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

Christopher J. Reading[1] & Gabriela M. Jofré[2]

[1] Centre for Ecology & Hydrology, CEH Wallingford, Benson Lane, Crowmarsh Gifford, Wallingford, Oxon, OX10 8BB, UK

Corresponding author: cjr@ceh.ac.uk

[2] c/o Centre for Ecology & Hydrology, CEH Wallingford, Benson Lane, Crowmarsh Gifford, Wallingford, Oxon, OX10 8BB, UK: gjofre@tiscali.co.uk

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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.

Key words: body condition, canopy cover, *Coronella austriaca*, growth rate, reproductive output, survivorship.

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 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 & 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 & 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 1.8m 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 10.45ha (mean=4.23ha; *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 92cm x 73cm) 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 10m apart, and covering an area of 0.29 hectares (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 & 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 & 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 & Burnham, 1999). Two ‘Goodness of Fit’ (GOF) tests for the data were run to estimate a Variance Inflation Factor (ĉ) using Programs RELEASE and U-CARE (Choquet et al., 2009). A third, MEDIAN ĉ, was also estimated using Program MARK. Program MARK was then re-run using the highest ĉ value (most conservative estimate) obtained from the three tests in place of the default value (ĉ=1) which assumes a perfect fit.

The number of smooth snakes leaving (mortality and/or emigration) either the heath or plantation study sites were estimated by counting all those individuals that were present in a particular year and not subsequently recaptured. Individuals that were not captured in a particular year but were subsequently recaptured were assumed to have been present in those years when they were not captured. The number of new smooth snakes entering the study sites was estimated by counting the number of individuals that had not been previously marked.

Linear regression analysis was used to describe the relationships between $\log_{10}$ SVL and $\log_{10}$ body mass (BM) of males and non-reproductive females. Gravid females were omitted from all analyses of SVL vs BM to prevent the inclusion of embryo mass in overall female BM and subsequent estimation of body condition (BC: residuals generated following regression analysis of $\log_{10}$ body mass against $\log_{10}$ SVL; Schulte-Hostedde, et al., 2005). Similarly, the BM of snakes containing a discernible meal were also excluded from the analysis of BC. Pseudo-replication within the data set, where individual snakes had been caught more than once in any year, was avoided by first calculating a mean SVL and mean BM for each individual snake in each year and using these values in subsequent regression analyses. The SVL vs BM data, for males and non-reproductive females, for all sites and in all years were pooled separately and the residuals obtained from each regression analysis used to investigate differences between plantation and heathland sites. For within year differences the data for individual years was pooled and the resultant residuals analysed. For between year differences within either plantations or heathland sites, the data for all years was pooled and the resultant residuals analysed. The number of each of the two prey categories found in faecal samples collected from both heathland and plantation snakes were compared using Chi-square analysis.

Snake growth rates were determined by calculating the difference in SVL recorded on consecutive captures of individual snakes and dividing this value by the number of days between captures. To reduce the effect of SVL measuring error only data collected from snakes that were captured at least 50 days apart were used in the analysis.

A possible consequence of reduced growth rates, in plantation snakes compared with those from heathland, is a change in the relationship between SVL and age. Growth curves were plotted for both males and females and related to known ages for individual snakes (those first captured within one year of birth) and/or ages extrapolated for older snakes so that their growth curves fitted those of known age snakes within a given habitat. Residual values resulting from a regression analysis of snake SVL against $\log_{10}$ age using pooled data for either females or males from heath and plantations were compared using Student's t-test.

Testing for equal variances between variables was done using Levene's test. Where appropriate, a general linear model (GLM) was used to analyse the relationships between a specific performance metric and potential covariates e.g. female SVL and the number of embryos palpated for each habitat type with female age as a covariate, after first determining if there was a statistically significant relationship between the potential covariate and the metric using linear regression analysis. Tukey's test was used to determine pairwise differences between groups.

All statistical tests were considered significant at $P<0.05$ and all statistical analyses were completed using Minitab 16 (Minitab, 2010).

3. Results

Over the eight year duration of these two parallel studies of smooth snakes in Wareham Forest a total of 74 individuals (males and non-breeding females) were captured on the heath and 136 individuals within 11 of the 20 forestry plantations. No smooth snakes were found in the other nine forestry plantations. With the exception of one mature plantation (>55 years old), which had a low density of trees, smooth snakes were all found in young plantations (<20 years old).

3.1. Smooth snake densities

The Kolmogorov-Smirnov test (*KS*) showed that the snake density data for the heath and plantation arrays were not normally distributed (heath mean=3.60; SD=2.443; n=88; *KS* statistic=0.166; $P<0.01$; plantation mean=3.41; SD=3.669; n=88; *KS* statistic=0.215; $P<0.01$). The Kruskal-Wallis test was therefore used to compare relative snake densities between years and habitats (H statistic_{years}=6.69; df=7; P=0.462; H $\text{statistic}_{habitat}$=3.47; df=1; P=0.062) and showed that none of the comparisons were different (Fig. 1).

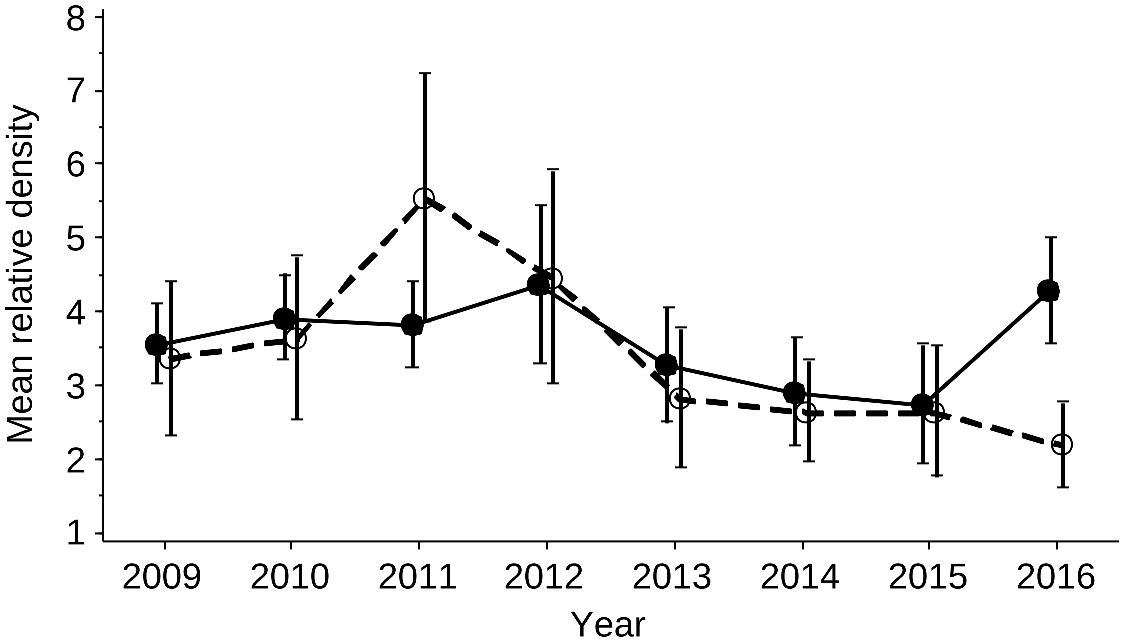


Fig. 1. Mean (±*SE*) annual relative smooth snake density in heathland (filled circles, solid line) and plantation (open circles, dotted line) arrays 2009-2016.

