Jofré, Gabriela M.; Warn, Mark R.; Reading, Christopher J. 2016. **The role of managed coniferous forest in the conservation of reptiles.**

The role of managed coniferous forest in the conservation of reptiles

Gabriela M. Jofré[a], Mark R. Warn[a] & Christopher J. Reading[b]

[a] Forestry Commission, South England Forest District, The Queen's House, Lyndhurst, Hants, SO43 7NH, UK. gjofre@tiscali.co.uk

Forestry Commission, South England Forest District, The Queen's House, Lyndhurst, Hants, SO43 7NH, UK. Mark.Warn@forestry.gsi.gov.uk

[b] Centre for Ecology & Hydrology, CEH Wallingford, Benson Lane, Crowmarsh Gifford, Wallingford, Oxon, OX10 8BB, UK. cjr@ceh.ac.uk (corresponding author)

Key words: canopy cover; habitat structure; lizard; plantation age; snake

Running page title: The use of managed coniferous forest by reptiles

Abstract Commercially managed coniferous forest is often considered detrimental to wildlife despite their early developmental growth stages being well utilised by some species from a number of different taxa. Our study investigated the use of different aged conifer plantations by reptiles in southern England using arrays of artificial refuges, placed within 20 plantations of varying age, to determine the presence of reptiles annually within each between 2009 and 2013. All six native British reptile species (adder *Vipera berus*, grass snake *Natrix natrix*, smooth snake *Coronella austriaca*, common lizard *Zootoca vivipara*, sand lizard *Lacerta agilis*, slow worm *Anguis fragilis*) occurred in conifer plantations. Excluding the slow worm, which occurred in plantations of all ages, the majority of reptile observations occurred in plantations up to 20 years old and where tree canopy cover was below 65% with the highest numbers occurring in 3-12 year old plantations with a canopy cover below 50%. The early stages of plantation growth are utilised well by reptiles but become increasingly unsuitable over time. Furthermore, the availability of suitable reptile habitat is transient, depending on the rate of tree growth, the timing and extent of tree thinning and felling operations, the size of the plantation units and their proximity to adjacent areas inhabited by reptiles.

Our study shows that coniferous forests can be managed so that both timber production and biodiversity conservation can be achieved through the formation of a mosaic of relatively small, multi-aged plantations and that small changes in ground preparation and habitat management practices may further enhance its suitability for reptiles and, by implication, for species from other taxa. The results of our study also have pertinence for species conservation and biodiversity within similar managed forestry throughout the world.

1. Introduction

Habitat change is the biggest threat to the conservation of many taxa worldwide including herpetofauna (Sala *et al*., 2000; Gardner, Barlow & Peres, 2007; Bohm *et al*., 2013; Reading & Jofré, 2015) with land use practices, including forestry, agriculture and domestic cattle grazing being some of the main drivers of this change (Lindenmayer & Fisher, 2006; Gardner, Barlow & Peres, 2007). Over the last 250 years the lowland heaths of southern England, the premier habitat for reptiles in the UK that supports all six native species (Jofré & Reading, 2012), have decreased significantly in area due mainly to fragmentation, the subsequent development of the resulting small fragments, and the loss of large areas to commercial forestry (Rose *et al*., 2000).

During the 20th century an increasing demand for timber led to a massive increase in the area of plantation woodland in Britain, including the planting of new coniferous plantations on open land such as heathland, dunes and moorland (Donald *et al*., 1998). In addition, much of the early planting of forests was in large, single-species, even-aged blocks of fast growing and mainly non-native conifers (Donald *et al*., 1998). However, by the end of the last century substantial changes were introduced into UK forestry policy and practices with biodiversity conservation becoming an important objective (Quine, Humphrey & Watts, 2004). Significant progress has been made since then in restoring habitats, where afforestation was considered inappropriate, and in restructuring some of the largest commercial forests by creating more heterogeneity in terms of the size, shape and age structure of forest compartments in order to increase and improve their perceived habitat conservation value (Donald *et al*., 1998). Unfortunately this change has occurred in the absence of a recognised need for detailed research into the specific habitat requirements of many species of conservation interest (Quine, Humphrey & Watts, 2004). As a consequence there remains a common perception that plantation forests are ecological deserts that do not provide habitat for valued organisms (Brockerhoff *et al*. 2008) despite assemblages of open-habitat taxa occurring in clear-felled and young pine stands worldwide (Barbaro *et al*., 2005; Wright *et al*., 2007; Wilson *et al*., 2009; Uribe & Estades, 2014; Calladine *et al*., 2015; Sharps *et al*., 2015).

Within the UK the habitat requirements of native reptile species, all of which also occur throughout Europe, occurring on lowland heathland (adder *Vipera berus* (L.), grass snake *Natrix natrix* (L.), smooth snake *Coronella austriaca* (Laurenti), common lizard *Zootoca vivipara* (Jacquin), sand lizard *Lacerta agilis* (L.) and slow worm *Anguis fragilis* (L.)) are relatively well known (Frazer, 1983; House & Spellerberg, 1983; Reading & Jofré, 2015; Reading & Jofré, *In Press*) and show that they all have a preference for a well-structured habitat (Spellerberg & Phelps, 1977; Edgar, Foster & Baker, 2010; Reading & Jofré, 2009; Reading & Jofré, 2015; Reading & Jofré, *In Press*) that meets their thermal requirements, offers foraging opportunities, and shelter (Spellerberg & Phelps, 1977; Edgar, Foster & Baker, 2010). Of these the sand lizard and smooth snake, both European protected species (EPS), are at the north-western edge of their geographical range and are heathland specialists in the UK.

Despite this, the use of conifer plantations by reptiles, during the different stages of the complete cycle of a commercial rotation (planting, thinning and final harvesting), has not previously been studied in the UK. The objective of this study was, therefore, to investigate how conifer plantations of different ages are used by the six native UK reptile species and how this use may change over time and provide insight for the conservation of species from other taxa that occur in managed forest worldwide.

2. Methods

2.1 *Study area and management*

This study was carried out between January 2009 and December 2013 in Wareham Forest (50^{o}44′N, 2^{o}08′W), a coniferous forest planted on lowland heathland, over tertiary deposits of acid sands and gravels (Mann & Putman, 1989), in southern England by the Forestry Commission. The forest is managed on rotation, with trees clear-felled at about 60 years, maintaining a mosaic of clear fell, tree stands of varying ages, open heath and permanent open ground. Some trees stands older than 60 years are kept to maintain a mosaic landscape design and to increase the amount of available dead wood habitat. The primary tree species is Corsican pine *Pinus nigra* (Melville). Sapling pine trees are planted, approximately 1.8m apart, in late winter/early spring one year after clear-felling plantations of mature trees, preparing the ground using a powered scarifier during the previous winter and sometimes spraying with herbicide. Following planting, the early years (≈0-12 years old) of forest growth are described in forestry as the 'pre-thicket' stage. During the following 'thicket stage' (≈10-30 years old), the trees form an increasingly dense canopy preventing most light from reaching the forest floor, resulting in an almost total absence of ground flora. Plantations are thinned for the first time after 25-30 years, by approximately 40%, and subsequently every five years. The 'high forest' stage (≈30-70 years old) results in a higher, often more open, canopy allowing more light to reach the forest floor and the re-establishment of some ground flora. This is most marked at the forest edge.

The ground flora growing within the plantations, and the area surrounding them, is that characteristic of dry and wet lowland heath communities comprising common heather *Calluna vulgaris* (L.), bell heather *Erica cinerea* (L.), cross-leaved heath *Erica tetralix* (L.), purple moor grass *Molinea caerulea* (L.) and bristle bent *Agrostis curtisii* (Kerguelen) as the dominant species. Dwarf gorse *Ullex minor* (Roth) and bracken *Pteridium aquilinum* (L.) are also common within the plantations.

2.2 *Project set-up*

In December 2008 twenty pine plantations of different ages were selected within Wareham forest (Fig. 1), and grouped into four broad age classes with five plantations in each: **Sites A:** planted between 1930 and 1966 (1A, 2A, 3A, 4A, 6A); **Sites B**: planted between 1975 and 1987 (2B, 3B, 5B, 6B, 7B); **Sites C**: planted in 1994 (4C, 6C1, 6C2) and 2001 (3C, 5C) and **Sites D:** planted in 2003 (4D) and 2006 (1D, 2D, 6D, 7D). The area of individual plantations, that included the 20 study sites, ranged between 0.61-10.45ha (mean=4.23ha; SD=2.671; n=20). Five plantations within each plantation age class category were selected to include a range of aspect and lowland heath plant communities that all provided potential habitat for reptiles.

