In Europe, the consequences of commercial plantation management for birds of conservation concern are poorly understood. The European Nightjar *Caprimulgus europaeus* is a species of conservation concern across Europe due to population depletion through habitat loss. Pine plantation-forest is now a key Nightjar nesting habitat, particularly in northwestern Europe, and increased understanding of foraging habitat selection is required. We radiotracked 31 Nightjars in an extensive (185-km²) complex conifer plantation landscape in 2009 and 2010. Home-range 95% kernels for females, paired males and unpaired males were an order of magnitude larger than song territories of paired males, emphasizing the importance of habitats beyond the song territory. Nightjars travelled a mean maximum distance of 747 m from the territory centre each night. Home-range placement relative to landscape composition was examined by compositional analysis. Pre-closure canopy forest (aged 5–10 years) was selected at all scales (MCP, 95% and 50% kernels), with newly planted forest (aged 0–4 years) also selected within 50% kernels. For telemetry fixes relative to habitat composition within 2 km of their territory centre, individuals again selected pre-closure and newly planted forest, and also grazed grass heath. Open ungrazed habitat was not selected, with implications for open habitat planning for biodiversity conservation within public-owned forests. Despite the Nightjars’ selection for younger growth, moth biomass was greater in older forest stands, suggesting that foraging site selection reflects ease of prey capture rather than prey abundance. Within large plantation-forest landscapes, a variety of growth stages is important for this species and our results suggest that grazing of open habitats within and adjacent to forest will additionally benefit the European Nightjar.

**Keywords:** foraging, habitat selection, moths, radiotracking.

Commercial forest management may represent a potential threat to temperate biodiversity, but also may provide opportunities for conservation management (Peterken 1996, Wallace 2011). Forest age structure, structural complexity and the availability of open habitats determine the species and trait composition of invertebrate (Koivula & Niemelä 2003, Pedley et al. 2013) and plant assemblages (Eycott et al. 2006). However, the implications of European forest management for bird assemblages are not well understood, in marked contrast to the robust evidence base regarding the effects of agricultural management and mitigation measures on farmland birds (e.g. Donald et al. 2001). A substantial body of research has examined the effects of area and landscape context on forest bird assemblages (Dolman et al. 2007, Dolman 2012) and avian responses to coppice management in semi-natural deciduous woodlands (e.g. Fuller et al. 2007, Holt et al. 2010). However, within managed coniferous plantation forests, avian responses to landscape composition and stand-level management have received scant attention (but see Donald et al. 1998, Fuller et al. 2007), despite their importance to numerous bird
species of conservation concern, including species otherwise associated with shrubland, heathland or farmland habitats.

During the 20th century, the European Nightjar *Caprimulgus europaeus* suffered a widespread population and range reduction across Europe, primarily due to habitat loss, and was subsequently categorized as a Species of European Conservation Concern (SPEC 2; Burfield & Van Bommel 2004) and protected under Annex 1 of the EC Birds Directive (EC 1979). European Nightjars breed in dwarf-shrub heathland and in pine plantation with sparse tree cover, particularly in northwestern Europe (Tucker et al. 1994); however, the extent to which populations breeding in conifer forests also depend on other foraging habitats in the wider landscape is unclear. Improved understanding of the foraging behaviour of forest-nesting Nightjars, including home-range extent, the relative importance of forest, heathland and other open habitats, and factors driving habitat selection, will provide an evidence basis for conservation management.

Although Nightjar song territories (including the nest-site) in plantation forests have been characterized (Ravenscroft 1989, Scott et al. 1998), home-range extent and habitat use beyond this are less well understood. Nightjars may forage short distances from the nest, particularly when they have eggs or young (Schlegel 1967, Cross et al. 2005), but they have also been recorded foraging an average distance of 3.1 km per night (Alexander & Cresswell 1990). Animal home-range size may vary between sexes due to differences in behaviour (e.g. Cresswell 1990). Improved understanding of the foraging behaviour of forest-nesting Nightjars, including home-range extent, the relative importance of forest, heathland and other open habitats, and factors driving habitat selection, will provide an evidence basis for conservation management.