3.2. Smooth snake daily growth rates

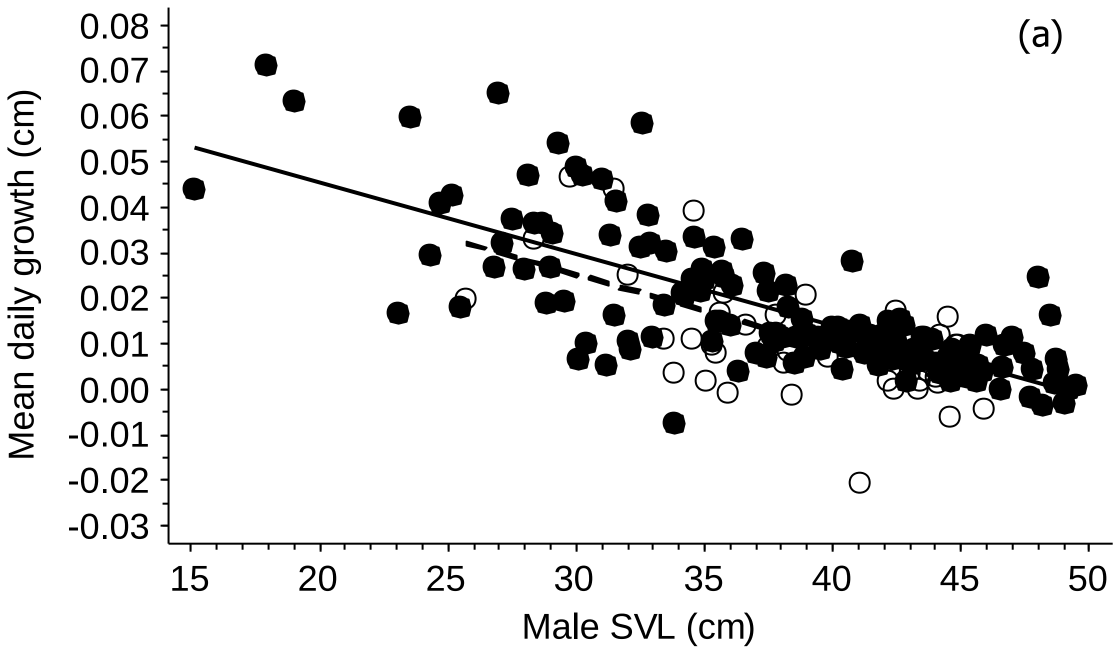
Growth rates were investigated in males and females separately as smooth snakes show sexual dimorphism with respect to SVL (Reading, 2004a). Levene's test showed that the variances between habitats did not differ for either males (test statistic=1.00; P=0.320) or females (test statistic=0.36; P=0.548). Initial GLM analysis of male mean daily growth rate against snake SVL between habitats, with habitat*snake SVL as an interaction factor, revealed that no between-habitat variation in growth was detectable (habitat*SVL interaction: F=0.00; P=0.944; df=1) and could be removed from the GLM. The GLM was then repeated without the interaction term and showed a statistically significant difference between habitats (F=7.07; P=0.009; df=1; Table 1).

Table 1

General Linear Model (GLM) results used for selecting which model best explained the observed variation for the parameter under examination. Best fitting models shown in bold.

Parameter	Model	df	F	p
SVL	Habitat	1	196.82	0.000
	Log_{10} age	**1**	**7096.92**	**0.000**
	Sex	1	784.77	0.000
	Error	499		
GROWTH	Habitat	1	18.87	0.000
	Sex	1	6.51	0.011
	SVL	**1**	**243.54**	**0.000**
	Error	304		
REPRODUCTIVE OUTPUT	Habitat	1	6.19	0.015
	Age	1	0.26	0.610
	SVL	**1**	**9.13**	**0.004**
	Error	67		
BODY MASS: Males	Habitat	1	24.06	0.000
	Log_{10} SVL	**1**	**5132.33**	**0.000**
	Error	311		
BODY MASS: Females	Habitat	1	2.57	0.112
	Log_{10} SVL	**1**	**934.70**	**0.000**
	Error	119		

Tukey's grouping information method showed that the mean daily growth rate for heathland males (0.01710 cm/day; n=137) was higher than that for plantation males (0.01245 cm/day; n=46; Fig. 2a). Similarly, no evidence for between-habitat difference of growth occurred in females (F=0.28; P=0.598; df=1) and the GLM was re-run with it removed. The subsequent GLM showed a statistically significant difference between habitats (F=12.93; P<0.001; df=1). Tukey's grouping information method showed that the mean daily growth rate for heathland females (0.02156 cm/day; n=87) was higher than for plantation females (0.01203 cm/day; n=38; Fig. 2b).



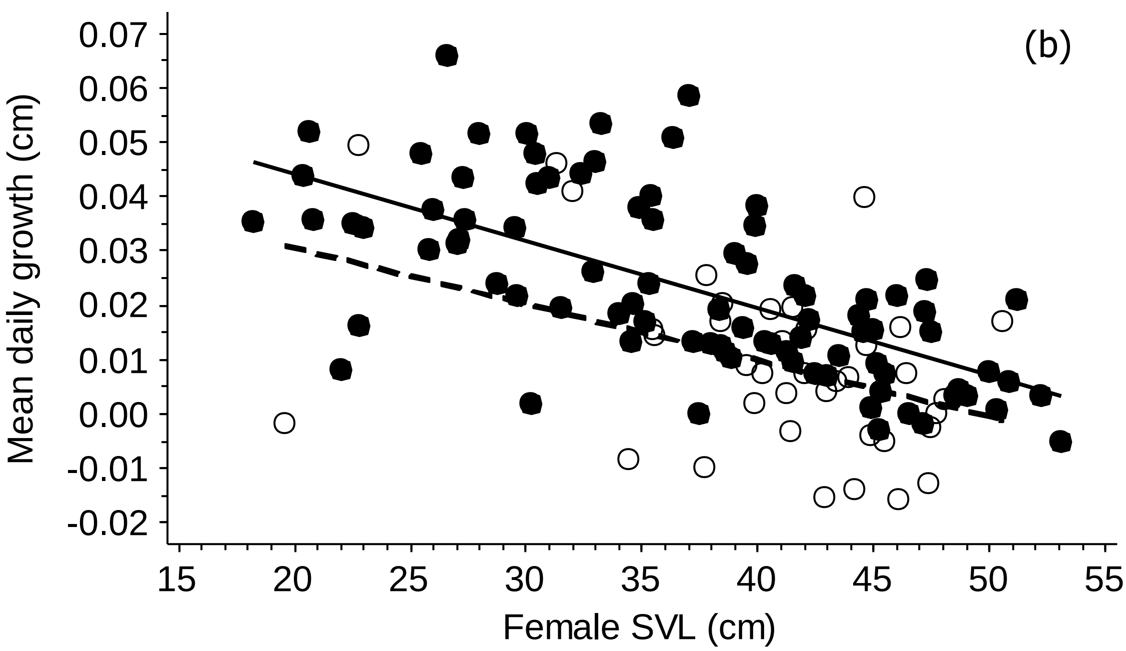


Fig. 2. Daily mean growth rates for smooth snakes from heathland (filled circle, solid line) and within plantations (open circle, dotted line). a) Males: Heath: Mean daily growth=0.08–0.001 male SVL; r^2=57.0%; P<0.001; n=137. Plantations: Mean daily growth=0.07–0.002 male

SVL; r^2=38.4%; P<0.001; n=46; b) Females: Heath: Mean daily growth=0.07–0.001 female SVL; r^2=42.6%; P<0.001; n=87. Plantations: Mean daily growth=0.05–0.001 female SVL; r^2=17.0%; P=0.01; n=38.

