.76$). It seems then that although radio telemetry allows individual churring birds to be clearly distinguished from others, the results from telemetry and territory mapping can be similar. Animals increase their territory size if a limiting resource is in short supply (Powell 2000) for example, shortage of females in the area for unpaired males and a shortage of another resource, such as food availability for paired males. Therefore, variations in individual territory size and overlap may be due to characteristics of the study area itself.

The mean longest dimension for all male song territories in this study was 533m (± 220 m sd , range= 295-1204m). In the last national nightjar survey in the UK (Conway et al. 2007), churring registrations that were >350 apart were counted as two separate birds. This was based on information from a number of studies. During the UK survey in 2004, the mean distance between simultaneous churring points was 360m ($n=331$, $sd=184.9$ m) (Conway et al. 2007). Bult (2002) found that the greatest diameter of nine nightjar song territories was 229m and therefore recommended that calls heard more than 300m apart should be counted as different birds. A previous radio-telemetry study in Thetford Forest recommended a distance of 400m to avoid

over-recording of nightjars (Bowden and Green, 1991). In order to provide a balance between over and under-estimating population size, a distance of at least 450m seems most suitable based on all results, including those from this study. A further method to provide an accurate distance would be to calculate the probability that if birds were registered as being the same at less than 450m, this would result in an over-estimate. However, this was beyond the scope of this study.

In summary, male nightjars with overlapping territory boundaries could cause a potential underestimate in numbers and surveyors must be aware of this. Both paired and unpaired males set up a single territory at a time and roaming males should not significantly affect census numbers. It is recommended that observers take time during surveys to record behavioural observations, in order to record the assumed breeding status of the male and any potential territory overlap. Radio telemetry provided clear information on the extent and longest dimension of nightjar territories, removing any uncertainty over the identity of individual birds. Territory sizes were similar to those found in other studies using territory mapping, therefore for the nightjar, territory mapping can provide an accurate representation of nightjar numbers (if overlapping is taken into account). The information from this study will be useful for future national nightjar surveys across Europe to ensure that nightjar populations can be monitored effectively. The methods in this study could be applied to other bird species to determine if the behaviour of paired and unpaired males could be affecting population estimates.

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Chapter 4: Home range and habitat selection of the European nightjar (*Caprimulgus europaeus*) in a heathland-plantation landscape

Abstract

The European nightjar (*Caprimulgus europaeus*) is widely distributed but is of conservation concern in Europe due to population depletion through habitat loss. Pine-plantation forest is a key habitat for nesting nightjars, particularly in north-western Europe and there is a need to understand nightjar foraging requirements in this habitat to provide management recommendations for the species. We radio-tracked 31 nightjars in 2009 and 2010 in an extensive (185km²) and complex conifer plantation landscape to determine home range extent and structure and investigate habitat preferences. Home range 95% kernels for females (mean 146ha, ± 119 sd), paired (mean 46ha, ± 33 sd) and unpaired males (mean 91ha, ± 54 sd) were an order of magnitude larger than male song territories (paired male: mean 9ha ± 6 sd, unpaired male: mean 7ha ± 5 sd), emphasising the importance of foraging habitat in the wider landscape. An investigation of nightjar breeding behaviour indicated that changing nest site and prospecting for mates could provide explanation for home range structure. Compositional analysis, in terms of home range placement in the landscape, showed that foraging nightjars selected pre-closure plantation forest (aged 5-10 years) and newly planted coupes (aged 0-4 years). Grazed grass-heath was also used, relative to availability, when within 2km of the territory centre. Open ungrazed and un-planted habitat is retained within the forest as a conservation measure but was avoided by nightjar, relative to availability. Results suggested that home range size may decrease with the percentage of key foraging habitats (pre-thicket, newly planted coupes and grazed grass-heath) within a 500m radius buffer from the territory centre, providing recommendations for forest design. Moth trapping indicated that nightjars may select foraging areas based on habitat structure rather than prey abundance. We demonstrate the importance for European nightjar of a large, structurally complex forest landscape with a variety of growth stages, which has relevance for conservation of the species across Europe.

Introduction

The European nightjar (*Caprimulgus europaeus*) is a cryptic, nocturnal species with over half of its global breeding range in Europe (Hagemeijer & Blair 1997). During the 20th century, the nightjar suffered a widespread population decline and range reduction across Europe, primarily due to

habitat loss and is subsequently a Species of European Conservation Concern (SPEC 2) (Burfield and Van Bommel 2004) and protected under Annex 1 of the EU 'Birds' Directive (EC 1992). The nightjar is found in dry, open habitats including dwarf-shrub heathland and clearings in scrub oak *Quercus* or mixed woodland (Cramp 1985). Open pine plantations with sparse tree cover are a key nightjar breeding habitat, particularly in north-western Europe (Tucker et al. 1994). In the UK for example, 57% of nightjars were associated with forest plantations in 2004 (Conway et al. 2007). Improved understanding of how nightjars use plantation forest landscape is required in order to inform appropriate conservation management practices for the species.

Although song territories, (which include the nest site) are well characterised for nightjar, home range extent and habitat use outside this are less understood. There was no difference between the song territory size of paired and unpaired male nightjars, with mean territory area $9\text{ha} \pm 6\text{sd}$ and $7\text{ha} \pm 5\text{sd}$ respectively (see Chapter 3). Nightjars forage short distances from the nest site, particularly when they have eggs or young chicks (Schlegel 1967, Cross et al. 2005), but can also forage several kilometres from the nest (Schlegel 1967, Alexander and Cresswell 1990). Use of habitat outside the immediate nesting or song territory can therefore be important to breeding populations, for example, Liley and Clarke (2003) found nightjar density in heathland patches to be positively related to the area of surrounding woodland within 500m of the patch boundary. Home range size and structure for nightjar is poorly known. The female nightjar's home range has not been quantified and results presented for males have been based on few individuals ($n=3$, Sierro et al. 2001, $n=4$, Spray 2006). Nightjar breeding systems also require investigation to provide further explanation for home range extent and structure. For example, females may change partner after the first brood (Cramp 1985) and prospecting females may leave the nest territory. A detailed investigation of the nightjar's home range and breeding behaviour is required to quantify the total area used and determine the relative importance of the nest territory and surrounding habitats for foraging.

Woodlands provide a heterogeneous landscape for birds, particularly plantation forests comprising stands of different ages as well as open areas. This "patchiness" can have important consequences on landscape suitability for a species (Dolman et al. 2007). The Open Habitats Policy of the Forestry Commission aims to recreate open habitats within existing forest plantations in the UK to benefit species such as the European nightjar (Driver 2010). Previous radio telemetry studies have found nightjars leaving mature coniferous plantations to feed in deciduous woodland in Dorset, UK (Alexander and Cresswell 1990), nesting in mixed age pine plantation and foraging in young forest and heathland in East Anglia, UK (Bowden and Green

1991), selecting open oak scrubland over vineyards and dense pine forest in the Swiss Alps (Sierro et al. 2001) and feeding primarily in young and open areas of conifer plantation forest, with some birds feeding in heathland and rough pasture in South Wales, UK (Cross et al. 2005). These contrasting results suggest that differences in forest landscape structure may affect the suitability of a site for foraging nightjars. These studies were not comprehensive however, with the number of birds being limited (n= 11, Alexander and Cresswell, 1990, n=3 Sierro et al. 2001) or radio-tracked birds being repeatedly lost due to difficult terrain (Cross et al. 2005). There is need to investigate foraging habitat selection, to determine the relative importance of forest, grass heath and other open habitats to nightjars in plantation forest.

Nightjar foraging habitat selection is thought to be based on habitat structure and prey abundance (Bowden and Green 1991, Sierro et al. 2001), with the insectivorous nightjar requiring habitat that enables prey capture against the light of the night sky. However previous studies were not extensive and results using moth trapping may be inaccurate due to moths being attracted to high powered traps from other habitats (Sierro et al. 2001). As moths are thought to be one of the key prey species for nightjars (Collinge 1920, Schlegel 1967), further examination of moth abundance in different habitats would enhance the current knowledge on nightjar habitat selection.

We used radio-telemetry to track a robust sample size of male and female nightjars in a complex plantation forest landscape in eastern England, which comprised stands of different growth stages, unplanted open habitat and adjacent areas of grazed grass-heath. Actinic moth traps (designed to have a low attraction radius) were placed in a variety of habitats within the landscape: grass-heath, ungrazed grassland and three forest growth stages spanning 0-80 years since planting. We quantified home range extent and prey abundance in different habitats and examined the relative importance of forest and grassland habitats for foraging nightjars, in order to provide management recommendations on the suitability of a forested landscape for this species.

Methods

Study site

The study was conducted in Thetford Forest (0°40'E, 52°27'N), the largest lowland commercial forest in the UK, covering 185km² of Breckland, East England. The forest contributes part of the

Breckland Forest Special Protection Area (SPA), designated in 2000 for its internationally important breeding populations of European nightjar and woodlark (*Lullula arborea*). Thetford Forest held c. 10% of the UK nightjar population during the last national survey in 2004 (Conway et al. 2007) but there has been a decline in numbers from 420 males in 1998 (Evans 2002) to 240 males in 2010 (Conway and Henderson 2010).

Thetford Forest is divided into blocks surrounded by a variety of different habitats, including agricultural land and heathland. Corsican (*Pinus nigra*) and Scots pine (*P. sylvestris*) comprise 85% of the planted area. The forest is managed by clear-felling (at economic maturity, currently 60-80 years) and replanting of even aged stands (mean coupe area 9.0 ha \pm 8.6 sd) of trees, creating a mosaic of growth stages. These can be classified as: Restock (0-4 years since planting); Pre-thicket (5-10 years); Thicket (11-20 years); Pole (21-44 years); Mature Conifer (\geq 45) following Hemami et al. (2004) (Supplementary material, Table S1). As coupes aged 30-44 years were thought to be structurally similar to pole stage trees, (pers. comm. N. Armour-Chelu), the age of mature trees was increased to >45 .

Radio-telemetry

See the General Methodology chapter for details of the procedures carried out during radio tagging and tracking.

A total of 36 birds were radio-tagged; 20 in 2009 (13 male and 7 female) and 16 in 2010 (12 male and 4 female). In 2009, two birds shed their tags and three were lost, leaving a total of 31 (21 male and ten female) for analysis.

Breeding status

During evening surveys and subsequently during radio-telemetry, male status (paired or unpaired) was judged using multiple criteria (General Methodology, Table 1) primarily based on behaviour exclusive of movement patterns to assure independence for analysis. The use of behavioural observations to identify the breeding status of male birds is widespread (Van Horn et al. 1995, Guillemain et al. 2003), however it should be noted that there is the possibility that some males may be misclassified or change status during the season. For the duration that a bird was being tracked, notes on the breeding status of the bird were taken, including any changes in behaviour or status, as this had the potential to affect home range size. These observations included the

recording of possible prospecting for a new mate, or the loss of a mate. Females were considered prospecting, if the individual: 1) had a recently fledged/failed nest, and 2) was recorded stationary near a churring male in a new area of the forest.

Nightjar ranging behaviour

As the focus of this study was foraging habitat use, active points (including foraging, flying between churring posts and patrolling the territory) were used to define the nightjar's home range. Firstly, Minimum Convex Polygons (MCPs) were created for home ranges. Although criticised for failing to describe space utilisation within the range (Worton, 1987), MCPs are considered comparable among studies (Kenward, 2001). The kernel density estimator (KDE) (Worton, 1989) is now accepted as a more accurate method for home range analysis (Seaman and Powell, 1996) and was calculated for females, paired and unpaired males. Fixed kernels were used as adaptive kernels over-smoothed data. As the data set contained clustered points and some birds had multi-modal home ranges, a fixed proportion of the h_{ref} value was used for all individuals (Bertrand et al. 1996, Kie and Boroski 1996, Kie et al. 2002, 2010) For each individual home range, the proportion of h_{ref} that best fitted the data was chosen such that the home range was not split into multiple small islands or included large unused areas and the mean value (0.3) was then applied to all individuals.

MCPs and kernels were produced in ArcGIS 9.2 using Hawth's Tools and HRT: Home Range Tool. Home range MCPs were calculated (n=28, mean number of fixes per individual=37, ± 16 sd, range=17-72 fixes), with three individuals excluded due to an insufficient number of fixes. Two separate MCPs were created for one female that relocated by 2.2 km during 2010, this individual appears twice in the analysis for MCP size (therefore, total n for MCPs=29).

A further set of MCPs was created with fixes for female birds split by stage in the breeding season. Three categories were created: non-nesting females, which included birds with no nest, eggs or chicks, at the beginning of the season, between nesting attempts or at the end of the season after chicks had fledged; incubating females; and provisioning females. There were not enough fixes to create MCPs for incubating females, therefore MCPs were compared for non-nesting (n=5) and provisioning females (n=4) only (mean number of fixes=28, ± 11 sd, range=17-42 fixes).

95% (outer range) and 50% (core range) kernels were calculated for all birds with at least 27 active positional fixes (n=19) (mean number of fixes=44.6, ± 15.6 sd) following Seaman et al.

(1999). Two males were excluded from the kernel analysis as they changed breeding status during the season; with insufficient fixes to create kernels for each status class. There were not enough fixes for each female to create home range kernels split by breeding stage. Kernels were rescaled to unit variance when the ratio of the standard deviation for x and y co-ordinates was <0.5 or >1.5 following Rodgers and Kie (2010) and the raster cell size used was 10m.

Compositional analysis

A GIS habitat layer was created (see Supplementary material), classifying the following habitat types: Restocked coupes; Pre-thicket; Thicket; Pole; Mature conifer; Mature broadleaf; Improved grassland; Grazed grass-heath (hereafter referred to as 'grass-heath'); Ungrazed rough semi-natural grassland; Scrub; Arable; Inaccessible; Urban and Water (Supplementary material, Table S2). Nightjar habitat selection was investigated on two levels of spatial scale following Johnson (1980); first considering territory placement (home range MCP 95% or 50% kernels) relative to habitat available within the study landscape and second, individual fix locations, relative to the habitat available to each individual.

For the first level, as tagged birds were aggregated in different blocks of the forest, three discrete study area MCPs were created based on pooled telemetry points across individuals from both years. Each study area MCP was buffered by 1.2km, based on distances travelled by nightjars in previous studies (Alexander and Cresswell 1990, Bowden and Green 1991) resulting in a mean distance of 1.98km (± 0.56 sd) from the territory centre to buffer edge for each individual within the MCP.

For the second stage of analysis, habitat available to each individual was considered as that within a fixed radius (2km) of the territory centre. This was considered preferable to using the individual home range MCPs or kernels as: 1) home ranges varied greatly in area (MCP, 27-380ha, 95% kernels, 14-189ha); 2) ad hoc kernel estimators produced multi-modal home ranges that delineated used habitat and excluded much of the traversed habitat not used for foraging and thus precluded examination of used vs. available; 3) home ranges of individuals excluded neighbouring habitat types, preventing compositional analysis to examine used versus available extent of less favoured habitats. The distance chosen is consistent with the study area buffers and encompassed 100% of fixes for 2009 and 98% for 2010.

The percentages of each habitat class available to birds and of fixes in each habitat were calculated using ArcGIS 9.2, excluding any inaccessible areas.

Hierarchical habitat selection was examined by compositional analysis (Aebischer et al. 1993) using 'Compos Analysis Version 6.2 Plus' (Smith Ecology 2004). Differences between habitats were determined using paired *t*-tests, with habitats ranked, independently of availability, based on the number of positive differences (Aebischer et al. 1993). A Habitat Preference Index was created based on the sum of the difference in log ratios between habitats produced from the compositional analysis (following Holt et al. 2010). Habitats were removed if availability was zero for more than half of individuals or if fewer than five individuals used the habitat, resulting in a final habitat set of: grazed grass-heath; ungrazed semi-natural grassland; restocked; pre-thicket; thicket; pole stage; mature conifer. As only three individuals were recorded using mature broadleaf, this category was excluded from analysis. Habitat use values of zero were substituted with a number an order of magnitude smaller than the values for available and used habitat (Aebischer et al. 1993) and 1000 iterations were chosen for data randomisation.

For the first level of analysis, data for all birds, years and study areas were considered (excluding birds lacking enough data with which to create MCPs and/or kernels). As all active points for each bird were used, the two males that were excluded from the kernel home range analysis (due to changed breeding status) were included in the compositional analysis. As equal composition accuracy for all animals is assumed (Aebischer 1993), for the second level of analysis, individuals were weighted according to the number of fixes obtained. Four birds were excluded from this level of analysis as they had no access to 'grass-heath' and three further birds were excluded as there were insufficient fixes to draw meaningful results (fewer than five).

In order to investigate if home range size varied with the availability of suitable foraging habitat, the percentage of key habitats (as determined by the compositional analysis) within a 500m (mean distance travelled by active birds in this study) radius buffer from the territory centre was also calculated for each bird. MCP home range size was then related to buffer composition.

Moth trapping

As moths are one of the key components of the nightjar diet (Collinge 1920, Schlegel 1967) moth trapping was used to investigate if nightjars select habitats due to high prey biomass or if there are other factors driving habitat preferences, for example, ease of prey capture.

Heath-type 15W actinic moth traps (Anglian Lepidopterist Supplies) were placed in five habitats available to foraging nightjars: grass-heath; ungrazed grassland; restocked; pre-thicket and old trees (including pole and mature trees, range=21-80 years) on five nights each week (where possible) from 15th June to 20th August 2009 and the 8th June to the 24th August 2010 (total

n=423). For each year, replicates of each habitat were chosen and traps alternated among these (\geq three in 2009, five in 2010). In 2009 a maximum of five traps were used each night (one in each habitat, alternating among replicate locations on different nights), while in 2010, a maximum of ten traps were placed each night with two in different patches of each habitat, located in different blocks of the forest where possible. The total sample size for each habitat was: grass-heath (n=78); ungrazed grassland (n=76); restocked (n=99); pre-thicket (n=96) and old trees (n=74). Truxa and Feidler (2012) used a mark and re-capture study to determine that the attraction radius for actinic traps was low, often below 10m, with very few moths being recaptured when released more than 40m from the light trap. Therefore moth traps were positioned 50m from the coupe edge, to ensure that moths were not attracted from neighbouring habitats. Traps were placed at dusk and emptied at dawn, with moths found inside the trap or on the box exterior recorded to family and size classes (Noctuid, $<$ or $>$ 2cm, Geometrid $<$ or $>$ 1cm, from head to abdomen tip) and where possible, to species (23% of all moths caught). Identification to species level was preferable as it provided information for subsequent moth biomass calculations, however due to time constraints and a large number (56% of all moths caught) of microlepidoptera being captured, (which require examination of the genitalia under a microscope for formal identification) (Waring and Townsend 2003), the majority of moths were identified to family and genus only.

Dry weights of moths collected from each main family group were used to determine moth biomass. Moth biomass was determined after freezing and then placing moths in an oven at 80 °C for 24 hours, removing to a dessicator to prevent moisture absorption, and subsequent weighing to 0.1mg. Three categories of moth contributed to the biomass calculations: a) individuals identified to species with dry weight known for that species (37% of total biomass from both years); b) individuals identified to species for which dry weight was unknown, therefore dry weight of species of similar abdomen size was used for biomass calculations (14% of total biomass); c) individuals identified to family or genus where the mean dry weight for representatives of that family (based on size class where possible) or genus, was used in biomass calculations (49% of total biomass, of which 22% of total biomass were micro-moths).

Temperature measurements

Temperature was recorded using data loggers (Lascar electronics, EI-USB-1). In 2009, three data loggers (one each in un-grazed grassland, restock and pre-thicket forest stands) were placed in the central area of Thetford Forest from July. In 2010, 20 data loggers were deployed in three

areas of Breckland (a max. of 10 km apart), in five habitats, (grazed grassland, un-grazed grassland, restock, pre-thicket and mature forest stands) from June.

For nights prior to placement of data loggers, nocturnal forest temperatures were predicted from hourly air temperature data from the British Atmospheric Data Centre (for Lakenheath weather station) based on the modelled relationship between forest temperature and those data, for hours when both were available (Data logger temp ($^{\circ}\text{C}$) = $1.25(\text{Met Office}) - 5.76$, $R^2=0.75$, $p<0.001$, $n=462$, 10 hours per day, 4/7/2009-19/8/2009).

Due to the small number of data loggers used in 2009 ($n=3$), temperature data was averaged for all habitats. For the 2010 temperature data, temperature varied with growth stage (GLM, $F_{(4,1346)}=14.81$, $p<0.001$), but not forest blocks (GLM, $F_{(2,1353)}=2.257$, $p=0.105$). Temperatures in the older trees were higher than those in other growth stages, (post-hoc Tukey, $p<0.05$ for all comparisons), but were similar among the other, more open, growth stages. However, inter-night temperature variation in the forest was high (mean midnight temp for all growth stages= 13.2°C , $sd=3.4$, range = $2-21^{\circ}\text{C}$) relative to the effect of growth stage on nightly temperature (mean nightly difference between midnight temp of old trees and all other growth stages= 1.17°C , $sd=1.45$, range= $0-5^{\circ}\text{C}$). Therefore, as the aim was to investigate differences in moth biomass from traps placed in different habitats, temperature effects on the overall abundance of moths on different nights were controlled for by considering the mean temperature per night (taking midnight temperature, averaging across growth stages) for both 2009 and 2010 data.

Statistical analysis

For females, paired males and unpaired males, home range area (square root transformed) was positively related to the number of active fixes available for the individual, considering both MCP ($n=29$, $R^2=0.141$, $p=0.045$), 95% and 50% kernels ($n=19$, $R^2=0.356$, $p=0.007$, $R^2=0.344$, $p=0.008$ respectively). Home range size (square root transformed) differences were investigated using a General Linear Model (GLM) with individual status (Female, Paired male or Unpaired male) as a fixed factor and number of fixes as a covariate, using PASW Statistics v. 17.0.3. Differences among each status class were examined using pair-wise comparisons of estimated marginal means. As Bonferroni corrections of confidence intervals can reduce power and increase the likelihood of a Type II Error (Nakagawa 2004), confidence intervals of the means were not adjusted. When females were split by breeding stage, differences in home range area (square root transformed) were investigated using a GLM that incorporated individual status as a fixed effect and number of fixes as a covariate (ΔAIC_i on removal of 'number of fixes' was 2.79).

To examine if MCP home range size varied with the habitats present within a 500m radius buffer, the relationship between home range area (square root transformed) and the percentages of key foraging habitats (as determined by compositional analysis) was investigated using a series of GLMs with Gaussian error, with percentage of habitat as a fixed effect, and controlling for the breeding status of each bird and the number of fixes obtained for each individual as additional fixed effects. Only the area of MCP home ranges was investigated; the number of females with enough fixes to allow calculation of kernel home ranges was too few to allow an equivalent model to be constructed.

Moth biomass (square root transformed) was compared among habitats using a General Linear Mixed Model (GLMM) with Gaussian error, including temperature and temperature² as fixed effects, an interaction between habitat and temperature, and coupe number as a random effect, using R (R Core Development Team 2011). Model selection was carried out by computing the Akaike Information Criterion, corrected for small sample size (AICc). When ΔAIC_i (difference in AIC from best model) <2, there is a substantial level of empirical support for the model (Burnham and Anderson 2002). To investigate the difference between habitat types, 95% confidence intervals (CI) of the habitat type coefficient estimates were used (Boughey et al. 2011). When the CI for a habitat type overlaps zero (CI >coefficient), there is no difference between that habitat and the habitat represented by the intercept.

Results

Breeding status

Of the tagged males, 11 birds were paired and the ten remaining were considered to be unpaired, with three of the paired males becoming unpaired during the season. Two of the ten nesting females moved to a new location, one after a successful nest and the other after a failed nest. Only one of these females had a large home range kernel due to this move (Fig. 2c) as the other moved before regular radio-tracking began. Three females were recorded as 'presumed prospecting' (including one of the birds that moved location). Three males continued to defend the territory, despite the loss of their mate.

MCPs and 95% kernels for males were an order of magnitude larger than song territory (paired male: mean 9ha \pm 6sd, unpaired male: mean 7ha \pm 5sd, see Chapter 3) (Fig. 1a & c). Female nightjars had home ranges twice the size of paired males in terms of MCP and over three times the size for 95% and 50% kernels (Fig. 1). Non-nesting and provisioning females had similar home range areas, larger than those of paired males and with no difference to those of unpaired males (Fig. 1b).

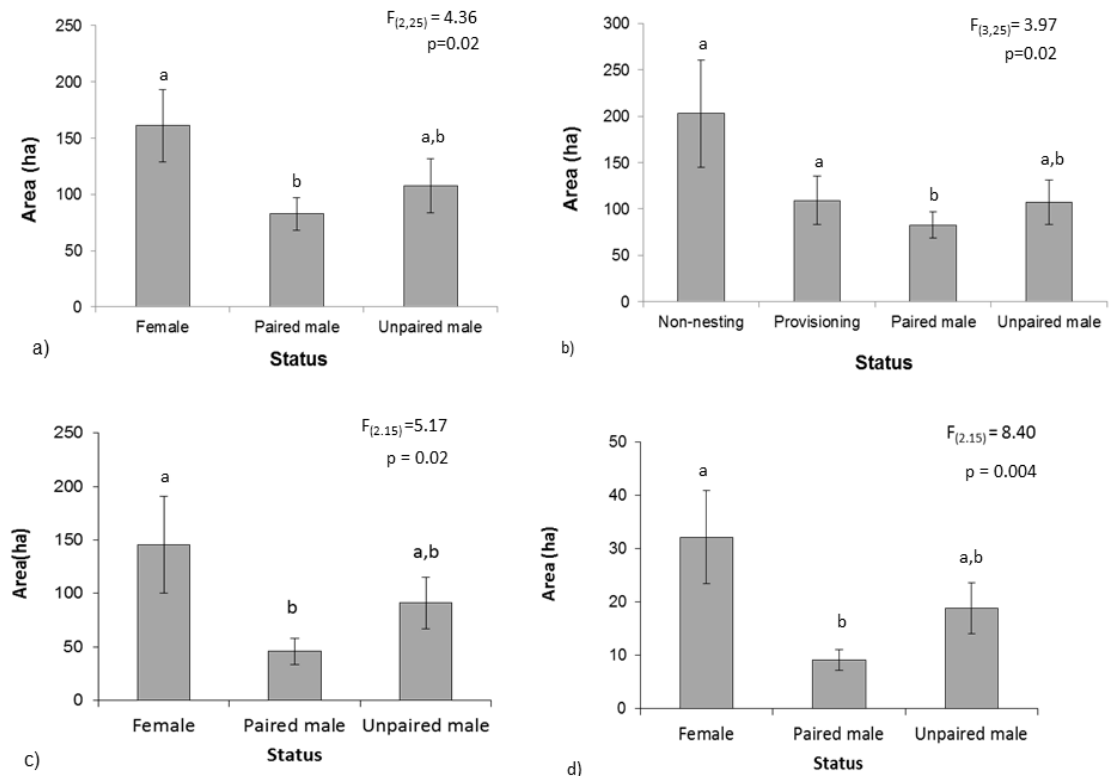


Figure 1. Mean area used by nightjars in Thetford Forest, showing a) home range MCP for female (n=11), paired male (n=10), unpaired male (n=8); b) home range MCP for non-nesting female (n=5), provisioning female (n=4), paired male (n=10), unpaired male (n=8); c) 95% kernel and d) 50% kernel for female (n =7), paired male, (n =7), unpaired male, (n=5). Error bars represent \pm se. Lower case letters indicate homogenous sub-sets from pairwise comparison of estimated marginal means.

Paired males had one core area centred on the song territory with a number of smaller core areas (Fig. 2.a) while female birds used a wide area outside the multi-modal 50% range (Fig. 2. b) &c). Unpaired males had multi-modal or large core areas (Fig. 2.d) and home range size intermediate

between that of females and paired males. The 50% kernel for all birds included the nest/song territory.