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Radiotracking studies of Nightjars nesting in plantation-forest have produced contrasting results for habitat selection. Birds left mature coniferous plantations to feed in deciduous woodland in Dorset, UK (Alexander & Cresswell 1990), and selected open oak scrubland in preference to vineyards or dense pine forest in the Swiss Alps (Sierro et al. 2001). In contrast, Nightjars nesting in mixed-age pine plantation foraged in young forest and heathland in East Anglia (Bowden & Green 1991) and in South Wales, UK (Cross et al. 2005), where they also utilized rough pasture. This suggests that Nightjar foraging behaviour may vary depending on the availability of habitats within the landscape and on the age structure of the plantation-forest itself. However, previous Nightjar radiotracking studies were limited by small sample sizes (n = 11 birds, Alexander & Cresswell 1990; n = 3, Sierro et al. 2001) or difficult terrain (Cross et al. 2005).

Nightjar foraging habitat selection may be based on prey abundance, but also the ease of capturing prey (Bowden & Green 1991, Sierro et al. 2001). As moths (Lepidoptera) are a key Nightjar prey (Collinge 1920, Schlegel 1967), examination of moth biomass within different habitats, particularly in plantations of different ages and heathland, would enhance current knowledge of Nightjar habitat requirements. In the UK, where the Open Habitats Policy aims to recreate open areas within existing forest plantation to benefit species, including the Nightjar (FE 2013), a clearer understanding of Nightjar foraging habitat is crucial.

To increase the knowledge base on the importance of management in coniferous plantations for bird species of conservation concern, we radiotracked male and female Nightjars in a complex plantation-forest comprising a mosaic of tree growth stages and patches of heathland in eastern England, UK. We examined home-range extent of females, paired males and unpaired males, distances travelled, and habitat use within the landscape, and used moth trapping to determine the relationship between habitat selection and available prey biomass.

**METHODS**

**Study site**

The study was conducted in Thetford Forest (52°27′N, 0°40′E), the largest lowland commercial forest in the UK, covering 185 km² of Breckland, eastern England (Fig. 1). This region is characterized by a semi-continental climate and sandy soils, and supports many species associated with heathland and ruderal land-uses (Dolman & Sutherland 1992). The forest constitutes part of the Breckland Forest Special Protection Area (SPA), designated under the EC Birds Directive (EC 1979) in 2006 for its internationally important breeding populations of Nightjar and Woodlark.
*Lullula arborea*. Thetford Forest held 349 male Nightjars (c. 10% of the UK population) in 2004 (Conway et al. 2007), representing a decrease from the 1998 total of 420 males (Evans 2002). Numbers have subsequently continued to decline, with 240 males counted in 2010 (Conway & Henderson 2010).

Thetford Forest is divided into discrete management blocks surrounded by predominantly agricultural land and heathland. All designated heathland is grazed by livestock. Additionally, restoration of seven previously forested areas (totalling 300 ha) to grazed heathland began in 2000. Corsican Pine *Pinus nigra* and Scots Pine *Pinus sylvestris* make up 85% of the planted area of the forest (Forestry Commission GIS database). Management by clear-felling (at economic maturity, currently 60–80 years) and replanting of even-aged patches of trees creates a mosaic of growth stages (Eycott et al. 2006). Such contiguous areas of trees planted in a single year are hereafter referred to as stands (mean area 9.0 ha ± 8.6 sd; Dolman & Morrison 2012). Forest growth stages, following Hemami et al. (2004), were classified as: restocked (0–4 years since planting); pre-thicket (5–10 years); thicket (11–20 years); pole (21–44 years); and mature conifer (≥ 45 years; Supporting Information Appendix S1, Table S1).