3.3. Smooth snake age

Plots of male and female SVL against estimated age (Fig. 3) suggest that for any given age heathland snakes are larger than those from plantations. Following a linear regression analysis of the pooled data for SVL against $\log_{10}$ age for males and females from heathland and plantations a comparison of the resultant residuals for each sex showed that heathland males and females were larger than plantation males and females (males: t=14.04; P<0.001; df=286; females: t=9.26; P<0.001; df=67).

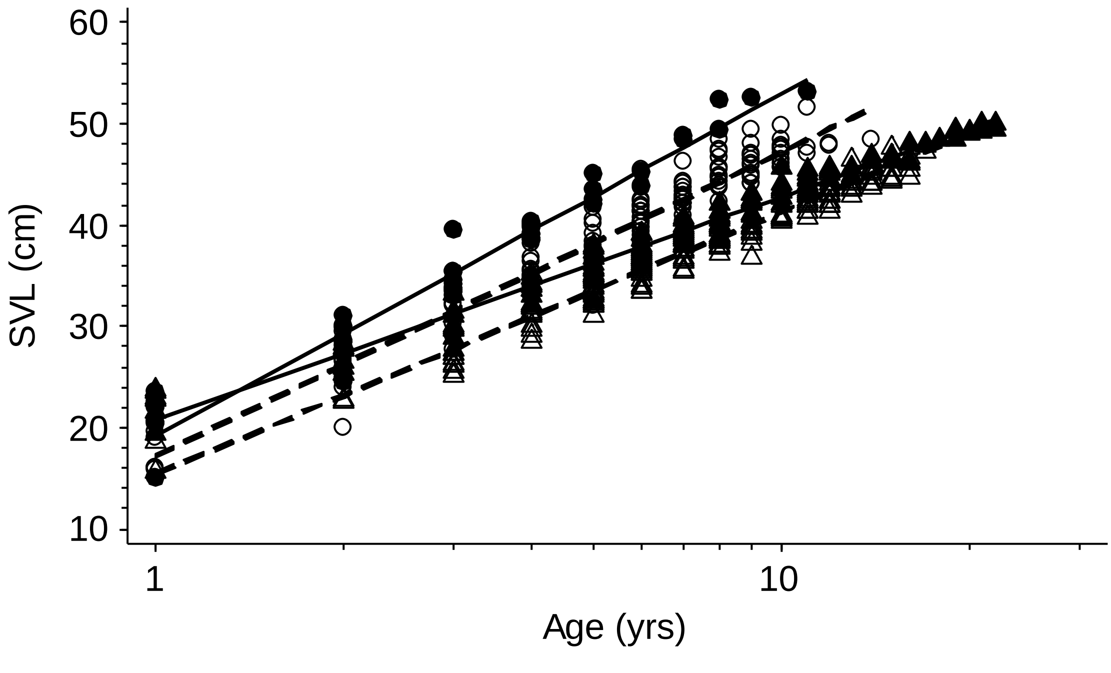


Fig. 3. Change in female (circles) and male (triangles) SVL with age on open heath (filled symbol, solid line) and in plantations (open symbol, dotted line). Fitted lines derived from regression plots: Heath females: SVL=19.2+33.7 Log_{10} age; r^2=96.4%; P<0.001; n=45.

Plantation females: SVL=17.2+30.0 Log_{10} age; r^2=93.5%; P<0.001; n=142.

Heath males: SVL=20.7+22.1 Log_{10} age; r^2=97.1%; P<0.001; n=127.

Plantation males: SVL=15.4+25.9 Log_{10} age; r^2=96.0%; P<0.001; n=189.

3.4. Reproductive output

A potential effect of reduced growth rates in plantation smooth snakes compared to those on heathland, is its impact on reproductive output in terms of the number of young produced by females of a given SVL (Fig. 4) with a potential covariate being female age. Levene's test showed that variances between habitats did not differ (test statistic=1.93; P=0.169). Regression analyses of the log_{10} number of palpated young against female age, and female SVL against female age, were both statistically significant allowing both to be entered into a GLM analysis

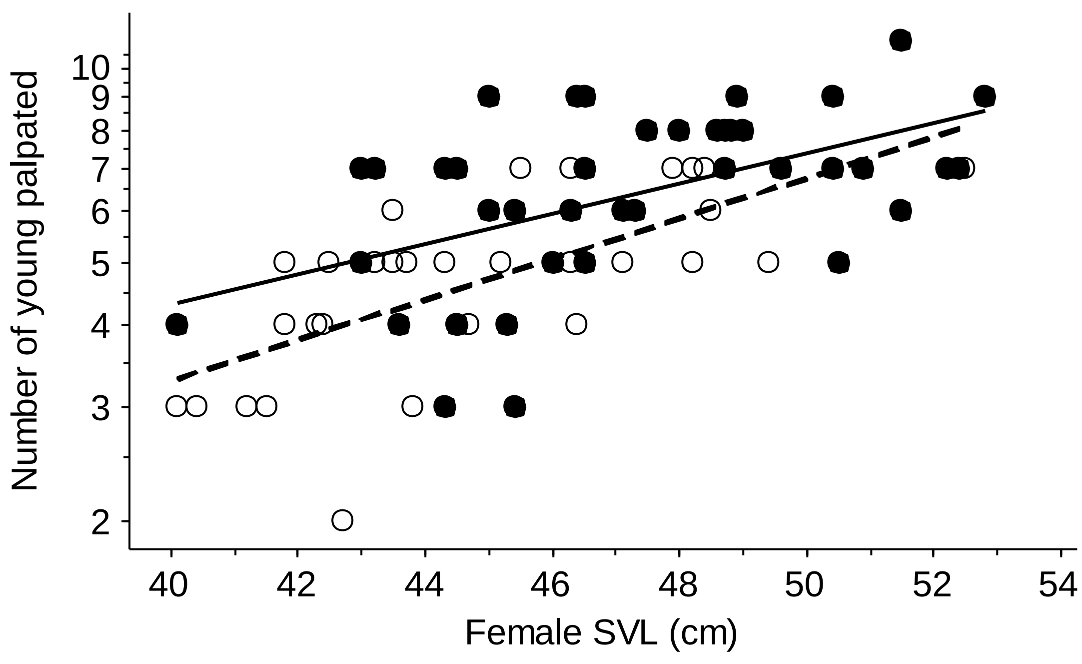


Fig. 4. Number of embryos determined by palpating gravid females inhabiting heathland (filled circle, solid line) and plantations (open circle, dotted line) with fitted regression lines.