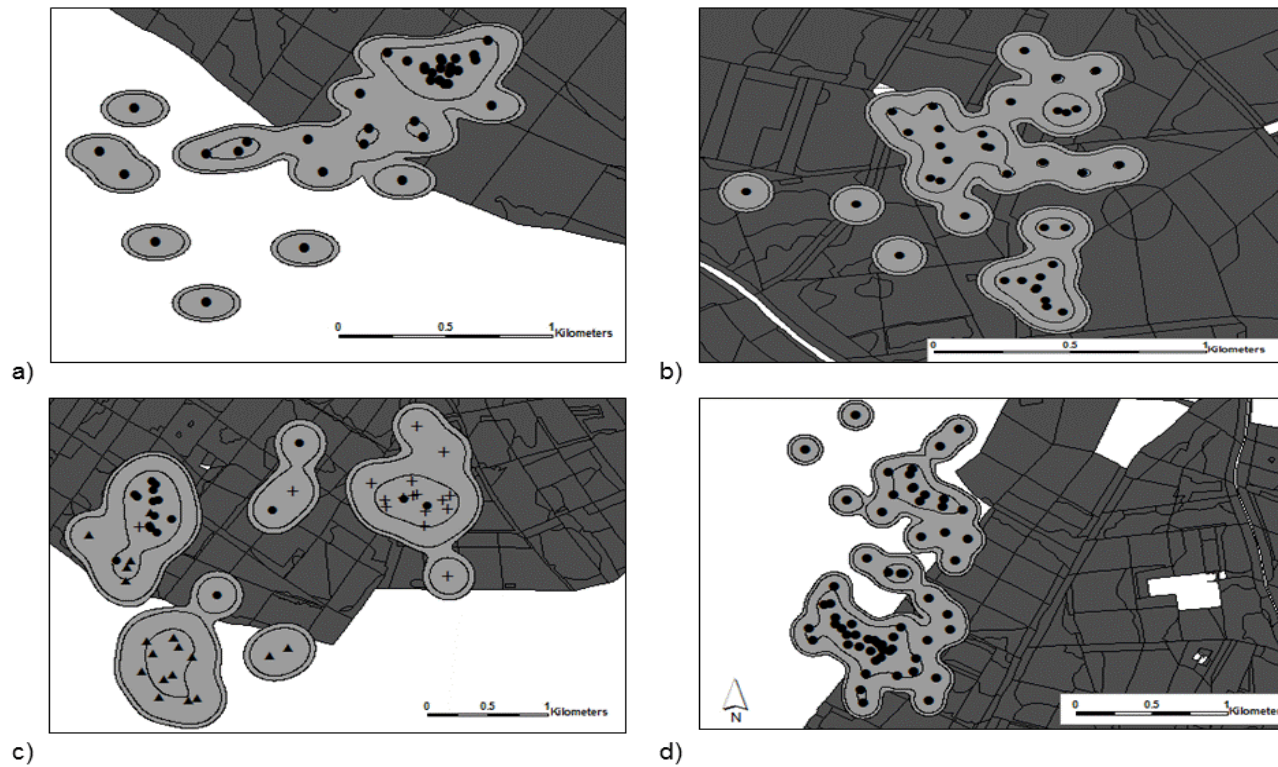


Figure 2. Nightjar home range kernel density estimates (outer isopleth representing 95% kernel and inner isopleth representing 50% kernel) for: a) a paired male; b) a female; c) a female that moved location, with points split by stage in the season, '+' = nesting in late June/early July, '●' = without nest in July, '▲' = without nest in August; d) an unpaired male.

Habitat selection

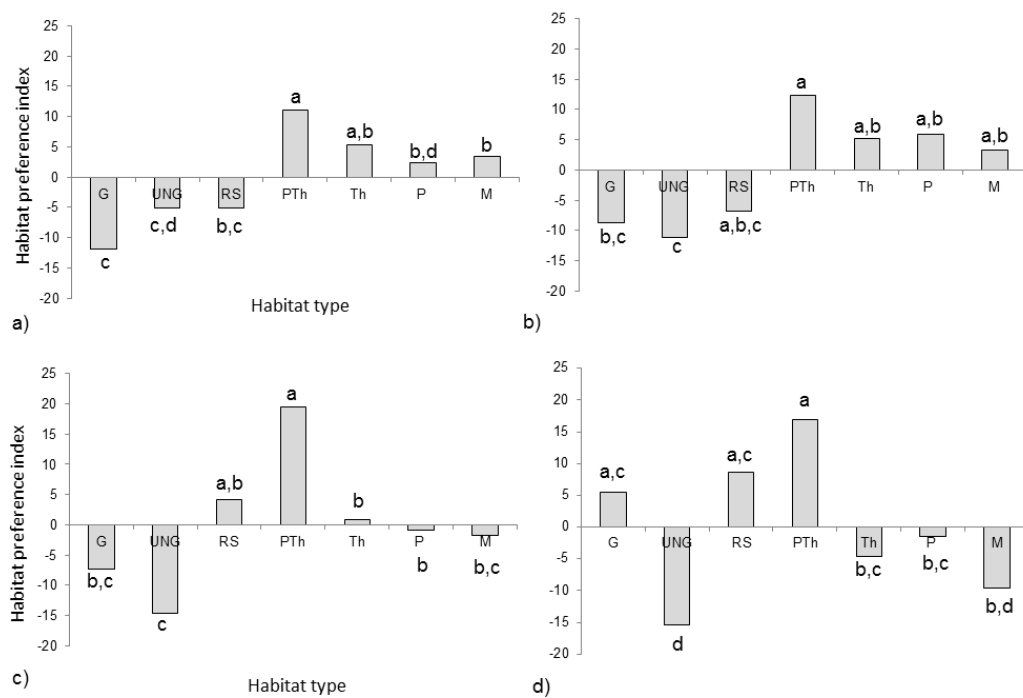


Figure 3. Compositional analysis of nightjar habitat use in Thetford Forest, a) MCP home ranges (n=29); b) 95% home range kernel (n=21); c) 50% core kernel (n=21), each compared with habitat availability across the study area; d) telemetry fixes for each bird compared with individual 2km buffers around territory centre (n=25). Habitat types: G= Grazed grass-heath, UNG= Ungrazed semi-natural grassland, RS=Restocked forest (0-4 years), PTh=Pre-thicket forest (5-10 years), Th=Thicket forest (11-20 years), P=Pole forest (21-44 years), M=Mature conifer (≥ 45). Lower case letters on the graph indicate differences among habitat types; classes that share a super-script do not differ significantly.

For habitat use within MCPs, relative to availability in the study area, pre-thicket plantation had the highest habitat preference index, being used significantly more than all other available habitats (except thicket), with both types of grassland used significantly less than other habitats (except pole stage and restocked) (Fig. 3a). For 95% kernels, while pre-thicket was again ranked the most preferred, there was no significant difference among the forest habitats, however pre-thicket was used significantly more than either grass-heath or ungrazed grassland (Fig. 3b). Within the 50% core range, pre-thicket was most preferred, followed by restocked coupes and the use of ungrazed grassland was significantly lower than that of other habitats except mature forest and grass-heath (Fig. 3c). For habitat use at individual fixes within the 2km buffer, the preferred

habitats were pre-thicket, restocked and grass-heath (with no significant difference among these), while ungrazed grassland was ranked as the least selected and was used significantly less than all habitats except mature forest (Fig. 3d).

The percentage of pre-thicket within a 500m radius buffer of the territory centre had no effect on home range size, with the best model containing only the breeding status of the bird and the number of fixes (on addition of the fixed effect of percentage of pre-thicket to the model, $\Delta AIC_i = 2.33$). The percentage of the three key foraging habitats (pre-thicket, restocked coupes and grass heath) was then summed (as % of suitable foraging habitat) and included in the model as a fixed effect. After controlling for the effect of breeding status and number of fixes, there was no clear difference between the model containing the percentage of suitable habitat and the one without (best model contained % of suitable foraging habitat but ΔAIC_i on removal of this variable = 0.97), suggesting that each model is equally plausible. Therefore the percentage of suitable foraging habitat within a 500m radius buffer of the territory centre may affect the home range size. Results suggest that home range size decreases as the percentage of suitable foraging habitat increases (Fig. 4).

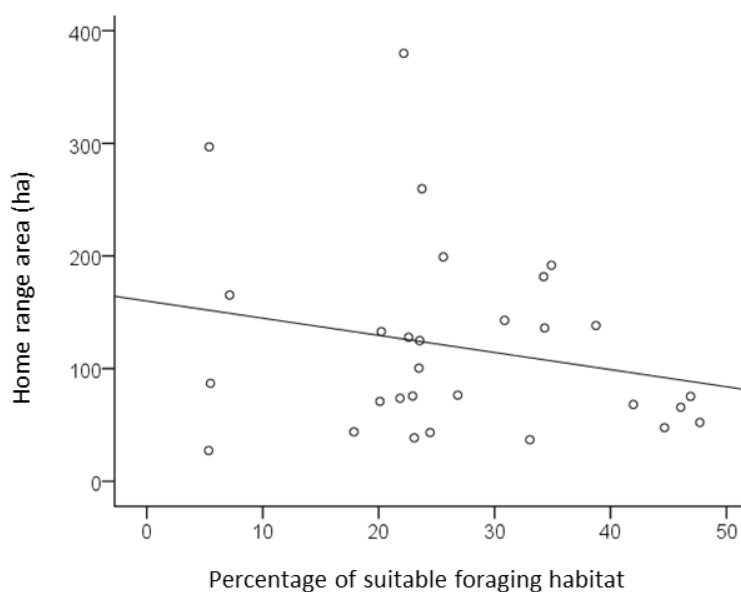


Figure 4. Variation in nightjar home range (Minimum Convex Polygon) size with the percentage of suitable foraging habitat (sum of pre-thicket, restocked coupes and grass heath) within a 500m buffer around the territory centre.

While there is considerable scatter in the graph of raw data (Fig. 4) due to variation in home range size with breeding status and number of fixes, the results suggest that as the percentage of

suitable habitat within the buffer increases to 40-50%, home ranges are at their lowest size. Within a 500m buffer from the territory centre, this represents an area of 31-39ha.

Moth biomass among habitats

The relative contribution of different families to total moth biomass was similar among habitats (Fig. 5). More moth biomass was captured on warmer nights (ΔAIC_i for model lacking temperature and temperature² =294), with a temperature increase of ten degrees more than trebling the total mean moth biomass caught (10°C, \bar{x} =1.21g night⁻¹, ± 0.91 sd; 20°C, \bar{x} =4.21 g night⁻¹, ± 3.56 sd). Moth biomass was greater in old trees than in young forest (both pre-thicket and restock) and ungrazed open habitats (ΔAIC_i for model lacking habitat=13.79), while biomass in grass-heath sites did not differ from that in either old trees, or young forest. There was an interaction between habitat and temperature, with old trees having higher moth biomass than other habitats on nights with low temperatures (ΔAIC_i for model lacking the interaction=5.13).

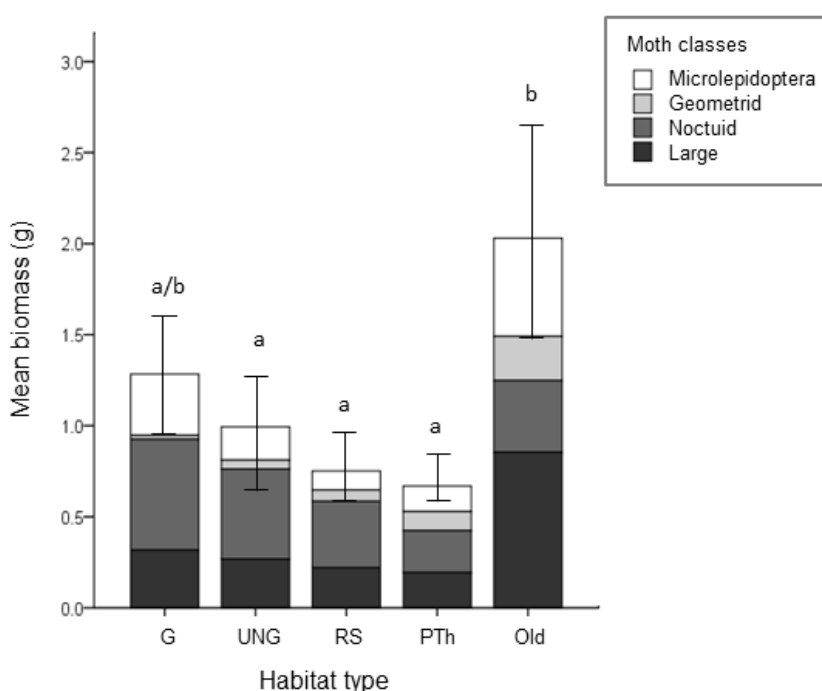


Figure 5. Mean moth biomass in different habitats, with bars made up of mean biomass of key moth groups. Habitat types: G=Grazed grass-heath; UNG= Ungrazed semi-natural grassland; RS= Restock stage forest (0-4 years); PTh= Pre-thicket stage forest (5-10 years); Old=Pole and Mature forest (21-80 years). For moth classes: Large= Sphingidae, Lasiocampidae, Arctiidae, Micro= Microlepidoptera, wingspan <20mm. Error bars are \pm se. Lower case letters indicate differences among habitat types; classes that share a super-script do not differ significantly.

Discussion

This study combines an investigation of range size, breeding behaviour, habitat use and potential prey availability to provide information to assist forest design recommendations for a breeding European Species of Conservation Concern. Using a robust sample size for male and female birds, nightjar home range areas were found to differ according to sex and were an order of magnitude larger than the male song territory. Key forest growth stages relative to their availability were restocked forest and especially young pre-thicket plantation. Interestingly, high moth biomass was not associated with these most visited forest habitats, implying that the birds' habitat 'preference' may have been related to prey accessibility rather than abundance. Grass-heath was also selected when within 2km of the territory centre, in contrast to the relatively small areas of ungrazed grassland (mainly forest rides) that were avoided by birds. Together, these results suggest that a heterogeneous forest landscape can support breeding and foraging nightjars and can be used to inform forest management planning.

Breeding status

Information on nightjar breeding behaviour provided understanding of differences in home range area between males and females. On the basis of the detection of new territory centres, female birds were recorded prospecting after their first nest, supporting the suggestion that females may swap partners between nests (Cramp 1985). Apparent prospecting did account for some of the outer points in the female home range, as did females visiting previous nest sites. In addition, two females moved nest site during the breeding season. These results must be interpreted with some care however as the possible negative effects of telemetry and regular nest monitoring (to assess nest survival) can't be ignored.

Nightjar home range

For both MCP and kernel home range analysis, bias has been found to decrease with larger sample sizes (Swihart and Slade 1997). There is no general consensus on the recommended sample size for MCPs, with variability between studies; for example, using area-observation curves of radio telemetry data and simulated locations, 100-200 points is suggested in order to reach asymptotic levels for the MCP (Bekoff and Mech 1984, Laundre and Keller 1984), whereas Arthur and Schwartz (1990) recommend >60 points to achieve both accuracy and precision. However, it can be difficult to achieve these sample sizes per animal when using radio-telemetry.

The use of GPS tags can vastly increase the number of data points collected (Arthur and Schwartz 1990, Kie et al. 2010) but the technology was not available for the size of satellite tag and battery life required for this study. Seaman et al. (1999) recommend a minimum of 30 observations per animal for home range kernels, as was followed for the kernels in this study. While the MCPs (n=29) did not meet this requirement for all birds (for n=7, number of fixes=17-25), home range size was similar using the two methods, with MCPs found to be slightly larger, as would be expected as kernels map the utilisation of space by birds rather than the total area within the outermost points.

The home ranges in this study were based on active fixes, which could represent foraging, prospecting or movement, including, for male birds, flying between churring sites. However, it is assumed that the majority of fixes represent foraging although these activities are not mutually exclusive. For example, territorial male birds were regularly recorded occupying the song territory for the duration of the night while only making short flights between churring posts, therefore birds were presumed to be foraging while defending the territory. The large size of the home ranges in comparison to song territory size confirms that nightjars are also regularly leaving the song territory to forage. Female home ranges (both MCP and 95% kernel) were larger than those of paired males. Home range sizes for non-nesting and provisioning females were similar, however, error bars were large due to low sample sizes. Visual inspection of the data suggested that differences between male and female home ranges may be primarily due to females ranging widely when they are not nesting, which could include females prospecting for mates or birds being less tied to the nest site after chicks have fledged. The 50% kernels were also larger for females and their multi-modal structure suggests that female birds had more than one regular foraging location throughout the season while the core area with the most activity for paired males was centred on the song territory. As paired males were found to remain at the territory even if the female had left the area, it seems that while the priority for the male is to guard the territory, the priority for female birds is to find optimal foraging sites. Unpaired males had intermediate home ranges, with individuals still defending a churring and potential nesting territory but ranging further than paired males, perhaps to increase the chance of locating a female. All birds, irrespective of sex and status, were regularly active in the song/nest territory. This suggests that nightjars in plantation forest may choose a territory based on its suitability both for nesting and foraging requirements.

The key habitat used by European nightjars in Thetford Forest was young plantation prior to canopy closure (pre-thicket), with newly planted coupes (0-4 years) also being preferred within the core (50% kernel) home range. There is no published evidence to indicate why birds may prefer these habitats, but the open canopy and access to bare ground structure may confer foraging advantages that increase ease of prey capture and perches for consumption of prey after capture. The presence of herbaceous vegetation and tree stumps may also provide an abundance of particular kinds of suitable prey. As the activity home ranges of birds of both sexes were centred on the song territory/nest site, young, open forest is suggested to be suitable for both nesting and foraging. Compositional analysis of territory placement within the study area indicated that grass-heath was not selected by all birds but was used when available within 2km of the territory centre. This habitat provides similar foraging opportunities as young forest stages.

For MCPs in the study area, both pre-thicket and thicket stage forest were preferred by birds but this may be because MCPs included habitat positioned alongside or between key habitats. When 95% probability density kernels (which provide a more accurate representation of space utilisation) were considered relative to the study area, there was no significant difference between all growth stages of forest. This may be because the forest contains a mix of growth stages and as birds were found foraging in a variety of these habitats, it is difficult to distinguish between forest habitats at this level of analysis.

In contrast to the birds in this study, Alexander and Cresswell (1990) found that nightjars were leaving nest sites within conifer forest to feed in deciduous woodland. However, the conifer forest in Alexander and Cresswell's study (Wareham, Dorset) contained mature conifers of a uniform age in contrast to Thetford Forest. Also, while all Thetford birds had areas of deciduous woodland within 2km of their territory centre, only three birds were recorded using this habitat, therefore it wasn't included in the final compositional analysis. This could have been because the individual size of patches of deciduous woodland was small (mean=2ha, ± 0.5 sd) and consisted mostly of narrow strips within the forest. Similarly, while birds in Switzerland avoided pine forest, trees in the forest were densely planted and the habitat deemed unsuitable for foraging nightjars (Sierro et al. 2001). Therefore the combined results suggest that forest structure is a key factor in nightjar habitat choice (Conway et al. 2007) and influences where birds forage in relation to the forest itself or adjacent habitats.

Nightjars in this study foraged on grazed grass-heath when it was available within a 2km radius buffer. Similarly, Schegel (1967) reported nightjars feeding near grazing animals. Grazing animals provide an additional source of nightjar prey due to the presence of dung beetles. In contrast, open habitat that was not grazed was avoided by foraging birds. Again, this is consistent with results recorded by Alexander and Cresswell (1990) in Dorset, with foraging nightjar avoiding ungrazed *Calluna* heathland. Although individual patches of ungrazed grassland were considerably smaller than those of grazed habitat (Supplementary material, Table S2) as they were largely comprised of forest coupe margins, any patches that were too small to detect nightjar foraging in (<20m wide and/or <0.5ha) were excluded from the GIS habitat layer; therefore birds were showing avoidance of ungrazed grassland. It may be more beneficial in terms of prey capture for birds to travel to larger areas of grass-heath to forage. It should be noted that when using compositional analysis to rank habitat preferences, as habitat use is compared to availability using proportions, habitat avoidance for rare habitats may be over-estimated because small differences between use and availability in absolute terms are proportionately larger than similar absolute differences between habitats that were more common (Marzluff et al. 1997). The mean value for available ungrazed grassland was only 5%, therefore this must be considered when interpreting results, however the overall outcome is the same, birds were not foraging in ungrazed grassland. It is also possible that birds are not using ungrazed grassland due to habitat structure. Nightjars have been recorded “hawking” for prey (Cramp 1985), which involves the birds sitting on the ground and swooping for flying prey. During our study, birds were recorded sitting at ride edges and “hawking” was witnessed. Also, birds foraging on grass-heath were often recorded as stationary and small bursts of movement from birds at the nest were regularly recorded. This behaviour may not be possible in ungrazed grassland due to vegetation height.

Results suggested that nightjar home range MCPs may decrease in size as the percentage of suitable foraging habitat close to the territory centre increases. It would be useful to investigate this further, with a larger sample size of birds, allowing 95% and 50% kernel areas to be investigated, as models results were equivocal. In addition, while these results can provide some guidance for habitat managers, the behaviour of birds (particularly females and paired males) during the breeding season was also found to have a strong effect on home range size, therefore habitat availability may not be the only factor to consider for forest design.

Moth biomass in habitats

Nightjars in Thetford Forest were not choosing habitats based solely on moth abundance as coupes containing old trees (pole and mature) had a higher moth biomass than pre-thicket coupes. These older growth stages were found to have greater moth biomass even on cold nights, presumably due to the dense canopy cover and bracken over the sandy soil keeping temperatures slightly higher than in other growth stages. As suggested by Bowden and Green (1991) and Sierro et al. (2001), nightjars may instead select foraging habitat due to the ease of catching prey, for example, pole stage coupes would be dark at night and difficult to manoeuvre amongst dense tree branches, whereas more open habitats such as pre-thicket and restocked coupes may be easier to forage in. In addition, habitats may be selected due to the abundance of other prey types such as beetles, another key component of nightjar diet (Cramp 1985; see also Chapter 5). Beetles are likely to be an important prey both in restocked and pre-thicket coupes due to the abundance of longhorn beetles (Coleoptera: Cerambycidae) emerging from cut stumps, and in grazed grass-heath, which supports dung-feeding beetles (principally Aphodiinae), although abundant deer populations (Hemami et al. 2004) also support dung-feeding beetles across a wide range of forest habitats (Stewart 2001). While foraging birds did not favour the older forest habitats, it is possible that they are still valuable habitats within the forest landscape as they may act as a reservoir for moths, with insects moving between forest habitats.

Conservation implications

This study emphasises the importance of investigating habitat use outside the song territory and demonstrates that radio-telemetry can add important understanding of habitat use relative to that obtained from territory maps. This is the case for a number of bird species, for example, chaffinches (*Fringilla coelebs*) foraged 1km from the song territory and home ranges included habitats not used for singing (Hanski and Haila 1988). Twite (*Carduelis flavirostris*) nesting in heather (*Calluna vulgaris*) foraged a minimum of 1km from the nest site on farmland (McLoughlin et al. 2010). The habitat requirements of a species must be understood to ensure that conservation measures are effective.

Understanding of nightjar habitat use in plantation forest provided by this study has widespread application, particularly in north-west Europe. While Gribble (1983) and Morris (1994) showed the importance of pine plantations to nesting nightjars based on surveys of churring males, this study demonstrated that plantations can provide nightjar with key habitat for both nesting and

foraging. Habitat structure is indicated as a factor determining nightjar habitat use. Nightjars would benefit from a large, structurally complex forest comprising a mosaic of growth stages and grazed grass-heath, with young forest habitats providing particularly suitable foraging sites and grazed grass-heath as an additional source of prey. Nightjar home range size may also decrease with an increased area of suitable foraging habitat close to the nest site, with results suggesting that an area of 31-39 ha foraging habitat within a 500m radius buffer around the territory centre may decrease the overall area required by the birds (with the caveat that model results were not strongly supported, thus further investigation is required to confirm the optimum area of foraging habitat required). Therefore the configuration of the habitat mosaic may also be important. As the forestry plantation management plans run on 60-80 year rotations, it would be difficult to re-structure the layout of growth stages. However, it may be possible to alter the size of each growth stage plot and the Forestry Commission also aims to recreate open habitat within plantation forest (Driver 2010), which could provide additional foraging resources for the nightjar, depending on the methods used in managing the habitat.

The structure and management regime for open habitat within plantation forest must be considered. The results of this study suggest that grazing of open habitat is important for foraging nightjars, either by lowering the height of vegetation or in providing sources of dung for dung beetle prey. The creation of open unplanted patches within the forest may not be beneficial if the vegetation is ungrazed. In addition to providing a further foraging resource for nightjars, the creation of grazed grass-heath also has potential benefits for regional biodiversity (Dolman et al. 2010), with heathland restoration and controlled levels of grazing advocated in lowland heathland Biodiversity Action Plans (BAPs). In terms of breeding nightjars, the use of grazing to maintain the vegetation structure of heathland will be beneficial as long as sufficient nesting habitat is also provided within c. 2km.

In summary, the creation of a heterogeneous mosaic within pine plantations and provision of open, grazed grass-heath areas for additional foraging opportunities will benefit this European Species of Conservation Concern.

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Supplementary material for Chapter 4

Habitat classification

Forest habitats were classified by growth stage (Table S1) and non-forest habitats were split into eight further classes (Table S2). A GIS habitat layer was created in ArcMap 9.2 by merging the Forestry Commission sub-compartment database for Thetford Forest (which provides spatially explicit data for all management units greater than 0.1ha, giving land-use and planting year for all planted areas), a layer of Sites of Special Scientific Interest (SSSI) containing heathland in Breckland (compiled from GIS data on Natural England website, <http://www.naturalengland.org.uk/publications/data/default.aspx>), a County Wildlife Site (CWS) layer for Norfolk (from Norfolk Wildlife trust) and Suffolk (compiled by Suffolk County Council), containing sites with grass heathland and the Land Cover 2007 (LCM2007) 25m by 25m raster maps (Centre for Ecology and Hydrology). LCM 2007 uses 23 habitat classes to map the land cover of the UK based on surface reflectance from images taken using satellite sensors (Morton et al. 2011). Land Cover data can contain errors in the classification of grassland (Morton et al. 2011) therefore classification was confirmed using images from Google Earth, Ordnance Survey 1:25000 data, local knowledge of the area and ground-truthing where necessary.

A set of rules was created, based on the probability of accurately locating the bird in a polygon of habitat using radio-telemetry. A minimum width and area rule for polygons was established, based on values for the minimum width and area used to define a piece of woodland in the National Forest Inventory (Whitton 2011). If a polygon in the GIS layer was not both 20m wide and 0.5ha in area, it was merged into the neighbouring habitat, as it would not be possible to determine accurately if the bird was present in these smaller polygons (mean telemetry error = $26.8\text{m} \pm 20\text{sd}$). This included small un-felled patches of mature conifers retained within felled and re-planted stands (mean area 0.34ha, ± 0.11 sd, $n=361$). Polygons of unplanted and ungrazed semi-natural grassland or other open habitats were also merged with restock habitat if they lay within a restock polygon or if they were <100m wide and shared the longest perimeter edge with the longest edge of a restock polygon. The larger value of 100m (rather than 20m wide) was used in these cases as open and restock habitats are similar in structure and if the two were adjoining, the bird may have been flying between both habitat types.

