Effects of large-scale heathland management on thermal regimes and predation on adders *Vipera berus*

Animal Conservation

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Figures & tables

Figure 1 Example female (brown) and male (grey) Plasticine model adders used in this study.

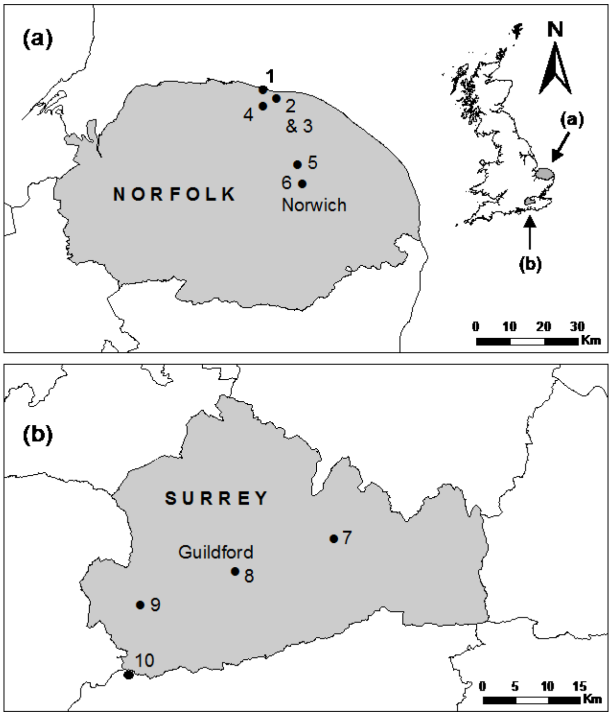


Figure 2 Locations of study heathlands in (a) Norfolk: 1 = Salthouse Heath, 2 = Kelling Heath 1, 3 = Kelling Heath 2, 4 = Holt Lowes, 5 = Buxton Heath, 6 = Horsford Woods and (b) Surrey: 7 = Headley Heath, 8 = Blackheath Common, 9 = Thursley Common, 10 = Marley Common. Inset shows study region locations within the UK.

Table 1 Attributes of the 10 lowland heathland sites included in this study

Site	Area (ha)	Grazing intensity (livestock ha^{-1})	Number of models
Horsford Woods	124	n/a	80
Buxton Heath	67	0.15	60
Holt Lowes	50	0.14	70
Salthouse Heath	95	n/a	90
Kelling Heath 1	89	n/a	90
Kelling Heath 2	89	n/a	70
Marley Common	21	0.14	70
Thursley Common	325	n/a	60
Blackheath Common	101	n/a	60
Headley Heath	204	n/a	120

Figure 3 Examples of areas of (a) cleared (a large recently mown area alongside a busy footpath at Blackheath Common) and (b) structurally complex heathland vegetation (Kelling Heath), and (c) a male adder crossing a large mown area (Kelling Heath, April 2015).