2.3 *Reptile surveys*

An array of artificial reptile refuges (corrugated steel sheet measuring 92cm x 73cm) was laid out in each of the 20 selected sites with each array consisting of a hexagonal pattern of 37 refuges, spaced 10m apart, and covering an area of 0.29 hectares (Reading, 1997). Refuges were individually numbered for reptile capture mapping purposes.

Sixteen reptile surveys were carried out annually (2009-2013), between the last week of April and the second week of October. Surveys were spaced at least one week apart to allow animals to change location and to avoid auto-correlation within the dataset (Swihart & Slade, 1985). During each survey all 20 arrays were visited and each refuge in each array was checked for reptiles by following a transect walk that visited each refuge in turn. All reptiles found on/under refuges, and seen within the array while walking between refuges, were identified and recorded. All captured snakes were individually marked with a pit-tag to provide individual recognition if recaptured.

2.4 *Array characteristics: tree canopy cover*

A Model ‘A’ spherical densitometer (canopy mirror: Lemmon, 1956) was used in each array to estimate percent tree canopy cover once each year between 2009 and 2013. Measurements were made from ground level at five fixed points corresponding to the centre of each array and each of the four cardinal points relative to the central refuge and at the edge of the array. The location pattern of the fixed points within each array was the same for all arrays. Four readings of the canopy cover, corresponding to each cardinal point, were made at each of the five fixed points giving a mean value for each from which an overall mean canopy cover for each array was estimated.

2.5 *Array characteristics: ground vegetation cover and height*

Vegetation surveys were completed annually in late summer using a 2m x 2m quadrat at each of 10 fixed locations within each of the 20 refuge arrays. The location pattern of the 10 quadrats within each array was the same for all arrays. The height and depth of live vascular plants, moss and litter and the percent cover of these and of bare ground were measured in each of the 200 fixed vegetation quadrats. All heights and depths were measured using a one metre rule and up to 12 measurements were taken for each plant species, in each quadrat, depending on its abundance. Since the vegetation cover, moss and litter layers overlapped vertically in many arrays the values for the total cover within these arrays exceeded 100%.

2.6 *Data analysis*

Data for the occurrence of each reptile species within each plantation were analysed against plantation age category. Bartlett's square root transformation was used to normalise the data for the total number of captures of each species, and the total number of individuals for the two snake species (Zar, 2010) and a one-way ANOVA was performed on the transformed data. Post hoc Tukey test was used to determine differences between reptile numbers and plantation age categories. Regression analysis was used to show trends in the relationships between canopy cover, mean ground vegetation cover and each ground cover plant species (including grass litter), against plantation age. Student's t-test was used to compare means.

The degree to which grass snakes and smooth snakes were 'residents', rather than 'transients', within the arrays was evaluated by comparing the mean annual number of captures of each individual within each array. All statistical tests were considered significant at $P<0.05$ and all statistical analyses were completed using Minitab 16 (Minitab, 2010).

3. Results

3.1 *Plantation ground cover*

The vegetation ground cover occurring within the sites varied in species composition and in structure (a combination of plant height and cover), both within sites included in the same age class category and between sites included in different age class categories (Table 1). Ground vegetation cover increased with plantation age reaching maximum values at 12 years (sites C) whilst ground cover by dead pine needles was greatest in sites B and the extent of bare ground greatest in sites D.

3.2 *Relationships between plantation age, tree canopy cover and ground vegetation cover*

During the first 10-12 years following the planting of pine saplings both tree canopy cover and ground vegetation cover increased (Fig. 2). In 11-13 year-old plantations, open habitat plant species, such as the heathers and gorse, started to decline and die whereas shade tolerant species, such as bracken *P. aquilinum* became dominant, even in closed canopy plantations, shading the ground even more. Tree canopy cover reached maximum values of about 90% in 20-30 year-old plantations (sites B) resulting in an almost total absence of heather in all sites, and of ground vegetation cover in some. In plantations older than 30 years, where tree thinning operations and storm damage had reduced canopy cover, allowing more light penetration, ground vegetation (e.g. heathers and grasses) started to reappear (Table 1).

As plantation age increased the height of the main ground cover plant species varied with that of the woody perennial plants, heathers (*C. vulgaris*, *E. cinerea* and *E. tetralix*) and gorse (*U. minor*) increasing rapidly over the first 10-12 years (sites D and C), shown by the a positive regression slope, before declining rapidly over the following 10-12 years (sites C), shown by a negative regression slope (Table 2). Once established within a plantation the height of these species was lowest in sites B, the densest of the plantations, and then started to slowly increase in the older plantations, after tree thinning had occurred, though subsequent heights did not approach those reached in sites C (Fig. 3). Although a similar pattern of changing plant height was also evident in bracken *P. aquilinum* the peak in its height was attained after about 18 years before declining to a minimum in 26-30 year old plantations. Gorse *U. minor* was not found in the oldest plantations. The pattern of change in height of these species was similar to that found for overall ground cover (Fig. 2) with the combination of these two aspects describing changes in habitat structure in the different aged plantations. The highest structural complexity occurring when both ground cover and plant heights were highest (sites C) and the lowest when both of these components were also lowest (sites B). The two grass species (*M. caerulea* and *A. curtisii*) and bracken *P. aquilinum*, though perennial, all died back during the late autumn, providing a layer of dead grass leaves and bracken fronds, before growing back the following spring providing additional layers that contributed to the overall structural complexity of the habitat.

3.3 *Habitat use by reptiles*

Although all six native British reptile species (adder *V. berus*; grass snake *N. natrix*; smooth snake *C. austriaca*; common lizard *Z.* vivipara; sand lizard *L. agilis*; slow worm *A. fragilis*) were observed annually the occurrence of adders was too low (23 individuals over the 5 years) to enable reliable analysis of their use of plantations. Data analysis was therefore restricted to the remaining five reptile species.

3.3.1 Smooth snake (C. austriaca)

Although smooth snakes occurred in all pine plantations with a mean tree canopy cover below 65% (Fig. 4a) they occurred first in the youngest plantations (sites D) with little or no tree canopy cover. Overall, significantly more captures (t=6.46; P<0.001; df=48) occurred in plantations with a tree canopy cover lower than 65% (mean=9.6; SD=10.20; n=49) than in those with a canopy cover greater than 65% (mean=0.14; SD=0.60; n=51). Similarly significantly more (t=6.97; P<0.001; df=49) individuals occurred in sites with a tree canopy cover below 65% (mean=4.5; SD=4.37; n=49) than above (mean=0.12; SD=0.47; n=51; Fig.5a).

There were significant differences between the numbers of smooth snake captures occurring in the different plantation age categories ($F_{3,96}$=15.91; P<0.001; r^2=33.21%) with categories A (mean=0.6; *SD*=0.22; *n*=25) and B (mean=0.03; *SD*=0.49; *n*=25) having significantly fewer captures than categories C (mean=6.5; *SD*=2.27; *n*=25) and D (mean=5.9; *SD*=2.21; *n*=25). As with captures there were also significant differences between the number of individual smooth snakes captured in the different plantation age categories ($F_{3,96}$=19.08; P<0.001; r^2=37.35%) with categories A (mean=0.4; *SD*=0.25; *n*=25) and B (mean=0.03; *SD*=0.49; *n*=25) having significantly fewer captures than categories C (mean=3.1; *SD*=0.14; *n*=25) and D (mean=3.5; *SD*=0.80; *n*=25).

Although smooth snakes occurred mainly in plantations younger than 20 years old (sites C and D; Fig. 4b and 5b) the highest number of captures, and individuals, occurred in 5-12 year old plantations (sites 4D, 6D, 3C, 5C) which were characterised by having a dense ground vegetation cover (cover range: 34.0-76.3%; Table 1) of relatively tall heather plants (height range: 24.7-52.7cm; Fig. 3). Maximum numbers of smooth snake captures and individuals occurred in an 8 year old plantation (site 4D) where heather *C. vulgaris* cover was relatively high (71.7%).

With the exception of an atypical open canopy mature plantation (site 3A: 55-59 years old) located adjacent to open heathland, and a single capture in a recently opened ride in a site B plantation, smooth snakes were absent from all plantations greater than 20 years old (sites A, B).

3.3.2 Grass snake (N. natrix)

Grass snake captures occurred first in new plantations with minimal tree canopy cover and numbers peaked in 4 year old plantations with a mean canopy cover of approximately 2% (Fig.

4c). Overall, significantly more captures (*t*=6.53; *P*<0.001; *df*=50) occurred in plantations with a tree canopy cover below 65% (mean=3.1; *SD*=2.97; *n*=49) than above 65% (mean=0.3; *SD*=0.49; *n*=51). There were also significantly more individuals (*t*=5.96; *P*<0.001; *df*=51) captured in plantations with tree canopy cover below 65% (mean=2.5; *SD*=2.61; *n*=49) than above (mean=0.3; *SD*=0.48; *n*=51; Fig. 5c).