Table S1. Classification of forest habitat growth stages in Thetford Forest (details from Hemami et al. 2004 and Eycott et al. 2006)

Forest class	Age (years)	Mean tree height (m)	Mean canopy cover (%)	Tree density (m ⁻²)	Ground cover
Restock	0-4	<1	0	0	Predominantly bare ground/moss with some herbs (~20%) and grasses (eg. <i>Deschampsia flexuosa</i> and <i>Holcus lanatus</i> , ~10%)
Pre-thicket	5-10	3	20	0.3	Increased grass cover (>50%), with bushes (eg. broom <i>Sarothamnus scoparius</i> , gorse <i>Ulex europaeus</i> and Oregon grape <i>Mahonia aquifolium</i> , 12%) and herbs (12%)
Thicket	11-20	12	90	0.3	Reduced grass cover (30%), bare ground/moss again dominant (>50%), with herbs (20%) and bushes (~5%) also present
Pole	21-44	18	90	0.15	Bare ground/moss dominant (>50%), some grasses present (25%), with bramble (<i>Rubus fruticosus</i> agg. 8%) and bushes (5%)
Mature	>45	30	80	0.07	Increased ground cover, with grasses ((27%), bracken (<i>Pteridium aquilinum</i> , 15%), herbs (15%), bushes (12%), bramble (5%)

Table S2. Classification of non-conifer forest habitat

Habitat class	Total area available (mean \pm sd for all study areas, ha)	Area of individual patch (mean \pm sd for all study areas, ha)	Description	Data Sources
Broadleaf woodland	294 \pm 158	2 \pm 0.5	Broadleaf woodland within the forest (>30 years since plant year) and broadleaf woodland exterior to Thetford Forest.	FC GIS layer, LCM 2007
Grazed grass-heath	430 \pm 230	60 \pm 130	Grazed rough, neutral, calcareous and acid grassland. Includes SSSI and CWS units that contain heathland habitat as a designated feature and heathland reversion sites within the forest.	SSSI heathland layer LCM 2007 County Wildlife sites layer
Un-grazed semi-natural grassland	200 \pm 110	1 \pm 4	Ungrazed rough, neutral, calcareous and acid grassland. Includes gardens, archaeological sites and open (un-planted) areas within the forest with >50% open un-wooded (non-scrub) ground	FC GIS layer, LCM2007, Google Earth
Improved grassland	44 \pm 14		Grassland improved by farming practices and amenity grassland, eg. car parks, picnic areas, campsites	LCM 2007, Google Earth
Scrub (within forest)	31 \pm 22		Open areas within the forest with >50% of polygon covered by shrubs, eg. Gorse (<i>Urex europaeus</i>), broom (<i>Cytisus scoparius</i>), hawthorn (<i>Crataegus monogyna</i>), young birch, (<i>Betula pendula</i>)	FC GIS layer, Google Earth
Arable	717 \pm 334		All land used for cereals, horticulture (eg. onions, sugar beet) and pigs	LCM 2007, Google Earth
Not accessible	70 \pm 81		Land that could not be accessed during radio-tracking	NA
Urban	148 \pm 104		Habitat polygons with >50% houses or open areas covered by gravel	LCM 2007, Google Earth
Water	8 \pm 4		Reservoirs, ponds, lakes	LCM 2007, Google Earth

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Chapter 5: Factors driving the generalist diet of an insectivorous summer migrant

Abstract

There can be a number of possible factors driving variation in the diet of birds, including changes in resource abundance, stage in the breeding season and available foraging habitat. We used the European nightjar (*Caprimulgus europaeus*), an Afro-Palearctic migrant, which preys on a variety of insects, as a study species to investigate dietary variation of a generalist. Nightjar faecal samples were collected from 61 nest and roost sites over three years (June to September, 2008-2010) in a conifer plantation forest (185km²) with adjacent patches of grass heathland, in eastern England. Moth trapping was carried out to investigate the changes in available biomass of Lepidopteran prey during the breeding season. Faecal pellets (n=1069) were dissected and moth scales were used as a non-linear indicator of moth biomass. Beetle fragments in the pellets were identified to family where possible and an index (based on different body parts) was created as a measure of relative beetle abundance. The abundance of moth scales in the faecal pellets peaked in the same week as moth trap biomass peaked, suggesting that nightjars forage opportunistically on available prey. Adult nightjars were found to be provisioning larger chicks with a higher abundance of beetles, with faecal pellets from nests containing adult nightjars and large young having greater beetle abundance than sites with adults only, or adults with young chicks. Comparison of the diets of nightjars with grass heathland available and those with only forest habitats available suggested that these habitats provide similar foraging resources for the nightjar. The results of this study suggest that the variation in the nightjar diet within the breeding season may be due to changes in resource abundance and varying requirements of chicks during the breeding season.

Introduction

Foraging behaviour can be understood in terms of economic decisions based on costs and benefits (Krebs & Davies 1993). The Optimal Foraging Model (MacArthur & Pianka 1966) predicts the level of diet specialisation based on prey search and handling time. In a productive, predictable environment, search time is reduced and an organism will have a narrower diet. Speculation remains over whether the specialist or generalist diet is a more efficient life history strategy in terms of evolutionary fitness (Woo et al. 2008). Dedicated specialists, with adapted

morphology and behaviour, spend less time searching for prey therefore foraging success may be greater than for generalists (Dukas and Kamil 2001). However, a specialist diet may lead to a decrease in fitness under certain circumstances, for example, when the preferred food source is scarce (Huckins 1997, Terraube et al. 2010). In reality, it is necessary to quantify the degree of specialisation and classify most species along a continuum between specialist and generalist (Sherry 1990). Whether or not a species is classed as a specialist depends on the species which it is compared to and the level of resource diversity (Recher 1990). For example, when the insectivorous diet of the Cocos flycatcher (*Nesotriccus ridgwayi*) was compared to that of mainland Costa Rican flycatchers, it was broader in terms of prey and foraging behaviour, however as the Cocos flycatcher preys only on insects, it is a specialist when compared to species feeding on both insects and fruit (Sherry et al. 1990). It is therefore necessary to examine diet in detail and specify the context of the study.

In the avian world, diet specialists range from the extreme Snail kite (*Rostrhamus sociabilis*), which feeds on one genus of freshwater snail (Beissinger 1990) to birds that specialise when a particular prey species is in high abundance for example, the tufted duck (*Aythya fuligula*) preying on zebra mussels (*Dreissena polymorpha*) (Olney 1968). For generalist species, variation in the diet can be due to a number of possible factors. Seasonal fluctuations in diet can occur in response to changes in weather and resource abundance, for example, the diet of insectivorous birds varies with seasonal fluctuations in insect abundance, especially in temperate regions (Morse 1971). Diet can vary with stage in the breeding season due to differing requirements of adults and chicks. Birds of the family Paridae feed chicks primarily Lepidopteran caterpillars (Wilkin et al. 2009) but also provided a higher proportion of spiders to younger chicks (3-9 days old) than older (>9 days old), unrelated to stage in season or spider availability (Cowie & Hinsley 1988, Arnold et al. 2007). Chicks can be fed different types/proportions of prey from adult birds, for example, while adult sandwich terns (*Sterna sandvicensi*) feed mostly on silversides (*Hypoatherinah arringtonens*) and sardines (*Harengula* and *Opisthonema* spp.) chicks were fed mostly sardines and dwarf herring (*Jenkinsial amprotaeni*) (Shealer 1998). The generalist diet can also be flexible depending on the availability of habitat and prey. The diet of purple herons (*Ardea purpurea*) varies according to available habitat, preying on fish in rivers and amphibians and crayfish in rice fields (Campos and Lekuona 2001). Therefore when investigating resource selectivity in a species, there may be multiple factors driving variation in the diet and the time scale and stage in the season must all be considered.

The European nightjar (*Caprimulgus europaeus*) is an insectivorous Afro-Palearctic migrant. Due to widespread population declines, the nightjar is a Species of European Conservation Concern

(SPEC2) (Burfield and Van Bommel 2004) and is red-listed in the UK. Analyses of adult stomach contents from European nightjars breeding in the UK (Collinge 1920) and in Germany (Schlegel 1967) showed that nightjars consume a wide variety of prey species during the breeding season, consisting primarily of Lepidoptera and Coleoptera but also Diptera, Trichoptera and Odonata, amongst others. Cramp (1985) suggests that diet varies seasonally, depending on the insect species available, but the evidence base for this assertion is unclear. Using faecal sample dissection from a limited sample (just two adults), Sierro et al. (2001) found that the primary component in the nightjar diet was Lepidoptera, which were abundant for all study months (June, July, August). Diet may vary with breeding stage; using neck collars (n=74 collars from 11 broods) at two days old, nightjar chicks were fed a larger proportion of small, soft bodied insects (Microlepidoptera, Diptera) than chicks aged 5-17 days and the proportion of other insects, e.g. Cerambycidae increased after chicks were 5 days old (Schlegel 1967). Nightjars can forage long distances from the nest in a variety of habitats, with birds breeding in a complex mosaic landscape foraging in both grazed heathland and open canopy plantation forest (See Chapter 4). Therefore the high level of variation in the nightjar diet may be due to seasonal fluctuations in insect emergence, changes in dietary requirements at certain stages in the breeding season or birds feeding on different prey depending on the available habitat. However, while habitats may be classified as distinct in terms of human land-use, (e.g. forestry versus heathland) whether these actually represent different foraging opportunities and prey spectra is unclear.

We investigated the diet of breeding nightjars foraging in a plantation forest containing a mosaic of growth stages, unplanted open habitat and bordered by patches of grazed heathland. Faecal samples were collected from a robust sample of 61 nest and roost sites over three years and moth traps were placed throughout the forest and in adjacent heathland to examine changes in the relative available biomass of Lepidopteran prey during the breeding season. We investigated if nightjars were using different resources: 1) at different times in the season; 2) when feeding chicks; 3) when able to forage in different habitats within the landscape.

Methods

Study site

This study was carried out in Thetford Forest, (0°40'E, 52°27'N) the largest lowland coniferous plantation in the UK (185km²). The forest was planted on grass heath and agricultural land within the biogeographic region of Breckland, Eastern England, characterised by a dry climate and sandy

soils (Dolman et al. 2010). Managed with clear-fell rotation and replanting of even-aged stands (mean coupe area 9.0 ha \pm 8.6 sd) Thetford Forest consists of a mosaic of growth stages, providing a variety of ground and canopy cover. Growth stages can be categorised as: Restock (0-4 years since planting); Pre-thicket (5-10 years); Thicket (11-20 years); Pole (21-44 years); Mature Conifer (\geq 45 years) (See Chapter 4 for more details).

In addition to heather dominated areas, Breckland grass heaths contain areas of calcareous and acidic grassland communities (Dolman and Sutherland 1992). A number of heathland remnants adjoin Thetford Forest; since the introduction of the Breckland Environmentally Sensitive Areas (ESA) scheme of 1988, all major designated heathlands have been managed by livestock grazing.

Thetford Forest forms part of the Breckland Forest Special Protection Area (SPA), designated in 2000 for its internationally important populations of breeding nightjar (*Caprimulgus europaeus*) and woodlark (*Lullula arborea*). In the 2004 national nightjar survey the forest contained 10% of the UK population (349 singing males) (Conway et al. 2007), however this number has declined to 240 males (Conway and Henderson 2010). The mosaic structure of the forest also provides a wide variety of habitats for Coleoptera and Lepidoptera, from closed canopy forest to open ground and ride margins; within the forest, 74% of vascular plant species recorded on Breckland grass heaths can be found (Eycott 2005). Diverse assemblages of carabid beetles are present in open forest habitats, for example, recently felled forest and restock stage trees, including species associated with coastal and heathland habitats as well as moorland and open woodland (Lin et al. 2007, Bertoncelj and Dolman, in press). Tree stumps provide an important habitat for saproxylic beetles, for example in Sweden 17 fungivorous and 8 predatory beetle taxa were found in “one summer old” stumps of Norway spruce (*Picea abies*) (Hedgren 2007). The presence of livestock (primarily sheep) on heathland within and surrounding the forest, as well as red (*Cervus elaphus*), roe (*Capreolus capreolus*), fallow deer (*Dama dama*) and Chinese muntjac (*Muntiacus reevesi*) feeding both within the forest (Hemami et al. 2004) and some adjacent areas of heathland, provides dung resources for Scarabaeidae beetles.

Faecal sample collection

Faecal samples (all pellets present at the site on a particular date) were collected from nest and roost sites of nightjars in Thetford Forest between May - September of each of 2008, 2009 and 2010 and stored in 70% ethyl alcohol. In 2008 and 2009, in a joint study between the UEA and BTO (see Chapter 6 for further details) nest cameras were set up at nightjar nests throughout the forest. Faecal samples were collected if present when the nest was found and a sample was also

collected when chicks were ringed (where possible). After chicks had fledged/the nest had failed, any intact faecal pellets present at the nest when the camera was removed were also collected. In 2010, nightjar nests were located by organised nest finding parties and nests monitored regularly (every 5 days where possible). Faecal samples were collected from the nest when present. Nightjar roost sites were most commonly found on nest finding days (across 2008-2010) or when searching for adults and chicks to determine if the nest had been successful. Therefore, samples were only collected on one occasion from the majority of roost sites. If faecal pellets were only collected on one occasion, then pellets could have potentially accumulated at the site for a number of weeks.

For each faecal sample (n=76, 1069 pellets in total), the collection date, location (forest block and coupe number), site (nest/roost) and status of the bird (roosting, incubating a clutch, provisioning chicks) was recorded. There were 61 sites in total, with each given a unique identifying number. For 75% of sites, a sample was collected only once, whereas for 25% of sites, samples were collected on multiple occasions (\bar{x} =2.4 collections per site, ± 0.63 sd, range=2-4). For sites that had repeated sample collection, the mean interval (days) between collections was=11.2 \pm 7.5sd days.

Faecal sample dissection

A pilot study was carried out, with faecal pellets teased apart using tweezers under a dissecting microscope, to confirm that insect fragments were present and identifiable. Moths and beetles were the key families found in the pellets. Further unidentifiable insect fragments were also present (in 24% of all pellets dissected in the main study) but were too fragmented for identification to be made with any certainty.

A reference collection of beetle and moth fragments was created by crushing into pieces a range of insect species known to be common in Thetford Forest (comprising one Noctuidae moth species: *Noctua pronuba* and eight beetle species; *Arhopalus rusticus* and *Strangalia maculata* from the Cerambycidae (Longhorns), *Amara plebeja* and *Pterostichus madidus* from the Carabidae, *Athous hirtus* from the Elateridae (Click beetles), *Aphodius rufipes* from the Scarabaeidae (Dung beetles) and *Quedius fuliginosus* and *Staphylinis olens* from the Staphylinidae). Photographs of segments were captured using the integrated camera of a Leica MZ75 microscope with a magnification range of x6.3 to x50. Additional identification aids included Ralph et al. (1985) and a bat faecal dissection guide (Shiel et al. 1997). Images of beetle fragments that appeared repeatedly in samples were posted to a photo-sharing website (<http://www.23hq.com/KatrinaEvans>) to invite identification from the entomological community.

I received feedback on the website from four specialists on beetle fragment and species identification (including palaeo-entomologists and county recorders). Identifications of key body parts or species were confirmed by more than one expert and cross-validated using the reference collection and samples of the insects suggested. Examples of characteristic fragments were the bi-lobed third tarsal segment of longhorn beetles (Cerambycidae), click mechanism of click beetles (Elateridae) and distinctive fore legs of dung beetles (Scarabaeidae) (Figure 1).

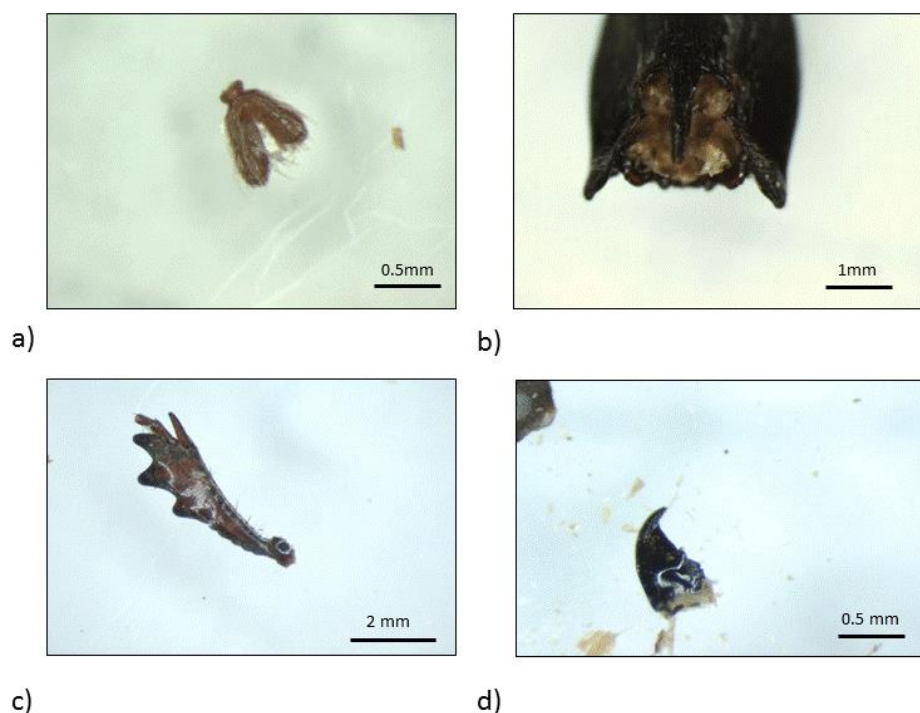


Figure 1. Characteristic beetle fragments found in nightjar faecal pellets, allowing identification of beetle families: a) Bi-lobed tarsal segment of longhorn beetle (Cerambycidae); b) Half of the click mechanism from a click beetle (Elateridae); c) Segment of a dung beetle fore leg (Scarabaeidae); d) Mandible of carabid beetle (Carabidae).

Each faecal pellet was placed on a piece of filter paper to remove excess alcohol, weighed and put in water in a petri dish (9cm internal diameter) with two drops of detergent added to reduce clumping of moth scales. Water was used rather than alcohol to reduce movement of the liquid and insect fragments due to evaporation. The faecal pellet was broken up using tweezers and stirred to disperse fragments and material evenly and fragments were then examined under a microscope for identification. All faecal pellet dissection and fragment identification was undertaken by one person. Where possible, ten pellets per sample were dissected, however on some occasions, multiple jars of pellets were collected at a site and therefore more than ten pellets (mean number of pellets dissected per sample dissected was 13 ± 10 sd, range=3-55).

Moth scales were chosen as a non-linear index of moth biomass in each pellet (Black 1974; Supplementary material). Although residual moth scales (a few scales per pellet) remain in the gut of bats up to 24 hours after moth consumption (Robinson and Stebbings 1993), when moths are freshly eaten, a “packed mass of scales” is present (Whitaker et al. 1996). We therefore expected a large range in frequency of moth scales, with large scores relating to recent foraging or provisioning compared to a ubiquitous background low level of scales. The petri dish was placed over a laminated grid of 5mm by 5mm squares. The number of moth scales in six randomly chosen squares was counted, under x10 magnification, with the petri dish contents stirred between each count. If there were greater than 100 scales in a square, 25% (visually estimated) of the square was counted and the number multiplied by four. For each pellet, the mean number of moth scales per 25mm² was re-scaled to the number of scales per petri dish and divided by pellet weight (to give a standard measure, scales per mg of faecal pellet). Between dissections, the petri dish and tweezers were washed with water to ensure that no moth scales remained from the previous faecal pellet (validated by examining a used petri dish under the microscope).

All identifiable beetle fragments visible in the entire pellet were recorded, distinguishing head, antennal segment, mandible, fore, hind and mid tibia, femur, coxa, claw, tarsal segment and carapace and other undifferentiated fragments; where possible fragments were identified to beetle family or species level. To provide an index of beetle frequency in the sample, firstly the frequency of each beetle piece in the faecal pellets was investigated to determine if there were any types of pieces found in the majority of samples that would therefore be a good indicator of beetle presence. None of the beetle pieces were found in all samples containing beetle fragments, therefore it was not possible to use the frequency of only one beetle piece as a measure of beetle abundance in the pellets. The correlation matrix, relating the frequency at which different parts were found (for all samples containing beetle pieces), was examined to determine which pieces were more likely to be found when other types of fragment were also present. From these a key set of beetle pieces with high frequency and correlation with other pieces was chosen: carapace, femur, fore tibia, mandible and tarsal segments (Supplementary material, Table S1). All other beetle pieces were pooled into the category “Other beetle pieces,” (which included antenna, coxa, claws, wing, head, mid and hind legs). Pieces of carapace showed strong correlations with other types of beetle fragments, however, because all relationships between carapace and other beetle pieces showed considerable scatter and as some samples contained different fragments of beetle exoskeleton but no carapace fragments (Supplementary material, Fig. S2) it was not possible to use carapace alone as an indicator of beetle abundance. As carapace fragments showed strong correlations with other types of beetle fragment and were numerous in the samples with a high standard deviation, carapace fragments were therefore

chosen to use as a common currency in which all other pieces could be expressed. Antennal segments (another common piece in the samples) were not chosen because there was a possibility that variation in the abundance of these pieces provided more information on the family of beetle present in the sample rather than the number of beetles present in the samples (Fig. S3). Separate linear regressions (with no intercept in the model, i.e. constrained through zero) were carried out between the number of carapace fragments and the number of each other class of pieces in the beetle set. The resulting equations were used to convert the number of all other pieces found in each faecal pellet into the equivalent 'number of carapace pieces' (Table 1). The totals for each faecal pellet were summed to provide the beetle index for each pellet.

Table 1. Regression results for beetle pieces, with carapace as dependent variable

	r^2	Beta	Se
Mandible	0.196	1.305	0.090
Fore	0.25	2.128	0.124
Femur	0.108	1.17	0.114
Tarsal	0.101	1.244	0.126
Other pieces	0.235	0.504	0.031

Beetle index values were only weakly related to sample weight (linear regression, $R^2=0.046$, $p<0.001$) and were therefore considered to represent the relative contribution of individuals and or biomass to recent prey consumption, rather than differences in the volume of faecal material comprised in the sample (Supplementary material Fig. S4).

Moth trapping

To investigate how available moth biomass varied with season, actinic heath moth traps (Anglian Lepidopterist Supplies), which allowed sampling of local habitat, were placed within three forest growth stages (restock, pre-thicket, old trees (>20 years)) in the forest blocks where radio telemetry was undertaken (See General methods chapter for details of methodology) and in surrounding grass heathland, five nights per week (where possible) from June until August 2009/10. For each year, replicates of all habitats were chosen and traps alternated among these (\geq three in 2009, five in 2010). A maximum of five traps per night was used in 2009, with a maximum of ten traps per night in the forest in 2010. Moths in the traps were identified to family

and size classes (Noctuid < or > 2cm, Geometrid < or > 1cm, from head to abdomen tip) and where possible, to species (23% of all moths caught). To determine moth biomass, dry weights of moths collected for four moth classes (Noctuid, Geometrid, Large (including Arctiidae, Lasiocampidae, Sphingidae) and Microlepidoptera (wingspan < 20mm) were used. (For further detail on the calculation of moth dry weights, moth biomass per habitat and nightjar foraging habitats, see Chapter 4).

Habitat classification

Using ArcGIS 9.2, a habitat layer was created by merging the Forestry Commission database, habitat data from CEH Landcover 2007, a layer of Special Sites of Scientific Interest (SSSIs) containing heathland (from the Natural England website:

<http://www.naturalengland.org.uk/publications/data/default.aspx>) and a layer of County Wildlife Sites for Norfolk (compiled by Norfolk Wildlife Trust) and Suffolk (compiled by Suffolk County Council) containing grass heath or lowland heathland. Grazed grass heath and heathland (including areas of re-created heathland within the forest landscape, all hereafter referred to as “grass heath”) was considered distinct from ungrazed grassland habitats that included open unplanted areas of the forest. The distance of each faecal sample site to the nearest area of grass heath and restock stage forest was calculated using ArcGIS. For 85% of collection sites, the GPS co-ordinates were known. For the remaining 25% of sites (all of which were roost sites), the centre of the forest coupe where the roost site was located was used to estimate the distance to the nearest area of grass heath. The mean dimensions for these forest coupes were 293m by 337m and thus the mean maximum error was approximately 150m. Sites were categorised as < or > 2km to grass heath, chosen as the 95th percentile of the maximum distance travelled per night by radio-tracked nightjars in Thetford Forest (see General Methodology chapter for details of radio telemetry). The percentage of grass heath within a buffer of 2km radius around each faecal sample collection site was also extracted from the ArcGIS habitat layer. As the percentage of restock forest in the buffer was similar for all birds (\bar{x} =3.2%, 2.0±sd, range=0-6), only the distance to the nearest restocked forest coupe was investigated.

Statistical analysis

To account for potential seasonal effects, the approximate midpoint of the period over which each sample may have accumulated was estimated and attributed as a continuous variable ‘Date,’ (number of weeks after May 1st). The maximum time that samples obtained from nests may have

accumulated was six weeks (based on two-three days at the nest scrape prior to laying, 18 days of incubation and 18-19 days until fledging (Cramp 1985)); however samples collected prior to fledging (e.g. at nest finding or during monitoring) will have accumulated for less time. For each nest, accumulation time was calculated based on the estimated first egg date, relative to the sample date. As birds can be faithful to roost sites (Cramp 1985 and verified in this study), accumulation periods were also applied to roost samples. Samples were collected for only one roosting female and the accumulation date was based on the date of nest failure as the female had moved to this roost site after the failure of a monitored nest). For roosting males, if there was evidence that the bird was paired with a female using a known nest site (from radio telemetry data (Chapter 4) or samples were found <50m from nest (males roost close to the nest site, Berry 1979)), then accumulation time for that roost was based on the stage of the nest. If there was no information on duration for which an individual male roost site was used, a value of six weeks accumulation time was allocated (based on the maximum time a male could have used the site if paired with a nesting female nearby), with the exception of samples collected early in the season, which were curtailed based on the mean expected arrival date of nightjars to the UK (15th May, based on information from BirdTrack (BTO/RSPB/BirdWatch Ireland/SOC 2012, www.birdtrack.net) and Greg Conway, BTO, pers. comm.).

Mass of faecal samples varied widely (\bar{x} =151mg \pm 89sd, range=17-959mg). We therefore examined whether it might be possible to distinguish faecal pellets from chicks and adults, according to their weight. To investigate if the mean faecal pellet weight was lower for nests containing chicks, faecal weights were compared among pellets obtained from adults with young and adults only (adults with eggs and roosting adults) using a General Linear Mixed Model (GLMM) with Gaussian error, including the fixed effects of accumulation time of samples at the nest (to control for any deterioration of samples) and date, with site identification number as a random effect. Controlling for the pseudo-replication of site (mean weight taken for pellets collected from the same site), pellets from adults (\bar{x} =184mg, \pm 61sd) were slightly larger than those from adults with chicks (\bar{x} =142mg, \pm 49sd) but with considerable overlap. However, due to the possibility of faecal pellet fragmentation in the field prior to collection (e.g. of older samples) and of deterioration and clumping of faecal pellets in storage jars, samples were not classified by weight.

To examine whether foraging or provisioning adults tended to specialise on either beetles or moths, we tested whether the abundance of these two main prey groups was negatively related in the pellets. The relationship between moths (response variable, scales mg⁻¹) and beetles (predictor variable, beetle index mg⁻¹) in the nightjar diet was examined using a GLMM with Gaussian error in 'lme4' for R (R Core Development Team 2011) (both variables were square root

transformed). A fixed interaction effect of site status (adults with young vs. adults) with beetle index was also added to the model. Lastly, a random effect of 'Site', allowing for a different level of moths for each site and a different response with varying beetle index (Beetle index|Site) was included.

For all remaining diet composition models, moths (scales mg^{-1} , square root transformed) was treated as a continuous response variable in a GLMM with normal error. As the response variable 'beetle index' consisted of the number of beetle fragments per pellet converted into the equivalent number of beetle carapace fragments to provide a single compound figure, this variable was treated as a count variable in a Zero-Inflated Generalized Linear Mixed Model (ZIGLMM) with negative binomial error (the non-zero element of the data was overdispersed), incorporating log (sample weight) as an offset using 'glmmADMB' in R.

Changes in abundance of moth scales in the faecal pellets with season were investigated, including a continuous fixed effect of date and date² and a random effect of site. Further models included the fixed effects of month, month² and/or year to investigate any further effects of time. A similar model was repeated using moth biomass (square root transformed) in moth traps, including a random effect for the trap location. As the key nightjar foraging habitats were found to be restocked forest coupes, pre-thicket and grass heathland, and there was no difference between moth biomass in these habitats (Chapter 4), moth biomass per night was pooled across these habitats and results from older trees excluded from the analysis. Seasonal changes in beetle index were then determined. When examining seasonal effects on diet, to remove any confounding effects of changes in diet between adult subsistence and chick provisioning later after clutches had hatched, models were repeated using samples from adult birds only (faecal material from nests sampled during the egg stage or that failed prior to hatching or from adult roosts).

To investigate dietary differences between nightjars of different breeding stages, the abundance of moth scales was compared among faecal pellets from nests that had contained hatched chicks (as well as the incubating female) and those from adults only (roosting and incubating), with site as a random effect. A sub-set of data (restricted to weeks 7-13) was used, as 'status' (adult or adult with young) was confounded with date. The fixed effects of date, date², month and/or year were also added to control for any effects of time. The model was repeated using beetle index with brood stage split between young (chicks ≤ 7 days old) and old (chicks > 7 days). To investigate any differences among bird statuses, 95% confidence intervals (CI) of the status coefficient estimates were used following (Boughey et al. 2011). When the CI for a status overlaps zero (CI

>coefficient), there is no difference between that status and the status represented by the intercept.