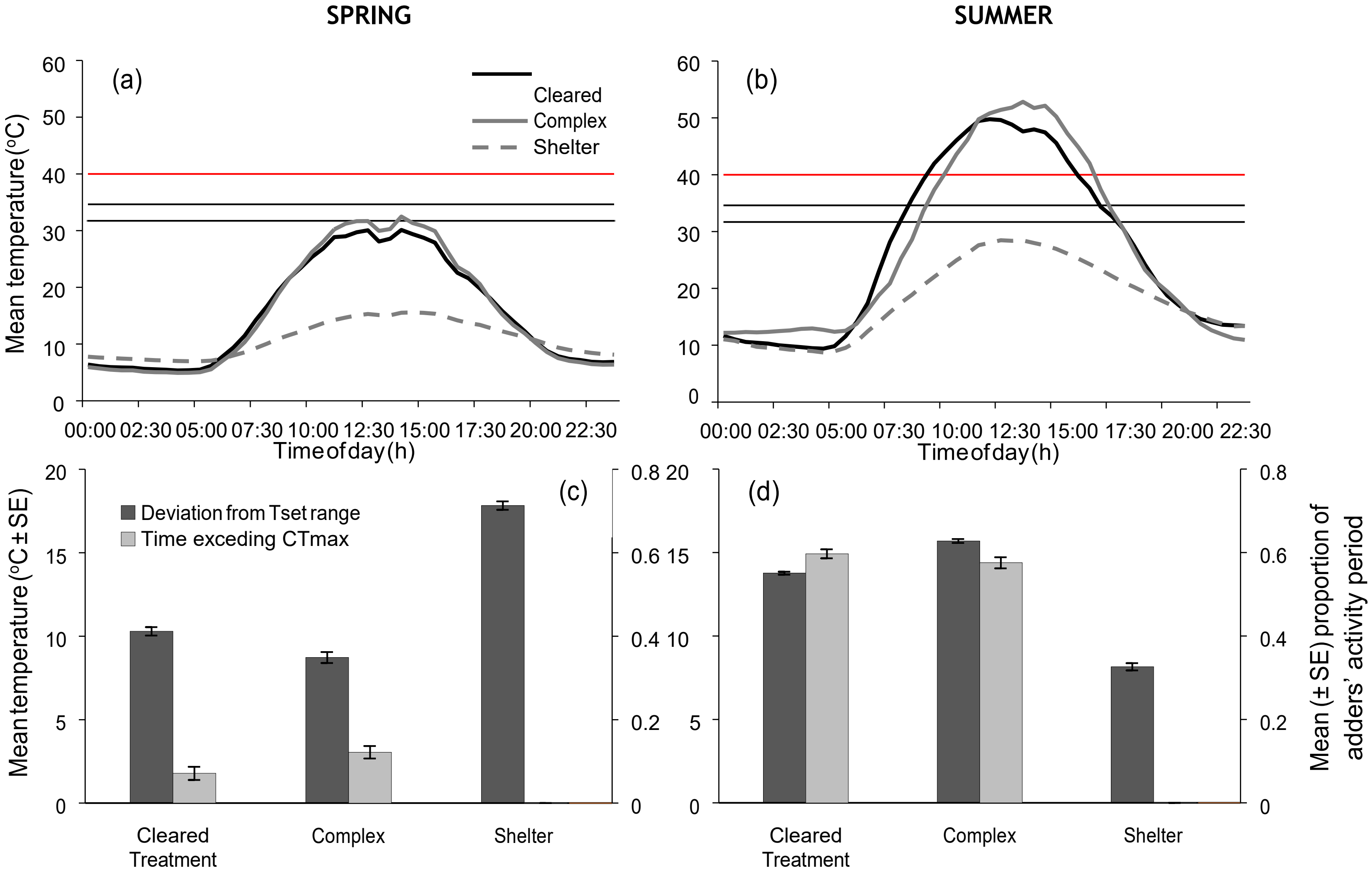


Figure 4 Daily cycle of operative temperatures (T_e: means per 30 minute interval) on cleared, complex and sheltered microhabitats on heathlands in (a) spring and (b) summer (black horizontal lines indicate adders' preferred temperature range (T_{set}) measured in a laboratory thermal gradient by Herczeg et al. (2007) and Lourdais et al. (2013), and red horizontal lines indicate the estimated critical thermal maximum temperature (CT_{max}) for adders (Brattstrom, 1965; Spellerberg, 1972)), and mean deviations of T_e from T_{set} during the diurnal activity period (08:00-20:00) and the proportion of the activity period in which T_e exceeds CT_{max} in (c) spring and (d) summer. **Operative temperature in sheltered areas was significantly lower than in cleared (GLMM post-hoc test, z = -8.259, p < 0.001) and complex areas (z = 9.104, p < 0.001), which were not significantly different from one another (z = 0.788, p = 0.711).**

Table 2 Model structures used in the analyses of variation in operative temperatures, the risk of attack on adders and the number of recreational visitors to heaths.