There were significant differences between the numbers of grass snake captures occurring in the different plantation age categories ($F_{3,96}$=21.06; *P*<0.001; r^2=39.70%) with categories A (mean=0.4; *SD*=0.30; *n*=25) and B (mean=0.16; *SD*=0.46; *n*=25) having significantly fewer captures than category C (mean=1.6; *SD*=0.11; *n*=25) and category C having fewer captures than category D (mean=3.3; *SD*=0.11; *n*=25). As with captures there were also significant differences between the number of individual grass snakes captured in the different plantation age categories ($F_{3,96}$=20.43; *P*<0.001; r^2=38.97%) with categories A (mean=0.3; *SD*=0.39; *n*=25) and B (mean=0.2; *SD*=0.46; *n*=25) having significantly fewer individuals than category C (mean=1.2; *SD*=0.20; *n*=25), and category C having fewer individuals than category D (mean=2.8; *SD*=0.06; *n*=25).

Although grass snakes were observed in plantations of all ages most captures and the highest number of individuals were recorded in 4-10 year old plantations (Fig. 4d, 5d).

3.3.3 Slow-worm (A. fragilis)

There were no significant differences ($F_{3,96}$=1.26; *P*=0.291; r^2=3.80%) between any of the plantation age categories and the number of slow worm captures (A: mean=41.3; *SD*=7.19; *n*=25; B: mean=28.6; *SD*=1.54; *n*=25; C: mean=32.2; *SD*=3.89; *n*=25; D: mean=27.6; *SD*=7.47; *n*=25). Slow worms were recorded from both open and closed canopy cover plantations (Fig. 6a) of all ages (Fig. 6b). However, the number of captures was slightly lower in most of the category B plantations and in one category A plantation, all of which had canopy cover values between 70-90% and where ground vegetation cover was minimal (Table 1).

3.3.4 Common lizard (Z. vivipara)

Although the number of common lizard captures did not differ significantly between plantation categories A (mean=2.3; *SD*=0.77; *n*=25), B (mean=0.7; *SD*=0.29; *n*=25) and C (mean=2.2; *SD*=1.74; *n*=25) significantly more did occur in category D (mean=17.8; *SD*=1.91; *n*=25) plantations ($F_{3,96}$=33.60; *P*<0.001; r^2=51.22%). However, most common lizard sightings were recorded from 3-12 year old plantations (sites D and some sites C) characterised by having low tree canopy cover (Fig. 6c and 6d). The number of observations peaked in two 6 year old plantations (sites 2D, 7D) where tree canopy cover was below 5 %, dead grass cover was the highest, and where the dominant ground cover species were heather and purple moor grass *M. caerulea* (23.4% and 42.9% respectively; Table 1). There were significant differences (*t*=6.69; *P*<0.001; *df*=30) in the number of captures occurring in plantations with a tree canopy cover below (mean=19.7; *SD*=14.40; *n*=30) and above 30% (mean=1.9; *SD*=3.44; *n*=70). Where common lizards occurred in plantations with a tree canopy cover above this value (sites 2A, 3A) they were always found associated with a high ground cover of purple moor grass *M. caerulea* (89.6% and 47.2% respectively; Table 1) and under gaps in the canopy.

3.3.5 Sand lizard (L. agilis)

There were significant differences between the number of sand lizard captures occurring in the different plantation age categories ($F_{3,96}$=31.22; *P*<0.001; r^2=49.38%) with the lowest numbers present in category A and B plantations and the highest in category D plantations. The number of captures in category C plantations (mean=1.5; *SD*=0.11; *n*=25) was significantly lower than category D plantations (mean=6.0; *SD*=0.78; *n*=25) and higher than category B plantations (mean=0.1; *SD*=0.47; *n*=25) but overlapped with category A plantations (mean=0.4; *SD*=0.36; *n*=25).

Significantly more (*t*=5.09; *P*<0.001; *df*=28) sand lizards captures occurred in plantations with a canopy cover below 25% (mean=7.2; *SD*=6.96; *n*=29) than above 25% (mean=0.6; *SD*=1.08; *n*=71). The majority of sand lizard observations were from 3-10 year old plantations (sites D), characterised by having relatively large areas of bare ground (17-38%; Table 1) and tree canopy cover below 25% (Fig. 6e). Although the number of captures peaked in a 4 year old plantation (Fig. 6f) most occurred in sites with a tree canopy cover below about 5%. In plantations with a canopy cover greater than 25% sightings were rare and always located close to plantation edges, in clearings or areas below gaps in the canopy.

3.4 *Snake captures vs individuals*

In all years the mean number of captures of individual grass snakes was significantly lower than that of smooth snakes (Table 3). There was no significant difference (*P*>0.05) between years in the mean number of captures/individual for grass snakes whilst that of smooth snakes increased significantly (*t*=-2.07, *P*=0.043, *df*=55) between 2009 and 2010 with no significant differences (*P*>0.05) thereafter.

Overall, only 9.9% of individual grass snakes were captured more than once compared to 46.0% of smooth snakes. The proportion of grass snake and smooth snake individuals captured more than twice was 1.6% and 26.2% respectively.

4. Discussion

The results of our study show that in plantations with trees that were too small to noticeably affect the re-establishment and growth of ground vegetation, both in terms of percent ground cover and plant height, each reptile species was found associated with heathland plant communities providing the same, or similar, structural attributes to those occurring on open heath (Spellerberg, 1975; Frazer, 1983; House & Spellerberg, 1983; Reading & Jofré, 2015; Reading & Jofré, *In Press*).

The importance of habitat structure for many reptile species is well documented (Martín & López, 2002; Amo, López & Martín, 2007; Garden *et al*., 2007; Palacios, Agüero & Simonetti, 2013; Reading & Jofré, 2015; Reading & Jofré, *In Press*) and has been demonstrated to be an important determinant of reptile survivorship (Bock, Smith & Bock, 1990), making such dependent species vulnerable to changes in the structure of vegetation ground cover (Amo, López & Martín, 2007). In Wareham Forest ground vegetation reached its maximum cover and structural complexity in 12-13 year old plantations after which it started to decline as tree canopy cover increased and gradually closed over, reducing the levels of light reaching the ground. Experimental research has shown that shade not only has a profound effect on the growth and morphology of heather *C. vulgaris* (Iason & Hester, 1993) but also appears to be a major factor leading to the death of heather plants growing beneath a developing tree canopy (Hester, 1987) with other factors, such as competition for water and nutrients also playing an important role (Jameson, 1967). This would explain our finding that the lowest structural complexity of the ground vegetation was found in closed canopy plantations, where most of the vascular plants had died back.

Although planted conifer forest, established on native open areas, such as heathland, are often regarded as particularly detrimental for 'valued wildlife' (Brockerhoff *et al*., 2008), the creation of early successional habitat, through clear-felling, appears to benefit reptiles

(Campbell & Christman, 1982; Greenberg, Neary & Harris, 1994; Todd & Andrews, 2008). The results of our study support this view. Within Wareham Forest all the plantations younger than 20 years old appeared to provide suitable habitat for reptile species (grass snake, smooth snake, common lizard sand lizard and slow worm) which occur on open lowland heath. In addition, forest racks, rides, areas located under canopy gaps and low tree density plantations older than 20 years, provide ephemeral patches of suitable reptile habitat (Dent & Spellerberg, 1988; Greenberg, 2001) which, although they appear to support only relatively low numbers of reptiles compared to younger plantations, may nevertheless act as corridors along which reptiles can access new areas. Thus, within a commercially managed coniferous forest, the length of time over which new plantations can provide suitable reptile habitat will be restricted to a period of approximately 15-20 years and will depend on soil conditions, topography and aspect, that may impact tree growth rates, thereby affecting the time taken for canopy cover to cause ground vegetation die-back.

However, with respect to the grass snake and smooth snake, for which individual based data were collected, their use of the plantations differed. Although grass snakes appeared to be transient visitors within individual plantations, some of the smooth snakes could be considered to be residents, as determined by the number of times individuals of each species were recaptured in particular plantations. This is not surprising given the ranging behaviour characteristic of the two species. Grass snakes are not heathland specialists and have large home ranges (Reading & Jofré, 2009) whilst smooth snakes are heathland specialists, in the UK, and have small home ranges (Reading, 2012).

The annual numbers of smooth snake captures recorded from plantations were similar to numbers found in identical sized arrays used in a study of reptiles on open heath, within Wareham Forest, between 2010 and 2013, once the difference in the annual number of surveys used in the two studies was allowed for (Reading & Jofré, 2015). The numbers of grass snake, common lizard and sand lizard were, however, higher in the plantations than on the open heath whilst the number of slow worm sightings was lower (Reading & Jofré, *In Press*). This suggests that the young plantations are potentially as attractive to most reptile species as the open heath though the open heath had been subject to cattle grazing for 13 years up to 2009 and this may have adversely affected reptile numbers (Reading & Jofré, 2015; Reading & Jofré, *In Press*).