Changes in moth abundance or beetle index, with distance to heathland (< or > 2km) were investigated, including the fixed effects of date and date² and the random effect of site. Models with the fixed effect of month and/or year were also fitted. Alternative formulations of these models were examined, either testing the distance to heathland (with models containing either a continuous or categorical distance variable) or using 'the percentage of heathland within the 2km buffer,' as the predictor variable. To investigate if moth or beetle abundance in the pellets varied with distance to restock stage forest, these models were repeated using the fixed continuous variable 'distance to restock.'

To determine if beetle families identified from samples (dung, longhorn, click and carabid) were more likely to be found in samples from birds closer to heath, presence/absence of each beetle family was related to the distance of the closest heathland in Generalized Linear Mixed Models (GzLMM) with binomial error and incorporating random effects of site and fixed effects of date, date² and month and/or year. To investigate if beetles from each family were more likely to be found in samples closer to restock stage forest, these models were repeated with 'distance to restock' as a fixed continuous variable.

For all model sets, the best model was chosen by examining the Akaike Information Criterion corrected for small sample size (AICc). If ΔAIC_i (difference in AIC from the best model) <2, there is no difference between the models with each having a similar degree of empirical support, (unless models differ by only one parameter, then the model with the higher AICc and number of parameters does not have support, as the increase in AICc is due to the increase in parameters only) (Burnham and Anderson 2002).

Results

During faecal sample dissection, 1069 pellets were examined from 61 distinct sites (39 nests and 22 roosts) throughout Thetford Forest. Virtually all of the samples (99%) contained evidence of moth consumption (Coefficient of variation of moth scales index=1.06, range=2-1018 scales mg⁻¹), while 81% contained beetle fragments (Coefficient of variation of beetle index=1.5, range=0-88). Beetle families identified in the samples included Carabidae, Cerambycidae, Elateridae, Scarabaeidae and Staphylinidae.

The abundance of moth scales and beetle fragments per pellet were not related (Fig. 2) with the best model of moth scales excluding beetle index (model including beetle index, $\Delta AIC_c = 1.06$, parameter difference=1).

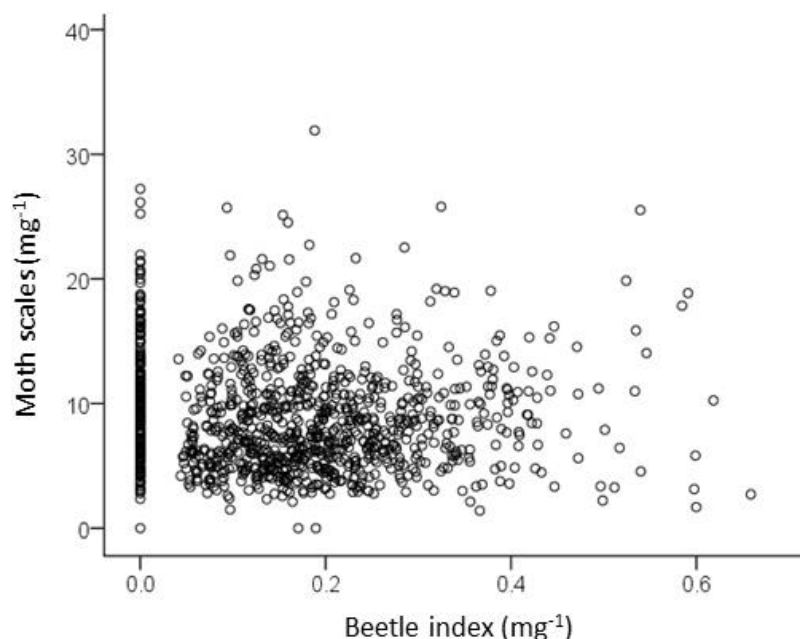


Figure 2. Relationship between the number of moth scales and index of beetle frequency (square root transformed) recorded from the dissection of nightjar faecal pellets (n=1069). The beetle index is calculated from the frequency of beetle fragments per faecal pellet, with a high frequency of beetle fragments resulting in a high beetle index.

Seasonal changes in diet

Moth abundance in the faecal pellets was related to stage in the season with the best model containing date and date², consistent with the observed peak in week 12 (17 -23 July) and subsequent decrease (Fig. 3a) (ΔAIC_c for model excluding date² =7.5, excluding both date and date² =20.53). There was no effect of month or year on moth scale abundance. There was no effect of season on moth scale abundance for pellets from adults only (best model excluded date, ΔAIC_c for model including date=1.66, parameter difference=1).

Moth trap biomass (square root transformed) also showed a uni-modal peak in week 12 (17th -23rd July) and a quadratic relationship with date (model excluding: date², $\Delta AIC_c = 23.13$; date and date², $\Delta AIC_c = 34.87$) (Fig.3b). The relative contribution of different moth classes to total moth biomass changed throughout the season as emergence periods began and ended, with the contribution of Geometrids and Large moths highest in June, micro-moths remaining constant

throughout the summer and Noctuids contributing the majority of moth biomass from mid-July to late-August (Fig. 3c).

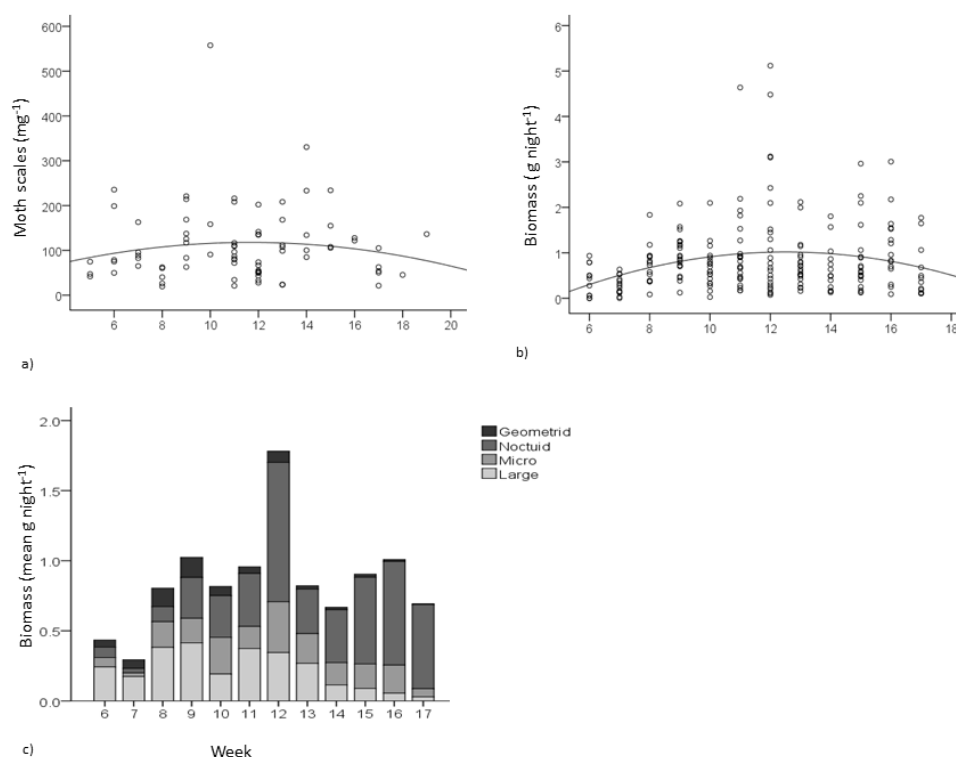


Figure 3. Changes in moth levels throughout the nightjar breeding season: a) Level of moth scales (scales mg⁻¹) in nightjar faecal samples varying with week; b) Moth biomass in moth traps varying with week; c) Changes in the biomass of different moth classes in moths traps with week; Micro = Micro-lepidoptera (wingspan <20mm) and Large= Sphingidae, Lasiocampidae, Arctiidae. Week = Number of weeks after 1st May. For plots a) & b), when faecal sample collection or moth trapping occurred in the same site during one week, the mean value of moth scales/ biomass per site was taken to remove pseudo-replication.

Beetle index decreased with year, with the mean index in 2008 ($\bar{x}=0.05 \pm 0.03\text{sd}$) slightly greater than in 2009 ($\bar{x}=0.04 \pm 0.03\text{sd}$) but more than double that of 2010 ($\bar{x}=0.02 \pm 0.02\text{sd}$) (ΔAIC_i excluding year= 5.32) (Fig. 4a). There was no effect of date or month. For data from adults only, there were no seasonal or year effects, (ΔAIC_i excluding year= 1.85, parameter difference=1).

In terms of beetle families, 2% of faecal pellets contained evidence of Carabidae, 12% of Cerambycidae, 6% of Elateridae and 16% of Scarabaeidae. Beetles from the family Staphylinidae were only found in 0.8% of pellets and were therefore not included in the data analyses. Models indicated that Elateridae presence decreased with month and the mean probability of presence in samples in 2009 ($\bar{x}=0.09 \pm 0.24\text{sd}$) was three times higher than 2008 ($\bar{x}=0.03 \pm 0.16\text{sd}$) and ten

times higher than 2010 ($\bar{x}=0.008 \pm 0.09\text{sd}$) (Fig. 4b (best model contained month and year, ΔAIC_i excluding: month =3.93, year=8.11). The mean probability of carabid presence in samples decreased with date in the season (ΔAIC_i excluding date=4.01) (Fig. 4c). There was no seasonal effect detected for Scarabaeidae or Cerambycidae.

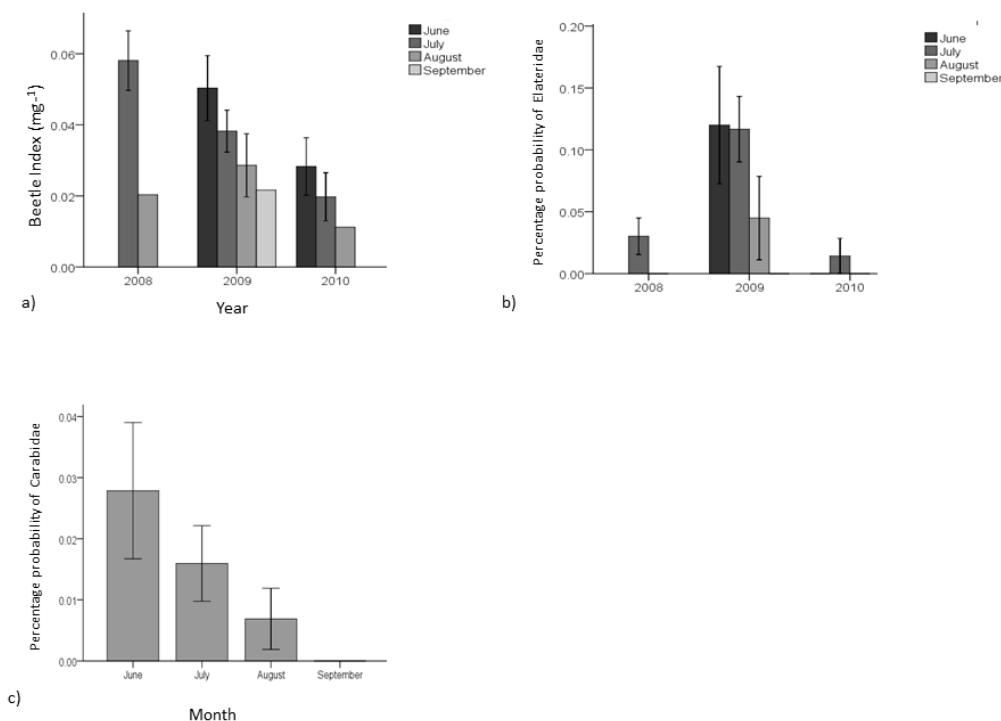


Figure 4. Varying beetle levels in nightjar faecal samples during the breeding season: a) Beetle index varying with year and split by month; b) Mean percentage probability of Elateridae presence varying with year and split by month; c) Mean percentage probability of Carabidae presence varying with month. Error bars $\pm \text{SE}$. For all plots, the mean value per faecal sample collection site was used to remove pseudo-replication.

Dietary differences between adults and chicks

The beetle index was higher in faecal pellets from nests with large chicks (>7 days old) than for nests with young chicks (≤ 7 days old), or solely adults (Fig. 5) (best model included status, ΔAIC_i excluding: status =4.27). Although the mean beetle index appeared lower in nests with young chicks than for solely adults, when the intercept was represented by 'Adults only' (i.e. taken as reference level for the status variable), the confidence interval of the coefficient estimate for 'Adults with young chicks' overlapped zero, indicating that there was no difference.

In contrast to beetles, the level of moth scales was similar for samples from adult birds only (roosting or incubating) and sites with both adults and young birds (best model did not contain status, $\Delta AICc_i$ with model containing status =1.87, parameter difference=1).

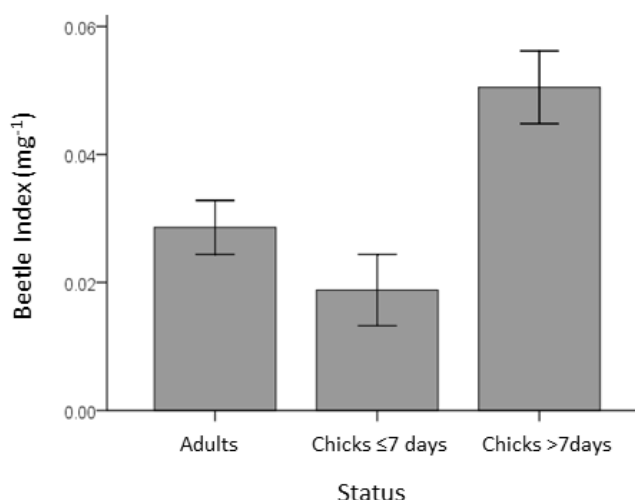


Figure 5. Beetle index (mg⁻¹) compared among nightjar faecal samples from adults only, adults with chicks ≤7 days old and adults with chicks >7 days old. The mean Beetle Index was taken for each faecal sample collection site to remove pseudo-replication. Error bars ±SE.

Dietary differences with available habitat

The abundance of moth scales in the faecal pellets was similar for all birds, irrespective of the proximity or extent of heathland available (best model included only date and date² and excluded all heathland variables; model incorporating percentage of heathland within 2km buffer, $\Delta AICc_i$ = 2.01, parameter difference=1; models incorporating distances to heathland: as a categorical variable, $\Delta AICc_i$ =1.93, as a continuous variable, $\Delta AICc_i$ = 1.96, each with a parameter difference of 1).

The beetle index did not vary either with the extent of heathland available to birds, with the best model containing only year (on addition of heathland variable, $\Delta AICc_i$ =1.13, parameter difference=1) or with distance to the nearest heathland as a categorical variable (on addition of heathland variable, $\Delta AICc_i$ =1.85, parameter difference=1) or as a continuous variable (on addition of heathland variable, $\Delta AICc_i$ =2.01, parameter difference=1).

Similarly, the abundance of moth scales and beetle fragments in the faecal pellets did not vary with distance to the closest restocked coupe, (on addition of 'distance to restock' to the best model of moth scale abundance (containing only date and date²), $\Delta AICc_i$ =0.94, parameter

difference =1; on addition to the best model of beetle index (containing only year), $\Delta AIC_c = 1.85$, parameter difference=1). While there was no difference between the distance to restocked coupes for sample collection sites in different years, (ANOVA, $p=0.27$, $F_{2,58}=1.35$), the data suggest that the distance to restocked coupes may have tended to be higher in 2010 (Fig. 6).

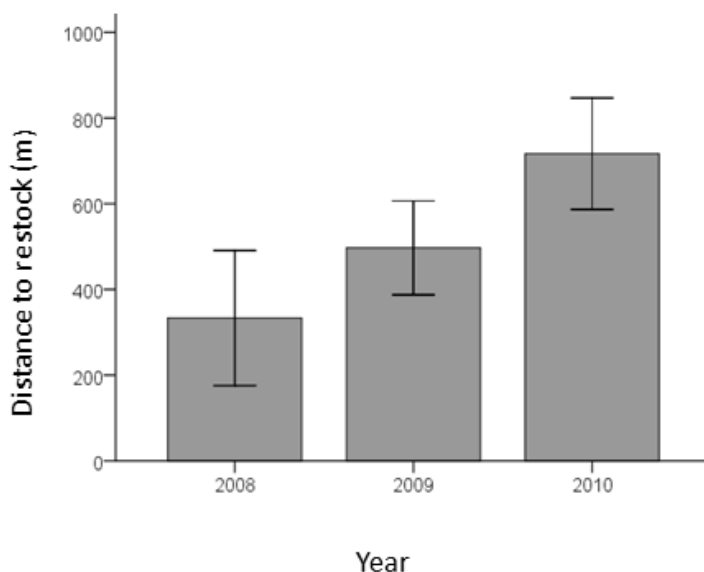


Figure 6. Distance (m) to the nearest restocked coupe for nightjar faecal collection sample sites, for each year. Error bars \pm SE.

The presence/absence of Carabidae, Elateridae and Scarabaeidae beetles was not affected by the percentage of or distance to heathland, with none of the best supported models containing fixed effects of percentage of heath, distance to heath (continuous or categorical) or distance to restocked coupes. The presence/absence of Cerambycidae was not affected by the percentage of heathland available or the distance to restocked coupes. However, distance to heathland was included in the best supported model for Cerambycidae, (on removal of distance to heathland as a continuous variable, $\Delta AIC_c = 0.18$, on removal of distance as a categorical variable, $\Delta AIC_c = 2.85$), with a higher probability of finding Cerambycidae in samples collected from nests/roosts <2000m from heathland (Fig. 7a). As Cerambycidae may also emerge from tree stumps left following felling and replanting, potential confounding effects of the distance to the nearest restocked coupes were examined. Nests/roosts <2000m from heathland were located at a similar distance from restocked coupes than those >2000m from heathland (Fig. 7b) (t -test, $t(45) = 1.83$, $p=0.075$).

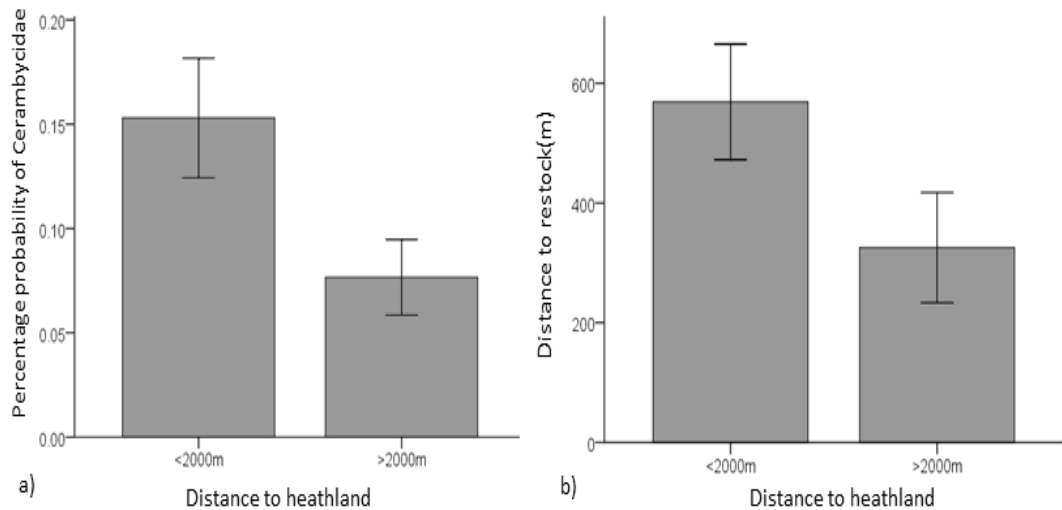


Figure 7. Nightjar dietary differences with habitat availability: a) percentage probability of the presence of Cerambycidae beetles in nightjar faecal samples and b) distance to restocked coupes; for faecal collection sites <2000m and >2000m from the nearest heathland. For both plots, pseudoreplication was removed by taking the mean percentage probability for each faecal collection site. Error bars are \pm SE.

Discussion

The results of this study suggest that nightjars forage opportunistically, preying on particular insects when they are in high abundance, however they may be selective during certain stages of the breeding season. In a complex landscape, heathland and forest appear to be largely similar in terms of foraging resources for nightjar, with the presence of grazing mammals and deer providing dung beetles as a source of prey across both habitats.

Dissection of nightjar faecal samples showed high abundance of both moths and beetles in the diet, confirming other studies that have indicated these insect orders are key prey species for European nightjar (Collinge 1920, Schlegel 1967). The presence of particular beetle families in the samples suggests important foraging resources in the landscape, with Cerambycidae and Scarabaeidae the most common families found. As wood borers, Cerambycidae are commonly found in the stumps of felled conifers and both the grazing sheep on heathland and deer within the forest provide a source of dung for Scarab beetles. Therefore habitats with easily accessible stumps, for example restocked coupes, provide the nightjar with access to Cerambycidae while

both forest habitats and grazed heathland are a source of scarab beetles associated with mammal dung.

As the number of moth scales and beetle index are each a measure of abundance in the samples, a negative relationship was expected between moths and beetles, as a foraging bird was assumed to consume either a high number of moths or beetles but not both. While this pattern seemed apparent in the data, the model showed no support for this relationship. This could be due to a high level of scatter in the relationship between the number of scales and moth biomass; the relationship between moth scales and biomass is predicted to be non-linear, as although larger moths will have a greater number of scales, some moths have large wings but a slender body (for example, geometrids). There could be a similar scatter in the relationship between the number of beetles eaten and thus the frequency of detecting beetle body fragments and actual beetle biomass consumed, with the possibility of a larger number of small beetles consumed resulting in a higher likelihood of a beetle fragment being found. Moth scales and beetle fragments may be retained in the gut as has been documented in bats (Robinson 1997) such that faecal samples may represent the diet over a period of days rather than the result of one foraging trip (Moreby and Stoate 2000). However it is also likely that the passage time of beetle fragments and moth scales through the gut differ, so that their relative frequency in a particular faecal pellet may not relate to synchronous relative diet contribution. This is a potential caveat of the study, however, the moth and beetle index varied from low to high magnitudes, suggesting that a large index indicates recent consumption over the number of days in the roosting or breeding period that each pellet represents.

Seasonal variation in diet

The agreement found between seasonal models of moth biomass availability and moth scale abundance in the diet suggests that nightjars take advantage of changing levels of moth abundance, as predicted for birds with an insectivorous diet (Morse 1971). This result also confirms that although moth scales may be retained in the gut, the moth scale index is changing as a response to moth consumption. Models indicated that moth consumption and biomass in the traps both peaked in week 12 (17-23 July). The summer months from May to August are the key periods for moth emergence and flight seasons in the UK (Waring and Townsend 2003). Moth trapping indicated that the proportion of moths from each family/class varied throughout the season, with Noctuidae comprising a large proportion of total biomass in week 12. The larger noctuids, for example, yellow underwings (genus *Noctua*) and Dog's Tooth (*Lacanobia suasa*) are in flight at this time and many of the smaller noctuids, for example, the Ear Moth (*Amphipoea*

oculea) emerge in late July (Waring and Townsend 2003). With their stout bodies (compared to the sligher bodies of geometrid moths), the noctuids may be a key source of prey for nightjar. Although the best model for abundance of moth scales in faecal pellets using data from 'adults only' did not require date, the pattern in those data was still present. It could be that the smaller sample size for adults only (nests or incubating adults, n=22) reduced statistical power.

While there was no seasonal effect on the abundance of beetle fragments in the faecal pellets, this may be because beetles from different families emerge throughout the season therefore a succession of beetles are available for nightjar consumption. The variation in the abundance of beetles with year could be due to the location of the faecal sample collection sites in each year. Although model results proved inconclusive, the data suggest that when the distance from the nest/roost to young restocked plantation is greater, the beetle index in the faecal pellets is lower. Restock stage forest provides a number of habitat types for a wide variety of beetles and is a key foraging habitat for nightjar (Chapter 4), therefore it is not surprising that nightjars with restock forest in close proximity may be feeding on more beetles. The variation in beetle index with year could also be due to other factors, for example, fluctuations in other insect populations or changes in weather.

When the presence of specific beetle families in the samples was investigated, the results suggested a seasonal pattern for carabid and elaterid beetles. Carabid beetles can be split into spring and autumn breeders, with some species emerging in May while others emerge in August (Lin 2005). As carabid fragments were only confirmed in a small number of samples (2%), the results from the samples may not represent the true seasonal relationship. The emergence time for species of Elateridae in the UK varies, with some species in flight between May-July and others April-August (Chinery 2005). However, as models indicated a strong effect of year, the seasonal effect for Elateridae appears to be due to the higher numbers found in pellets in 2009 rather than a true effect of month (Fig. 4c). Again, this may be partly due to the differing location of faecal sample sites and proximity to restock stage forest between years. However, both distance to restock and the presence of Elateridae were low in 2008. Some species of Elateridae are associated with wood but others are associated with grass roots (Chinery 2005), therefore nightjars have potential access to these beetles throughout the forest and grass heath. The effect of year may be due to some other factor, for example, weather. There was no seasonal effect for Cerambycidae or Scarabaeidae, however this is expected as the emergence time for Cerambycidae varies with species, with the majority in flight between May and August, and Scarabaeidae are in flight between April – October (Chinery 2005).

Differences between the diet of adults and chicks

There was no difference in moth abundance between the samples for adults only and those from adults with young in the nest. As moths are soft bodied, they will be suitable prey for both adults and young birds, with the main dietary difference between breeding stages being moth size rather than moth abundance (Schlegel 1967). It was not possible to determine any details on moth size from the faecal samples as the scales for one individual moth can vary in size and shape (Black 1972). The higher abundance of beetle fragments in the faecal pellets collected from nests that accumulated material from both adult birds and large chicks suggests that adult nightjars are preferentially provisioning larger chicks with beetles. Similarly, Schlegel (1967) found that feeding with Cerambycidae increased after chicks were 5 days old. Adult birds have been found to provision chicks with specific prey for nutritional purposes, for example, Arnold et al. (2007) found that blue tits (*Cyanistes caeruleus*) feeding more spiders to young chicks led to higher levels of the amino acid taurine in the chicks' diet during early development.

Variation in diet with habitat availability

Faecal dissection in the current study revealed no difference in terms of the abundance of moths, abundance of beetles or particular beetle families (with the exception of Cerambycidae) in samples from birds with varying levels of access to heathland. This could be because the heathland patches adjacent to Thetford Forest have many similar properties to the young plantation forest, in terms of the vascular plant species present, the extent of bare, sandy soil and the presence of dung from mammals. Nightjar faecal samples were more likely to contain Cerambycidae when they were obtained from sites closer to heathland. While heathland lacks the systematic tree stumps created by felling operations in the forest, retention of mature conifers and standing dead wood on heathlands nevertheless provides opportunities for saproxylic beetles. In addition, although there was no difference between the distance to restocked coupes for birds <2000m or >2000m to heathland, visual inspection of results suggested that birds nesting closer to heathland were more likely to be slightly further from restocked coupes (mean distance to restock=569m, ± 97 sd). However, 569m does not represent a long foraging distance for a nightjar, (mean foraging distance for all active birds=500m) therefore both groups of birds (<2000m and >2000m to heathland) could also have been feeding on Cerambycidae within restocked coupes.

This study has investigated the diet of the nightjar during the breeding season, spanning a five month period, with results suggesting that variation in the diet may be due to changes in prey

abundance and requirements of chicks at certain stages. As with all diet studies, these results must be put into context. Although the nightjar has a varied diet, this species feeds only on insects thus a diet comparison would yield varying results depending on the species compared. While in this study forest and heathland habitats were similar in terms of foraging resources, the diet of nightjars in other habitats may vary, for example, in deciduous woodland. Also, this study investigated the nightjar diet in the UK during the breeding season. When the nightjar is overwintering in Africa, there may be other factors controlling variation in the diet. Lastly, another possible factor affecting the nightjar diet is weather, for example nightly temperature changes and levels of rainfall. It was beyond the scope of this study to investigate the effect of variation in weather on nightjar diet, however this could potentially affect the insects preyed upon by nightjars on a daily basis.