**Radiotracking**

Nightjars were captured in three areas (Fig. 1), containing similar configurations of habitat, chosen to maximize the number of Nightjars captured and based on areas of suitable nesting habitat and accessibility. Birds were located through initial surveys conducted 1 h before and after sunset during late May 2009 and 2010. Where Nightjars were present, capture was attempted using playback lures (consisting of contact and courtship calls, wing clapping display and male churring) placed at the mid-point of a mist-net. Radiotags (Pip Ag-392, Biotrack, Wareham, UK), with an above-ground detection range of 0.5–1.2 km, were attached to the central tail feather following Bowden and Green (1991). Tags weighed 1.5 g, within the recommended threshold of 2% (Kenward 2001) of adult body-weight (mean = 74.25 g ± 7.14 sd, range = 65–95 g, n = 33). All tagged birds were ringed, and therefore birds were individually recognizable. As females responded less than males to the lure, further attempts were made to catch females in the vicinity of active nests.

Nightjars roost during daylight (Cramp 1985), so to investigate foraging habitat use, tagged Nightjars were tracked from sunset until sunrise between 25 May and 28 August 2009 and 2010 using a Biotrack Sika receiver and three-element Yagi antenna (see Appendix S2, Table S3 for monitoring dates for individuals). Between one and three independent tracking teams of two people each operated each night. Each team tracked one tagged bird per night, with information on the location of other tagged birds in the search area recorded where possible. Birds were tracked using...
the burst sampling method following Barg et al. (2005), with bursts lasting approximately 8 h, from just before individuals became active at sunset (c. 21:00 h) until sunrise (c. 05:00 h) with the last fix taken after the bird was roosting. Fixes were taken every 10 min from sunset to dusk and from dawn to sunrise, and reduced to every 30 min between dusk and dawn, when the birds were generally stationary (with the exception of 30 min between dusk and dawn, when the birds were moving. The bird was sighted or heard). Fluctuations and changes in signal volume indicated that the bird was moving. The bird’s activity was classed as stationary, churring, active or interactive (flying in a group, wing clapping or pursuing another bird; Supporting Information Appendix S2). Fix locations were subsequently determined from bearings using LOCATE III (Pacer Co., Tatamagouche, Nova Scotia, Canada). Tracking error was measured by comparing locations estimated from triangulation (using either two or three bearings) to the known location of stationary tags (n = 32, measured using hand-held GPS with an error < 10 m), held by a colleague at ground level in a variety of forest growth stages (restocked, pre-thicket, thicket, mature; n = 8 per habitat).

Breeding status

Male status (paired or unpaired) was judged using multiple criteria (Supporting Information Appendix S3, Table S4). Although behavioural observations are commonly used to identify the breeding status of male birds (e.g. Van Horn et al. 1995, Guillemain et al. 2003), we acknowledge that some males may have been misclassified or changed status during the season.

Nightjar ranging and habitat use

Both male and female Nightjars spend a large proportion of time stationary near the nest (Cramp 1985). As home-ranges based on all tracking fixes would be defined by the nest-site rather than foraging locations, only active fixes were used in the analysis. Although criticized for failing to describe space utilization within the range (Worton 1987), minimum convex polygons (MCPs) are considered comparable among studies (Kenward 2001). Male song territory MCPs were created using fixes for churring locations. Home-range MCPs were also calculated (n = 29, mean fixes = 37 ± 16 sd, range = 17–72), with three individuals excluded due to an insufficient number of fixes. The kernel density estimator (Worton 1989) is now accepted as a more biologically meaningful method for home-range analysis (Seaman & Powell 1996) and was calculated for females, and paired and unpaired males using fixed kernels based on a constant proportion of $h_{ref}$ for all individuals (Bertrand et al. 1996, Kie et al. 2002, see Appendix S4 Fig. S1). Females were not split by nesting status due to insufficient sample size. Home-range kernels at 95% (outer range) and 50% (core range) were calculated for all birds with at least 27 active positional fixes (n = 19, mean fixes = 44.6 ± 15.6 sd, range = 27–72) following Seaman et al. (1999). MCPs and kernels were produced in ARCGIS 9.2 using Hawth’s Tools and Home-Range Tool (Rodgers & Kie 2011).