Heath: Log_{10} no. embryos=-0.30+0.023 SVL; r^2=27.1%; P<0.001; n=41.

Plantations: Log_{10} no. embryos=-0.73+0.031 SVL; r^2=46.3%; *P*<0.001; *n*=30.

as covariates. In addition, interaction terms between habitat and both SVL and age were also included. Following an initial GLM analysis, and with the exception of SVL, all the interaction terms were statistically non-significant and were therefore removed from the GLM one at a time before further analysis. The final GLM showed a statistically significant (*F*=34.64; *P*<0.001; *df*=1) effect of female SVL, between habitat types (*F*=7.50; *P*<0.001; *df*=1; Table 1), on the number of young palpated. Tukey's grouping information method showed that the mean number of embryos found in heathland females was higher than the number found in plantation females (heath: mean=6.304; *n*=41; plantations: mean=5.318; *n*=30).

3.5. Survivorship

The capture data for males and females were analysed separately using Program MARK to estimate the survival rate of each sex within the two habitat types. Of the three GOF tests used to estimate ĉ (RELEASE: ĉ-males=0.7473; ĉ-females=0.1888; U-CARE: ĉ-males=0.8298; ĉ-females=0.2602; MARK: median ĉ-males=1.0536; median ĉ-females=1.1092) the median ĉ value (White & Burnham, 1999) for both males and females was selected and inserted into program MARK before re-running the analysis. The resultant best model for males (Table 2: $QAIC_c$ *weight*=0.714) was with survival rate (*Ø*=0.6407; *SE*=0.02725; *n*=7) independent of time or habitat and recapture rate independent of time but dependent on habitat ($p_{(heath)}$=0.9356; *SE*=0.04410; *n*=7: $p_{(plantations)}$=0.6610; *SE*=0.05798; *n*=7). The best model for females (Table 3: $QAIC_c$ *weight*=0.389) was with both survival rate (*Ø*=0.6048; *SE*=0.04766; *n*=7) and recapture rate (*p*=0.7263; *SE*=0.07014; *n*=7) independent of time and habitat.

Table 2 Model selection criteria for male smooth snake survival and recapture rates resulting from data analysis using Program MARK. Best fitting model, using a median deviance inflation factor (median ĉ=1.0536), estimated using Program MARK, is shown in bold.

Model	Model Rank	QAICc	Delta QAICc	QAICc Weight	Model likelihood	No. of parameters	Model Deviance
Phi(.) p(h)	**1**	**448.5934**	**0**	**0.71388**	**1**	**3**	**121.747**
Phi(h) p(h)	2	450.6148	2.0214	0.25983	0.364	4	121.7042
Phi(t) p(h)	3	456.6807	8.0873	0.01252	0.0175	9	117.1953
Phi(.) p(.)	4	457.3404	8.747	0.009	0.0126	2	132.542
Phi(h) p(.)	5	459.0178	10.4244	0.00389	0.0054	3	132.1715
Phi(.) p(h*t)	6	463.6474	15.054	0.00038	0.0005	15	110.8883
Phi(.) p(t)	7	465.5826	16.9892	0.00015	0.0002	8	128.2465
Phi(h) p(h*t)	8	465.8464	17.253	0.00013	0.0002	16	110.81
Phi(t) p(.)	9	466.0815	17.4881	0.00011	0.0002	8	128.7454
Phi(h) p(t)	10	467.3864	18.793	0.00006	0.0001	9	127.901
Phi(h*t) p(h)	11	468.6177	20.0243	0.00003	0	16	113.5812
Phi(t) p(h*t)	12	469.8000	21.2066	0.00002	0	20	105.4595
Phi(t) p(t)	13	471.7093	23.1159	0.00001	0	13	123.4481
Phi(h*t) p(.)	14	477.6003	29.0069	0	0	15	124.8412
Phi(h*t) p(h*t)	15	481.8064	33.213	0	0	26	102.8978
Phi(h*t) p(t)	16	483.9109	35.3175	0	0	20	119.5705

φ: Survival rate; p: Recapture rate; (h): Habitat; (.): denotes that the preceding parameter is constant over time; (t): denotes that the preceding parameter varies over time.

Table 3 Model selection criteria for female smooth snake survival and recapture rates resulting from data analysis using Program MARK. Best fitting model, using a median deviance inflation factor (median ĉ=1.1092), estimated using Program MARK, is shown in bold.

Model	Model Rank	QAICc	Delta QAICc	QAICc Weight	Model likelihood	No. of parameters	Model Deviance
Phi(.) p(.)	**1**	**221.5801**	**0**	**0.38926**	**1**	**2**	**88.3166**
Phi(h) p(.)	2	222.0537	0.4736	0.30718	0.7891	3	86.6949
Phi(.) p(h)	3	223.4714	1.8913	0.1512	0.3884	3	88.1126
Phi(h) p(h)	4	224.1791	2.599	0.10614	0.2727	4	86.6918
Phi(.) p(t)	5	227.437	5.8569	0.02082	0.0535	8	81.0868
Phi(h) p(t)	6	228.0602	6.4801	0.01524	0.0392	9	79.4027
Phi(t) p(.)	7	229.7875	8.2074	0.00643	0.0165	8	83.4374
Phi(t) p(h)	8	231.5751	9.995	0.00263	0.0068	9	82.9177
Phi(t) p(t)	9	234.2178	12.6377	0.0007	0.0018	13	75.9368
Phi(h) p(h*t)	10	236.9531	15.373	0.00018	0.0005	16	71.0113
Phi(.) p(h*t)	11	237.2284	15.6483	0.00016	0.0004	15	73.8846
Phi(h*t) p(.)	12	239.3832	17.8031	0.00005	0.0001	15	76.0394
Phi(h*t) p(h)	13	241.9475	20.3674	0.00001	0	16	76.0057
Phi(t) p(h*t)	14	244.4231	22.843	0	0	20	67.6169
Phi(h*t) p(t)	15	245.1465	23.5664	0	0	20	68.3403
Phi(h*t) p(h*t)	16	256.287	34.7069	0	0	26	61.6171

φ: Survival rate; p: Recapture rate; (h): Habitat; (.): denotes that the preceding parameter is constant over time; (t): denotes that the preceding parameter varies over time.