Model response	Distribution	Model structure
Operative temperature (T_e)	Normal	Time of day + Treatment * Season + (1 | Day) + (1 | Logger ID) + (1 | Site)
Attack rate	Binomial (logit)	Region + Site + Sex + Distance to path * Treatment
Number of people	Poisson (log)	Day + Site + Activity

Table 3 Results of a generalised linear mixed model of variation in operative temperatures (T_e) of biophysical models on lowland heaths in different management treatments (cleared, complex, shelter) throughout the day (30 min periods between 08:00 and 20:00) in spring (April) and summer (July). Significant variables are highlighted in bold.

Variable	Estimate	SE	DF	T	P
(Intercept)	7.63	1.07	18	7.148	<0.001
Treatment	**0.54**	**0.08**	**2322**	**6.966**	**<0.001**
Time of day	**-0.42**	**0.008**	**2322**	**-49.537**	**<0.001**
Season	**17.11**	**0.19**	**2206**	**89.607**	**<0.001**
Treatment * Season	0.16	0.19	2322	0.805	0.421

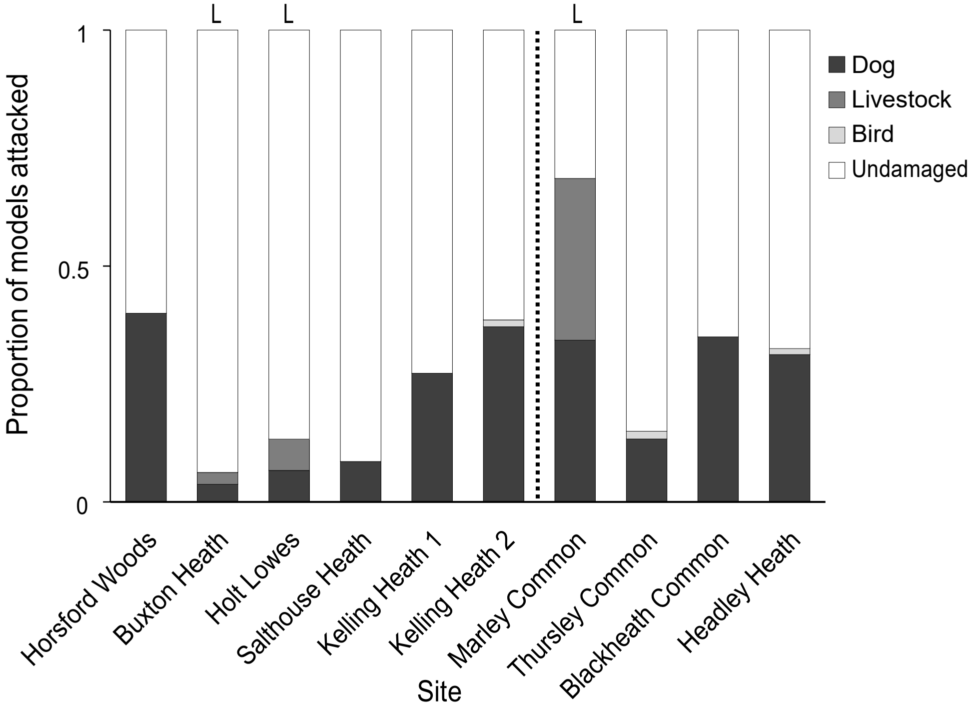


Figure 5 The proportion of adder models attacked on each of the ten heathland sites and the relative proportion attacked by dogs and birds and trampled by livestock (L = sites with grazing livestock) . The dotted line divides the six Norfolk sites and four Surrey sites.

Table 4 Results of generalised linear mixed models of the risk of attack of adder models by all predators combined, and attacks by dogs and livestock trampling separately, in different management treatments (cleared and complex) and at different distances from footpaths on lowland heaths. Significant variables are highlighted in bold.

