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The relative performance of smooth snakes inhabiting open heathland and conifer plantations

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ABSTRACT

Different habitat types that support similar densities of a particular species may not be equally suitable for that species and this may impact on the ability of that species to grow, reproduce, and survive. Here we investigate the impact of habitat quality on the performance of the UK's rarest snake which inhabits both lowland heath and adjacent areas of managed conifer plantation located on former lowland heath. Annually, over an 8 year period (2009–2016), we recaptured known individual smooth snakes (*Coronella austriaca*) in these two habitat types and compared their survivorship, using Program MARK, and growth rates, estimated ages, reproductive outputs, emigration/immigration, and body condition, using regression analysis and GLM. When compared with snakes from plantations those inhabiting open heathland had higher growth rates, were larger for any given age, had a higher body condition and females produced more embryos for a given body size. Smooth snake survivorship rates within the two habitats were similar. Whilst the body condition of snakes in heathland did not change during the study it declined in plantations and this decline was correlated with increasing plantation age and tree canopy cover. Our data show that although smooth snakes occur in both habitat types the overall quality of open heathland is superior to that of plantations, particularly in the long term.

This study has potentially important implications for the conservation of smooth snakes and other reptile and vertebrate species inhabiting coniferous plantations, where management practices aimed at reducing ground vegetation cover, such as cattle grazing and the use of herbicides, are also used. The combination of increasing canopy cover and these additional ground vegetation control measures are likely to significantly reduce further the time period over which plantations can be utilised by these taxa.

1. Introduction

One of the major threats to biodiversity generally, and to the conservation of many taxa worldwide, is habitat change (Sala et al., 2000) for which there are many causes including human land use practices, such as commercial forestry (Lindenmayer & Fischer, 2006; Böhm et al., 2013). However, although plantation forests are generally considered to be of lower quality than natural forests for forest species they may, nevertheless, provide valuable habitat for some endangered or threatened species (Brockerhoff et al., 2008; Jofré et al., 2016) though the evidence for this is relatively scarce given the recognised need for detailed studies of the habitat requirements of many species of conservation concern (Quine et al., 2004).

Habitat quality and its impact on either individual, or population, performance within a particular habitat type has been investigated in many taxa and has, to a large extent, concentrated on measuring habitat attributes, such as the presence and/or abundance of competitors or predators and habitat structural features such as vegetation cover and type. Fewer have focussed on measuring a species performance within a particular habitat type e.g. reproductive output, growth rate and survivorship, all of which may be dependent on an individual's ability to obtain food with the best measure of this being body condition (Johnson, 2007). In addition, most studies that have compared a species performance within different habitat types have done so in those habitats that are relatively stable (e.g. Morris, 1989; Mosser et al., 2009; Sasaki et al., 2016; Allen et al., 2017) whilst fewer have attempted to do so where at least one of the habitat types under investigation is transient (Welsh et al., 2008; Rotem et al., 2013).

To date many studies have compared habitat quality by measuring the relative density of a particular species within two or more different habitat types and then inferred that the habitat with the lower density is the one with the lower quality (Morris, 1989). However, assuming a direct relationship between density and habitat quality can be misleading (Van Horne, 1983) and therefore the use of a single proxy of

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habitat quality, such as density, may not provide a reliable assessment (Gaillard et al., 2010). A better approach is one that uses measures of a species performance e.g. reproductive output, growth rates, mortality/survivorship, and body condition, as these may be better at identifying causal factors implicit in the long-term persistence of a population within a particular habitat type (Van Horne, 1983; Vickery et al., 1992; Hall et al., 1997; Mosser et al., 2009).

Studies attempting to link habitat quality to a species performance can be particularly problematic in those species that migrate between winter and summer habitats, or have large home ranges e.g. many birds and some large mammals, as defining their precise habitat at all times can be difficult. An additional potential complication concerns estimating a species performance, over prolonged periods of time, when that species occurs in different habitats but at similar relative densities. Are the habitats of equal quality over time? Ideally, metrics relating to the performance of an animal species within different habitat types should be studied over the same period of time and be based on known individuals within each population (Gaillard et al., 2010; Homyack, 2010). This approach overcomes potential errors arising from temporal changes in habitat quality when measures of performance are based on unknown individuals over different periods of time.