Management recommendations

The results of this study have a number of conservation management implications. For the nightjars of Thetford Forest, heathland habitats serve as an additional foraging habitat (Chapter 4). The diets of nightjars with varying access to heathland were found to be similar, which was concluded to be because young forest and heathland habitats were similar in terms of resources for the birds. Therefore grassy, grazed heathland, with bare patches of sandy soil, a variety of herbaceous plants and standing wood provides a suitable foraging habitat for nightjars. The results of this study may have differed if carried out elsewhere in the UK, for example in an area with heather-dominated heathland. Alexander and Cresswell (1990) found that nightjars avoided heather-dominated heathland and foraged 1.5km from the nest in deciduous woodland, suggesting that the properties of this form of heathland were unsuitable for foraging nightjars. Heather-dominated heathland differs in structure from the heathland patches adjacent to Thetford Forest, with the former lacking bare patches of soil and having less variety of vascular plants. Therefore, heathland management is a key factor when considering suitable foraging habitat for the nightjar.

Results also suggest that birds nesting/roosting closer to restocks may have a higher abundance of beetle fragments in their faecal pellets. Therefore a forested landscape with a mosaic of growth stages is important for foraging nightjars as young, open patches of forest provide many habitats for beetles. Additionally, nightjars foraging in the forest had access to dung beetles, due to the presence of deer. There is strong evidence of a negative impact of increasing numbers of deer on woodland birds due to intensive browsing of understory vegetation (Holt et al. 2011). However,

the results of this study suggest that the presence of deer may have a positive impact on nightjar by providing an additional prey resource for birds foraging within the forest.

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Supplementary material for Chapter 5

Moth Index

As moths do not have the hard, chitinous bodies of beetles, moth legs and heads did not appear regularly in the samples. Both moth scales and moth frenula (spines connecting fore and hind wing) were present in samples. However, frenula number can vary between moth species, between the sexes (Acharya 1995) and within the females of a family (Yang and Brown 2009). There was a positive but weak relationship between the number of moth scales (mg^{-1}) and the number of frenula (mg^{-1}) in the faecal pellets ($r^2 = 0.022$, $p < 0.01$), with a lot of scatter around the fitted regression line (Fig. S1). Moth scales, rather than frenula, were therefore chosen as the main indicator of moths in the samples (following Black 1974).

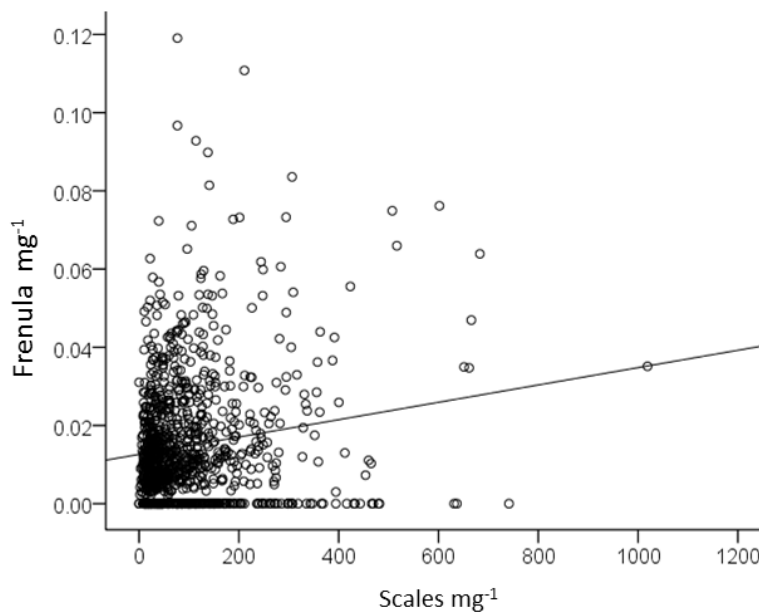


Figure S1. Moth frenula (mg^{-1}) and scales (mg^{-1}) in nightjar faecal pellets ($n=1069$) collected from roosts and nests ($n=61$) in Thetford Forest, Eastern England.

Table S1. Correlation matrix of beetle pieces in nightjar faecal pellets

					Correlation matrix					
Beetle piece	Frequency	Mean	Sd	Max/sample	Carapace	Femur	Fore	Mandible	Tarsal	Other pieces
Carapace	604	2.56	3.97	52	1	0.33	0.50	0.44	0.32	0.48
Femur	367	0.69	1.11	8	0.33	1	0.40	0.39	0.23	0.41
Fore	228	0.42	0.93	8	0.50	0.40	1	0.42	0.33	0.40
Mandible	219	0.46	1.34	23	0.44	0.39	0.42	1	0.26	0.57
Tarsal	202	0.42	0.93	9	0.32	0.23	0.33	0.26	1	0.37
Other pieces	690	2.93	4.12	39	0.48	0.41	0.40	0.57	0.37	1

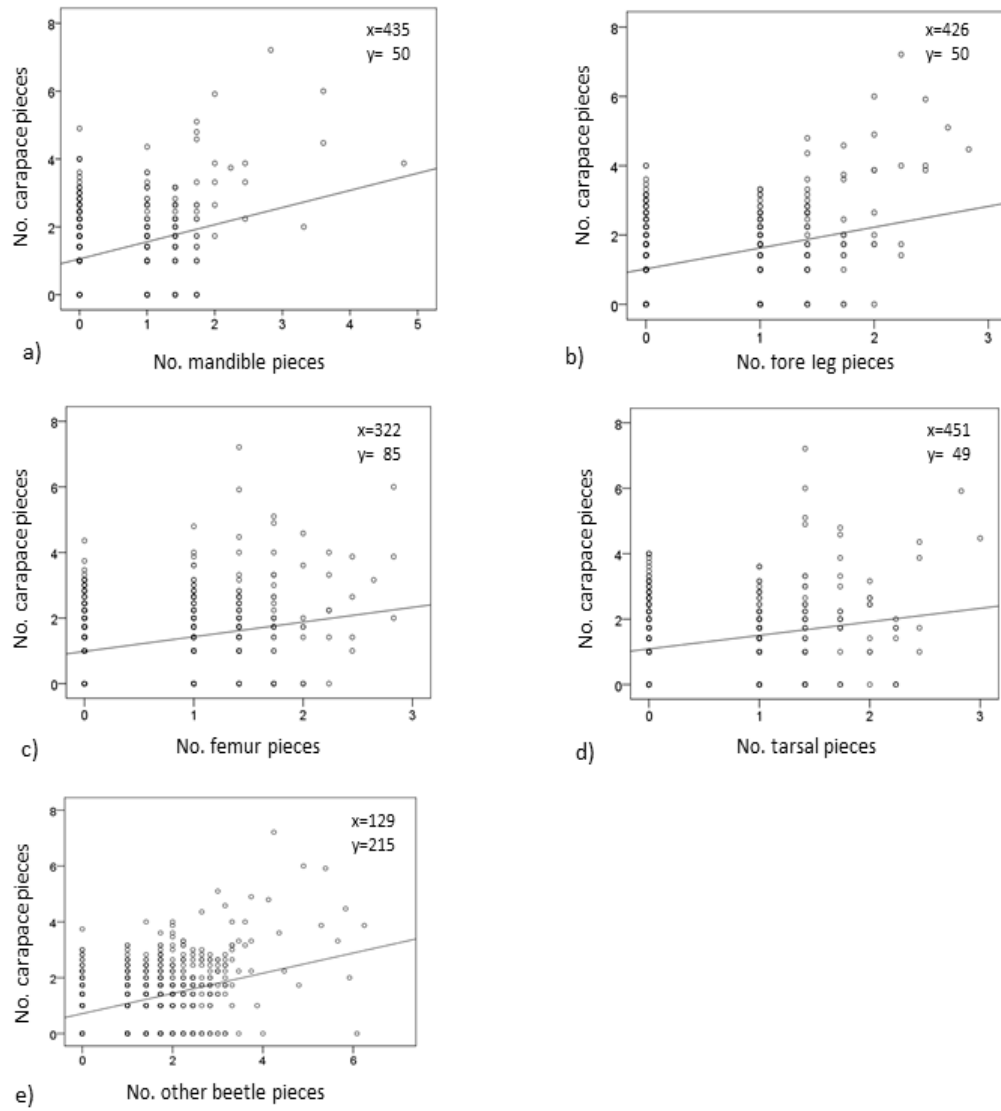


Figure S2. The relationship between the number of beetle carapace pieces and the number of other beetle fragments in nightjar faecal pellets: a) mandible pieces; b) fore leg pieces; c) femur pieces; d) tarsal pieces; e) other beetle pieces (including antenna, coxa, claws, wing, head, mid and hind legs). For all plots, x =Number of pellets with zero of the predictor variable but >0 carapace pieces, y =Number of pellets with zero carapace pieces but >0 of the predictor variable.

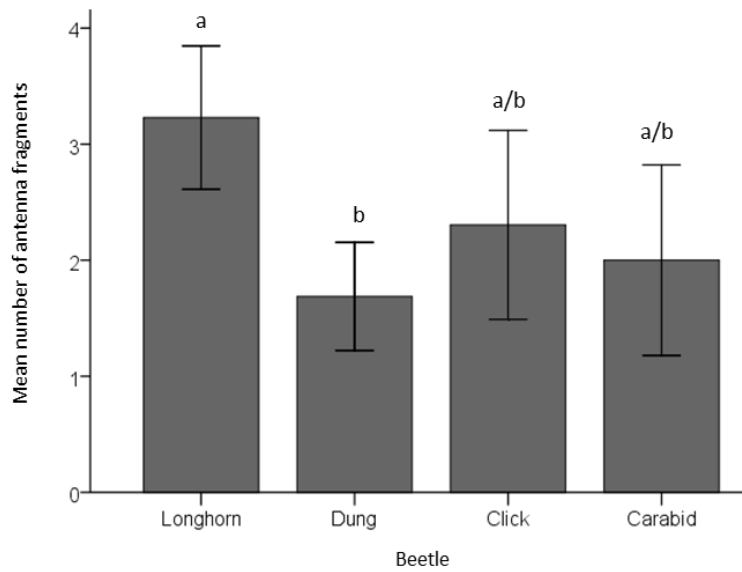


Figure S3. Mean number of antennal fragments in nightjar faecal pellets containing beetles from identified families. Lowercase letters indicate significant differences.

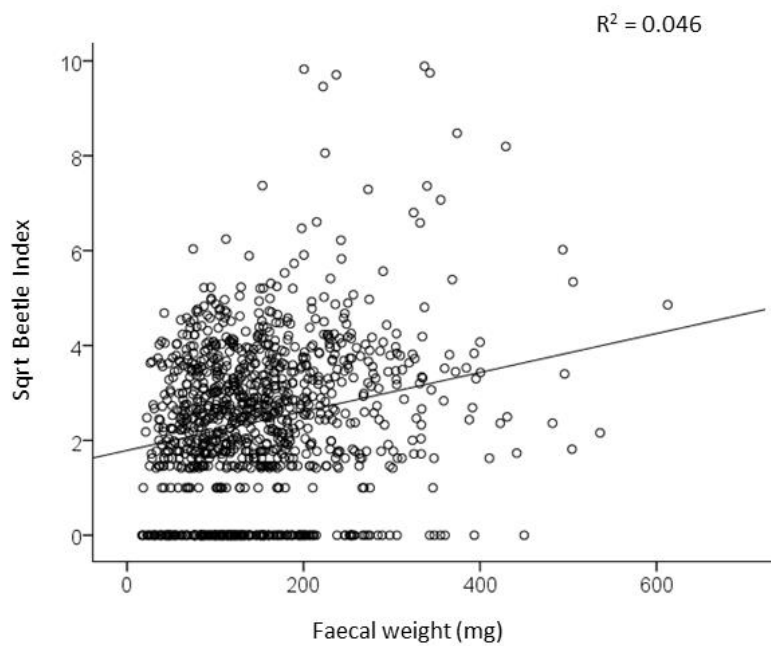


Figure S4. Changes in beetle index (square root) in nightjar faecal pellets with faecal weight.

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Chapter 6: Investigating the effects of reproductive stage and temperature on parental non-attendance at the nest in nightjars, using nest cameras and radio telemetry

Abstract

Studies of animal behaviour can provide information which is relevant for conservation management. However, in addition to collecting behavioural data, it is also important to understand the factors driving changes in behaviour before recommendations can be made for conservation practices. As avian reproduction is energetically costly, adults face multiple trade-offs, for example, between self-maintenance and egg chilling during incubation and chick provisioning and the risk of predation. During this period, adults must achieve a balance between time spent absent from the nest with the requirements of the eggs and chicks. Environmental factors such as temperature can also influence the duration of time that adult birds leave the nest unattended. Nocturnal birds may face differing pressures compared to diurnal species, with less risk of frequent visits to and from the nest attracting the attention of predators. Using nest cameras and radio telemetry, we examined the nesting behaviour of the nocturnal, ground nesting European nightjar (*Caprimulgus europaeus*), which is Red-Listed in the UK. Male nightjars were involved in both incubation and chick provisioning, with their presence at the nest greatest during the latter, however there were times during each night when the nest was left unattended by both parents. The duration for which the nest was left unattended was shortest when the nest contained young chicks (≤ 3 days old) and increased with chick age, presumably because larger chicks are less susceptible to chilling and provisioning requirements increase with chick size. Adult behaviour at the nest varied depending on incubation stage, with results suggesting that when the temperature was low, adults devoted more time to self-maintenance during the early stages of incubation, however as incubation progressed, egg brooding took priority. Adult nightjars were found to leave the nest unattended frequently for short periods of time during chick rearing, demonstrating that this nocturnal species is not at risk from attracting the attention of predators at the nest as diurnal species are. Overall, the key factors influencing the duration and frequency of adult non-attendance at the nest in nightjars are the stage in incubation, temperature and chick requirements. This behavioural information can be used to inform conservation management for this species, with results suggesting that adult nightjars would benefit from having suitable foraging habitat near the nest at certain times during the breeding season.

Introduction

Behavioural studies can provide important information for conservation management. Sutherland (1998) outlines 20 areas where the study of behaviour can help solve conservation problems, including understanding small population extinctions and reducing predation. There are numerous studies demonstrating the relevance of behavioural research in guiding conservation management practices. For example, by studying the reproductive behaviour of Barrow's Goldeneye (*Bucephala islandica*) Eadie et al. (1998) determined that the use of clumped and visible nest boxes would be a valuable conservation strategy, due to the low levels of conspecific brood parasitism and strong territorial behaviour during nesting for this species. Similarly, a study on the effectiveness of translocation demonstrated the value of considering social interactions and relationships within family groups when moving animals, with black-tailed prairie dogs (*Cynomys ludovicianus*) translocated as a family being five times more likely to survive than those moved without their family (Shier 2006). In addition to collecting data on animal behaviour, it is important to understand the factors driving behavioural decisions, how such behaviours can vary, for example, during the breeding season and the resulting impact on the requirements for conservation management of a species.

Reproduction requires high levels of energy expenditure from adult birds. Trade-offs are a key theme in life-history theory (Charnov and Krebs 1974, Bell 1980). There can be numerous trade-offs during breeding; examples include the risk of egg/brood chilling balanced against parental foraging needs (Conway and Martin 2000) and frequency versus the duration of absences from the nest (Vleck 1981b). The optimal decision in reproductive trade-offs can also be influenced by external factors, for example, fluctuations in environmental temperature and the presence of predators (Conway and Martin 2000, Fontaine and Martin 2006). The outcome of such trade-offs will ultimately affect the success of the reproductive effort.

Incubation of eggs was long assumed to require less energy expenditure than provisioning chicks, due to the lower level of parental activity (Walsberg 1983, Gill 1990). However, warming eggs requires an increase in adult metabolic rate during a period when available foraging time is already reduced by incubation behaviour (Monaghan and Nager 1997). The level of male assistance during nesting varies between avian species. Polygynous males devote time to maximising reproductive potential and attracting new mates, therefore not all broods receive the same level of male parental care (Muldal et al. 1986), whereas monogamous males may be present in the nesting territory throughout incubation and provisioning, though whether they

contribute to both nesting stages nevertheless varies between species. In addition, studies on the frequency of extra pair copulations (EPCs) have indicated that the level of male parental care can be dependent on certainty of paternity (Westneat 1988, Møller and Birkhead 1993).

For species for which incubation is solely by the female, time off the nest must be balanced between self-maintenance and care of the offspring; a small number of long nest absences reduces the number of times the female rewarms the clutch (Vleck 1981b) (which can be energetically costly) (Vleck 1981a), however, long nest absences may cause embryo development to slow due to egg cooling (Haftorn 1988). Parental attendance at the nest can also vary during incubation, for example, nest absences decreased as incubation progressed for Cassin's auklets (*Ptychoramphus aleuticus*) (Ronconi et al. 2009). Astheimer (1991) suggests that the level of parental care increases as incubation progresses because eggs are less resistant to chilling during the later stages of development. Similarly, in a review of studies of variation in egg temperature with age, Webb (1987) considered that increases in temperature and precision of regulation with incubation arose due to an increase in parental investment with time, which may in part be related to age-related embryo intolerance of low temperatures.

For many birds, provisioning of chicks requires high energy expenditure (Drent and Dan 1980). Frequency of foraging trips can vary with reproductive stage, both between clutch and brood stages, and subsequently as chicks progressively develop. For the Wandering albatross (*Diomedea exulans*), provisioning trips were shorter in both duration and distance covered, compared to foraging trips made during incubation, as chicks needed to be fed frequently, constraining time at sea (Shaffer et al. 2003). Growing chicks require an increasing level of prey biomass, in contrast, young chicks can chill easily and rapidly (Ricklefs 1974) and therefore can't be left exposed for long periods. It is therefore common for young chicks to be brooded for long periods, while parental absence increases as chicks develop and food demands increase. For example, Adelie penguins (*Pygoscelis adeliae*) made shorter foraging trips when chicks were young with distance increasing as chicks aged (Kerry 1995). In addition, there can also be constraints on the size of prey that chicks can ingest, for example, in Caspian terns (*Hydroprogne caspia*) (Quinn 1990), therefore as chicks develop and energy demands increase, it is suggested they must be fed more frequently rather than with larger items (Anderson et al. 2005).

Fluctuations in environmental temperature can affect the level of parental nest attendance, with parent birds acting to ensure that eggs are not chilled or do not overheat, depending on the geographic location of the nesting species. For example, in British Columbia, Canada, the burrow nesting, nocturnal Cassin's Auklet was less likely to leave eggs unattended when temperatures

were low (Ronconi et al. 2009), contrary to the prediction that during low temperatures, egg neglect would increase due to self-maintenance demands of the parent birds. Similarly, during incubation, individual absences from the nest by diurnal female goldcrests (*Regulus regulus*) in Kjaebu, Norway, were also longer at warmer temperatures (Haftorn 1978). Conversely, parental nest attendance for the Kentish plover (*Charadrius alexandrinus*) nesting in the Arabian desert increased during the hottest temperatures of the day, with both parents working together to ensure that eggs were not left exposed to the high ambient temperatures (AlRashidi et al. 2010).

For diurnal avian species, the need for parents to leave the nest must also be balanced with the risk of nest predation. Avian nest predators, such as corvids or raptors, which hunt using visual cues, present a high risk for birds leaving the nest during daylight hours as repeated parental visits to the nest can attract the attention of predators (Eggers et al. 2005). Fontaine and Martin (2006) experimentally reduced the risk of nest predation in 12 species of coexisting passerines and found that parent birds in a safer environment increased the rate of visits to the nest to provision chicks. Similarly, in a meta-analysis of North American female-incubating passerines (n=97 species), birds with a higher predation rate left the nest less frequently and spent longer off the nest when they did so (Conway and Martin 2000). For nocturnally foraging birds, the threat of nest predation from visually searching avian predators is low; for example, in a nest camera study investigating predation in four different habitats (marsh, meadow, scrubland and forest) in Ontario, Canada, the majority of nocturnal predation on artificial nests containing Japanese quail (*Coturnix japonica*) eggs, was by mammals (Picman and Schriml 1994). As nocturnal mammals use olfactory cues to hunt, parental absences from the nest would not affect predation risk therefore the parental response to the threat of predation may differ between diurnal and nocturnal birds. Parental nest attendance strategies may be more influenced by temperature fluctuations in nocturnal birds compared to diurnal foragers, as there is a higher variability in temperature between mild and cold nights. In contrast, for diurnal species nest attendance strategies likely represent a complex trade-off between chilling, provisioning, maintenance and predation risk.

Parental resource allocation and reproductive trade-offs have been examined in passerines (for example, Haftorn 1988, Conway and Martin 2000) and seabirds (Shaffer et al. 2003, Williams et al. 2008); however, nocturnal birds have not been studied extensively. The European nightjar (*Caprimulgus europaeus*) is a nocturnal, ground nesting, insectivorous summer migrant that winters in sub-Saharan Africa and breeds throughout much of the Western Palearctic. As a Species of European Conservation Concern (SPEC 2) (Birdlife International) and a red-listed species in the UK (Gregory et al. 2002), the collection of behavioural data on the nightjar during

the breeding season could also provide useful information for conservation management. In a nest camera study in eastern England, European nightjar nests were predated only by mammalian predators, especially fox and badger (Dolman 2010). Primarily active at dusk and dawn, nightjars forage for only a short period each night, therefore a fine balance must be achieved between adult foraging and incubating eggs. The key foraging habitats for the nightjar have been described (Chapter 4), however an investigation of the factors driving nightjar behaviour at the nest may provide an understanding of any variation in the length of time birds have available for foraging throughout the breeding season, which may affect the optimum configuration of foraging habitat in the landscape for this species. Nightjars are insectivorous, preying primarily on beetles and moths (Cramp 1985), with chicks fed a saliva-covered food ball (Cleere and Nurney 2000). Using counts of moths in horizontal light beams, Bowden and Green (1991) found that there was a nightly peak in moth abundance (just after sunset), which corresponded to the peak in nightjar activity at the beginning of the night; however there was no equivalent pre-dawn peak in moth abundance. Using observations from a hide, Schlegel (1967) found that the male nightjar relieved the female during incubation but usually left before the female returned from foraging, therefore eggs can be left unattended for varying periods of time. However, using radio telemetry, male birds were found to rarely incubate eggs at dusk (Cross et al. 2005). While radio telemetry provides a more detailed and accurate account of male activity at the nest, it is possible that male presence at the nest varies with stage in incubation, temperature or with other behaviours such as territory guarding. Using spot checks of radio-tagged birds (with their position and activity sampled every 10 minutes), Bowden and Green (1991) found that females with chicks >13 days old (i.e. within a week of fledging) were more active in the middle of the night than incubating adults and birds with young chicks. For two radio-tagged female nightjars in Dorset, birds were found to be most absent from the roost/nest site in the pre-egg stage (mean of 79% for searches recording absence in the early, mid and late periods of the night), less absent when they had young (mean= 27%) and least absent when they had eggs (mean=17%). When relative absences per night third were considered for nine tagged birds in one study area, there were fewer absences in the middle of the night than in either the early or late periods of the night (Alexander and Cresswell 1990). However, previous nightjar research is based on small sample sizes (e.g. n=2 females monitored for the complete breeding season, Alexander and Cresswell 1990) and more detailed information on nest attendance could be extracted from continuous or burst sampling radio telemetry data rather than using spot checks, which do not provide a complete account. The effect of temperature on nightjar presence at the nest has not been investigated.

During incubation, the nightjar nest will be left unattended if the female is absent on a foraging trip and the male either has not taken over or has subsequently departed. We predicted that eggs would be incubated throughout the central period of the night, with adult non-attendance at the nest at the beginning and end of the night only. This is due to changes in abundance of nightjar prey (Bowden and Green 1991) and temperature throughout the night (Supplementary material, Fig.1), (with the coolest temperatures in the middle of the night and just before dawn), and also for energetic reasons. The female was considered likely to require a foraging trip at dusk, for sustenance after the long daylight incubation period (approximately 15 hours, from c. 5:00 until c.20:00) and again at dawn, in preparation for incubation that day. This can be compared with the incubation behaviour of diurnal birds; while Skutch's (1957) review of avian incubation outlines a number of different patterns depending on the division of male and female care for diurnal species, eggs are kept covered for the duration of the night. For example, using temperature probes attached to data loggers, which were inserted into nests, Joyce et al. (2001) demonstrated that diurnal female black-throated blue warblers (*Dendroica caerulescen*) incubate throughout the night, with little variation in nest temperature during that period. For the nocturnal nightjar, on colder nights, eggs were predicted to be left unattended less overall per night, or only briefly per absence and with even less absence in the middle part of the night.

During chick provisioning, the nightjar nest will be unattended if the female is absent to provision chicks and the male is also absent (either foraging to provision chicks or guarding the territory). We predicted that chicks would be left unattended less when first hatched, as they require less prey biomass and are also more vulnerable to chilling. Further, we predicted that young chicks would be left unattended even less when temperatures were lower. As chicks grow, the number of periods of short parental non-attendance was predicted to increase as chicks require more prey biomass but can only be fed small amounts at a time, and still require brooding for thermal protection; however the frequency of short periods of parental non-attendance was predicted to decrease as chicks grow larger, as they can be left for longer and can ingest a greater volume of prey biomass per provisioning bout.

By combining nest camera footage and radio telemetry, we aimed to investigate nightjar parental non-attendance at the nest throughout the breeding season. Specifically we: 1) investigated the level of male parental care during incubation and provisioning; 2) compared differences in duration and frequency of parental non-attendance at the nest amongst birds of different breeding stages and during different periods of the night; and 3) investigated the effect of temperature on the length of time the nest was left unattended by both adults. In addition to

providing an increased understanding of the breeding behaviour of this nocturnal species, the results of this study can also be used to provide recommendations for conservation management plans.

Methods

Study site

Thetford Forest (0°40'E, 52°27'N), in Breckland, East England, is the largest lowland commercial forest in the UK, covering 185km². The forest consists of discrete blocks with adjacent habitats including agricultural land and heathland. The two primary tree species in the forest are Corsican (*Pinus nigra*) and Scots pine (*P. sylvestris*), covering 85% of the planted area. The forest is managed by clear-felling of trees at economic maturity (currently 60-80 years) and replanting even aged stands (mean coupe area 9.0 ha \pm 8.6 sd). The Breckland Forest Special Protection Area (SPA) was designated under the EC Birds Directive in 2000, due to internationally important breeding populations of nightjar and woodlark (*Lullula arborea*). In 2004, Thetford Forest held c. 10% (349 churring males) of the UK nightjar population (Conwy et al. 2007) but nightjar numbers in the forest are declining, from 420 males in 1998 (Evans 2002) to 240 in 2010 (Conway and Henderson 2010).

Nightjar nest cameras

In a collaborative project between the University of East Anglia (UEA) and the British Trust for Ornithology (BTO), miniature digital infra-red nest cameras were mounted at 45 nightjar nests in Thetford Forest during May-August of 2008/9 (Dolman, 2010). A MemoCam DVR image storage unit (Video Domain Technologies Ltd., Petah Tikva, Israel) was used to store video footage, which could be downloaded to a computer using a card reader. The video motion detection (VMD) facility was used to record images when there was movement at the nest. To reduce the recording of irrelevant footage triggered by the movement of vegetation/insects, the VMD was configured so that recording was only triggered by movement in the central third of the image (Bolton et al. 2007, Dolman 2010). For each event, the units were configured to record 6 images at 0.3 second intervals. The first image showed the nest at a point between 0 to 0.3 seconds before the motion was detected and the following 5 images (spanning 1.5 seconds) recorded what occurred subsequently. In order to reduce recording of duplicate events and to reduce the

rate at which memory cards were filled up by repeated events triggered by movement of vegetation (which runs the risk of important events being overwritten once the card is full), a delay was introduced between each set of recordings. This was set at 4 seconds in 2008 and reduced to 2 seconds in 2009 (Dolman 2010). Precautions were taken to minimise the visibility of the cameras to potential predators: cameras were placed inside rain guards (total dimensions of the unit c6cm x 2cm x 2cm), painted in camouflage colours and installed against vegetation, but in a position with a clear view of the nest, approximately 0.5m away. The MemoCam unit and a 12v battery were connected to the camera using a waterproof cable, placed in a waterproof box, and buried 10m from the camera (Bolton et al. 2007, Dolman 2010). Each camera installation was carried out by one trained person (BTO members of staff) in the shortest possible time (c.20 minutes).