3.6. Numbers of individuals entering and exiting arrays

Between 2009 and 2016 the number of individual smooth snakes entering and exiting the heathland arrays (Fig. 5) did not vary across years (Number entering = -400.2 + 0.20 Year; r^2=11.6%; P=0.410; n=8; Number exiting = -64.7 + 0.03 Year; r^2=0.1%; P=0.940; n=7) and

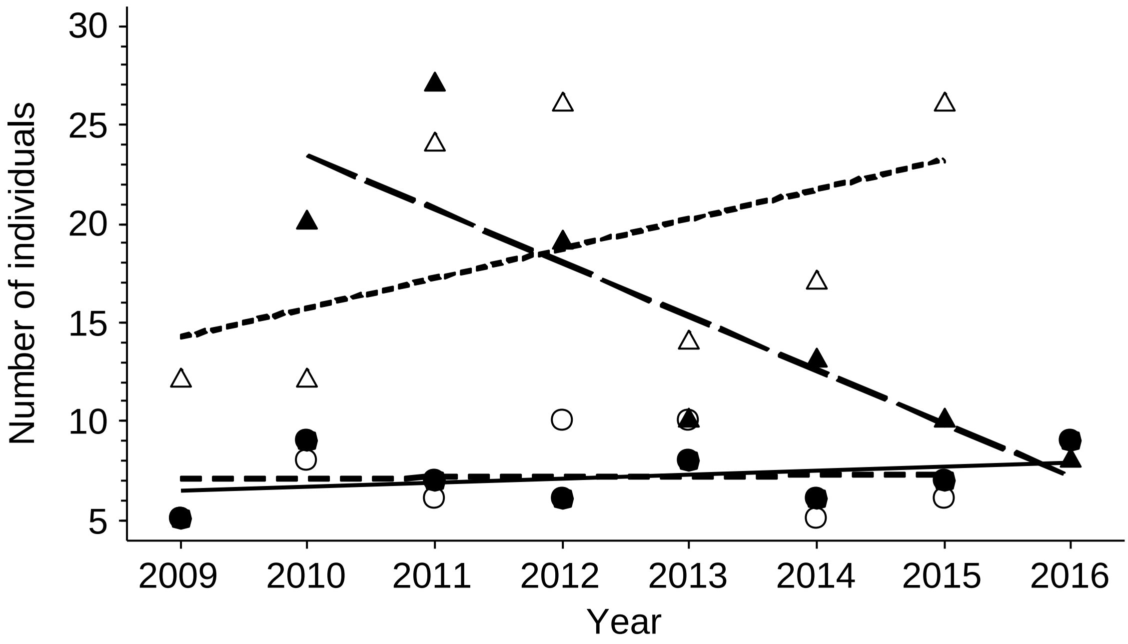


Fig. 5. Total number of smooth snake individuals exiting (Heath: open circle, short-dash line; Plantations: open triangle, dotted line) and entering (Heath: filled circle, solid line; Plantations: filled triangle, long-dash line) the heathland and plantation arrays each year.

were similar (Number entering: mean=7.13; *SE*=0.52; *n*=8; Number exiting: mean=7.14; *SE*=0.83; *n*=7; *t*=-0.02; *P*=0.986; *df*=10). In contrast, the number of snakes entering the plantation arrays declined over time (Number entering = 5479 - 2.71 Year; r^2=71.8%; *P*=0.016; *n*=7) whilst the number exiting showed an apparent, though not statistically significant, increase over the same period (Number exiting = -2999 + 1.50 Year; r^2=25.3%; *P*=0.25; *n*=7).

There was a statistically significant negative relationship between the number of individual smooth snakes entering the plantation arrays (No. entering=39.2–0.59 %Canopy Cover; r^2=64.2%; *P*=0.030; *n*=7) and tree canopy cover within them (Fig. 6). There was no detectable relationship between the number of individual snakes exiting the plantations arrays and tree canopy cover (No. exiting=2.1+0.461 %Canopy Cover; r^2=33.5%; *P*=0.17; *n*=7) though the overall trend was for the numbers exiting to increase as canopy cover increased (Fig. 6).

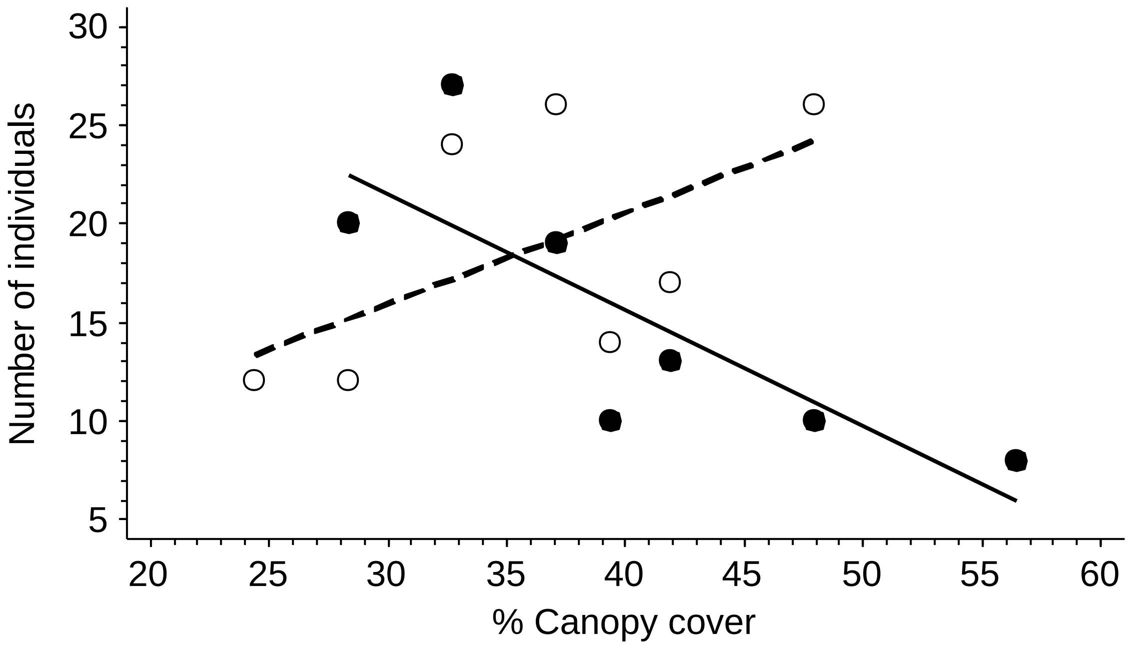


Fig. 6. Relationship between the total numbers of smooth snake individuals exiting (open circle, dashed line) and entering (filled circle, solid line) the plantations and % tree canopy cover.

3.6. Snake body mass and body condition

Levene's test showed that the variances of the heathland and plantation BM data were not statistically different (Test statistic=3.49; *P*=0.062). Regression analysis of $\log_{10}$ BM (males and non-breeding females) against $\log_{10}$ SVL for both habitats were statistically significant (*P*<0.001) enabling the data from the two habitats to be analysed using GLM with $\log_{10}$ SVL as the covariate and two interaction terms: habitat*$\log_{10}$ SVL and habitat*sex. The results showed that neither the allometric relationship between mass and SVL nor the relationship between mass and sex differed between habitat types and so the GLM was re-run with these terms removed. The results of the second GLM showed statistically significant differences between habitats in both the BM-SVL and BM-sex relationships (BM-SVL: F=5317.71; P<0.001; df=1; BM-sex: F=101.50; P<0.001; df=1). The data for males and females within the