A good example of a relatively long-lived vertebrate that is known to have a small home range and is relatively site faithful as an adult, is the smooth snake (*Coronella austriaca*), and for which marked individuals inhabiting an area of open lowland heath have been studied intensively since 1992 (Reading, 1997, 2004a, 2004b, 2012; Reading and Jofré, 2013). Over an eight year period (2009–2016) a parallel study was also undertaken on marked individual smooth snakes inhabiting managed conifer plantations in close proximity to the heathland study population (Jofré, 2016; Jofré et al., 2016). These two studies provided a rare opportunity to investigate, simultaneously, different measures of performance for a vertebrate occurring in two distinct habitat types, one being relatively stable (managed heathland) and the other transient (conifer plantations) and how the overall performance of individuals, indicated by survivorship, reproductive output, growth, and body condition, within each habitat type might change in relation to changes in habitat metrics over time.

2. Materials and methods

This investigation was carried out between January 2009 and November 2016 in Wareham Forest (50°44′N, 2°08′W), and is based on two parallel studies, the first on a 10 ha area of lowland heath and the second within adjacent or nearby plantations of managed coniferous forest.

2.1. Conifer plantations and lowland heath study sites

The conifer plantations were planted on former lowland heath, over tertiary deposits of acid sands and gravels (Mann and Putman, 1989), in southern England by the Forestry Commission. The forest is managed on rotation, with trees clear-felled at about 60 years old, thereby maintaining a mosaic of clear fell, tree stands of varying ages, forest rides, open heath, and permanent open ground (heathland). The primary tree species is Corsican pine *Pinus nigra* (Melville) which are planted, as saplings, approximately 1.8 m apart in late winter/early spring one year after clear-felling plantations of mature trees and preparing the ground during the previous winter. Following planting, the 'pre-thicket' stage (≈0–12 years old) is characterised by relatively small trees with a good ground cover of heathland plants. During the following 'thicket stage' (≈10–30 years old), the trees form an increasingly dense canopy that reduces light levels resulting in an increasing absence of ground flora over time.

The ground flora occurring within the plantations, and the nearby lowland heath, 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.), bristle bent *Agrostis curtisii* (Kerguelen), and dwarf gorse *Ullex minor* (Roth) as the dominant species. Bracken *Pteridium aquilinum* (L.) is also common within the plantations.

In December 2008 twenty pine plantations of different ages were selected within Wareham Forest and grouped into four broad age classes (see Jofré et al., 2016 for a more detailed description). The area of individual plantations, that included the 20 study sites, ranged between 0.61 and 10.45 ha (mean = 4.23 ha; $SD = 2.67$; $n = 20$). 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.

2.2. Reptile surveys

An array of artificial reptile refuges (corrugated steel sheet measuring 92 cm × 73 cm) was laid out in each of the 20 selected sites, within the conifer plantations, and at 11 locations within an area of heathland close to the plantation sites. Each array consisted of a hexagonal pattern of 37 refuges, spaced 10 m apart, and covering an area of 0.29 ha (see Reading, 1997 for a detailed description).

Sixteen reptile surveys were carried out annually (2009–2016), between the last week of April and the second week of October, in the plantations and 21 surveys annually on the heathland sites. Surveys were spaced at least one week apart and during each survey all 31 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 snakes were captured, sexed, weighed to the nearest gram (g) using a spring balance, and the snout-vent length (SVL) and tail length measured to the nearest millimetre (mm). Each snake was implanted with a PIT (Passive integrated transponder) tag for individual recognition when recaptured (see Reading and Davies, 1996 for a full description). All captured snakes were palpated to determine whether or not they contained a discernible meal and, for adult females, whether or not they were gravid and, if so, the number of embryos they were carrying.

The prey taken by smooth snakes inhabiting the heathland and plantations was investigated between 2009 and 2015 by analysing faecal samples collected from captured snakes (see Reading and Jofré, 2013 for a full description of methodology). For the purposes of comparison, between the two habitat types, the prey were placed into two broad categories 1: all Lacertidae (common lizard *Zootoca vivipara*, sand lizard *Lacerta agilis*) and 2: all small mammals (common shrew *Sorex araneus*, pygmy shrew *S. minutus*, wood mouse *Apodemus sylvaticus*, short-tailed field vole *Microtus agrestis*).

2.3. Tree canopy cover

A Model 'A' spherical densitometer (canopy mirror: Lemmon, 1956) was used to estimate percent tree canopy annually (autumn) between 2009 and 2016, in each plantation array. 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 (see Jofré et al., 2016 for a more detailed description).

2.4. Data analysis

Annual mean smooth snake densities in the heathland and plantation arrays were estimated from the number of individual snakes captured in each array for a given habitat. Annual snake survivorship and recapture rates within the plantations and on open heath were estimated using Program MARK v.8.2 (White and Burnham, 1999). Two 'Goodness of Fit' (GOF) tests for the data were run to estimate a