The management of Wareham Forest has resulted in a changing mosaic of both suitable and unsuitable habitats for reptiles. The availability of suitable habitats is transient and depends not only on tree growth rate but also on forestry management practice (e.g. the timing of first thinning) that allows developing plantations to remain undisturbed for approximately 25 years. It also depends on the size and proximity of mature plantations, which will be clear-felled and subsequently replanted, to younger maturing plantations which are declining in their suitability as reptile habitats and which can act as source populations for the recolonization of the replanted ones by reptiles, and other species. As long as the conservation of the appropriate habitat-based biodiversity continues to be an important objective guiding forestry management practice, resulting in a continued maintenance of a heterogeneous mosaic of relatively small plantations of different ages interconnected by heathland forest rides, lowland heathland reptiles will be able to use such managed forests in addition to their natural habitat.

It may be argued that the length of time over which plantations can provide suitable habitat for reptiles could be lengthened if tree thinning were to occur after about 12-15 years, thereby reducing tree canopy cover and extending the period over which ground vegetation cover could persist. We reject this argument on economic, silviculture and reptile conservation grounds. Planted forests are grown for commercial reasons with the thinning of young trees likely to result in poor timber quality and reduced profitability. Early thinning is therefore likely to be resisted by foresters on both economic and silvicultural grounds. In addition, the use of heavy tree felling machinery to thin and remove trees, in areas known to be inhabited by reptiles, would inevitably result in significant habitat damage and potentially cause direct harm to them whilst coincidentally contravening the current legal guidelines concerning the two European protected species (sand lizard *L. agilis* and smooth snake *C. austriaca*).

Although our study investigated reptile habitat use during the spring and summer months, and as a consequence provided no data about their hibernation site preferences, it did show that common lizards and sand lizards moved into very young plantations and may, therefore, hibernate in them. This suggests that it would be best if the ground in clear-felled plantations were prepared for replanting almost immediately following tree removal, or during the following winter, in order to minimise the chance of reptiles recolonizing these areas before ground preparation practices commence.

Potential threats to the continued long-term success of managing a coniferous forest that sustains reptile populations, and other taxa by implication, if too long a period is left between clear-felling and replanting, are the use of herbicides (Uribe & Estades, 2014) and changes in silviculture establishment practices that increase the risk of harming hibernating reptiles or those sheltering below ground. Following scarification, and in the absence of herbicides, remnants of vegetation remain that enable a more rapid return to a well-structured heathland habitat suitable for colonisation by reptiles and other wildlife. Additional concerns, that warrant ongoing and careful monitoring, are changes to conservation policy and the introduction of untested habitat management practices, such as cattle grazing, which may have detrimental effects on ground vegetation cover and structure, and as a consequence, on wildlife in general and reptile populations in particular (Jofré & Reading, 2012; Reading & Jofré, 2015; Reading & Jofré, *In Press*).

4.1 *Conclusions*

The early successional stages of coniferous plantation growth are well utilised by reptiles and suggests that this may be equally true for other open-habitat taxa. However, this use is relatively short-lived being dependent on tree growth rates and the subsequent increase in tree canopy cover that is inversely correlated with the presence of ground vegetation cover. Given these restrictions a forest comprising a mosaic of relatively small compartments of varying age and shape, as opposed to large even-age blocks, will enhance the conservation value of managed forests in terms of both individual species of concern, and species diversity for many taxa including reptiles. The study reported here concerned native British reptiles in southern England that are likely to be adapted to, and have, different habitat and thermal requirements to reptile species occurring in other parts of the world. It is therefore essential that species specific habitat and thermal requirements are determined, and accounted for, when assessing the time period over which managed forests, comprised of tree species with varying canopy cover attributes, may be considered suitable for these species.

The results of our study are not restricted solely to reptiles and coniferous forest management within the UK but have implications for the conservation of all wildlife inhabiting managed forests worldwide.

Acknowledgements

The reptile surveys were funded by the Forestry Commission (Contract No. 304/NF/11/385) and undertaken by G.M.J. The capture of all protected species was done under licence from Natural England.

References

Amo, L., López, P. & Martín, J. (2007). Natural oak forest vs. ancient pine plantations: lizard microhabitat use may explain the effects of ancient reforestations on distribution and conservation of Iberian lizards. Biodivers Conserv 16: 3409-3422.

Barbaro, L., Pontcharraud, L., Vetillard, F., Guyon, D. & Jactel, H. (2005). Comparative responses of bird, carabid, and spider assemblages to stand and landscape diversity in maritime pine plantation forests. Ecoscience 12: 110-121.

Bock, C.E., Smith, H.M. & Bock, J.H. (1990). The effect of livestock grazing upon abundance of the lizard, *Sceloporus scalaris*, in southeastern Arizona. J Herpetol 24: 445-446.

Böhm, M., Collen, B., Baillie, J.E.M., Bowles, P., Chanson, J., Cox, N., Hammerson, G. *et al*. (2013). The conservation status of the world's reptiles. Biol Conserv 57: 372-385.

Brockerhoff, E.G., Jactel, H., Parrotta, J.A., Quine, C.P. & Sayer, J. (2008). Plantation forests and biodiversity: oxymoron or opportunity? Biodivers Conserv 17: 925-951.

Calladine, J., Bray, J., Broome, A. & Fuller, R.J. (2015). Comparison of breeding bird assemblages in conifer plantations managed by continuous cover forestry and clearfelling. For Ecol Manage 344: 20-29.

Campbell, H.W. & Christman, S.P. (1982). Field techniques for herpetofaunal community analysis. Herpetol Comm 193-200.

Dent, S. & Spellerberg, I.F. (1988). Use of forest ride verges in southern England for the conservation of the Sand lizard *Lacerta agilis* L. Biol Conserv 45: 267-277.

Donald, P.F., Fuller, R.J., Evans, A.D & Gough, S.J. (1998). Effects of forest management and grazing on breeding bird communities in plantations of broadleaved and coniferous trees in western England. Biol Conserv 85: 183–197.

Edgar, P., Foster, J. & Baker, J. (2010). *Reptile Habitat Management Handbook.* Amphibian and Reptile Conservation, Bournemouth.

EPS. http://www.biodiversityplanningtoolkit.com

Frazer, D. (1983). *Reptiles and Amphibians in Britain*. The New Naturalist No 69. Collins,

London.
Garden, J.G., McAlpine, C.A., Possingham, H.P. & Jones, D.N. (2007). Habitat structure is more important than vegetation composition for local-level management of native terrestrial reptile and small mammal species living in urban remnants: A case study from Brisbane, Australia. Aust Ecol 32: 669-685.

Gardner, T.A., Barlow, J. & Peres, C.A. (2007). Paradox, presumption and pitfalls in conservation biology: The importance of habitat change for amphibians and reptiles. Biol Conserv 138: 166–179.

Greenberg, C.H. (2001). Response of reptile and amphibian communities to canopy gaps created by wind disturbance in the southern Appalachians. For Ecol Manage 148: 135-144.

Greenberg, C.H., Neary, D.G. & Harris, L.D. (1994). Effect of high-intensity wildfire and silvicultural treatments on reptile communities in Sand-pine scrub. Conserv Biol 8: 1047-1057.

Hester, A.J. (1987). Successional vegetation change: the effect of shading on *Calluna vulgaris* (L.) Hull. Trans Bot Soc Edinburgh 45: 121-126.

Iason, G.R. & Hester, A.J. (1993). The response of heather (*Calluna vulgaris*) to shade and Nutrients- -Predictions of the carbon-nutrient balance hypothesis. J Ecol 81: 75-80.

Jameson, D.A. (1967). The relationship of tree overstory and herbaceous understory vegetation. J Range Manage 20: 247-249.

Jofré, G. M. & Reading, C. J. (2012). *An assessment of the impact of conservation grazing on reptile populations.* Amphibian & Reptile Conservation Research Report 12/01.

Lemmon P.E. (1956). A spherical densitometer for estimating forest overstory density. For Sci 2: 314-320.

Lindenmayer, D.B. & Fischer, J. (2006). Habitat fragmentation and landscape change – An ecological and conservation synthesis. Island Press. Washington. DC 20009.

Mann, J.C.E. & Putman, R.J. (1989). Patterns of habitat use and activity in British populations of

Sika deer of contrasting environments. Acta Theriol 34: 83-96.

Martín, J. & Lopez, P. (2002). The effect of Mediterranean dehesa management on lizard distribution and conservation. Biol Conserv 108: 213-219.

Minitab.16 Statistical Software (2010). [Computer software]. State College, PA: Minitab Inc. (www.minitab.com).