Home-ranges analysed in this study were restricted to stable periods for individuals with consistent breeding status. For four male birds that changed from paired to unpaired breeding status during the season, only one song territory and home-range (that with the most fixes) was analysed. Multiple nesting attempts within the original song territory (n = 3, mean distance from previous nest = 88 m ± 76 sd) were included in one home-range. One female moved territory centre by 2161 m after fledging a first brood; two MPCs were created for this individual but insufficient fixes were available to calculate two kernels, and therefore one large kernel was created. Two males that changed breeding status (resulting in insufficient fixes per status class) were excluded from the kernel analysis.

To investigate Nightjar foraging distances, the distance between every active fix and the territory...
centre (roost or nest-site) was calculated using Hawth's Tools with ARCGIS 9.2. Periods of absence (no signal) during tracking were also recorded. The longest distance travelled from the roost/nest per night for each bird was calculated (excluding nights where the bird had no signal for > 10 min). Due to extreme values, both mean and median distances are reported.

**Moth trapping**

To compare biomass of a commonly exploited prey, moths (Collinge 1920, Schlegel 1967), between habitat classes, Heath-type 15-W actinic moth traps (Anglian Lepidopterist Supplies, Hindolveston, UK) 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) between the beginning of June and the end of August in 2009 and 2010 (n = 423 trap-nights).

The attraction radius for actinic traps is low, with few moths recaptured when released more than 40 m away (Truxa & Fiedler 2012), and therefore to sample moths from the target habitat only, traps were placed ≥ 50 m from the stand edge. Traps were positioned at sunset and emptied at sunrise, with moths inside the trap or on the box exterior recorded. Temperature was recorded using data loggers (El-USB-1, Lascar Electronics, Salisbury, UK). In 2009, three loggers (one each in ungrazed grassland, restock and pre-thicket forest) were placed in the central forest block. In 2010, 20 loggers were deployed in three forest blocks, in five habitats, (grass-heath, ungrazed semi-natural grassland, restock, pre-thicket and mature forest; n = 4 per habitat).

As moth abundance in Thetford Forest peaks at dusk (Bowden & Green 1991), the daily time for the end of evening twilight (the final stage of dusk) was obtained from www.timeanddate.com (Norwich, UK) and the mean dusk temperature from all data loggers was used for the nightly temperature. Dry weights of moths collected from each family group were used to determine moth biomass (Supporting Information Appendix S5).

**Statistical analysis**

Song territory size (square root-transformed) was compared between paired and unpaired males using a general linear model (GLM), with male breeding status as a fixed effect, and number of fixes as a covariate. Home-range size (square root-transformed) was compared among females, paired males and unpaired males using a GLM, again controlling for number of fixes as a covariate. Differences among classes were examined using pairwise comparisons of estimated marginal means. GLMs were conducted in PASW STATISTICS v. 17.0.3 (SPSS Inc., Chicago, IL, USA).

Compositional analysis (Aebischer et al. 1993) was used to investigate selection of foraging habitat, initially considering all birds rather than splitting by sex or status, due to limited sample sizes. Habitats within the study area were classified using GIS (Tables S1 and S2). Those with < 2% availability within the study area were excluded (scrub, improved grassland, inaccessible (tourist complex), urban and water), retaining the following for analysis: grazed grass-heath (including heathland within and adjoining the forest, referred to as grass-heath hereafter), ungrazed semi-natural grassland, restocked stands, pre-thicket, thicket, pole stage, mature conifer, arable and mature broad-leaved woodland (broadleaf hereafter).