Predator	Variable	Estimate	SE	Z	P
All attacks					
	(Intercept)	**1.6**	**0.48**	**3.36**	**<0.001**
	Treatment	**-2.01**	**0.42**	**-4.75**	**<0.001**
	Dist. to path	**-0.09**	**0.01**	**-7.57**	**<0.001**
	Sex	0.4	0.21	1.89	0.06
	Treatment * Dist. to path	0.02	0.02	0.96	0.33
Dogs					
	(Intercept)	**1.71**	**0.49**	**3.5**	**<0.001**
	Treatment	-0.83	0.56	-1.49	0.14
	Dist. to path	**-0.1**	**0.01**	**-7.61**	**<0.001**
	Sex	0.4	0.24	1.64	0.1
	Treatment * Dist. to path	**-0.08**	**0.04**	**-2.3**	**0.02**
Livestock					
	(Intercept)	-0.61	1.26	-0.49	0.63
	Treatment	-0.49	1.05	-0.47	0.64
	Dist. to path	-0.03	0.02	-1.59	0.11
	Sex	-0.78	0.48	-1.62	0.11
	Treatment * Dist. to path	0.02	0.03	0.55	0.58

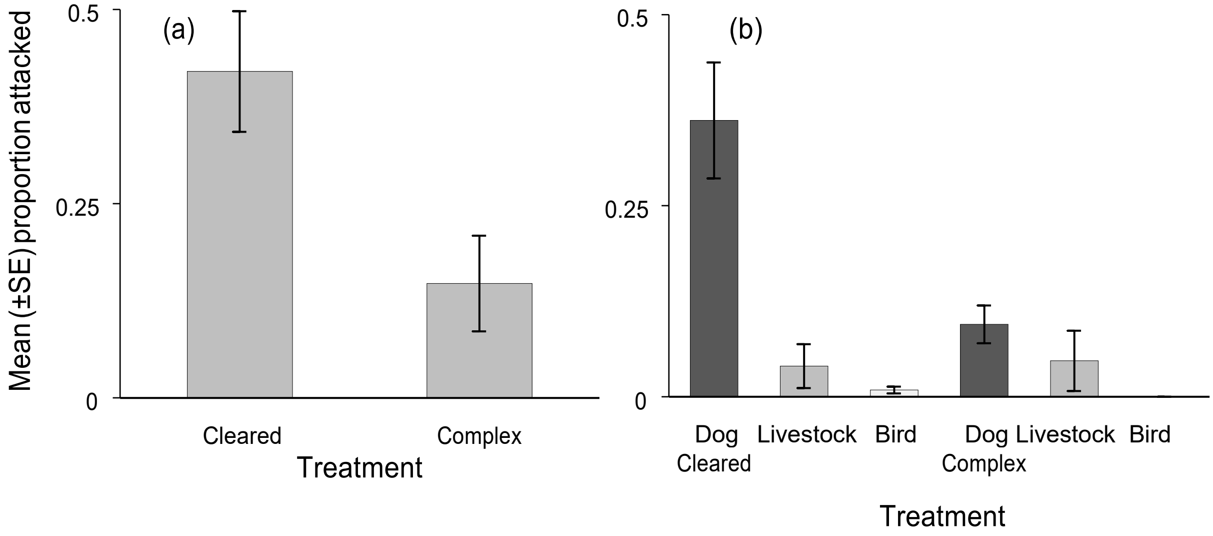


Figure 6 The mean (±SE) proportion of adder models (a) attacked, and (b) attacked by dogs, birds and livestock, in cleared and complex areas across 10 heathland sites.

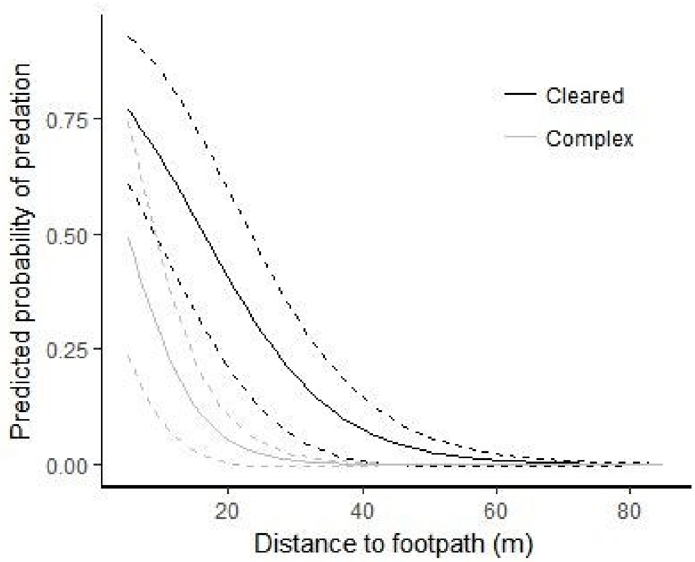


Figure 7 Variation in the risk of attack of model adders by dogs in relation to distance to the nearest footpath, on cleared and complex areas of heathland. Dotted lines indicate 95% confidence intervals.