Palacios, C.P., Agüero, B. & Simonetti, J.A. (2013). Agroforestry systems as habitat for herpetofauna: is there supporting evidence? Agrofor Syst 87: 517-523.

Quine, C.P., Humphrey, J.W. & Watts, K. (2004). Biodiversity in the UK's forests—recent policy developments and future research challenges. In: Paivanen R, Franc A (eds) Towards the sustainable use of Europe's forests-forest ecosystem and landscape research: scientific challenges and opportunities. European Forest Institute, Joensuu, pp 237–248.

Reading, C. J. (1997). A proposed standard method for surveying reptiles on dry lowland heath. J Appl Ecol 34: 1057-1069.

Reading, C.J. (2012). Ranging behaviour and home range size of smooth snake inhabiting lowland heath in southern England. Herpetol J 22: 241-247.

Reading, C. J. & Jofré, G.M. (2009). Habitat selection and range size of grass snakes *Natrix natrix* in an agricultural landscape in southern England. Amphibia-Reptilia 30: 379-388.

Reading, C. J. & Jofré, G.M. (2015). Habitat use by smooth snakes on lowland heath managed using 'conservation grazing'. Herpetol J 25: 225-231.

Reading, C. J. & Jofré, G.M. (*In Press*). Habitat use by grass snakes and three sympatric lizard species on lowland heath managed using 'conservation grazing'. Herpetol J

Rose, R.J., Webb, N.R., Clarke, R.T & Traynor, C.H. (2000). Changes on the heathlands in Dorset, England between 1987 and 1996. Biol Conserv 93: 117-125.

Sala, O.E., Chapin, F.S., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F., Kackson, R.B., Kinzig, A., Leemans, R., Lodge, D.M., Mooney, H.A., Oesterheld, M., Poff, N.L., Sykes, M.T., Walker, B.H., Walker, M. & Wall, D.H. (2000). Global biodiversity scenarios for the year 2100. Science 287: 1770-1774.

Sharps, K., Henderson, I., Conway, G., Amour-Chelu, N & Dolman, P.M. (2015). Home-range size and habitat use of European Nightjars *Caprimulgus europaeus* nesting in a complex plantation-forest landscape. Ibis 157: 260-272.

Spellerberg, I.F. (1975). Conservation and management of Britain's reptiles based on their ecological and behavioural requirements: a progress report. Biol Conserv 7: 289-300.

Spellerberg, I.F. & Phelps, T.E. (1977). Biology, general ecology and behaviour of the snake, *Coronella austriaca* Laurenti. Biol J Linn Soc 9: 133-164.

Swihart, R.K. & Slade, N.A. (1985). Testing for independence of observations in animal movements. Ecology 66: 1176-1184.

Todd, B.D. & Andrews, K.M. (2008). Response of a reptile guild to forest harvesting. Conserv Biol 22: 753-761.

Uribe, S.V. & Estades, C.F. (2014). Reptiles in Monterey pine plantations of the coastal range of central Chile. Rev Chil Hist Nat 87: 1-8.

Wilson, M.W., Irwin, S., Norriss, D.W., Newton, S.F., Collins, K., Kelly, T.C. & O'Halloran, J. (2009). The importance of pre-thicket conifer plantations for nesting Hen harriers *Circus cyaneus* in Ireland. Ibis 151: 332-343.

Wright, L.J., Hoblyn, R.A., Sutherland, W.J. & Dolman, P.M. (2007). Reproductive success of Woodlarks *Lullula arborea* in traditional and recently colonised habitats. Bird Study 54: 315-323.

Zar, J.H. (2010). Biostatistical analysis. 5th Edition. Pearson Education Ltd., London.

Table 1. Mean % ground cover (±*SD*) of the main plant categories within each plantation (n=50 for all categories). Cv/Ec/Et: *C. vulgaris*+*E. cinerea*+*E. tetralix*; Um: *U. minor*; Ac: *A. curtisii*; Mc: *M. caerulea*; Pa: *P. aquilinum*; BGr: bare ground; Pneed: pine needles; DGr: dead grass.

Site		Cv/Ec/Et	Um	Ac	Mc	Pa	Moss	BGr	PNeed	DGr
1A	Cover	2.31	0.36	0.19	-	-	18.65	3.54	82.23	-
	SD	*4.943*	*1.366*	*0.637*	-	-	*21.329*	*11.877*	*25.362*	-
2A	Cover	1.06	0.31	2.29	89.59	-	0.56	0.13	40.13	95.86
	SD	*4.992*	*0.998*	*3.040*	*10.658*	-	*2.808*	*0.850*	*44.672*	*10.715*
3A	Cover	5.68	-	0.02	47.18	43.23	0.32	8.73	21.7	44.24
	SD	*9.424*	-	*0.141*	*40.468*	*36.869*	*1.584*	*24.296*	*35.565*	*46.210*
4A	Cover	65.55	-	-	0.07	0.01	36.43	2.1	87.37	0.04
	SD	*20.570*	-	-	*0.286*	*0.071*	*40.594*	*10.442*	*29.515*	*0.283*
6A	Cover	37.51	-	3.72	8.65	2.17	7.28	0.28	89.17	15.64
	SD	*24.441*	-	*9.453*	*15.801*	*3.938*	*20.055*	*1.457*	*17.797*	*28.326*
2B	Cover	0.36	-	0.58	56.48	1.28	4.35	2.18	67.89	40.39
	SD	*1.463*	-	*1.792*	*31.917*	*3.833*	*11.011*	*9.393*	*39.413*	*39.777*
3B	Cover	0.02	6.01	0.12	21.52	28.2	18.18	6.45	88.00	3.6
	SD	*0.100*	*42.425*	*0.372*	*14.941*	*23.186*	*26.814*	*22.414*	*31.102*	*12.249*
5B	Cover	1.38	-	-	10.18	1.1	8.82	5.58	91.64	4.9
	SD	*3.790*	-	-	*17.743*	*3.174*	*18.609*	*20.335*	*19.867*	*18.803*
6B	Cover	5.94	0.37	0.12	1.03	0.86	6.35	1.44	95.00	-
	SD	*8.175*	*1.624*	*0.848*	*4.110*	*2.087*	*15.011*	*7.282*	*16.413*	-
7B	Cover	0.06	-	1.42	52.5	1.99	0.34	0.52	98.28	48.65
	SD	*0.260*	-	*4.342*	*16.813*	*5.346*	*1.364*	*2.936*	*5.782*	*30.178*
3C	Cover	76.29	0.7	0.08	6.43	9.32	32.33	6.59	60.43	4.53
	SD	*15.613*	*1.896*	*0.340*	*10.948*	*13.654*	*33.226*	*9.794*	*34.998*	*12.276*
4C	Cover	0.64	4.81	0.34	1.62	65.96	36.58	1.00	92.1	0.32
	SD	*1.702*	*8.272*	*0.783*	*4.675*	*20.456*	*36.149*	*7.071*	*21.855*	*1.634*
5C	Cover	74.08	9.15	0.43	8.03	6.54	68.5	1.73	15.11	2.28
	SD	*12.14*	*8.676*	*1.301*	*7.074*	*9.093*	*36.963*	*3.520*	*24.082*	*4.012*
6C1	Cover	26.12	2.13	0.02	0.20	23.38	45.75	4.34	61.3	-
	SD	*22.468*	*4.796*	*0.141*	*0.528*	*23.107*	*34.467*	*9.702*	*37.113*	-
6C2	Cover	0.48	6.57	12.22	16.02	12.43	14.25	2.72	91.58	6.36
	SD	*1.026*	*9.097*	*12.027*	*17.374*	*20.075*	*24.374*	*13.182*	*22.049*	*13.674*
1D	Cover	39.03	0.28	5.88	1.59	-	28.41	19.32	1.15	4.9
	SD	*27.269*	*1.016*	*15.166*	*4.183*	-	*33.941*	*20.737*	*3.820*	*14.690*
2D	Cover	33.98	4.46	10.36	27.34	5.59	4.84	17.73	1.56	23.44
	SD	*21.857*	*8.438*	*11.810*	*19.940*	*8.792*	*10.478*	*16.539*	*3.759*	*27.289*
4D	Cover	71.7	-	-	5.8	-	42.38	17.83	4.11	6.24
	SD	*16.029*	-	-	*13.404*	-	*28.202*	*16.578*	*9.628*	*16.355*
6D	Cover	31.69	2.53	3.54	16.72	2.63	4.55	38.26	1.74	12.92
	SD	*20.323*	*3.500*	*9.296*	*14.226*	*5.616*	*8.476*	*26.399*	*4.646*	*17.143*
7D	Cover	22.26	1.83	6.90	43.99	10.81	3.14	17.18	0.82	42.92
	SD	*19.126*	*4.936*	*9.046*	*31.452*	*22.612*	*10.484*	*23.215*	*3.341*	*38.694*

Table 2. Regression equations for data shown in Figs 2 and 3. Significant values shown in bold. Heather: *C. vulgaris+E. cinerea+E. tetralix*; Um: *U. minor*; Ac: *A. curtisii*; Mc: *M. caerulea*; Pa: *P. aquilinum*; DGr: dead grass.