The female nesting habitat and, for male birds, the primary habitat (> 80%) within the song territory was extracted using GIS. Nightjar foraging habitat selection was investigated at two levels of spatial scale following Johnson (1980): considering home-range placement (MCP, 95%, 50% kernels) relative to habitat available within the study area; and individual fix locations relative to the habitat available to that 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 fixes across individuals from both years (Fig. 1). To encompass habitat that was potentially available to the birds, each study area MCP was buffered by 1.2 km, based on distances travelled by Nightjars in this and previous studies (Alexander & Cresswell 1990, Bowden & Green 1991), resulting in a mean distance from the individual territory centre to the buffered edge of the study area of 1.98 km (± 0.56 sd).

For the second stage of analysis, habitat available to each individual was considered to be that within a fixed radius (2 km) of the territory centre. This was considered preferable to using individual MCPs or kernels, as home-range size varied more than 10-fold among individuals, and as $h_{ref}$
kernel estimators produced multi-modal home-ranges that delineated used habitat and excluded much of the traversed habitat not used for foraging, thus precluding examination of used vs. that available at the scale of the fix. The distance chosen was 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 inaccessible areas.

Hierarchical habitat selection was examined using COMPOS ANALYSIS VERSION 6.2 PLUS (Smith Ecology 2004). 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). 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 randomization. Individuals were weighted according to the number of fixes obtained (Aebischer et al. 1993).

As birds were not split by status for the analysis of home-range kernel placement within the study area, two males excluded from the kernel home-range area analysis (due to changed breeding status) were included. When considering individual fixes within a 2-km buffer, four birds were excluded as they had no access to grass-heath and three further birds were excluded as there were insufficient fixes (< 5) to draw meaningful results. As it was difficult to differentiate between male foraging activity and territorial behaviour, the compositional analysis containing all birds may be biased towards habitats within the song territory. Female birds were considered more likely to be foraging when active, due to constraints of incubation and chick-rearing, relative to territorial males, and therefore analyses at scales of MCP placement and individual fixes were repeated using female data only. Analysis of female kernel placement relative to available habitat was not possible, as the number of habitats (n = 9) was greater than the number of female kernels (n = 7), violating compositional analysis rules (Aebischer et al. 1993).

Moth biomass (square root-transformed) was compared among habitats using a general linear mixed model (GLMM) with Gaussian errors, including dusk temperature and temperature² as fixed effects, an interaction between habitat type and temperature, and forest stand as a random effect. Model selection was carried out by examining the change in the Akaike information criterion corrected for small sample size (AICc) on each variable removal, following Burnham and Anderson (2002). To investigate the difference in moth biomass among habitat types, we assessed whether 95% confidence intervals of the habitat coefficient estimates overlapped zero, sequentially changing the reference habitat to undertake pair-wise comparisons (following Boughhey et al. 2011). Mixed models were conducted using package lme4 in R (R Development Core Team 2012).

RESULTS

Thirty-six birds were radiotagged, 20 in 2009 (13 males and seven females) and 16 in 2010 (12 males and four females). In 2009, two birds shed their tags and three were lost, leaving a total of 31 (21 males and 10 females) for analysis. No individuals were tracked in both seasons. The total recording effort (duration of nightly fieldwork) was 1518 h. In trials with stationary tags, mean tracking error was 26 m (± 20 sd, range = 2–99 m) and did not differ with bearing number ($F_{1,56} = 0.317, P = 0.576$) or forest growth stage ($F_{3,56} = 1.237, P = 0.305$). This error may vary depending on the distance and activity of the bird (Supporting Information Appendix S2). Of the tagged males, 11 were initially paired and 10 were considered to be unpaired, with four of the paired males becoming unpaired during the season. Two of the eight unpaired males included in the analysis had extensive song territories, with one bird recorded churring 3.6 km from the territory centre (on one occasion) and a second bird increasing the size of its song territory (fourfold) towards the latter half of the breeding season. Two females moved territory after the fledging (2161 m) or failure (819 m) of the first nest, the latter before regular radiotracking began.