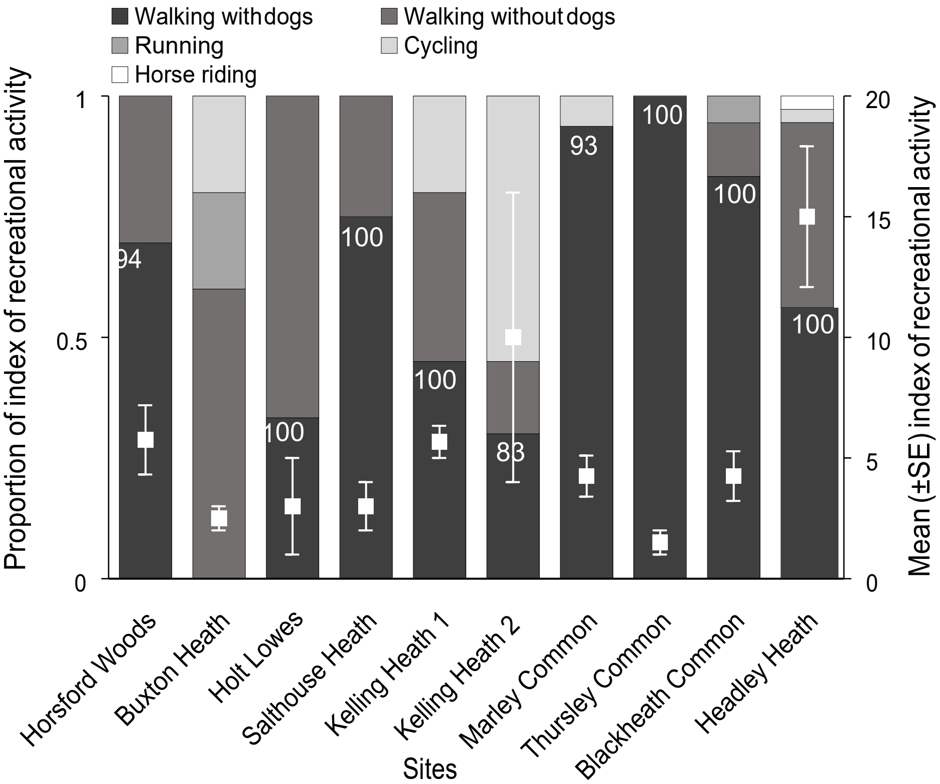


Figure 8 The mean index of recreational activity at each of the ten heathland sites studied in May 2015 and the relative contribution of each of the five constituent components of the index, on each of the sites. The percentage of dogs off-lead is also given for each of the sites where walking with dogs occurred.

Table 5 Results of a general linear model of the number of human visitors undertaking different activities (see Fig 8) recorded during surveys of recreational activity on 10 lowland heathland sites. Significant variables are highlighted in bold.

Variable	DF	Deviance	Residual DF	Residual deviance	P
Day	3	7.211	41	136.896	0.065
Site	**8**	**79.307**	**33**	**57.589**	**<0.001**
Activity	**4**	**30.118**	**29**	**27.471**	**<0.001**