Fig.	Array/ Age	Equation	r^2 (%)	*P*	*n*
2	A	% Vegetation cover = 5.35 + 1.07 Plantation age.	18.6	**0.031**	25
	B	% Vegetation cover = 6.75 – 0.72 Plantation age.	1.2	0.605	25
	C	% Vegetation cover = 207.53 – 6.59 Plantation age.	12.7	0.161	17
	D	% Vegetation cover = 14.37 + 13.50 Plantation age.	72.8	**<0.001**	33
	A+B	% Canopy cover = 88.35 – 0.19 Plantation age.	13.4	**0.009**	50
	C+D	% Canopy cover = –22.77 + 5.35 Plantation age.	84.2	**<0.001**	50
3	0-14yrs	Heather height = 6.73 + 3.88 Plantation age.	79.2	**<0.001**	34
	15-20yrs	Heather height = 195.40 – 9.08 Plantation age.	46.4	**0.005**	15
	22-40yrs	Heather height = 21.48 – 0.10 Plantation age.	0.4	0.795	20
	42-85yrs	Heather height = –4.26 + 0.47 Plantation age.	46.6	**<0.001**	24
	0-10yrs	Um height = 4.92 + 2.96 Plantation age.	27.4	**0.006**	26
	11-20yrs	Um height = 58.37 – 1.93 Plantation age.	52.4	**<0.001**	19
	22-40yrs	Um height = 19.95 – 0.20 Plantation age.	2.3	0.808	5
	42-85yrs	Um height = –1.92 + 0.40 Plantation age.	30.7	0.097	10
	0-20yrs	Ac height = 18.98 – 0.31 Plantation age.	16.5	**0.014**	36
	21-85yrs	Ac height = 12.69 + 0.04 Plantation age.	3.8	0.340	26
	0-85yrs	Mc height = 31.25 + 0.05 Plantation age.	2.2	0.159	92
	0-7yrs	Pa height = 20.09 + 7.44 Plantation age.	40.9	**0.010**	15
	8-19yrs	Pa height = 20.34 + 4.96 Plantation age.	40.0	**0.001**	25
	20-38yrs	Pa height = 94.72 – 1.07 Plantation age.	3.4	0.401	22
	55-83yrs	Pa height = 161.91 – 1.45 Plantation age.	78.5	**0.001**	10
	0-85yrs	DGr height = 13.61 – 0.04 Plantation age.	2.8	0.201	61

Table 3. Mean number of times individual grass snakes and smooth snakes were captured within each array each year (2009-2013). Significant values (P<0.05) shown in bold

Year	Grass snake Mean *SD : n*	Grass snake Range Min-Max	Comparing means *t* : *P* : *df*	Smooth snake Mean *SD : n*	Smooth snake Range Min-Max
2009	1.07 *0.258 : 29*	1-2	3.67 : **0.001** : 42	1.61 *0.838 : 36*	1-4
2010	1.08 *0.277 : 25*	1-2	4.13 : <**0.001** : 40	2.26 *1.743 : 39*	1-7
2011	1.16 *0.602 : 37*	1-4	3.44 : **0.001** : 75	1.98 *1.624 : 56*	1-8
2012	1.09 *0.301 : 21*	1-2	4.40 : <**0.001** : 53	2.29 *1.837 : 49*	1-9
2013	1.20 *0.410 : 20*	1-2	3.35 : **0.002** : 35	2.34 *1.860 : 32*	1-7
Overall	1.12 *0.410 : 132*	1-4	8.23 : <**0.001** : 251	2.09 *1.641 : 212*	1-9

Figure legends

Fig. 1. Map of the study area within Wareham Forest showing the positions of the 20 reptile refuge arrays relative to each other. Site age categories: A-△; B-▲; C-○; D-●.

Fig. 2. Relationship between tree canopy cover (open symbols, dotted regression lines) and vegetation ground cover (solid symbols, solid regression lines) with planation age (2009-2013). Regression equations shown in Table 2.

Site age categories: A-▼,▽; B-■,□; C-▲,△; D-●,○.

Fig. 3. Relationship between mean vegetation height and plantation age (2009-2013). Regression equations shown in Table 2. Heather: *C. vulgaris+E. cinerea+E. tetralix*; Um: *U. minor*; Ac: *A. curtisii*; Mc: *M. caerulea*; Pa: *P. aquilinum*; DGr: dead grass. Site age categories: A-△; B-▲; C-○; D-●.

Fig. 4. Relationship between the total number of smooth snake (Ca) and grass snake (Nn) captures and plantation canopy cover (a, c) and plantation age (b, d). Site age categories: A-△; B-▲; C-○; D-●.

Fig. 5. Relationship between the total number of smooth snake (Ca) and grass snake (Nn) individuals and plantation canopy cover (a, c) and plantation age (b, d). Site age categories: A-△; B-▲; C-○; D-●.

Fig. 6. Relationship between the total number of slow worm (Af), common lizard (Zv) and sand lizard (La) captures and plantation canopy cover (a, c, e) and plantation age (b, d, f). Site age categories: A-△; B-▲; C-○; D-●.

Fig. 1

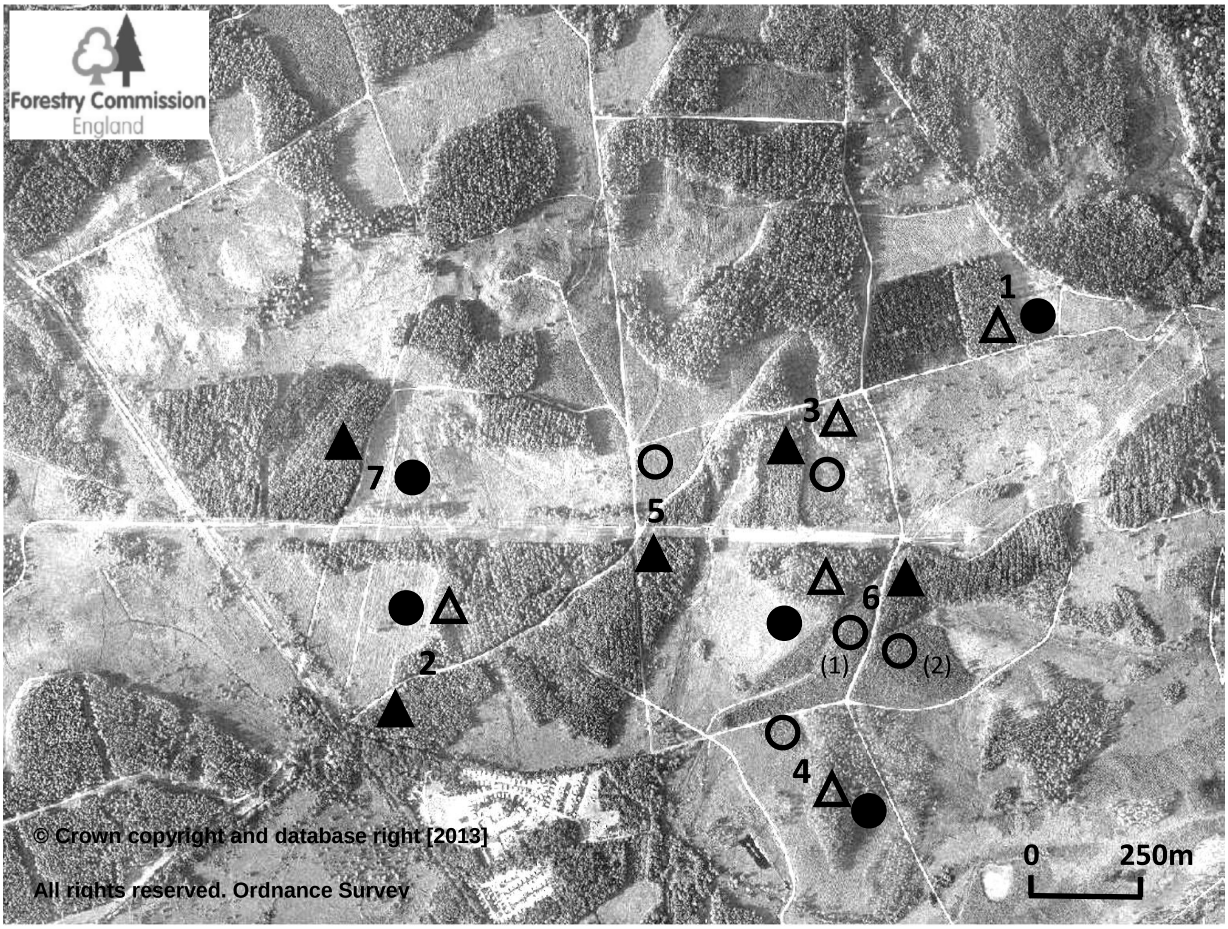

Forestry Commission
England
1
3
7
5
6
2
(1)
(2)
4
© Crown copyright and database right [2013]
All rights reserved. Ordnance Survey
0
250m