Song territory size did not differ between paired males and those considered unpaired (Fig. 2a) and was positively related to the number of fixes ($F_{1,16} = 5.2, P = 0.03$). Home-range area for MCPs, and 95% and 50% kernels increased with the number of fixes ($F_{1,25} = 8.9, P < 0.01$, $F_{1,15} = 12.5, P < 0.01$, $F_{1,15} = 14.6, P < 0.01$, $F_{1,15} = 14.6, P < 0.01$).
respectively). Controlling for fix number, home-range MCP and 95% kernels for males were an order of magnitude larger than the song territories of paired males (Fig. 2b,c). Females 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. 2). Home-range size (MCP and kernels) for unpaired males was intermediate and did not differ from female or paired male ranges (Fig. 2b–d). While the 50% kernel for all birds included the nest/song territory, females had multi-modal 50% kernels and paired males tended to have one central 50% range within the song territory (Appendix S4, Fig. S1).

Figure 2. Mean area used by Nightjars in Thetford Forest, showing (a) song territory MCP for paired males (n = 11) and unpaired males (n = 8); (b) home-range MCP for females (n = 11), paired males (n = 10) and unpaired males (n = 8); (c) 95% kernel and (d) 50% kernel for females (n = 7), paired males (n = 7) and unpaired males (n = 5). Model-derived means are back transformed from square root-transformed data. Error bars represent 95% confidence intervals. Within each plot, classes sharing a lowercase letter do not differ significantly (P > 0.05).

Habitat selection

Nest and song territories were recorded in pre-thicket (n = 15 birds), restocked (n = 9) and thicket (n = 5) habitats. For home-range MCPs, relative to availability in the study area, pre-thicket plantation had the highest habitat preference index and was used significantly more than grass-heath, ungrazed grassland, arable, broadleaf and restocked stands. No significant difference was found among pre-thicket, mature, pole and thicket forest stages (Fig. 3a). For 95% kernels, pre-thicket was again ranked the most selected, with no significant difference among the forest habitats (except for mature). However, pre-thicket was used significantly more than grass-heath, ungrazed grassland, arable and broadleaf (Fig. 3b). Within the 50% core range, pre-thicket was the most selected, followed by restocked stands, with ungrazed grassland, arable and broadleaf being the least selected (Fig. 3c). For habitat use at individual fixes within the 2-km buf-
fer, pre-thicket, restocked and grass-heath were selected (no significant difference among these); there was no difference between ungrazed grassland, pole, thicket and mature, with arable and broadleaf ranked as the least selected (Fig. 3d).

Compositional analysis restricted solely to females showed a similar pattern of habitat selection (Fig. 3a,d), with pre-thicket the most strongly selected at all stages of analysis. However, low sample size resulted in fewer significant differences among habitats.

**Moth biomass among habitats**

Moth biomass in old trees was more than double that of young forest (both pre-thicket and restock) and ungrazed open habitats, whereas biomass in grass-heath sites did not differ from that in either old trees or young forest (Fig. 4). More moth biomass was captured on warmer nights ($\Delta$AICc for model lacking temperature and temperature$^2 = 246$). Old stands had greater moth biomass than other habitats on nights with low temperatures ($\Delta$AICc for model lacking the interaction between habitat and temperature = 8).

**DISCUSSION**

The home-range of European Nightjars in mixed plantation was an order of magnitude larger than the song territories of paired males. However, the mean recorded maximum foraging distances per night were shorter than those recorded in other
UK Nightjar populations. Results show that a complex forest landscape can provide the Nightjar with habitat for both nesting and foraging, and that the outcomes of this study can be used to inform habitat management.