In 2010, an M.Sc. student working under the supervision of Katrina Sharps examined and extracted observation data from all MemoCam events recorded during 1569 nocturnal hours of monitoring from 21 nests (Wilshaw 2010). Further events from 2126 diurnal hours of monitoring from 22 nests were also extracted (Wilshaw 2010, Dolman 2010) but were not used in analysis of nest attendance behaviour in the present study. Observations from the remaining 23 camera installations were not used for this study due to unclear footage or failure to record bird movements accurately.

Movement by either the adult(s) or chicks triggered an event and therefore the capture of images. Diurnal events (n=50) often comprised the female adjusting position on the nest (for example as the sun and thus her shadow tracked round), were triggered by vegetation movement or were occasionally (n=12) caused by the flushing of the adult bird by potential nest predators, (deer and rat) (Wilshaw 2010). Nocturnal events (n=1845) were primarily triggered by the wing movements of adults taking off from, or landing at the nest. While the adults were absent from the nest, images of the unattended nest could be triggered by chick movements, confirming the continued absence. Only very rarely was the departure of an adult missed (this could occur, for example, if the departure took place within the unit 'sleep period' following capture of provisioning or a movement that had just triggered a previous image, or if the female was present in the vicinity of but not brooding in the centre of, the nest). Thus by examining and noting the timing and nature of each sequential event (e.g. adult leaving, adult returning, incubating bird adjusting position, adult leaving) a continual log of nest attendance and provisioning could be created for each hour of the night.

Unfortunately it was difficult to distinguish between the sexes of the adult birds at the nest, due to the infra-red light reflecting off the bird's feathers and the quick movements of the birds, especially at the chick stage (Wilshaw 2010); however, where possible the sex of the bird leaving and returning to the nest was recorded. The key information analysed from the footage therefore centred on the duration and frequency of periods when the nest was left unattended with both parents absent from the nest and eggs/chicks left exposed. These periods of non-attendance represented the decision of both parents to be absent from the nest and could be due to: the gap during parental swap-over at the nest, female foraging for self-maintenance or to provision chicks (with short absences from the nest to catch passing insects or forage briefly in the immediate vicinity of the nest, and longer absences to commute to and forage in optimal foraging habitat), or interactions with other birds (involving territory guarding for male birds). The duration of absence from the nest by both parents was taken as the difference between the time when the attending adult was seen leaving the nest and the time when an adult next returned to the nest. For some of the cameras, the VMD was found to occasionally miss behavioural events, for example, a bird would be observed returning to the nest with no record of the departure. If this occurred for more than three absence bouts per night for two consecutive nights, the data from this camera was not included in the analysis (this criteria excluded 8 of the 23 camera installations not included in this study) (Wilshaw 2010). All absence bouts with uncertainty over the duration (6% of all events, during 19% of periods and on 37% of nights) were excluded from the dataset before analysis. As there was only a small percentage of total events with uncertainty and no reason why these events should be biased towards short or long periods of parental non-attendance, the removal of these events should not affect results.

For each night of footage, from 20:00 to 05:00, the total duration that the nest was left unattended per night was calculated. Classes were based on the quartiles (25, 75, 95) of the data for both 2008/9: <30s, 31-120s, 121-600s, >600s, which allowed for examination of nest absences of varying duration, from very short (which may represent either parental swap overs at the nest or brief fly catching trips by the female) to longer absences. For each night, the frequency of parental non-attendance events in each class was calculated per hour. Parental non-attendance at the nest spanning two hours, e.g. beginning at 22.50 and ending at 23.05, were treated as an event and attributed to the hour in which they began. The night was split into three periods of varying duration, based on the nightly activity pattern of the nightjar (Bowden and Green 1991)– early (20:00-22:59), mid (23:00 –02:59) and late (03:00-04:59).

Radio telemetry

See the General Methodology chapter (Chapter 2) for details of radio telemetry methods.

For each full night of telemetry data for nesting females ($n=10$), the 'total female absence from the nest per night' was calculated. Female nest absence included when the female was recorded active in the nest territory or in other areas of the forest and also when the female was stationary in the nest territory but sitting away from the nest. As the mean telemetry error was 26.76m (± 20.08 m sd, range=2-99m) it was sometimes difficult to say for certain if the female was sitting on the nest. Therefore if the female was stationary in the nest territory, in the direction of the nest and the positional fix was <100m from the actual nest site, the bird was not recorded absent from the nest. If the bird was active or absent from the territory at the beginning of a ten minute period (the start of the absence was missed) or the exact return time to the nest was not known (the end of the absence was missed, for example if an active bird returned to the nest territory before the observer arrived back from the foraging location), the midpoint between the time of the previous fix and the current one was taken as the beginning/end of the absence. This occurred often (92% of absences) however the mean value for the maximum potential error of female nest absence was only 5.6 minutes (± 5.4 sd). Only 16% of these potential over/under-estimates were >10 minutes, with a maximum value of 31.5 minutes.

In 2008/09, the status of each nest ($n=10$ in 2008, $n=11$ in 2009) for all nightjar pairs included in the study (for example, stage of incubation or the chick age) on a particular date could be determined using the nest camera footage. Nest cameras were not placed at nests ($n=4$) in 2010 due to logistical and time constraints, but nests were regularly monitored, with the status of each nest being checked every five days where possible. When the exact date of egg laying and hatching was not known, the date of an event (for example, egg hatching or predation) was taken as the mid-point between the last nest check and the current one, unless an earlier or later likely hatch date was indicated by the stage of development of the chicks.

Temperature

Data on the hourly air temperature from Lakenheath weather station (to the south west of the forest, $0^{\circ}35'E$, $52^{\circ}25'N$) was provided by the British Atmospheric Data Centre. The temperature at

midnight was used as a measure of the nightly temperature (See methodology in Chapter 4 for more details). On nights when there was no record of midnight temperature (20%), the mean of the temperature at 11pm and 1am was calculated. For the temperature during each period of the night (early, mid, late) the mean of the hourly temperatures per period was calculated.

Statistical analysis

Nest camera and telemetry comparison

The results for parental non-attendance from the nest camera footage and radio telemetry results were compared, providing an opportunity to validate the two methods. There were four nights of data from 2009 with both nest camera and radio telemetry for the same bird (n=3 individual females). The null hypothesis that there was no difference between the relative frequencies of detection of camera non-attendances of different duration (two minutes or under, three to ten minutes, greater than ten minutes) using radio telemetry, to their relative frequencies detected by nest cameras, was tested using a Fisher's Exact Test (performed on a 3x2 contingency table of duration class x detected by telemetry x not detected by telemetry) in the statistical program R (R Core Development Team 2012).

Seasonal variation in parental non-attendance at the nest

As nightjars are active only at dusk and dawn, the length of time available to nightjars for foraging varies throughout the breeding season. It was therefore necessary to control for the stage in the season in models investigating cumulative simultaneous parental absence from the nest. As the variable 'Week after May1st' was correlated with midnight temperature ($r^2 = 0.3$, $p < 0.001$), it could not be included as a control for season in the majority of the models. Therefore for each night of observation, a Seasonal Discrepancy value was calculated, representing the difference between the length of that night (taken as the interval from sunset to sunrise) and the mean length of nights across the season. Times of sunset and sunrise (for Norwich, UK) for the summers of 2008-2010 were obtained from www.timeanddate.com.

It was noted that male presence was recorded on some nest cameras more than others (Wilshaw 2010). To examine if this was because the male was present at these nests more often (with their attendance replacing female absences, so that these nests would be left unattended less overall) or alternatively whether males were present to a similar degree at all nests but with some

cameras able to provide clearer footage (with the diagnostic white wing flash of the male more easily seen), cameras (n=21) were split into four groups based on the quartiles (25, 50, 75, 95) of the mean frequency of detected male presence at the nest per night. If male presence actually varied between nests, the cameras with the lowest frequency of visible male presence at the nest are expected to have more frequent non-attendance (simultaneous absence of both parents from the nest). A General Linear Mixed Model (GLMM) with normal error distribution related 'Total parental non-attendance per night' to 'Camera group' and 'Nest stage' (incubating or provisioning, determined separately for each night of nest footage) as predictor variables, with Week and Nest ID included as random effects.

Short periods of adult non-attendance at the nest may be due to parental swap-overs or short foraging trips by the female. In order to examine short periods of adult non-attendance of the nest in more detail, it was necessary to determine if male presence at the nest varied with the length of the parental nest absence. Information on male presence at the nest was extracted from the five cameras with the clearest footage (highest frequency of male visibility at the nest). Male involvement during non-attendance was considered if the female left the nest and the male was the next bird to land at the nest, or if the parental non-attendance was between the male leaving and female arriving back at the nest, (less than the full duration of the female absence). If there was no evidence of the male on either side of the parental non-attendance, which represented the female leaving and subsequently returning, this was classed as no male involvement. A GzLMM with the response variable 'Male involvement during absence' (binomial error: 1=yes/0=no) was fitted with the categorical predictors 'Absence length' and 'Nest stage' (incubation or provisioning). The categorical variable 'Period of the night' was also included (with an interaction with season) and Nest ID was added as a random effect. Initial investigations revealed that there was no difference between the two shorter absence categories (for <30s and 31-120s, the confidence intervals overlapped zero) therefore these categories were pooled to make one 'short absence' category. Thus only three main absence categories: short (<2 minutes); intermediate (two to ten minutes) and long (>ten minutes); were used for all following analyses.

The nest camera data were then used to determine if nest stage, temperature and period of the night affect parental non-attendance of the nest by carrying out a series of models (Table 1). The incubation period for nightjar is 18 days however nest camera footage for incubating birds only spanned 14 to 0 days before hatching. Therefore when included in models as a categorical variable, incubation was split into 'early' (14 to 8 days before hatching) and 'late' (7 to 0 days before hatching). The range of chick ages from the nest camera footage was 0 to 12 days. Very

young chicks were predicted to have less parental absence at the nest, with Cramp (1985) suggesting that chicks are brooded continuously until they are a few days old. When chick age was included as a categorical variable, it was therefore split between young (≤ 3 days old) and older (> 3 days old). As the periods of the night (Early, Mid, Late) spanned different durations (3, 4 and 2 hours), an offset of the 'Number of hours per period' was added to all models investigating the frequency of parental non-attendance per period of the night.

Models were fitted to test if the duration the nest was left unattended by both adults per night (Models 1&2), the frequency of short (< 120 s) parental non-attendances per period of the night (Model 3) and the frequency of intermediate (Model 4) and long parental non-attendances per period of the night (Model 5) differed among nest stages, and if this varied with period of the night (for 3, 4 and 5) and temperature. The telemetry data from nesting females was used to investigate if similar effects of nest stage could be detected using another data collection method (Model 6).

Data from incubating birds was used to determine if eggs were left unattended for less time when temperatures were low (Models 7-9) and if there were fewer longer parental non-attendances in the middle period of the night during incubation when temperatures were lower (Models 10-13). Using data from nests containing chicks, models were used to test if chicks were left unattended for less time when they were at a young age, by investigating how the total parental non-attendance per night (Models 14&15), the frequency of short parental non-attendance (per night) (Models 16-18) and the frequency of longer parental non-attendance per night (Models 19&20) increased with chick age. Lastly, to investigate the effect of low temperatures on adults brooding young chicks, models were fitted to determine: if the total parental non-attendance per night was less for young chicks on nights with low temperatures (Model 21); if the frequency of short parental non-attendances (per night and per period of the night) was greater for young chicks at low temperatures (Models 22-23, 26) and if there were fewer long parental non-attendances for young chicks at low temperatures (per night and per period of the night) (Models 24,25,27,28).

Table 1. Structure of models used to determine if nest stage, temperature and period of the night affect simultaneous nest absences by both parents in nightjars. See footnote for explanation of variables and coding.

Mod	Response variable	Type	Error	Predictor variables			Temp	Period *Discrepancy	Interactions	Random Nest ID	Discrepancy
				Stage	Egg (Days)	Chick age (Days)					
1	Duration nest left unattended (SQrt)	GLMM	Normal	X (3)			X(B)		X(A)	X	
2	Duration nest left unattended (SQrt)	GLMM	Normal	X (4)			X(B)		X(A)	X	
3	Freq of short absence per period	GzLMM	Neg. binomial	X(3)			X(A)	X	X(A-D)	X	
4	Freq of intermediate absence per period	GzLMM	Neg. binomial	X(3)			X(A)	X	X(A-D)	X	
5	Freq of long absence per period	GzLMM	Neg. binomial	X(3)			X(A)	X	X(A-D)	X	
6	Female absence per night (SQrt)	GLMM	Normal	X(3)							X
7	Duration nest left unattended (SQrt)	GLMM	Normal				X(B)			X	
8	Duration nest left unattended (SQrt)	GLMM	Normal	X(2b)			X(B)		X(A)	X	
9	Duration nest left unattended (SQrt)	GLMM	Normal		X		X(B)		X(A)	X	
10	Freq of intermediate absence per period	GzLMM	Neg. binomial				X(A)	X	X(C)	X	
11	Freq of intermediate absence per period	GzLMM	Neg. binomial	X(2b)			X(A)	X	X(A-D)	X	
12	Freq of long absence per period	GzLMM	Neg. binomial				X(A)	X	X(C)	X	
13	Freq of long absence per period	GzLMM	Neg. binomial	X(2b)			X(A)	X	X(A-D)	X	
14	Duration nest left unattended (SQrt)	GLMM	Normal			X				X	
15	Duration nest left unattended (SQrt)	GLMM	Normal	X (2c)						X	
16	Freq of short absence per night	GzLMM	Poisson			X				X	
17	Freq of short absence per night	GzLMM	Poisson			X + X2				X	
18	Freq of short absence per night	GzLMM	Poisson	X(2c)						X	
19	Freq of longer absence per night	GzLMM	Poisson			X				X	
20	Freq of longer absence per night	GzLMM	Poisson	X(2c)						X	
21	Duration nest left unattended (SQrt)	GLMM	Normal			X	X(B)		X(A)	X	
22	Freq of short absence per night	GzLMM	Poisson			X	X(B)		X(A)	X	
23	Freq of short absence per night	GzLMM	Poisson	X(2c)			X(B)		X(A)	X	
24	Freq of longer absence per night	GzLMM	Poisson			X	X(B)		X(A)	X	
25	Freq of longer absence per night	GzLMM	Poisson	X(2c)			X(B)		X(A)	X	
26	Freq of short absence per period	GzLMM	Neg. binomial			X	X(A)	X	X(A-D)	X	
27	Freq of intermediate absence per period	GzLMM	Neg. binomial			X	X(A)	X	X(A-D)	X	
28	Freq of long absence per period	GzLMM	Neg. binomial			X	X(A)	X	X(A-D)	X	

Footnote for Table 1.

Response variables: 'Duration nest left unattended' = the total time per night that the nest was left unattended by both parents (minutes), using nest camera data. 'Female nest absence per night' = the total time that the female was absent from the nest per night (minutes), using telemetry data. 'Freq. of short absence per period (or per night)' = the frequency of short (<2 minutes) parental non-attendances of the nest per period of the night (or per night), using nest camera data. 'Freq. of longer absences per night' = the frequency of longer (>2 minutes) parental non-attendances of the nest per period of the night, using nest camera data. 'Freq. of intermediate absence per period' = the frequency of intermediate (2-10 minutes) parental non-attendances of the nest per period of the night, using nest camera data. 'Freq. of long absences per period' = the frequency of long (>10 minutes) parental non-attendances of the nest per period of the night (or per night), using nest camera data.

Predictor variables: Egg (days) = the number of days before the eggs hatched. Period = Period of the night: Early (20.00-22.59hrs); Mid (23.00-02.59hrs); Late (03.00-04.59hrs). The interaction term 'Disc' (Seasonal Discrepancy) was included to control for the stage in the season. The categorical predictor 'Stage' (Nest stage) has five alternatives: 2a=Incubating and provisioning; 2b=Early incubation and late incubation; 2c=Young chicks (≤ 3 days old) and older chicks (>3 days old); 3=Eggs, young chicks, older chicks; 4=Early and late incubation, young and old chicks. The continuous predictor variable of 'Temperature' has two alternatives: A=Mean hourly temperature per period; B=Temperature at midnight. There were four possible interactions in the models: A=Nest stage *Temperature; B=Nest stage*Period of the night; C=Period of the night*Temperature; D=Nest stage*Period of the night*Temperature.

For all model sets, the best model was chosen by examining the Akaike Information Criterion corrected for small sample size (AICc). If ΔAIC_i (difference in AICc between Model i and the best model) < 2 , then both models are plausible and have a similar level of empirical support (unless models differ by only one parameter, then that with the higher AICc and number of parameters has no support, as the increase in AICc is only due to the addition of a further parameter) (Burnham and Anderson 2002). For each model set, ΔAIC_i was reported for key models. When ΔAIC_i was reported for the removal of an interaction term, this represented only the removal of the interaction (*) between the variables, while the additive terms of these variables were still retained in the model. When investigating differences between categorical variables, for example, the frequency of absences per night among different nest stages, 95% confidence intervals (CI) of the status coefficient estimates were examined (following Boughey et al. 2011). When the CI for a nest stage overlapped zero (CI $>$ coefficient), it was concluded that there was no difference between that nest stage and the nest stage represented by the intercept. The packages lmer4 (for GLMMs) and glmmADMB (for GzLMMs) for the program R (R Core Development Team 2012) were used to fit all models.

Results

Investigation of male attendance

There was no effect of camera group (in quartiles of apparent male attendance) for the total length of time (per night) that the nest was left unattended by both adults (best model did not contain camera group, ΔAIC_i on addition of camera group = 5.47). It is therefore likely that the frequency of male presence was similar for all nests, but that some cameras provided clearer footage than others, allowing the male to be distinguished more easily.

For the sub-set of five nest camera installations with the clearest images, male presence at the nest was least likely for the longest nest absences (> 600 s), (the best model contained 'Length of parental non-attendance', on removal of this variable = 44.67). Models with and without nest stage (incubating and provisioning) were equally plausible (the best model contained nest stage but ΔAIC_i on removal of nest stage = 1.8) therefore there may be a difference between male involvement during absences at different nest stages.

When the two longer absence categories (121-600s and >600s) were pooled, short absences (< two minutes) from the nest were more likely to involve male presence at the nest than longer parental non-attendances (>two minutes) (Fig. 1). Male involvement occurred in approximately half of short parental non-attendances at the nest but in <20% of long absences, suggesting that a large proportion of short absences represent change-over events rather than brief foraging trips by the female.

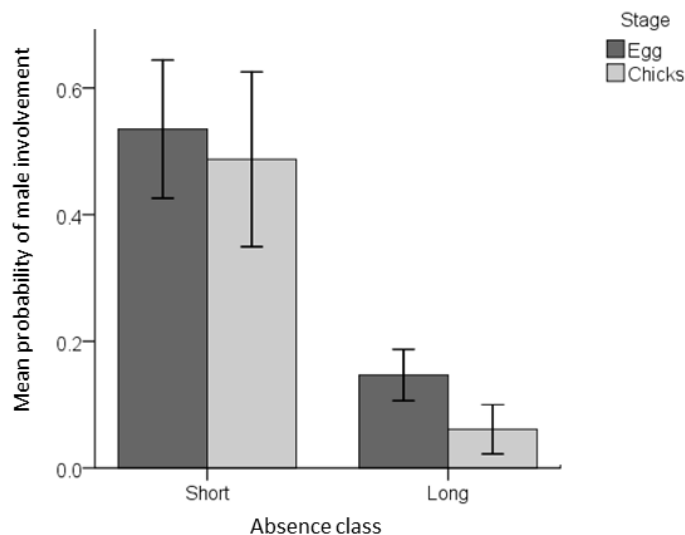


Figure 1. The mean probability of a male nightjar being involved with a parental nest absence for short (<120s) and long (>120s) periods of parental non-attendance at the nest, for nests containing eggs or chicks; $n = 6$ nests, 135 nest nights in total, 341 absence events in total. To control for the pseudo-replication of nest site, the mean probability of male involvement was taken per nest, for each absence class and nest stage. Error bars are \pm SE.

The probability that absence of the female was detected by telemetry, during simultaneous absences by both parents as detected by the nest cameras, differed depending on the absence duration ($n=3$ nests, 4 nights in total) ($p<0.001$). While 100% of absences greater than ten minutes ($n=10$) recorded by the cameras were also detected by the telemetry, only 10% of absences lasting two minutes ($n=11$) or less detected by camera were also recorded by telemetry, and none of the absences between three and ten minutes ($n=9$) recorded by camera were recorded by telemetry. Thus nest cameras provide valuable information on parental non-attendance of the nests that was not detected by telemetry using a regular fix interval of ten minutes.

Comparing the total length of time when both adults were absent from the nest per night from the camera data to total female absence per night from the telemetry data, provided information on the level of male parental care at different nest stages. This suggests that males were present at the nest (incubating or brooding) for a large proportion of the female absence, ranging from half (49.5%) of the female absence during incubation, to 60% for young chicks and 62% for older chicks (Table 2).

Table 2. Comparison of two methods investigating nightjar absence from the nest, using nest cameras to determine cumulative simultaneous absence of both parents from the nest per night and radio telemetry to determine cumulative female absence from the nest per night. The difference represents the time spent at the nest by the male bird.

Nest stage	Camera :	Telemetry:	Male presence (mins.)
Discrepancy:	Both absent (mins.)	Female absent (mins.)	
Egg	51 \pm 4 SE	101 \pm 18 SE	50
Chicks<3 days	26 \pm 3 SE	65 \pm 10 SE	39
Chicks>3 days	61 \pm 6 SE	162 \pm 22 SE	101

Comparison of absence frequency and duration between nest stages

Young chicks were left unattended for less time per night than were eggs and older chicks (Fig. 2a). Counter-intuitively, the total length of time that the nest was left unattended simultaneously by both adults (per night) decreased with increasing temperature (Fig. 2c), with temperature affecting cumulative absence similarly across nest stages (best model contained nest stage and temperature, Δ AIC_c on removal of: nest stage=26.13, temperature =6.44, on addition of interaction between nest stage and temperature =1.94). When the model was repeated with a fourth nest stage, splitting incubation between early and late stages, there was no difference in the total length of time that the nest was left unattended by both adults (per night) between incubation stages (when the late incubation stage was the reference, the confidence interval of the early incubation stage coefficient overlapped zero), (Fig. 2b), and again a negative effect of

temperature; however the best model contained an interaction between temperature and nest stage (ΔAICc_i on removal of the interaction = 1.99). However, the AICc value for the best model when incubation was split was lower than the best model when incubation was not split ($\Delta \text{AICc} = 106$), suggesting that there may be a difference between the two incubation stages but that the dataset is not large enough to test this.

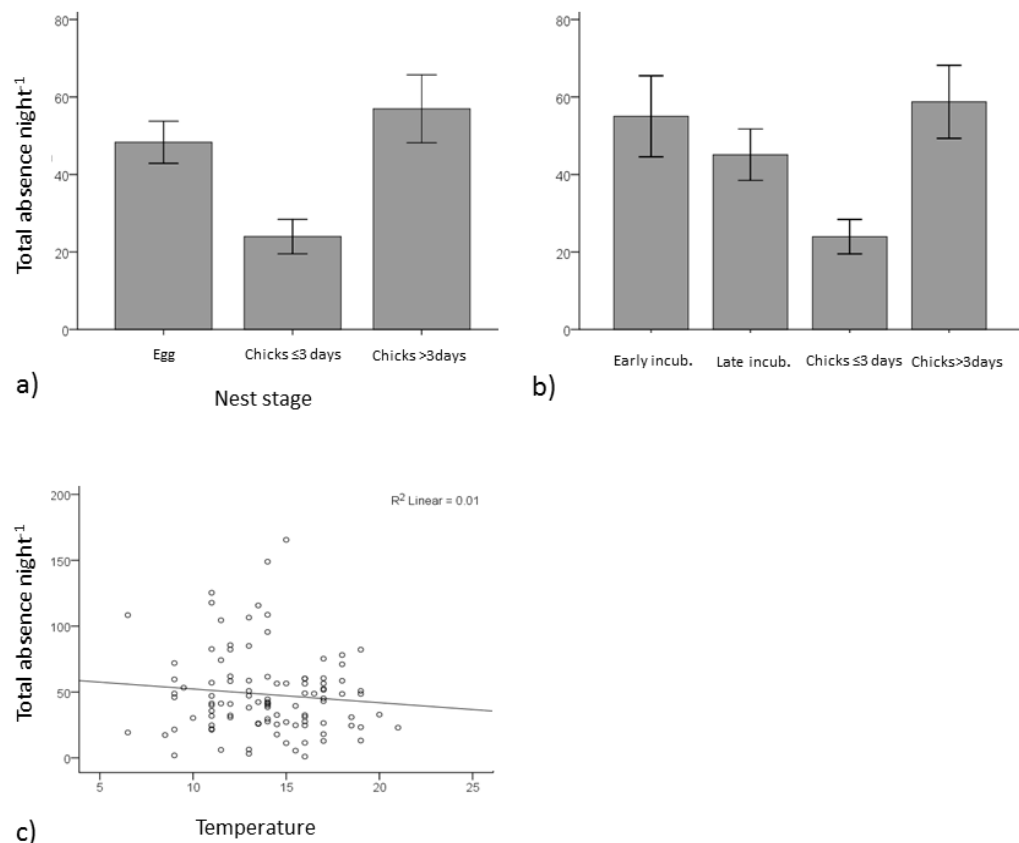


Figure 2. Total length of time that nightjar nests were left unattended by both adults (per night; minutes): a) Parental non-attendance for each nest stage; b) Parental non-attendance for each nest stage with incubation split into early and late; c) Variation in total parental non-attendance with temperature, with all nest stages pooled. Error bars for a) & b) \pm SE.

Using the telemetry data ($n=6$ nesting females, a total of 21 nights) to determine the cumulative female absence from the nest (per night), a similar pattern was found as shown by cameras for the cumulative absence for both adults, with the greatest female nest absence (minutes per night) for nests containing older chicks, nests with eggs having an intermediate level of absence and those containing younger chicks the lowest nightly absence. Although, the best model did not contain nest stage (ΔAICc_i on addition of nest stage = 1.07), the low ΔAICc_i value indicated that

this and the model incorporating stage were equally plausible. The contrast to the camera measures of combined parental non-attendance, where nest stage was strongly supported, likely reflects smaller sample size and weaker power of the model of telemetry data.

The frequency of short parental non-attendances per period of the night differed among nest stages, with nests containing eggs having fewer short absences overall, than nests containing chicks of either age class (Fig. 3a). There was an effect of the period of the night in the model, with the greatest number of short parental non-attendance during the early period of the night for all nest stages. There was a weak positive effect of temperature (i.e. more frequent short absences on warmer nights) and no interactions between temperature, night period or nest stage (best model contained nest stage, night period and temperature, ΔAIC_c on removal of temperature=2.2, on addition of interaction between period of the night and temperature=3.8, on addition of interaction between nest stage and temperature=2.3, on addition of interaction between nest stage and period of the night=4.7).

For parental non-attendances of intermediate duration (two to ten minutes) per period of the night, nests containing older chicks had the greatest number of parental absences, while there was no difference between nests containing eggs or young chicks (Fig. 3b). Overall, parental absences of intermediate length were more frequent during the early and late periods of the night, compared to the middle period. However, there was an interaction between the period of the night and nest stage, with a greater frequency of absences during the early period of the night for nests containing older chicks, and no clear effect of temperature (best model contained nest stage*period of the night, and temperature, on removal of temperature=0.2, on removal of nest stage=57.4, on removal of period of the night=106.0, on replacement of nest stage*period with nest stage* temp=19.0, on replacement of nest stage*period with period*temperature =16.1, on removal of the interaction between nest stage and period of the night=19.8, on addition of a three way interaction between nest stage, period of the night and temperature=6.9).

In contrast, for the longest class of parental non-attendance at the nest (greater than ten minutes) per period of the night, nests containing young chicks had fewer parental absences than either nests with eggs or nests with older chicks (confidence intervals for the nest stage coefficients did not overlap zero when 'nests with young chicks' was the reference) for all stages of the night (Fig. 3d). Again, simultaneous absences of both parents were less frequent during the middle period of the night, for all nest stages. As with the models for intermediate parental

absences, there was no effect of temperature (best model contained only nest stage and period of the night (on addition of temperature =1.6 (difference of one parameter), no interaction between nest stage and period of the night, on addition =1.71, on removal of nest stage=16.9, on removal of period of the night=102.9, on addition of the temperature term and an interaction between temperature and nest stage=3.8, on addition of the temperature term and an interaction between temperature and period of the night=5.3).