Fig. 2

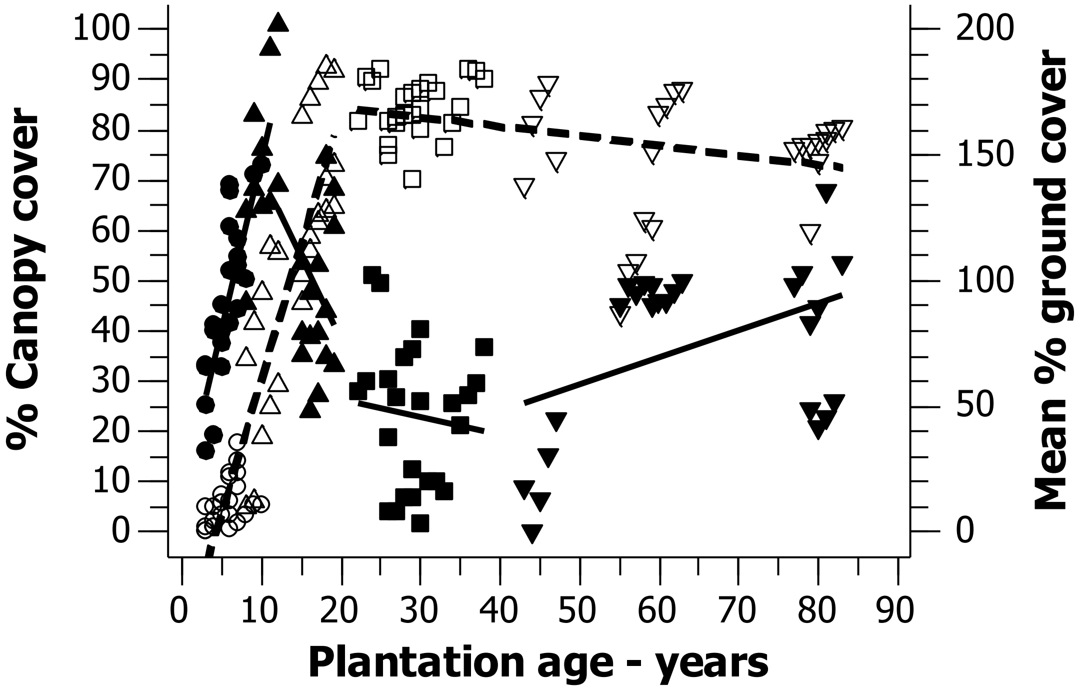

% Canopy cover
Mean % ground cover
Plantation age - years
0
10
20
30
40
50
60
70
80
90
100
0
50
100
150
200

Fig. 3

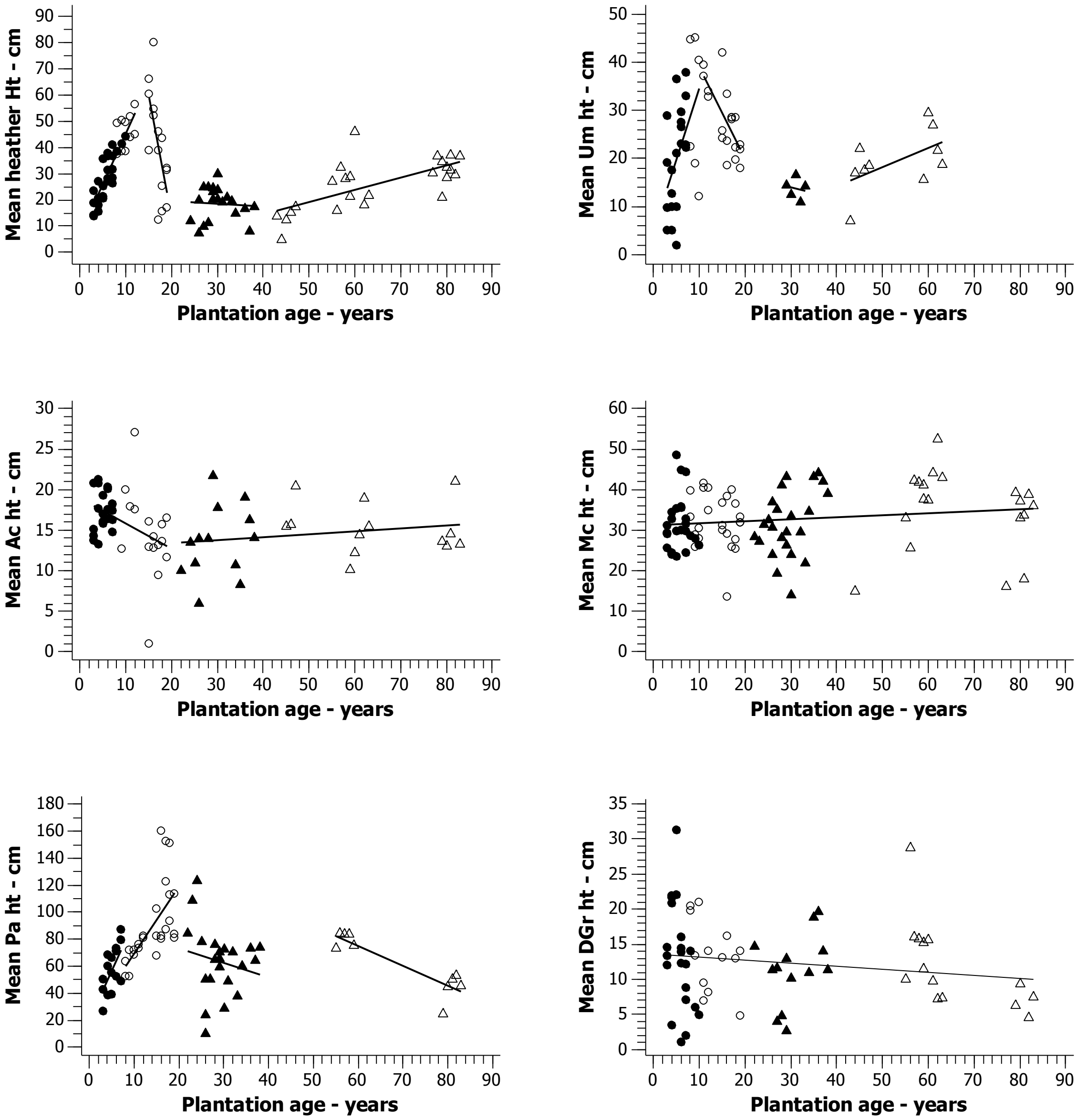

Mean heather Ht - cm
Plantation age - years
Mean Um ht - cm
Plantation age - years
Mean Ac ht - cm
Plantation age - years
Mean Mc ht - cm
Plantation age - years
Mean Pa ht - cm
Plantation age - years
Mean DGr ht - cm
Plantation age - years