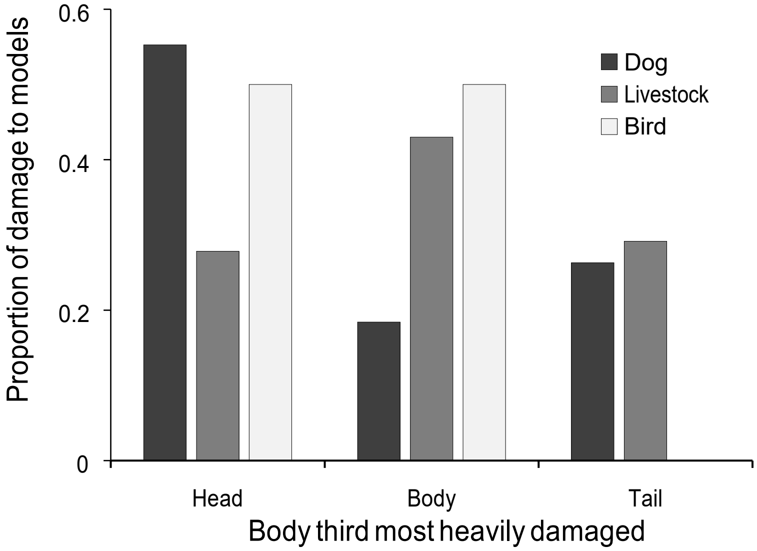
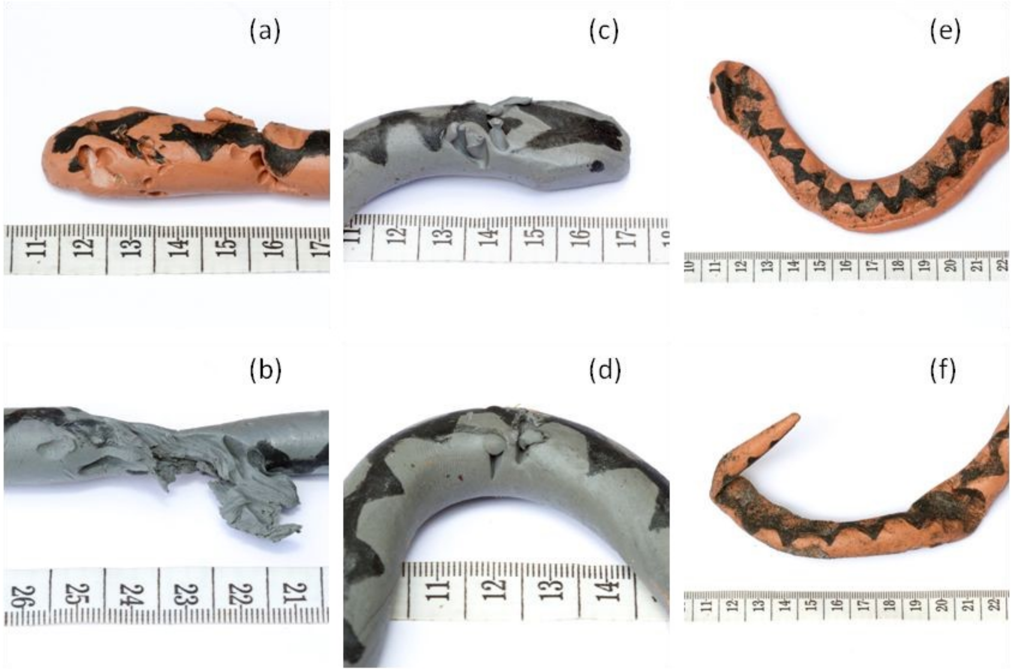


Figure 9 The proportion of damage to body sections among model snakes attacked by dogs and birds, and trampled by livestock.

Appendices



Appendix 1 Imprints left on adder models showing (a & b) tooth marks from dog attack, (c & d) bill marks from bird attack, and hoof marks from trampling by grazing (e) cattle and (f) pony.

Appendix 2 Dead adders found on heaths by JWH showing injuries apparently consistent with (a) dog attack and (b) trampling by grazing livestock.

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Short title: Effects of heathland management on the adder

Key words: habitat management, heathland, conservation, thermoregulation, predation, reptile, adder

Abstract

Management prescriptions for species of conservation concern often focus on creating appropriate habitat conditions, but the spatial scales over which these actions are applied can potentially impact their success. In Northwestern Europe, preventing further loss of lowland heathland through successional changes often involves the mechanical removal of vegetation, creating large blocks of open homogenous habitat. We investigate the influence of this broad-scale habitat management on a heathland specialist, the adder *Vipera berus*. By deploying temperature loggers and Plasticine adder models in heathland areas with and without complex vegetation cover, we show that (1) cleared areas lack both the temperature variation adders need to thermoregulate effectively and suitable refuges from dangerously high summer temperatures, and (2) attacks by dogs and trampling by grazing livestock are significantly more frequent in cleared areas and closer to footpaths. Habitat management strategies that retain some structural complexity of vegetation within cleared areas, and diverting footpaths away from cleared areas and/or strategic placement of barrier hedging around these areas could potentially reduce the exposure of adders to high predation risk and thermal extremes.