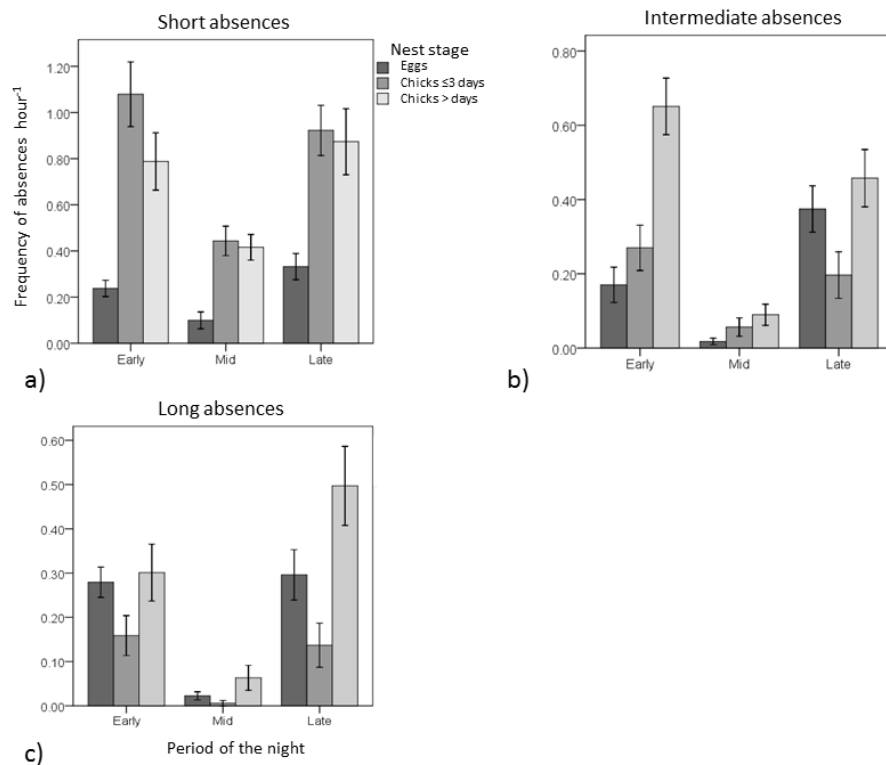


Figure 3. Variation in the mean frequency (per hour) of absences from the nest by both adults for nightjars at different stages in the breeding season, during different periods of the night (Early 20.00-22.59 hrs; Mid 23.00-02.59 hrs; Late 03.00-04.59 hrs), showing: Frequency of a) short parental non-attendances at the nest (<two minutes); b) intermediate parental non-attendances between two and ten minutes; c) long parental non-attendances >10 minutes. Error bars are $\pm 1SE$.

Models of parental non-attendance during incubation

Incubating birds did not spend less time away from eggs when temperatures were lower, with a rise in temperature causing a negative effect on the total duration nests were left unattended by

both adults (per night) (Fig. 4a) (best model included temperature, ΔAIC_c on removal of temperature=6.5). However, during the early stages of incubation, a decrease in temperature caused an increase in the total length of time both adults were absent, whereas as incubation progressed, the level of parental absence remained constant, despite changes in temperature (pooling data for both stages, whether incubation was coded as early versus late (categorical), or in terms of days (continuous), the best models contained an interaction between incubation stage and temperature; on removal of the interaction AIC_c =3.4 or 5.1 when incubation stage was categorical or continuous respectively).

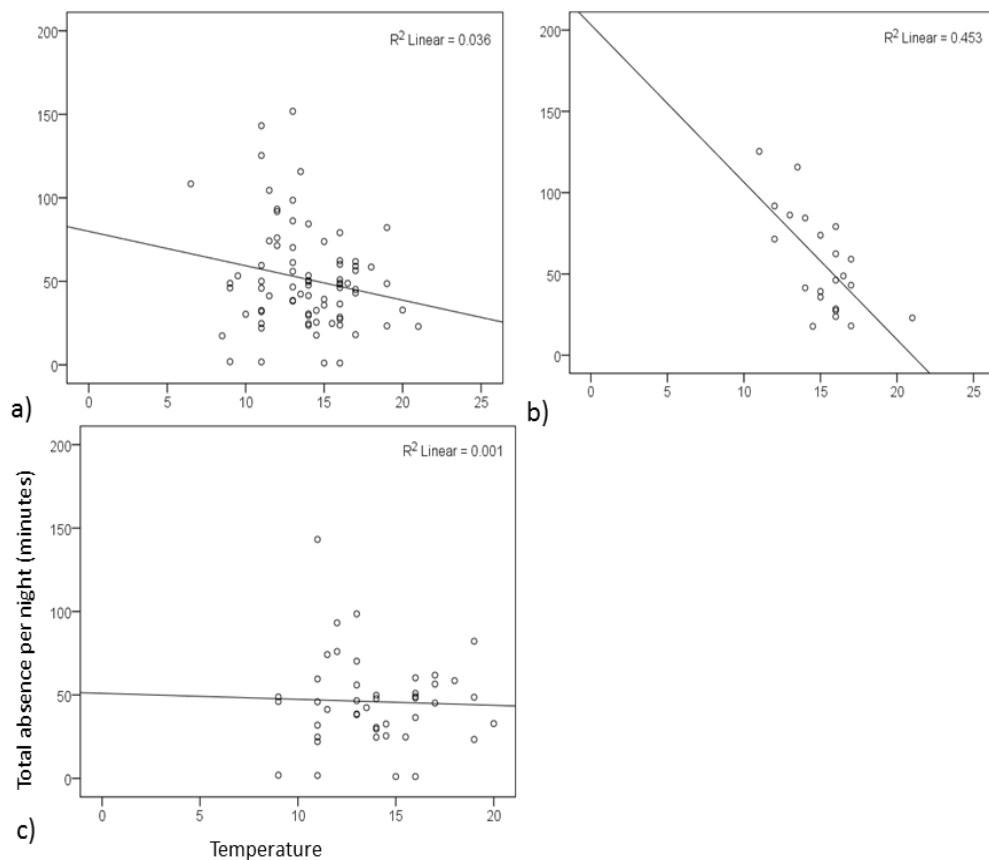


Figure 4. Variation in the total length of time both adults were absent from the nest (per night) during incubation with increasing temperature: a) all stages of incubation; b) early incubation (14 to 8 days before eggs hatch); c) late incubation (7 to 0 days before the eggs hatch).

For incubating birds, parental absences between two and ten minutes were most frequent during the early and late periods of the night. Overall, there was a weak positive effect of temperature on the frequency of intermediate absences and the possibility of there being less frequent absences during the early periods of the night at intermediate temperatures (best model

contained an interaction between night period and temperature (on removal of temperature, $\Delta \text{AICc}_i = 5.0$, on removal of night period = 103.5, on removal of the interaction term between night period and temperature, $\Delta \text{AICc}_i = 0.4$). There was no clear difference in the frequency of parental non-attendances at the nest between two and ten minutes between birds in the early and late stages of incubation and no interaction between temperature, incubation stage or the period of the night (best model contained only time of night and temperature, on addition of nest stage = 1.8, removal of temperature = 2.9, on removal of night period = 78.8, on addition of an interaction between period of the night and temperature = 0.06, on addition of nest stage and an interaction between nest stage and temperature = 3.8, on addition of nest stage and a three way interaction between nest stage, time of night and temperature = 7.2).

For incubating birds, the frequency of parental absences greater than ten minutes varied only with the period of the night, with the lowest level of absence in the mid period of the night (best model contained only night period, on addition of temperature = 1.7, on addition of temperature and an interaction between night period and temperature = 4.5). The frequency (per period of the night) of parental absences greater than ten minutes did not differ between early and late stage incubating birds and there was no interaction between temperature, incubation stage or the period of the night (the best model contained only night period: on addition of temperature = 1.9, on addition of nest stage = 1.9, on addition of temperature and an interaction between night period and temperature = 4.6, on addition of temperature and nest stage and an interaction between temperature and nest stage = 8.8, on addition of temperature and nest stage and a three way interaction between nest stage, temperature and night period = 13.7).

Models of parental non-attendance at the nest during the chick stage

There was a strong positive relationship between the duration (per night) that the nest was left unattended by both adults and chick age (Fig. 5a). The best model contained chick age (ΔAICc_i on removal of continuous chick age variable = 17.2 and for categorical chick age variable = 21.2). The frequency (per night) of short absences was not greater when chicks were young, however this pattern could be weakly seen in the data (Fig. 5b). When chick age was considered as a continuous variable, the best model incorporated chick age, however, ΔAICc_i on removal of chick age was only 0.08 indicating negligible support for its effect, with the null model equally plausible. When chick age squared was added as a further continuous variable, the best model contained chick age squared but ΔAICc_i of the removal of this variable (while keeping the linear age term)

was only 0.88. When chick age was included as a categorical variable, it was not included in the best model, however, ΔAIC_c of addition of chick age was only 0.22, again indicating equivocal support.

In marked contrast, the frequency of longer (>2 minutes) absences per night increased with chick age (Fig. 5c). The best model required chick age (ΔAIC_c on removal of continuous chick age variable =46.3 and on removal of the categorical chick age variable =34.86).

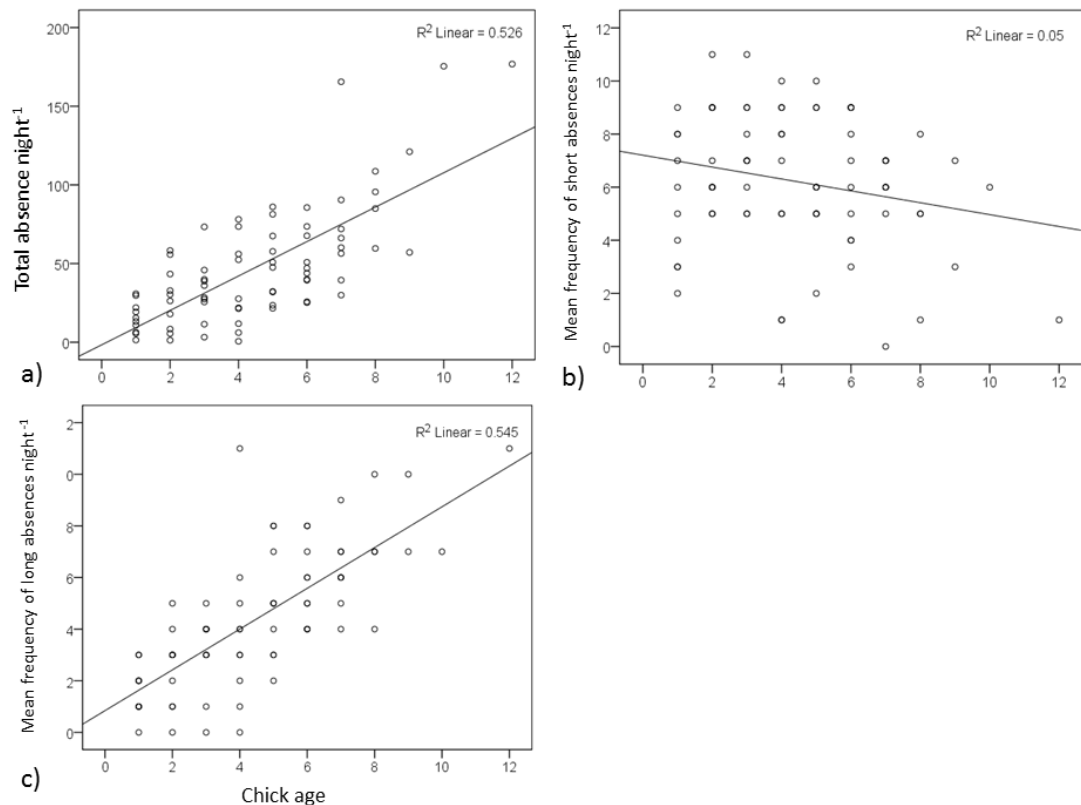


Figure 5. Changes in the duration and frequency of absences from the nest by both adults with increasing age of chicks in nightjars: a) Total absence from the nest (mins) per night; b) Frequency of short absences (<120sec) per night; c) Frequency of long absences (>120 sec) per night.

For nests containing chicks, there was no effect of temperature on the length of time (per night) that the nest was left unattended by both adults and no interaction between chick age and temperature (best model contained only chick age, ΔAIC_c on addition of temperature and an interaction between chick age and temperature = 2.9). However, Fig. 6a suggests a weak increase in total parental nest absence per night with temperature for nests containing young chicks, while Fig. 6b suggests a weak decrease in total parental nest absence per night with temperature for

nests containing older chicks. There was also no effect of temperature on the frequency per night of short absences and no interaction between chick age and temperature. The best model did not contain chick age or an interaction with temperature (ΔAIC_c on addition of the interaction with temperature with chick age as a continuous variable = 2.8, with chick age as a categorical variable=3.02). However, Fig. 6c suggests a weak decrease in the frequency of short parental non-attendances at the nest per night with temperature for nests containing young chicks, while Fig. 6d shows no relationship between temperature and the frequency per night of short parental absences for nests containing older chicks. There was no effect of temperature on the frequency per night of long parental non-attendances at the nest and no interaction between chick age and temperature. The best model contained only chick age (ΔAIC_c on addition of temperature and an interaction between temperature and chick age as a continuous variable = 2.40, with chick age as a categorical variable = 3.56). However, Fig. 6e suggests a weak increase in the frequency per night of long parental absences with temperature for nests containing young chicks, while Fig. 6f suggests no relationship between the frequency per night of long parental absences with temperature for nests containing older chicks.

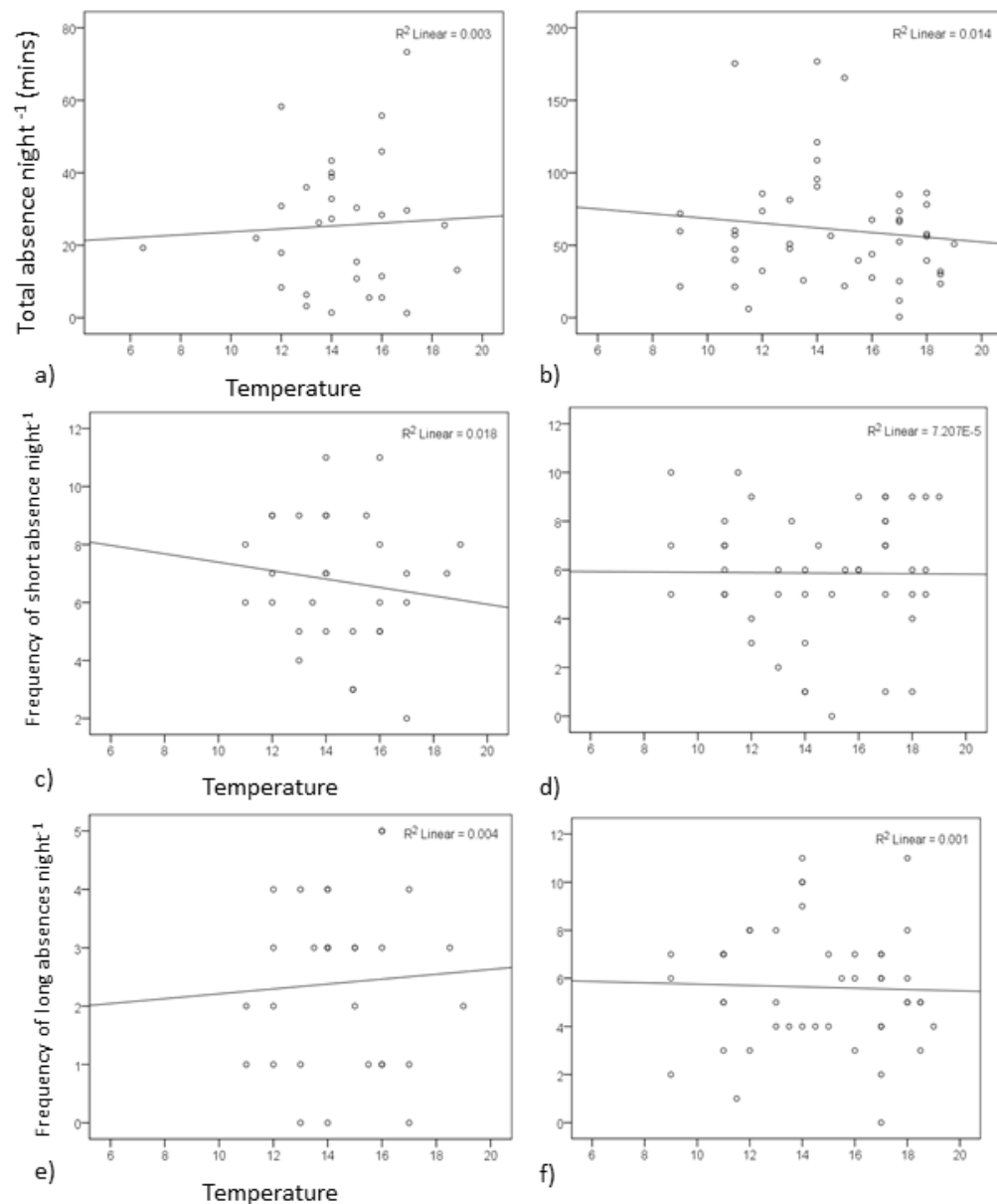


Figure 6. The effects of temperature on duration and frequency of simultaneous nest absences by both adults in nightjar nests with young (≤ 3 days) and old (> 3 days) chicks; Total length of time the nest was left unattended by both parents (per night) for: a) young chicks; b) for older chicks; Mean of the frequency of short (< 120 sec) parental absences per night for: c) young chicks; d) older chicks; Mean of the frequency of long (> 120 sec) parental absences per night for: e) young chicks; f) older chicks.

There was no clear evidence of an effect of temperature on the frequency per period of the night of short parental absences. The best model contained an interaction between chick age and period of the night, and temperature. However, while temperature was included in the best model and Fig. 7a indicates a weak negative relationship between temperature and the frequency

of short parental absences, ΔAIC_c on removal of temperature=1.6, therefore both models are equally plausible. Visual inspection of the data (Fig. 7b) suggested that there may have been more short absences for older chicks at lower temperatures. Further investigations revealed that this may have been due to an increase in short absences during the middle period of the night when parents have older chicks (Fig. 7d), while for parents with younger chicks, there were more short absences during the early period of the night, but this relationship was not significant (Fig 7c). However, overall, there was no strong evidence for an interaction between chick age and temperature (on replacement of chick age*period with chick age*temp +period, ΔAIC_c =2.1) and no need for a three-way interaction, (on replacement of chick age* period with chick age*period*temp, ΔAIC_c =8.5). The best model only contained an interaction between chick age and period, with a greater frequency of short parental absences during the early period of the night for nests containing young chicks (Fig. 3a), however ΔAIC_c on removal of the interaction between chick age and period =1.5, therefore again, the null model is equally plausible.

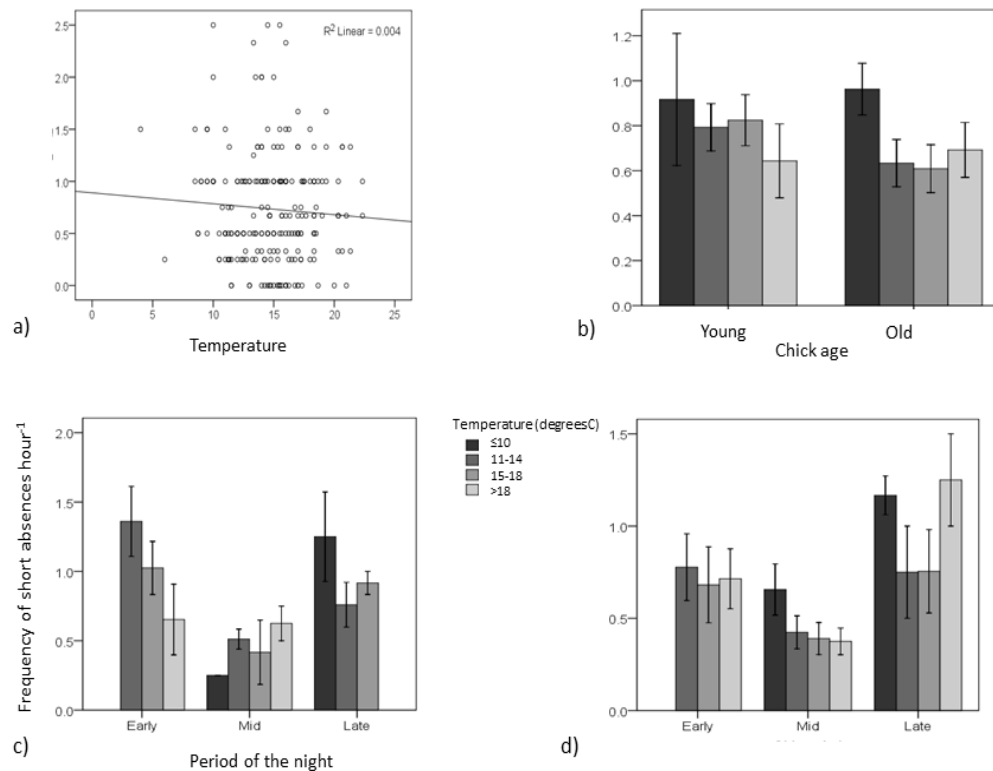


Figure 7. Variation in the mean frequency of parental absences less than two minutes per hour (per period of the night) (Early 20.00-22.59 hrs; Mid 23.00-02.59 hrs; Late 03.00-04.59 hrs) : a) with increasing temperature; b) for young (<3 days) and older (>3 days) chicks at different temperatures; c) for young chicks during different periods of the night at different temperatures; d) for older chicks during different periods of the night at different temperatures. Error bars are \pm SE.

For nests containing young chicks, there were more intermediate parental absences during the early period of the night when temperatures were highest (Figure 8) (best model contained a three way interaction between chick age, period of the night and temperature, ΔAIC_i on removal: of the interaction term for temperature=7.7, of the interaction term for period of the night=18.3, of the interaction term for chick age=10.9, of all interactions=14.8).

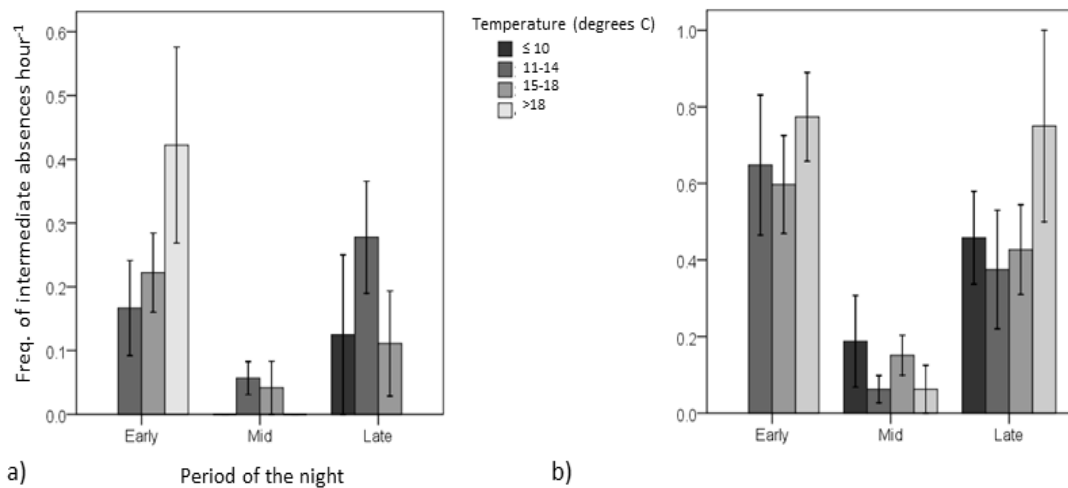


Figure 8. Variation in the mean frequency of intermediate parental absences (two to ten minutes) from the nest (per hour) for each period of the night (Early 20.00-22.59hrs; Mid 23.00-02.59hrs; Late 03.00-04.59hrs): a) young (<3 days); and b) older (>3 days) chicks, during different periods of the night and at different temperatures. Error bars are \pm SE.

Changes in temperature did not affect the frequency of parental absences greater than ten minutes (best model contained only chick age and night period, Δ AIC_c on addition of temperature=1.63, on addition of temperature and an interaction between temperature and chick age=2.1, on addition of temperature and an interaction between temperature and night period=5.5, on addition of temperature and an interaction between temperature, night period and chick age=10.4).

Discussion

This is the first study to examine how the attentiveness of nocturnal birds at the nest is affected by temperature during the breeding season using a combination of radio telemetry and nest camera footage. Male nightjars provided parental care during both incubation and chick provisioning, with their attentiveness during female absences apparently greater during the chick than during the egg stages. However there were times when the nest was left unattended simultaneously by both parents. Young chicks were left unattended for less time (per night) than clutches or older chicks. The response of adults to changes in temperature differed depending on the stage of incubation; during early incubation, results suggested that adults focused on self-maintenance at low temperatures with less non-attendance as temperature increased, however

as incubation progressed, there was no change in the total duration of absence from the nest by both adults with decreasing temperature. Chicks were left unattended in the nest for longer per night as chick age increased. As chicks increase in size their ability to thermoregulate increases, which subsequently decreases the need for parental brooding and attendance at the nest (Visser 1998). Larger chicks will also require greater provisioning effort by adult birds. Nocturnal birds provisioning chicks at the nest are not at risk from attracting predators as diurnal avian species are. This was reflected in the number of frequent short absences by both adults (considered to largely represent swap overs by adult birds, but also including brief foraging trips by the female) when chicks were both young and old.

Comparing the four nights with both telemetry and camera data, all absences of greater than ten minutes detected by the cameras were also detected by the radio telemetry protocol. However, none of the absences between two and ten minutes recorded by the nest cameras were recorded by the radio telemetry of the female (the female was recorded as absent but for a period >ten minutes). This could be for two reasons; firstly, it was difficult to detect short absences using the telemetry, both because readings were taken every ten minutes and also because small movements could represent small movements at the nest site or a short absence from the nest. Secondly, as it was difficult to distinguish male and female birds on the nest camera, the bird returning to the nest during the shorter absences may have been the male. This is supported both by the lack of difference in the length of time that the nest was left unattended per night between the camera groups with varying male visibility and by the major discrepancy between the total nightly absence from the nest by the female birds using telemetry and the total absence by both adults from the nest cameras. While it was unfortunate that males and females could not always be identified on the nest camera, the combined data from the nest cameras and radio telemetry provided useful information on the decisions by both parents to leave the nest unattended.

The telemetry data on total female nest absence per night showed similar results to the nest camera footage, with nests containing young chicks having the lowest duration of non-attendance. Using radio telemetry, Alexander and Cresswell (1990) found that the lowest percentage of nest checks where females were found absent occurred during incubation, however, the total absence from the nest per night by the female was not investigated and nests at the chick stage were not split by chick age as in this study. The comparison between camera and telemetry data indicated the level of male parental care at different breeding stages. As suggested in previous studies, the male nightjar did not incubate eggs and brood chicks continuously when the female left the nest and there were times when the nest was left exposed.

This could be because male birds are focused on guarding the territory. Male presence at the nest was greater during the chick rather than the egg stage. In a review of male parental behaviour in birds, Ketterson and Nolan (1994) suggest that incubation is the most restrictive of male parental care behaviours as it is time consuming and can't be postponed. The greater male presence at the chick stage in nightjars may also be because female require more assistance during this stage, to provision chicks with increasing need for biomass as they age.

Differences in duration and frequency of parental absence between nest stages

There was strong evidence for differences among nest stages for the total length of time the nest was left unattended by both adults per night and the effect of temperature. Nests containing chicks ≤ 3 days old had the least parental absence per night. This is in support of avian physiology, because young chicks are susceptible to chilling due to the high ratio of surface area to volume and must be brooded by parents to avoid excessive cooling (Visser 1998). However, while Cramp (1985) suggests that chicks are brooded continuously for the first few days, chicks were left exposed for a mean of 26 minutes per night. Therefore the female did come off the nest during this time and the male did not cover the chicks during a large part of the female absence. While the models showed no difference for the total length of time nests were left unattended by both adults per night between nests at the early and late incubation stages, the data indicated increased parental care as incubation progressed, with less parental absence for nests during the later stages of incubation. Irrespective of nest stage, the total time that the nests were left unattended per night decreased with temperature. This may be because adults can find insect prey more quickly at higher temperatures, for example, moth biomass in moth traps was greater at higher temperatures (Chapter 4) and adults may also have greater prey requirements for maintenance at lower temperatures. However, it is nevertheless surprising that nests were left simultaneously unattended by both parents for longer on cold nights and that the male did not cover the nest during the female absence, and feed later, after her return. It appears that during colder conditions, the male is foraging during a large part of the female absence from the nest, rather than taking over and investing greater parental care. It may be that the peak activity of prey during a short early evening period constrains both adults to forage then, especially when prey encounter rates are low, so that the male simply can't afford to incubate or brood the nest for the entire duration that the female is absent from the nest.