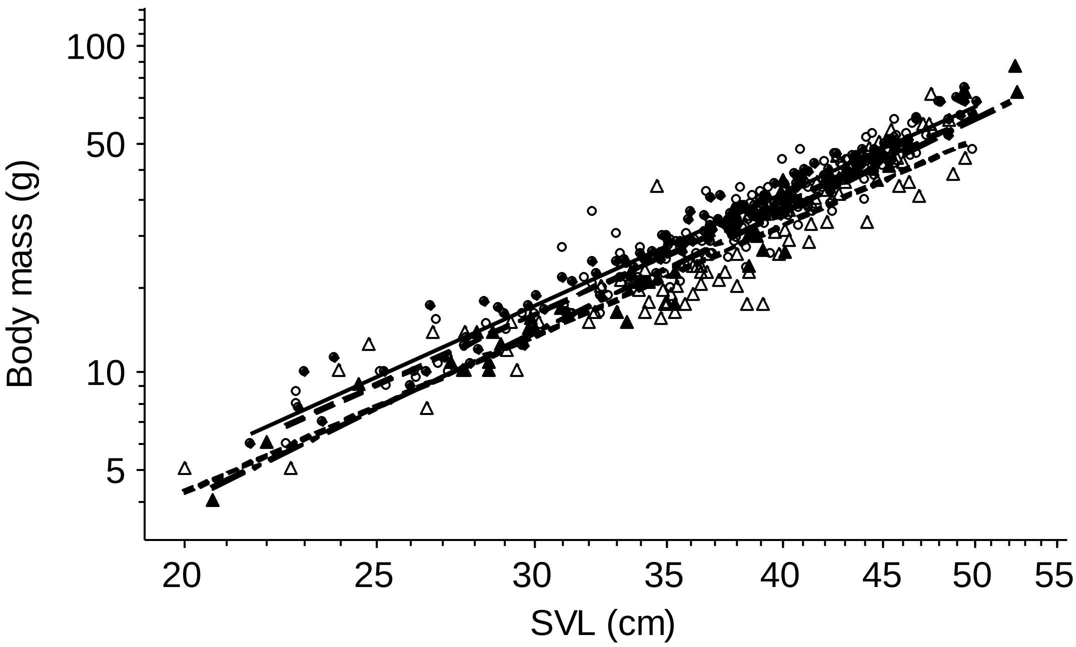


Fig. 7. Snake body mass (BM: gms) against snake snout-vent length (SVL: cm).

Heath males: (filled circle, solid line): $\log_{10}$ BM=-2.89+2.77 $\log_{10}$ SVL; r^2=96.6%; P<0.001; n=145. Plantation males: (open circle, dashed line: $\log_{10}$ BM=-2.87+2.74 $\log_{10}$ SVL; r^2=91.8%; P<0.001; n=169. Heath females: (filled triangle, dashed and dotted line: $\log_{10}$ BM=-3.27+2.97 $\log_{10}$ SVL; r^2=95.4%; P<0.001; n=37. Plantation females: open triangle, dotted line: $\log_{10}$ BM=-2.92+2.73 $\log_{10}$ SVL; r^2=85.0%; P<0.001; n=86.

two habitats were subsequently analysed separately with habitat*SVL as the interaction term in both. In both analyses the relationships between mass and SVL did not differ between habitats and so both GLM's were re-run with this interaction term removed (Table 1). Overall heathland males had a greater BM, in relation to SVL, than plantation males whilst there was no detectable difference for females between habitats (Fig. 7).

Levene's test for the homogeneity of variances for BC between heathland and plantation

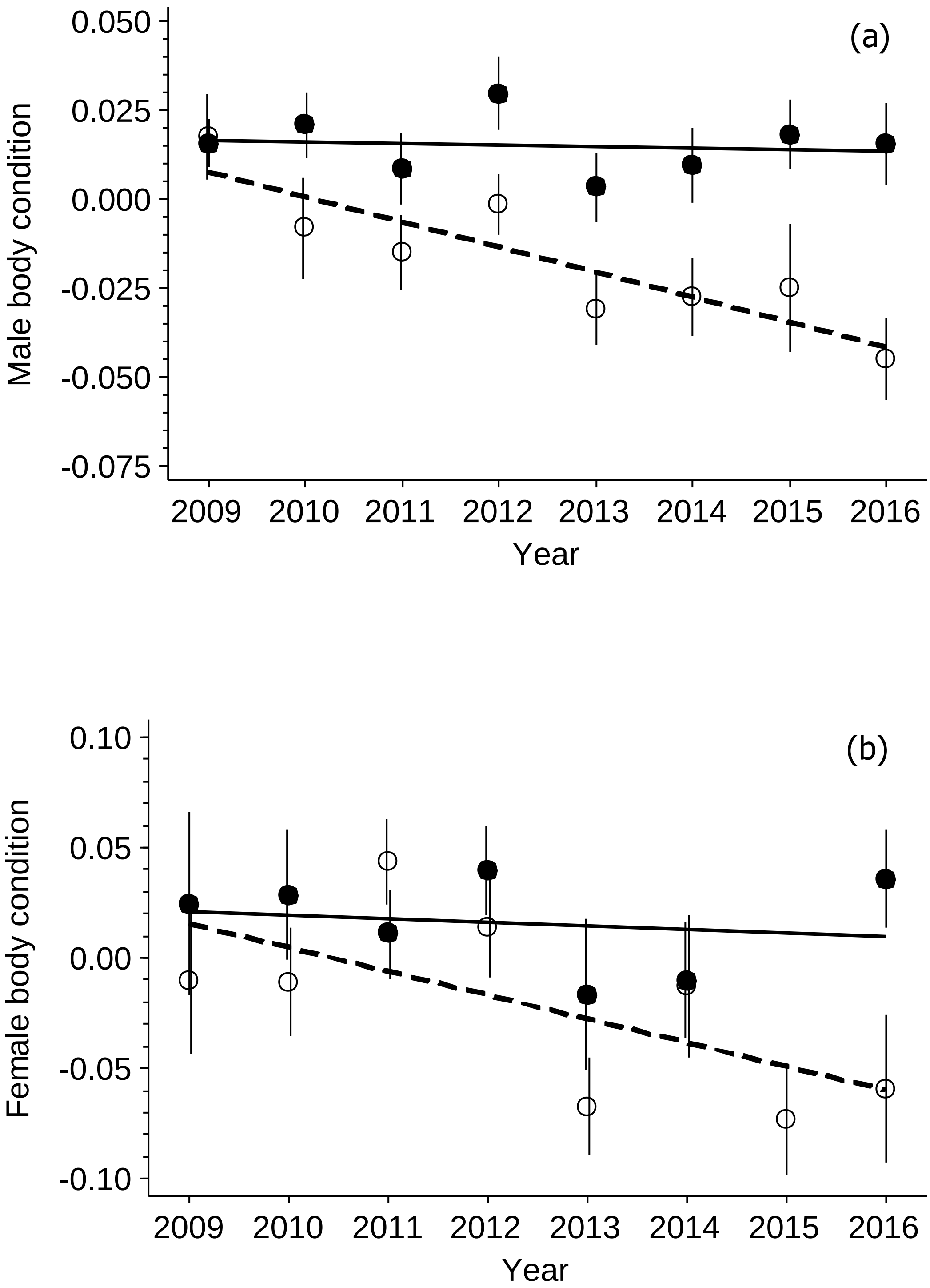


Fig. 8. Variation of mean (±*SE*) smooth snake body condition (BC) on heathland (filled circle, solid line) and within plantations (open circle, dotted line) between 2009 and 2016.
a) Males: Heath: BC=0.89-0.0004 year; r^2=1.7%; P=0.760; n=8. Plantations: BC=14.1-0.0070 year; r^2=77.4%; P=0.004; n=8; b) Females: Heath: BC=3.06-0.0015 year; r^2=2.7%; P=0.724; n=7. Plantations: BC=21.6-0.0108 year; r^2=40.5%; P=0.09; n=8.

snakes showed that they did not differ statistically (Test statistic=1.31; P=0.190). Regression analysis of BC against year for males (Fig. 8a) within each habitat showed that within the heathland male BC did not change over time (r^2=1.7%; P=0.760; n=8) whilst within the plantations there was a statistically significant decline (r^2=77.4%; P=0.004; n=8). Although the equivalent analysis for females (Fig. 8b) showed no statistically detectable changes in BC over time in either habitat type (Heathland: r^2=2.7%; P=0.724; n=7; Plantations: r^2=40.5%; P=0.090; n=8) the declining trend in their BC over time within the plantations was similar to that of males.