**Nightjar ranging behaviour**

The home-ranges in this study were based on active fixes, with the majority assumed to represent foraging. However, social contact may have also influenced ranging behaviour. These activities may not be mutually exclusive, however, with territorial males recorded occupying the song territory all night, only making short flights between churring posts, and thus birds were presumed to be foraging while defending the territory. Although song territory size did not differ between paired and unpaired males, two (of eight) unpaired males were recorded churring outside the song territory towards the end of the season. Thus, although unpaired Nightjars hold a territory, they may leave or extend their song territory as the season progresses, as do Nightingales *Luscinia megarhynchos* (Amrhein et al. 2007).

The larger size of the home-ranges confirmed that Nightjars were leaving the song territory, presumably to forage. Females’ 95% home-range kernels were larger than those of paired males, with wide-ranging active fixes, which may represent travel to optimal foraging grounds. One female had a large kernel primarily as a result of moving to a new territory. Cresswell and Alexander (1990) document a case of a female Nightjar swapping partners between nesting attempts, so mate prospecting may account for some of the outer home-range points of other females. Whereas female 50% kernels were large due to their multimodal structure, for paired males the core (50%) area was centred on the song territory. It may be that while a priority for the male is to guard the territory, for females it is to find optimal foraging sites. Unpaired males defended a territory but ranged 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, suggesting that Nightjars in plantation-forest may choose a territory based on its suitability for both nesting and foraging.

Whereas Alexander and Cresswell (1990) recorded a mean maximum distance per night of 3.1 km ± 1.2, the mean maximum distance for Nightjars in Thetford Forest was 747 m ± 513 sd. Due to challenges of relocating birds within the forest and surrounding landscape when their position was unknown, birds were recorded as out of range for > 10 min at 10% of attempted active fixes, and on 34% of tracking nights. Such points may have been external to the forest, but were mostly related to unpaired males and two females (one after moving nest territory, another after the failure of the second nest); these birds may not have been solely foraging. Although these absences must be taken into consideration, Nightjars nesting in mixed pine-plantation were not found to leave coniferous forest on the majority of foraging trips, in contrast to patterns found in other populations (Alexander & Cresswell 1990, Sierro et al. 2001).

**Nightjar habitat selection**

For the placement of MCPs within the study area, there was no significant difference in habitat selection among pre-thicket, thicket, mature and pole stage forest. However, this may be because MCPs included areas alongside or between key habitats. Similarly, when 95% kernels were considered relative to the study area, there was no significant difference among the majority of forest growth stages. As the forest contains a mosaic of growth

![Figure 4. Model-derived mean moth biomass in different habitats.](image-url)
stages and kernels represent the likelihood of locating the bird 95% of the time (birds were recorded active at least once in all forest growth stages), it may have been difficult to distinguish between forest habitats at this level of analysis.

Pre-thicket stage forest was found to be the most strongly selected habitat for all stages of compositional analysis, with restock also selected within 50% kernels, relative to the study area. The key foraging habitats in this study are similar to preferred Nightjar song territory habitats (young forest aged 0–10 years, e.g. Ravenscroft 1989). The majority of territories (nest and song) in the current study were based in restocked and particularly pre-thicket habitats and it was difficult to separate foraging and male territorial activity. It is therefore possible that the compositional analysis including all birds may be biased by song territory location. However, when the females were off the nest and more likely to be foraging (compared with male birds), they showed similar habitat selection.

Nightjars selected grazed grass-heath (relative to availability) when available within a 2-km radius. Livestock dung in grazed habitats may provide beetle prey for Nightjars (Schlegel 1967). In contrast, ungrazed grassland was one of the least selected habitats. Similarly, Alexander and Cresswell (1990) recorded foraging Nightjars avoiding ungrazed Calluna-dominated heathlands. Nightjars have been recorded ‘hawk-wing’ for prey (Cramp 1985), which involves swooping for flying insects from (or close to) the ground. This may be more difficult in taller, denser ungrazed grasslands.