Fig. 4

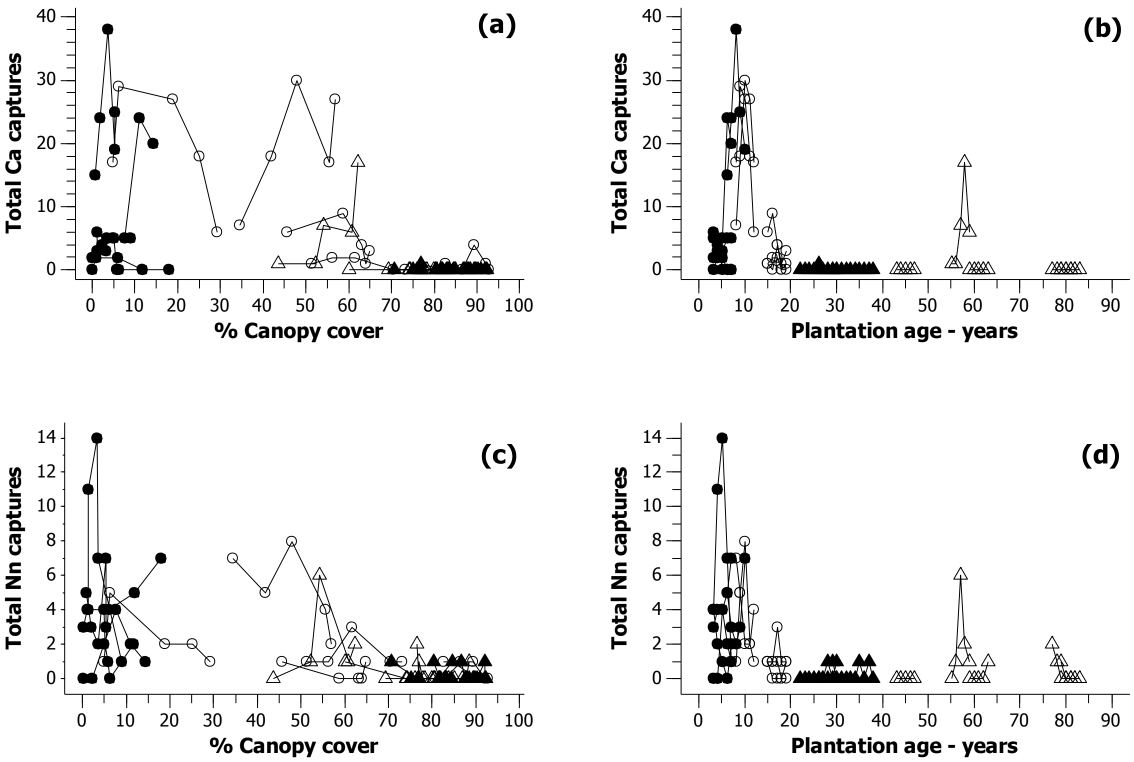

(a)
(b)
(c)
(d)
Total Ca captures
Total Nn captures
% Canopy cover
Plantation age - years
0
10
20
30
40
50
60
70
80
90
100
0
2
4
6
8
10
12
14

Fig. 5

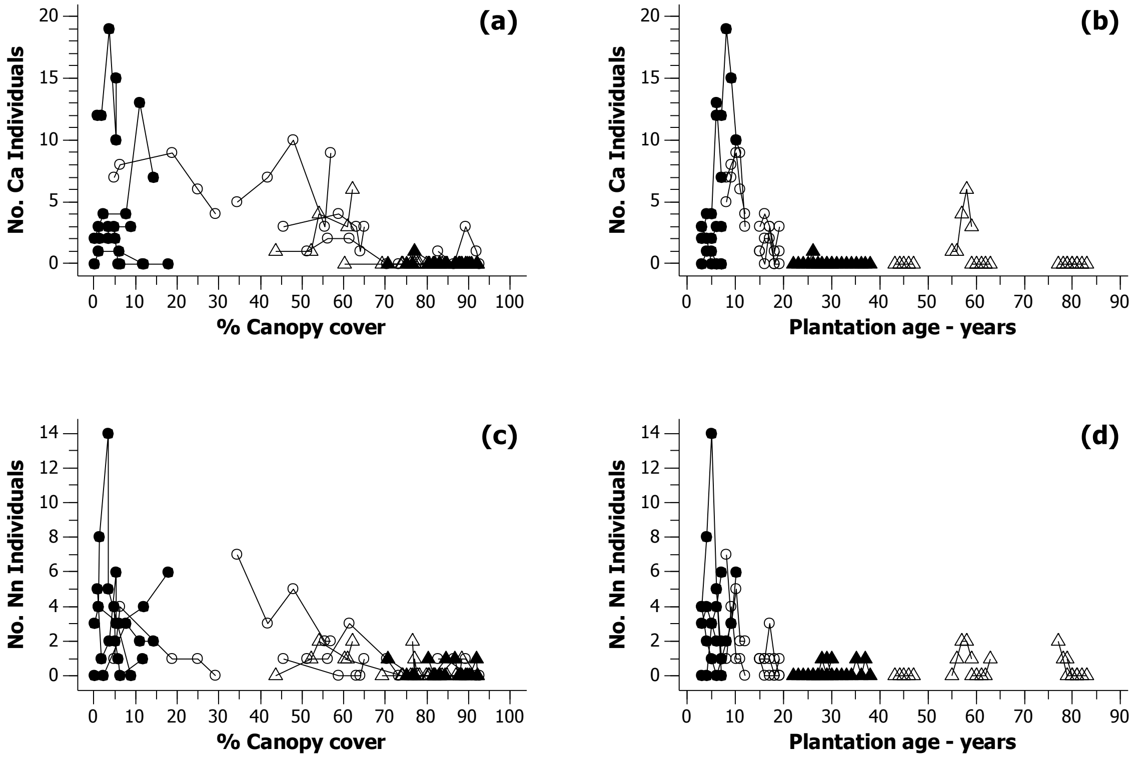
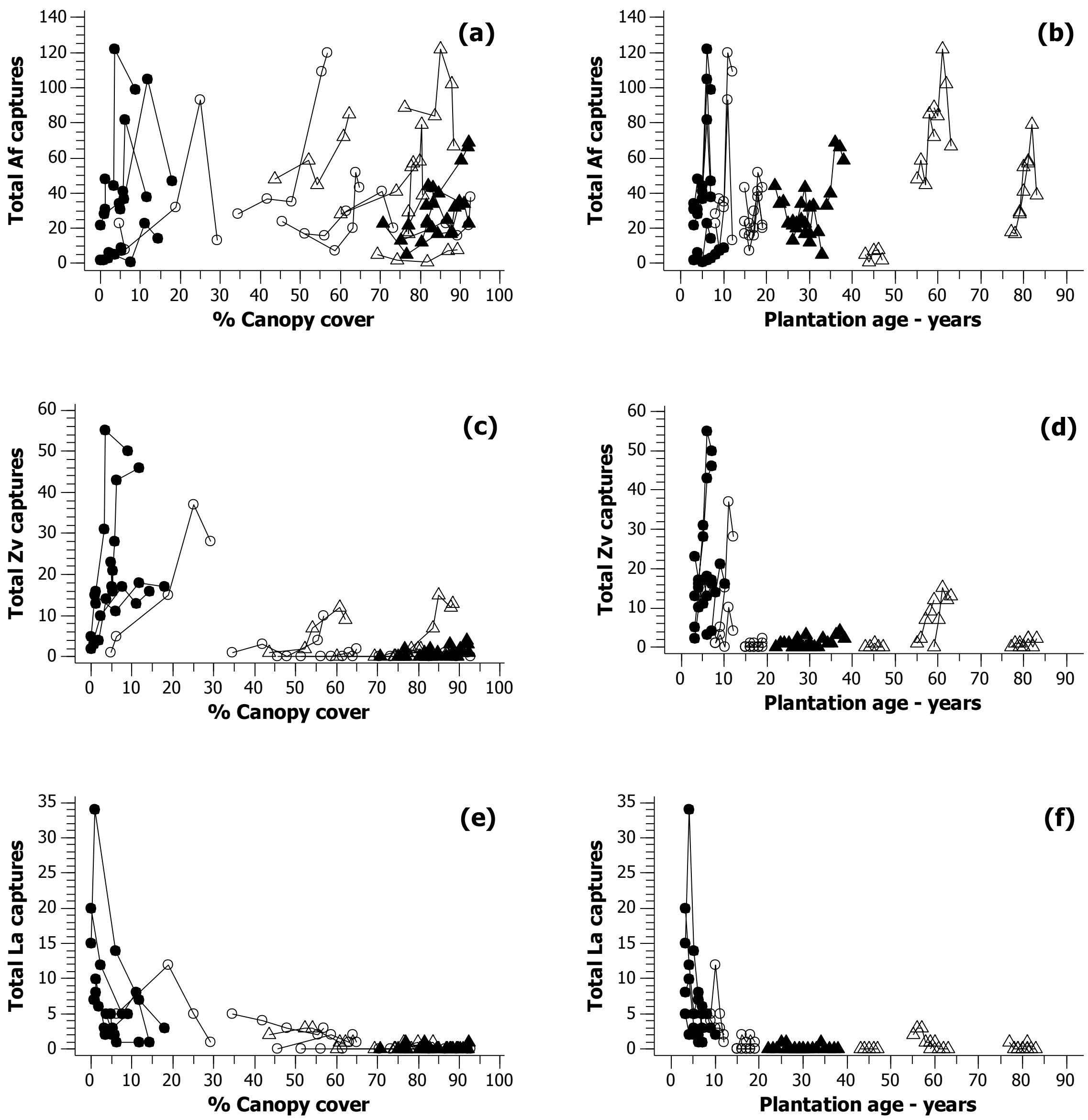

(a)
No. Ca Individuals
% Canopy cover
(b)
No. Ca Individuals
Plantation age - years
(c)
No. Nn Individuals
% Canopy cover
(d)
No. Nn Individuals
Plantation age - years

Fig. 6


(a)
Total Af captures
% Canopy cover
(b)
Total Af captures
Plantation age - years
(c)
Total Zv captures
% Canopy cover
(d)
Total Zv captures
Plantation age - years
(e)
Total La captures
% Canopy cover
(f)
Total La captures
Plantation age - years