Between 2009 and 2016 the mean plantation tree canopy cover increased (Mean % Canopy Cover = -839 + 4.19 Year; r^2=97.0%; P<0.001; n=8) from approximately 24% in 2009 to approximately 56% in 2016 with a resultant statistically significant negative relationship between mean snake BC and mean % tree canopy cover in males (r^2=75.4%; P=0.005; n=8) but not in females (r^2=37.6%; P=0.106; n=8: Fig. 9).

3.7. Snake diet

Between 2009 and 2015 a total of 145 faecal samples were collected from heathland smooth snakes and 165 from plantation smooth snakes. No statistically significant difference (χ^2=1.10; df=1; P=0.29) was found between the proportions of Lacertids and small mammals (adult, juvenile and nestling *S. minutus* and *S. araneus*, and nestling *A. sylvaticus*, *M. agrestis*) found in the diet of heathland and plantation snakes. Nor did the proportion of Lacertids and small mammals in the diet of plantation snakes differ significantly between years (χ^2=4.26; *df*=6; *P*=0.64).

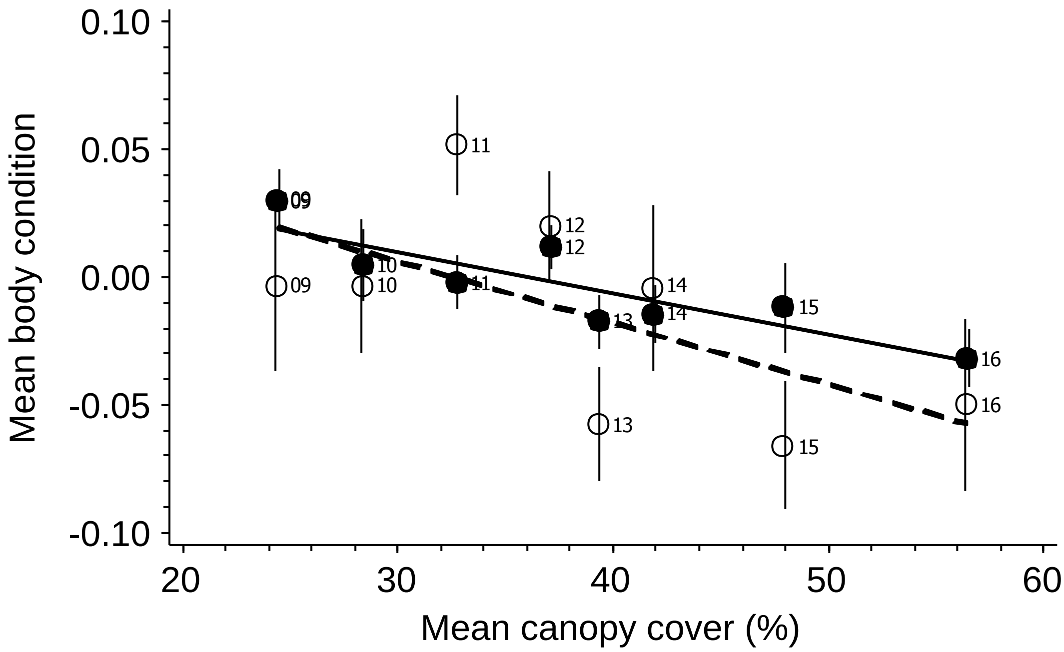


Fig. 9. Mean male (filled circle, solid line) and female (open circle, dotted line) body condition (BC±*SE*) of plantation snakes in relation to mean % tree canopy cover (2009-2016). Years are shown against each point. Male BC=0.0583-0.0016 Canopy cover; r^2=75.4%; *P*=0.005; *n*=8. Female BC=0.0783-0.0024 Canopy cover; r^2=37.6%; *P*=0.106; *n*=8.

4. Discussion

There has been, and continues to be, ambiguity in the terminology used in studies investigating a species performance within given habitat types (Murphy & Noon, 1991; Hall et al., 1997). For the purposes of this paper we are using the terms habitat 'quality' rather than 'suitability' and individual and/or population 'performance', rather than 'fitness' to describe the impact of habitat attributes on individuals and, as a consequence, on populations within a given habitat type.

Performance of an individual, or population, of an animal species should be measured in terms of their growth rate, reproductive output, body condition, and survivorship within the habitat type under investigation and over a prolonged period of time (Gaillard et al., 2010).

We estimated the annual number of snakes that ceased to be captured within individual arrays, and therefore assumed to have either emigrated or died, and the number of new snakes recruited into the heathland and plantation arrays each year. Within the heathland the number of smooth snakes remained relatively stable, with emigration/mortality being counterbalanced by recruitment, suggesting that this habitat was at, or about, carrying capacity over the duration of the study. This differed from the plantations where emigration was, at best, stable though the data hinted at increasing emigration over time, but where there was a detectable decline in recruitment. This suggests that the carrying capacity of the plantations was declining and that their quality, with respect to smooth snakes, was diminishing as a result of factors other than snake density. Indeed, we found a negative correlation between the declining number of new arrivals to the plantation arrays and increasing tree canopy cover within them. A similar negative impact of increasing canopy cover has also been reported for open-habitat reptile assemblages in south-eastern New South Wales, Australia (Pike et al., 2011).

We also found that the daily growth rates of both female and male smooth snakes were, on average, lower for those individuals from plantations than those from heathland and that plantation males also had a lower BM for a given SVL than those from heathland whilst in females there was no difference. Either taken individually, or together, these findings suggest that the energy intake rate, in terms of the availability and/or quality of prey, may have been lower in the plantations than on the open heath. The negative impact of reduced energy intake on BC and growth rate has also been reported for a population of western cottonmouths

(*Agkistrodon piscivorus leucostoma*) in the Ozark Mountains of the USA (Hill & Beaupre, 2008). Evidence supporting the cause of reduced BC in the smooth snake being related to a reduction in prey availability was found in a previous study, within the same study sites, that investigated how reptiles utilise conifer plantations of varying age (Jofré et al., 2016) and where the relative density of common lizards (*Z. vivipara*), an important prey species for smooth snakes (Reading & Jofré 2013), reached peak densities in relatively young plantations (3-12 years old), with a tree canopy cover of approximately 10%, before declining sharply in older plantations (>12 years old) where canopy cover exceeded approximately 30%. The decline in common lizard numbers in relation to plantation age and tree canopy cover also preceded the decline in smooth snake numbers within the same plantations (Jofré et al., 2016). Additionally, we found that the point at which the decline in the number of new smooth snakes entering the plantations fell below that of the number leaving coincided with a tree canopy cover of approximately 35% and the subsequent reduction in ground vegetation cover (Jofré et al., 2016).