Although Nightjars have been found to regularly leave territories within conifer forest to feed in atypical habitats (Alexander & Cresswell 1990, Sierr et al. 2001), those forests were of uniform age and densely planted, in contrast to the mixed-age structure of Thetford Forest. Broadleaf woodland was ranked as one of the least selected habitats in the current study, but was the preferred Nightjar foraging habitat in Dorset, UK (Alexander & Cresswell 1990). This may be because broadleaf patches in Thetford Forest primarily comprise dense mature Sycamore Acer pseudoplatanus or Beech Fagus sylvatica rather than mixed semi-natural deciduous woodland. Overall, results suggest that habitat structure may influence the extent to which Nightjars forage in the wider forest landscape.

Moth biomass in habitats

Nightjars in Thetford Forest were not choosing habitats based solely on moth abundance, as stands containing old trees (pole and mature) had a greater moth biomass than younger stands. Older forest growth stages were found to have relatively greater moth biomass even on cold nights; presumably denser canopy cover kept temperatures higher than in other growth stages. This supports the inference that Nightjars select habitat based on the ease of prey capture rather than abundance, with older forest growth stages avoided due to the difficulty of finding and capturing prey among dense branches (Bowden & Green 1991, Sierr et al. 2001).

Habitats may also be selected due to the abundance of other prey types such as beetles, another key component of the Nightjar diet (Cramp 1985, Sharps 2013). Beetles may be an important prey both in restocked and pre-thicket stands due to the abundance of saproxylic beetles (e.g. Cerambycidae) emerging from cut stumps (Hedgren 2007), and in grazed grass-heath, which supports dung-feeding beetles (Aphodinae; Menéndez & Gutiérrez 1996), although abundant deer populations (Wäber & Dolman 2013) also support dung-feeding beetles in forest habitats (Stewart 2001).

Conservation implications and recommendations

The understanding of European Nightjar habitat use in plantation-forest provided by this study has widespread applications, particularly in northwestern Europe. While Gribble (1983) and Morris et al. (1994) showed the importance of pine plantations to nesting Nightjars, this study demonstrates that mixed-age plantation-forest can provide both nesting and foraging habitat for this species. Nightjars were found to be foraging in forest habitats outside the song territory. Forest-nesting Nightjars would therefore benefit most from a large forest comprising a mosaic of growth stages, for which rotational clear-felling and replanting of large, even-aged stands (rather than group selection) is ideal. The configuration of growth stages within the forest mosaic may also be important for the Nightjar; stands of young forest clustered together would provide female Nightjars with multiple foraging opportunities in close proximity.
The results of this study suggest that the grazing of open habitats is important for foraging Nightjars, whereas creation or retention of ungrazed, unplanted patches within the forest may not be beneficial. The introduction of further patches of grazed heathland reversion within and adjacent to the forest would provide additional foraging resources for Nightjars and benefits for regional biodiversity (Dolman et al. 2012). 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. 2 km.

In summary, this study demonstrates that the management of commercial plantation-forest has important implications for maintaining populations of this species of conservation concern. The creation of a heterogeneous forest mosaic is important for foraging Nightjars, reducing the need for birds to leave the forest to reach suitable foraging habitat and allowing both foraging and nesting habitat for this species to be supported by one land owner/manager.

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**SUPPORTING INFORMATION**

Additional Supporting Information may be found in the online version of this article:

- **Appendix S1.** Habitat classification.
- **Appendix S2.** Radiotracking methodology.
- **Appendix S3.** Male breeding status.
- **Appendix S4.** Nightjar home-range kernels.

- **Appendix S5.** Moth trapping.
- **Table S1.** Classification of forest growth stages.
- **Table S2.** Classification of non-forest habitat.
- **Table S3.** Monitoring information for tagged Nightjars.
- **Table S4.** Male breeding status criteria.
- **Figure S1.** Nightjar home-range kernel density estimates.