Nests containing chicks had the highest number of short parental absences for all periods of the night. These short parental absences represented either short foraging trips made by the female or a swap-over between the male and female bird. The higher frequency during provisioning reflects the need of the parents to provision chicks frequently and/or could also indicate that the male bird was more likely to be present at the nest when the nest contained chicks.

The frequency of parental absences lasting between two and ten minutes did not differ between nests containing eggs and those with young chicks for absences. These absences may represent brief self-maintenance foraging absences by the female, which have no negative effect on either the eggs or young chicks. The interaction between nest stage and period of the night was due to the higher frequency of parental absences between two and ten minutes for nests containing older chicks at the beginning of the night. This may be due to parents taking advantage of the higher peak in moth abundance at the beginning of the night when chicks were larger and required a greater biomass of prey per night. Nests containing young chicks had the lowest number of parental absences greater than ten minutes, as chicks could not be left exposed for long periods due to the risk of chilling and the requirement to be fed frequently.

Parental non-attendance during incubation

During incubation, the negative relationship between temperature and the total length of time the nest was left unattended by both adults per night was the reverse of that expected if adults must incubate eggs against a greater risk of chilling on colder nights. This may be because when the temperature is higher, the female does not have to search as long for prey items, with an increased availability of moth prey at higher temperatures (Chapter 4). Alternatively, it may be possible that the minimum nocturnal temperatures recorded were not critical for nightjar eggs or that nightjar eggs can be exposed to low temperatures without adverse effects on embryo development, as for other bird families, for example, Procellariiformes (Boersma and Wheelwright 1979). When incubation was split into stages (early and late), the models showed no difference between the total parental-non-attendance at the nest per night, however this model was a better model than that containing nest stage split into only three stages (incubation, chicks ≤ 3 days, chicks > 3 days). This suggests that there may be a difference in parental non-attendance between incubation stages, with examination of the data suggesting that parental absence is greater during early incubation, however the sample size may not be large enough to show this result in the models. Adults spent more time away from the eggs at cold temperatures in the early

stages of incubation (with strong support for the importance of the interaction between temperature and incubation stage). As there was no indication that this occurred only in the early stages of the night before temperatures dropped to their lowest, it appears that the female's behaviour is governed by the necessity of self-maintenance during this time. However, as incubation progressed, there was no increase in nest absence despite changes in temperature, suggesting that the priority of adult birds changed to egg brooding as incubation progresses.

The frequency of longer parental absences (between two and ten minutes and greater than ten minutes) in the middle of the night did not decrease during lower temperatures, contrary to expectation. Model results suggested the possibility of less frequent parental absences between two and ten minutes during the early period of the night at intermediate temperatures. However, as there was very little absence of this duration during the early and middle periods of the night during the incubation stage, it was difficult to investigate the true effects of temperature. There did seem to be a general positive effect of temperature on the frequency of parental absences per period of the night between two and ten minutes for incubating birds (contrary to the overall decrease in total time that the nest was left unattended with temperature). This effect may be due to birds increasing the frequency of these intermediate absences at higher temperature but the total duration of each parental absence is shorter, possibly because it is easier to find prey at warmer temperatures.

Parental non-attendance during the chick stage

As predicted, the total length of time that nests were left unattended by both adults increased with chick age; as the chicks grew less susceptible to chilling and required less frequent but greater amounts of prey, adult birds were absent from the nest for longer. It was predicted that the frequency of short parental absences per night may have been higher when the chicks were younger as parent birds would have more swap-overs, with the male brooding the susceptible chicks during female absence and/or because the female may be more likely to make short, local trips to capture passing moths and avoid longer foraging absences. The frequency of short parental absences per night was not related to chick age. However, when the frequency of short parental non-attendances at the nest per period of the night was examined for nests containing chicks, there was support for an interaction between chick age and period of the night. This appears to be because there were more short parental absences for nests containing young chicks than older chicks in the early period of the night. This may be due to adults provisioning younger

chicks more frequently during the peak in moth abundance at the beginning of the night. The frequency of longer parental non-attendances at the nest increased with chick age as predicted.

No interactions between chick age and temperature were supported for any of the models of absences per night, although the predicted patterns appeared present on visual inspection of the data. In particular, for birds with young chicks, the total length of time that the nest was left unattended by both adults appeared to increase with temperature. Adults with young chicks were expected to have more short parental absences when the temperature was lower but as the temperature rises, the female can afford to go on longer absences and fewer shorter ones, or there is no need for the male to be present at the nest when the female is absent.

Models investigating the effect of temperature on the frequency of short parental absences during each period of the night indicated that there may be an effect (models with and without temperature were equally plausible) and inspection of the data indicated a weak negative relationship between the frequency of short parental non-attendances at the nest and temperature. This is in support of the result for the frequency of short absences per night; overall, parents with chicks increase the frequency of shorter absences when the temperature is lower. Model results also indicated that interactions between chick age and temperature and/or chick age and period of the night were plausible. Inspection of the data suggested that there were more short parental absences for nests containing older chicks when the temperature was lower, however the effect was dependent on the time of night. For nests containing younger chicks, the frequency of short parental non-attendances at the nest was higher at cold temperatures at the beginning and end of the night, whereas for nests containing older chicks there was no difference between the frequency of short parental absences with temperature at the beginning and end of the night, only the middle period. While these results were as predicted for young chicks, adults with young and older chicks left the nest for short times during all periods of the night, therefore this may not be a complete result due to the lack of a wide range of temperatures for each period of the night.

For parental absences between two and ten minutes at nests containing chicks, there was a three-way interaction between chick age, temperature and stage of the night. Inspection of the data suggested that this may be because when the nest contained young chicks, there were more medium absences during the early stage of the night when the temperature was warmer. As young chicks can't be left unattended for long periods when the temperature is low, adult birds may have only left chicks on longer provisioning absences when the temperature was higher.

Overall, as predicted, parental nest absence behaviour in the nocturnal nightjar differs from that of some diurnal species, most likely due to the lack of pressure from predators searching visually for prey. Thus parental absence from the nest is dictated by stage in incubation, with an apparent increase in parental care as incubation progresses; temperature, with results suggesting that adults leave eggs (in the later stage of incubation) and young chicks unattended less at lower temperatures; and chick requirements, with parents leaving the nest for longer periods as chicks require a higher level of biomass.

Management implications

This increased understanding of the factors driving nightjar behaviour at the nest can be used to inform conservation management plans. Using radio telemetry, female birds were found to forage frequently in the nest territory and in a number of other habitats outside the territory, with the core home range showing a multi-modal structure (Chapter 4). In support of the telemetry data, the nest cameras provided evidence of parental non-attendance of varying lengths, with investigations of male presence at the nest suggesting that the shortest of these absences were either swap-overs between adult birds or short absences by the female, presumably to forage in the nest territory. The nest camera results provide an increased understanding of the variation in absence lengths, suggesting that both breeding stage and temperature influence parental non-attendance at the nest. Therefore, the foraging habitats selected by the female nightjar each night may vary with temperature or the stage of the nest (e.g. incubation, young chicks, large chicks) with females foraging closer to the nest when temperatures are lower and/or when they are provisioning young chicks. This information can contribute to forest design plans for the nightjar, with results suggesting that it is important to have sufficient suitable foraging habitat close to the nest site to allow for short parental absences from the nest at certain times during the breeding season. This behavioural study also provides supportive evidence for the findings in chapter 4, with results suggesting that birds with a higher percentage of suitable foraging habitat within 500m of the territory centre may have a smaller home range size. The availability of sufficient suitable foraging habitat close to the nest site (see Chapter 4 for a suggested recommendation of a suitable area) may reduce the foraging distances birds have to travel and the resulting efficiency in chick provisioning at a crucial time in the breeding season could potentially lead to an increase in nightjar breeding success.

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Chapter 6: Supplementary material

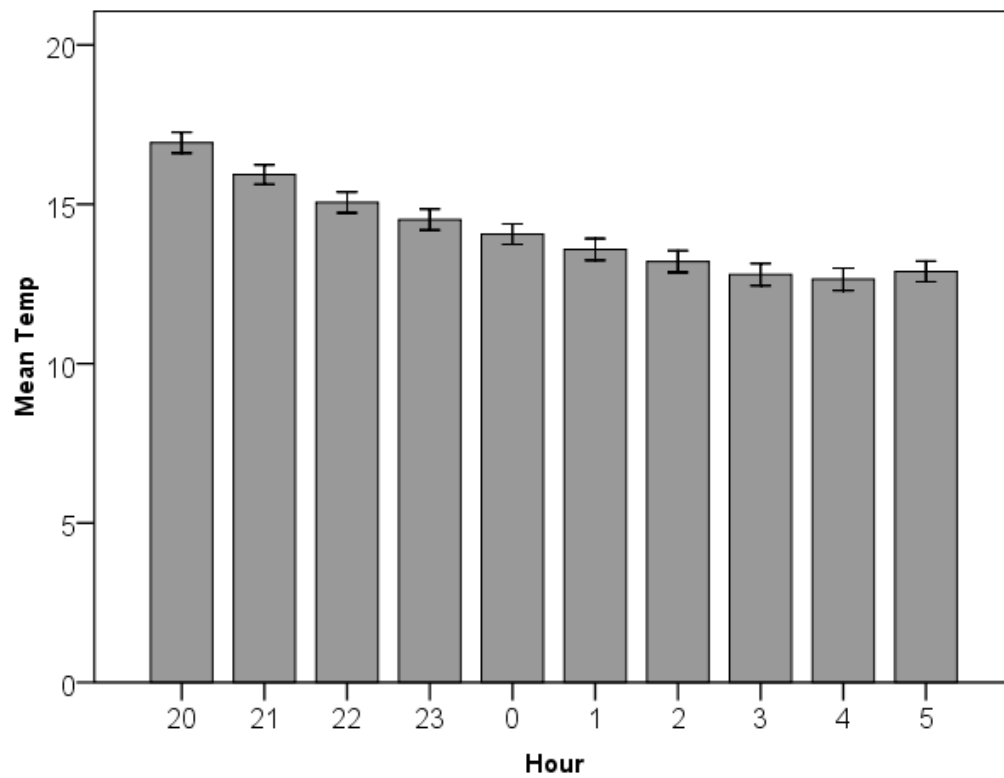


Figure S1. Mean hourly air temperature for 1st May – 30th August 2008. Data from Lakenheath weather station.

Chapter 7: Discussion

Summary of key findings

Using a variety of techniques, including field observation, radio telemetry, faecal dissection and nest cameras combined with robust data analysis, this thesis provides novel, detailed knowledge on the ecology of nightjars breeding in a heathland-plantation mosaic. These findings add to the current understanding of this species, and also provide support to the results of previous studies.

For the first time, both the male and female nightjar home range size and structure have been described, with the home range being much larger than the song territory, emphasising the importance of foraging habitat in the wider landscape. Males had smaller home ranges than females, which were centred on the song territory. Female birds had multi-modal home ranges, with birds foraging in a number of key sites. These results suggest a difference in behaviour and priorities between the sexes during the breeding season. In comparison to other populations of nightjar (Alexander and Cresswell 1990, Sierro et al. 2001), forest habitats were of key importance for foraging, with birds preferring open canopy plantation forest (aged 5-10 years) and recently planted coupes (aged 0-4 years). Plantation forest with a variety of growth stages can provide both nesting and foraging habitat for nightjar. A more thorough understanding of the requirements of nightjars foraging in open habitats was achieved, with grazed-grass heath selected when present within 2km of the territory centre but open ungrazed and un-planted habitat avoided, relative to availability, suggesting the importance of habitat management. Results suggest that home range size may decrease as the percentage of suitable foraging habitat within a 500m radius of the home range increases, however further work is required to confirm the optimum area of suitable habitat as models did not have strong support. In agreement with the findings of Bowden and Green (1991) and Sierro et al. (2001), moth trapping results suggested that nightjars did not prefer habitats containing the greatest moth biomass, therefore birds may select foraging habitat based on the ease of prey capture rather than prey abundance.

There was no difference between the song territory size of paired and (assumed) unpaired male nightjars and males defended a single territory at a time. However territories were found to overlap during a single four week period. Two unpaired males were found churring >1km from their territory, however this only occurred once for each bird. While further research is required to investigate the chances of an observer encountering overlapping birds on the same night and to determine the length of time observers should spend at a territory, these results can provide guidance for national nightjar surveys. Surveyors must be aware of the potential for territory

overlap, however, results suggest that the chance of an over-estimate due to roaming unpaired males is low.

There was a high abundance of both moths and beetles in the nightjar diet, confirming the results of previous studies (Collinge 1920, Cramp 1985). Results suggest that the variation in the nightjar diet during the breeding season may be due to changes in the availability of prey and as a response to varying chick requirements, with more beetles found in the diet of adults with older chicks than adults with young chicks and lone adults. A comparison of the diets of birds nesting/roosting at varying distances from heathland suggested that grazed grass-heathland and forest habitats may be similar in terms of foraging resources for nightjars. Again, the importance of habitat management is implied, with foraging nightjars in Dorset avoiding heathland that was not grazed, whereas grazed heathland provided an additional foraging resource for nightjars in Thetford Forest.

An investigation of nightjar behaviour during nesting suggested that the main factors influencing the frequency and duration of parental non-attendance were incubation stage, temperature and chick provisioning requirements. Male nightjars were present at the nest during both incubation and provisioning, however there were times when the nest was left unattended by both parents. Results suggested that nesting nocturnal birds do not face the same pressures as diurnal birds, with behaviour at the nest in the former not influenced by the threat of visually oriented diurnal predators. In addition to providing novel information on nightjar breeding behaviour, this study can be used to contribute to habitat management recommendations for the nightjar, with results suggesting that female birds may require suitable foraging habitat close to the nest at certain times during the breeding season.

Together, these findings on nightjar home range and habitat use, diet and breeding behaviour can be combined and used as an evidence base for nightjar conservation practices and recommendations. However, there is also potential for further work to add to these results.

Chapter synthesis

The exploration of nightjar habitat use and diet provide key understanding on nightjar habitat preferences. Nightjars were found to forage in both heathland and early growth forest habitats and the results of the dietary study indicate that there is no difference in the resources that these habitats provide. Although generally these habitats may not be considered similar, in Thetford Forest, both have sandy soil, contain grasses and various herbs, contain trees with open space

between them and have a source of dung beetles (from grazing animals on the heathland and deer in the forest).

Evidence of moth consumption was found in the majority of nightjar faecal pellets, confirming that moths are an important component of the diet and supporting the results from the nest camera footage, with adult nightjars thought to be taking advantage of the peak in moth abundance during the early stages of the night described by Bowden and Green (1991), at particular nesting stages. Moth biomass in moth traps was found to be greater on warmer nights, again supporting the interpretation of parental non-attendance at the nest, with adults predicted to spend longer searching for prey when temperature were lower.

Using radio telemetry, female birds were found to forage frequently within the nest territory and also in areas outside the territory, with the home range showing a multi-modal structure. Nest camera footage provided evidence of periods of parental non-attendance of varying lengths, which were found to either represent swap-overs between adult birds at the nest or short absences by the female, presumably to forage in the nest territory. The frequency and duration of parental non-attendances at the nest was found to vary with the stage of nesting (eggs, chicks ≤ 3 days or chicks > 3 days) and temperature. Therefore the foraging habitats selected by the female nightjar on a nightly basis may also be dependent on temperature or stage of nesting, with females foraging closer to the nest when temperatures are lower and when they are provisioning chicks.

This confirmation of the need for foraging habitat close to the nest at particular times in the breeding season also provided supporting evidence for the suggested decrease in home range size with an increasing percentage of suitable foraging habitat within a 500m radius buffer of the territory centre.

Review of thesis methods

The nocturnal nightjar can be a difficult species to study and the use of radio telemetry allowed the habitat use of active birds to be investigated. When using radio telemetry, it was important to attempt to gather a large sample of active fixes per bird in order to be able to analyse home range size and composition. This was sometimes difficult due to the short periods of time that the birds were active per night. The use of satellite tags to investigate habitat selection is becoming more common (for example, Kotzerka et al. 2010, Paiva et al. 2010), which allows a much greater number of fixes per animal to be achieved. However, when the fieldwork for this project was

being carried out, the technology for a tag of the correct size and with a suitable battery life did not exist. The size of satellite tags is becoming smaller and the technology more advanced (Vandenabeele et al. 2013), so this may be an option for the future.

The choice of home range analysis was based on the structure of the nightjar telemetry data and the smoothing factor used was decided upon after investigating a variety of possible options. Many studies do not explain reasoning behind the selection of the method for creating home ranges, as reviewed by Laver & Kelly (2008). The choice of smoothing factor is also important and can affect the size and shape of the KDE produced (Worton 1995, Seaman & Powell, 1996). Again, many studies do not specify the smoothing factor, suggesting that some home range analyses may have been carried out without consideration of the methods behind the technique and results may not be a true representation of the home range.

As nightjars feed chicks a saliva enveloped bolus (Cleere and Nurney 2000), the use of faecal pellet dissection was the main option available to investigate the nightjar diet. The extraction of insect DNA from the faecal samples was considered as an alternative, however the process was concluded to be too expensive, time consuming and unfortunately beyond the scope of this study. Although insect fragments were often highly fragmented, preventing identification, the method of counting moth scales allowed the biomass of soft bodied moths to be estimated reduced the level of bias that may occur due to differential digestion (Moreby & Stoate 2000). Overall, some very useful results on the nightjar diet were obtained using this method.

The nest cameras provided an opportunity to investigate parental non-attendance at the nest and added additional information in support of the radio telemetry. Cameras did malfunction, were occasionally not placed in the correct position (meaning that the nest could not be viewed clearly) and the sex of the bird at the nest could often not be distinguished. However, camera footage still allowed a detailed exploration of the factors influencing parental non-attendance at the nest and male parental care in the nightjar.

Management recommendations

The results of this thesis demonstrate that gaps in the ecological knowledge of a cryptic, nocturnal species can be filled using a variety of well-documented methods in order to provide an evidence base on habitat use and dietary requirements for conservation practitioners.

Dolman and Morrison (2012) found that the decline in nightjar population in Thetford Forest was proportional to the decline in habitat. Therefore it was important to determine the habitats that nightjars require in a heathland-plantation mosaic and to understand the reasons why birds select these habitats.

Based on the habitat requirements of nesting nightjars, Conway et al. (2007) and Langston et al. (2007b) provide management guidance for the nightjar, with recommendations including further restoration of heathland habitat and ensuring the continuation of a mosaic of growth stages in plantation forest.

This thesis adds to these recommendations by providing information on the key foraging habitats for nightjars and how habitat management can enhance the suitability of a site for the species. The primary management recommendation from this thesis is that results suggest nightjar foraging habitat preferences are based on habitat structure, with birds choosing habitats which enable ease of access to insectivorous prey. Open, early growth stage forest is the preferred foraging habitat for nightjars in plantation forest, with grazed grass heathland providing an additional (similar) foraging resource for the birds. The key habitat components that nightjars require are open ground, to allow 'hawking' for insects and open canopy, which has been suggested to allow birds to see insects against the night sky (Bowden and Green 1991).

The configuration of suitable foraging habitat within the forest landscape may also be important. Results suggest that home range size may decrease with an increasing percentage of suitable foraging in the range, indicating that birds may benefit from having a large area of suitable foraging habitat close to the nest site, resulting in shorter foraging distances and smaller home ranges. A recommendation of 31-39ha of suitable foraging habitat within a 500m radius of the territory centre was made based on results in Chapter 4, (with the caveat that the models results were not strongly supported, therefore further investigation of the optimum area would be beneficial).

Similarly, nest camera data indicated that short parental absences from the nest increase when the temperature is low and/or when birds are provisioning chicks, suggesting the importance of the provision of suitable foraging habitat close to the nest. While it would be difficult to change the layout of plantation forests, due to the long (60-80 years) rotation time of growth stages, it may be feasible to alter the size of particular growth stage plots and to re-create open habitats within the forest as planned and outlined by the Forestry Commission (Driver 2010). The management of these open habitats is important, as results suggested that foraging nightjars

avoided open habitat that was not grazed. Grazing of open habitats within the forest would decrease the height of vegetation making the sites more suitable for foraging nightjar and the dung of grazing animals provides an additional source of nightjar prey.

The extent of clear-felled areas and restocked habitats within forests in the UK has decreased, after a peak in the late 1980s/early 1990s due to storm damage. However, the clear-fell rotation system currently practiced in the majority of Forestry Commission forests provides a steady source of clear-fell and open canopy forest for the nightjar. A movement towards continuous cover forestry (CCF) has been suggested by the Forestry Commission (Mason & Kerr 2004) with a number of sites in north-west England already converted to this alternative management system. If there was a shift in management, it could take 30-40 years for continuous cover forests to become established, however in the long term, it may lead to a reduction in availability of nightjar habitat for both nesting and foraging, depending on the CCF methods used.

This study has indicated that nightjars are opportunistic feeders and previous research has shown that the diet of this species can be varied (Collinge 1920, Schlegel 1967) however results of this study suggest that a source of beetle prey is important for the nightjar as beetles were selected when birds were provisioning older chicks. Potential sources of beetles that were shown to be consumed by nightjars in this study are grass roots (Chinery 2005), recently felled tree stumps (Hedgren 2007) and the dung of grazing animals such as sheep, or deer.

Stump removal has taken place in some areas of Thetford Forest for four decades, to reduce the spread of the root rot fungus *Heterobasidion annosum* (Gibbs et al. 2002). While this process is ceasing in the forest now, the Forestry Commission is reviewing the possibility of stump harvesting as a source of renewable fuel (Forestry Commission 2009). Stump harvesting can negatively affect soil structure and removes a source of deadwood for biodiversity (Moffat et al. 2011). As the results of this thesis suggest that tree stumps are a foraging source for nightjar, this process will also reduce prey abundance for this species.

Future research

There are some areas of the research in this thesis that would benefit from further investigation.

The first key area requiring further work is the interpretation of nightjar census results and the potential for over or under-counting churring males. It is essential to have an accurate estimate of the number of nightjars in the UK, as the population must be monitored effectively to determine if conservation measures are successful and targets are being met. While radio telemetry data

indicated overlap between the territories of churring males (Chapter 3), an estimate of the probability of an observer encountering the same two birds in one territory on one night is needed. This would involve taking a random sample from the data for churring males and recording the location of the males in neighbouring territories, then repeating this process many times, in order to calculate the probability of territory overlap, based on the frequency of two males overlapping in territory.

In addition, further work is needed to determine the distance for which two calls heard separately are counted as two different birds, as the recommended distance varies between studies (Bowden and Green 1991, Bult 2002, Conway et al. 2007) and based on the mean longest distance between churring points for male nightjars in Thetford Forest in this study (533m, ± 220 sd), this may need to be increased when interpreting results of the national survey. Again, this could be done by sampling the male churring data at random, repeatedly, and calculating the probability that if birds were registered as being the same at less than a set distance (for example, 450m), this would result in an over-estimate, and then repeating for a number of other distances (e.g. 300m, 350m). These calculations may be possible with the current churring male data set, however, it would be preferable to obtain a much larger data set of radio tagged males, with consecutive nights of churring locations for each male bird throughout the breeding season. However, as the number of radio tagged males and observers with telemetry equipment is limited by equipment costs and the practicalities of field studies, it may be difficult in practice to collect a larger data set for these investigations.

Lastly, it may improve survey accuracy if observers were given a recommended time period to spend at each potential territory. An appropriate time period could be calculated by spending a number of hours (from sunset until dusk) at each potential site, recording the number of males. This visit could be repeated three times (as for the most recent national survey) (Conway et al. 2007). Then the number of males recorded after e.g. 10, 20, 30 minutes, 1 hour and 2 hours could be calculated for the total number of visits per site. If this was repeated for a large number of territories, this would provide an average for the optimum period of time to spend at territories to ensure that all males were counted. If observers were given a recommended period of time to spend at each territory, the uncertainty associated with potential male territory overlap could be reduced and there would also be time to record detailed behavioural observations on the breeding status of the bird (as discussed in Chapter 3). While this may increase the overall time taken to complete the national survey, it is important to provide as accurate an estimate as possible.

The behavioural study on nest attendance suggested that the habitats around the nest territory may be important for adults making short foraging trips (Chapter 6). It would be useful to investigate the effect of habitat around the nest territory on parental attendance at the nest in more detail. This could be done by calculating the percentages of key foraging habitats within, for example 2km, of the nest territory for all nests with valid camera data ($n=21$). Then the relationship between parental non-attendance at the nest (total per night, number of absences of different lengths per period of the night) and the percentage of key foraging habitat, for example, pre-thicket stage forest or newly planted coupes, could be tested (controlling for the fixed effects of temperature and the stage of nesting, e.g. incubation, provisioning or chick age). Another option would be to use both telemetry and camera data to determine which habitats radio-tagged females are using when they leave the nest for long or short periods. This would provide further information on the importance of habitats close to the nest. This was not possible with the current data set as the sample size of tagged females with cameras at the nest was low and short nest absences recorded by nest cameras were often missed using radio telemetry (Chapter 6). Further investigations could also be made between variations in nest attendance and nest success, for example, if the birds with the highest level of parental non-attendance at the nest also had lower levels of nest success, and how this related to the habitats available within 2km of the nest territory and/or prey availability. Further, to provide more detailed recommendations on the optimal area of suitable foraging habitat close to the nest site, a larger sample size of nightjar home ranges would be required. This would allow a more thorough investigation of the variation in MCP, 95% and 50% kernel home range size with the percentage of available foraging habitat.

Additionally, there are other aspects of nightjar ecology that were beyond the scope of this study but would provide further, useful information for conservation practitioners.

The results of this study have shown the key foraging habitats used by nightjars in the heterogeneous mosaic landscape of Thetford Forest. However, other studies have indicated that nightjars can forage in habitats that birds in this study did not use extensively, for example, deciduous woodland (Alexander & Cresswell 1990) and open oak scrubland (Sierro et al. 2001). It would be useful to compare the diets of birds feeding in these habitats with the diet of the birds in Thetford Forest, to investigate if the birds are feeding on different resources and to determine if there is an optimal nightjar foraging habitat or if diet is similar among all habitats.

Although it was not possible for this study, an examination of the insect DNA in nightjar faecal pellets would provide extremely fine scale information on the diet and indicate if there are any subtle differences in insect species consumed by nightjars in forest and heathland. Clare et al.

(2009) extracted DNA from insect fragments in the guano of the eastern red bat (*Lasiurus borealis*) and identified 127 different prey species (mostly Lepidoptera but also including Coleoptera and Diptera). As bats have similar habits and diet to the nightjar, future investigations could apply such techniques to nightjar faecal pellets.

Compositional analysis of nightjar habitat use at different stages in the breeding season (for example, birds brooding eggs and birds provisioning young) would provide more detailed information on changes in habitat requirements. The sample size for birds at different breeding stages was not large enough to allow this to be done in this study but again, it would be possible and would provide additional useful information for habitat managers.

Lastly, although the nightjars in Thetford Forest have declined due to a lack of suitable habitat, nightjar populations in other areas of the UK are also decreasing (Conway et al. 2007). While possible explanations for these declines in the UK are lack of available prey (Langston et al. 2007b) or recreational disturbance (Langston et al. 2007a), another possible cause is that declines are occurring in nightjar wintering grounds or on migration routes. While nightjars have been recorded wintering in the northern Afrotropics, the eastern half of Southern Africa and a small number in West Africa (Cramp 1985), little is known about the exact location of the wintering grounds of nightjars that breed in the UK. Initial studies are currently being carried out by the BTO in collaboration with Biotrack, using geolocators, which record light levels, to investigate where birds from known populations in the UK are wintering.

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