Analysis of the frequency of prey types found in the faeces of plantation snakes showed that their diet was not markedly different from that of heathland snakes. One possible consequence of the declining abundance of Lacertids (*Z. vivipara* and *L. agilis*) in plantations in relation to increasing plantation age and canopy cover (Jofré et al., 2016) that might have been expected would be an increase in the frequency of small mammals in the diet. This was not found and suggests that the abundance of small mammals might also have declined with increasing plantation age and canopy cover. This possibility is supported by previous work on small mammal assemblages (rodents and insectivores) in Ethiopia (Tilahun et al., 2012) and Malawi (Happold & Happold, 1987) where the number of species and their densities were all lower in plantations than in natural habitats and also declined with increasing plantation age.

An additional consequence of the reduced growth rates found in plantation snakes, compared to heathland snakes, was the smaller SVL for both females and males for any given estimated age. The significance of this lies in its potential impact on the age at which females, in particular, reach sexual maturity. The attainment of sexual maturity in smooth snakes is related to SVL (Reading, 2004a), with females starting to breed at an SVL of approximately 40cm. The number of offspring produced by females is also positively correlated with female SVL (Reading, 2004b). This would predict that plantation females should breed at a greater age, and/or produce fewer young for a given age, than heathland females. This prediction is supported by our finding that, for any given female SVL, fewer embryos were palpated in plantation females than heathland females.

All three life history traits (growth rate, reproductive output, and survivorship), usually used as a measure of habitat quality, are dependent to varying degrees on an animal's BC (Shine et al., 2001; Litzgus et al., 2008; Harrison et al., 2011; Gallego-Carmona et al., 2016; Sasaki et al., 2016) which in turn reflects the availability of energy, in terms of food/prey abundance and quality, within the habitat. Our study shows that the BC of heathland snakes remained relatively constant whilst that of plantation snakes, which was initially similar to that of heathland snakes, declined with increasing plantation age and was negatively correlated with increasing tree canopy cover. Reduced female BC resulting from poor pre-breeding rates of energy intake have been shown to adversely affect reproduction in a wide range of 'capital breeding' vertebrate taxa (Harrison et al., 2011) including the smooth snake (Reading, 2004b).

The survival rates of both females (60.5%) and males (64.1%) were similar in both habitats and implies that although snake growth rate and reproductive output, both dependent on body condition, may be negatively impacted by a sub-optimal habitat this need not reduce survivorship, as might have been expected, at least in the short term (8 years in the current study). Given that smooth snakes can attain ages in excess of 15 years (Reading, 2004a), prolonged survivorship at a lower body condition, but with a reduced growth rate and/or reproductive output, may enable an animal to take advantage of improving habitat conditions, should they subsequently occur.

With the exception of survivorship we found detectable differences in all of the 'performance' metrics we investigated for smooth snakes inhabiting the two habitat types within Wareham Forest. This suggests strongly that although young plantations, with short trees, low canopy cover, and high ground vegetation cover, may have a similar quality, with respect to smooth snakes, as open lowland heath, their quality declines over time and this decline may be due to the impact of increasing tree canopy cover on prey availability, particularly that of common lizards and possibly small mammals, through its impact on ground vegetation cover (Reading & Jofré, 2016). Managed conifer plantations may therefore represent an example of a 'type 2' habitat trap (Robertson & Hutto, 2006) i.e. after a species has colonised a particular habitat type on the basis of its quality at the time of colonisation, the habitat parameters then change over time reducing its quality for that species. A similar reduction in BC with increasing forest age (increasing canopy cover) was found in the salamander *Plethodon elongatus* though not in *P. stormi* inhabiting forest in the Pacific northwest of the USA (Welsh et al., 2008). However, these inferences, with respect to smooth snakes, are based on correlations which do not necessarily imply causality although the decreasing common lizard density within the plantations, in relation to plantation age and tree canopy cover, is a strong indication that this may be the case (Jofré et al., 2016).

Further strong evidence supporting this proposed causality would be to find a reduction in the feeding frequency of smooth snakes, over time, within the plantations compared to the open heath, assuming prey quality remained unchanged. Unfortunately, it was not possible to determine feeding rates or meal size/quality as the individual snakes were not radio-tracked, and could not therefore be continuously monitored.

Although different habitat types may support similar densities of a particular animal species their qualities may not be equal for that species. Our results suggest that, though not increasing snake performance within plantations to those levels found on open heath, reducing canopy cover might be beneficial for the conservation of Britain’s rarest snake by lengthening the time period over which the plantations remain suitable for them. However, we do not think that reducing canopy cover is either feasible, advisable, or acceptable on economic, silviculture or conservation grounds (Jofré et al., 2016). To maximise the period over which reptiles can utilise the plantations, management practices that reduce ground vegetation cover, critical for supporting smooth snake prey species (e.g. lizards and small mammals; Reading & Jofré, 2013), should be discontinued. The density of smooth snakes, and other reptile species, inhabiting lowland heath are known to be positively correlated with the structure (height and cover) of the ground vegetation (Reading & Jofré, 2015, 2016) as is the relationship between ground vegetation cover and tree canopy cover that was clearly demonstrated in a previous study of how reptiles use conifer plantations of varying ages in Wareham Forest (Jofré et al., 2016). The importance of natural vegetation over either a sown monoculture crop or no vegetation cover, for reptile diversity in commercial plantations has been clearly demonstrated in Spanish olive groves (Carpio et al., 2017). Forest management practices that have a negative impact on ground vegetation cover and structure within plantations e.g. cattle grazing (Reading & Jofré, 2015, 2016) and the use of herbicides, will reduce reptile density and diversity and also the time period over which they are utilised by reptiles. Plantations with a combination of high canopy cover and low ground vegetation cover will support the fewest reptiles over the shortest period of time. Despite this, a managed forest comprising a mosaic of relatively small plantations of varying ages may, nevertheless, represent an important sustainable source of reptiles potentially able to colonise new areas as and when they become available.

5. Conclusions

Our study of smooth snakes inhabiting lowland heath and conifer plantations has shown that although their densities did not differ significantly between habitats, the heathland snakes performed better than those in plantations having higher growth rates, being larger for any given age, having a higher body condition and females producing more young for a given body size. The number of new individuals entering and leaving the heathland were similar over time suggesting that this habitat was at carrying capacity whilst the number of new individuals entering the plantations declined significantly and the number leaving showed an increasing trend over time suggesting that the plantations were becoming less suitable. The body condition of the heathland snakes also remained relatively constant whilst that of the plantation snakes, though initially similar to that of heathland snakes, declined progressively and this decline was correlated with increasing canopy cover and suggested that the energy intake of plantation snakes was less than that of heathland snakes. A possible cause of this was the observed decline in the number of common lizards in the plantations, a critical prey species for smooth snakes. Despite these differences in snake performance metrics between habitats we found no evidence for reduced snake survivorship in the plantations compared to the open heath.

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