Introduction

The physical structure of habitats in anthropogenic landscapes is often dependent on human-directed disturbance regimes (Faegri, 1988; Lawton, 1999). Management that provides structural complexity can be important for wildlife because heterogeneous habitats typically provide more niches and resources (e.g. Simpson, 1949; Macarthur & Wilson, 1967; Lack, 1969; Bazzaz, 1975), and can benefit both faunal abundance and community diversity (Davidowitz & Rosenzweig, 1998; Tews *et al*., 2005). However, the spatial scale at which such management should operate is often unclear. Coarse-filter approaches to vegetation management are often employed to create appropriate conditions for a range of species characteristic of an area (Simberloff, 1998; Groves, 2003; Wiens *et al*., 2008). However, such generic management prescriptions can potentially lead to unintended consequences for species of conservation concern (Dolman, Panter & Mossman, 2012).

Lowland heathland of north-western Europe developed ~4000 years ago as a result of forest clearance, and has been maintained since by disturbance regimes including livestock grazing, burning, turf-cutting and harvesting of heather and bracken (Gimmingham, 1972; Webb, 1998). Over the last century, declines in these traditional land management practices have resulted in successional vegetation changes (Skogen, 1987; Webb, 1998; Mitchell *et al*., 2000; Fagúndez, 2013) and significant loss and fragmentation of heathland (Rose *et al*., 2000; Alonso, 2004; Newton *et al*., 2009). The UK has ~20% (58 000 hectares) of the remaining lowland heathland in north-western Europe (UK Biodiversity Steering Group, 1995), **often occurring in relatively small patches covering tens of hectares.** Consequently, it is listed under Annex I of the EU Habitats Directive and a priority habitat under the UK Biodiversity Action Plan.

Mimicking traditional land-use, various management practices have been applied to halt the loss of heathland, including grazing at different stocking rates (Bokdam & Gleichman, 2000; Pakeman *et al*., 2003), burning (Hobbs & Gimingham, 1984a, 1984b; Mallik & Gimingham, 1985; Britton *et al*., 2001), mechanical cutting (Calvo, Tarrega & de Luis, 2002) and turf stripping (Bokdam & Gleichman, 2000). While these modernised management systems can achieve economies of scale and efficiency, they are generally less diverse in terms of disturbance regimes and fine-scale temporal and spatial variability (Webb, 1998), and often reduce the complex structure of vegetation or remove it entirely (Newton *et al*., 2009; Edgar, Foster & Baker, 2010). However, there has been little investigation of the impacts of these modern management regimes on heathland wildlife.

Reptiles can be particularly impacted by changes to habitat structural complexity (Pianka & Pianka, 1970; Huey & Slatkin, 1976). Reductions in vegetation complexity can reduce the availability of locations with differing thermal conditions, making effective thermoregulation more difficult (Huey & Slatkin, 1976; Row & Blouin-Demers, 2006; Elzer *et al*., 2013). Habitat simplification can also increase predation risk (or perception of predation risk), by reducing refuge opportunities and/or increasing encounter rates between predators and prey (Murdoch & Oa, 1975; Gotceitas & Colgan, 1989; Irlandi, 1994). These effects may be especially pronounced for reptiles in temperate climates because they must balance the risk of predation with the need to thermoregulate (often basking in exposed areas) in highly variable thermal conditions (Huey, 1974). Basking poses significant risks to survival, but capitalising on favourable thermal conditions is vital for energy assimilation and growth (Olsson, Madsen & Shine, 1997; Lourdais *et al*., 2004; Herczeg *et al*., 2007).

Many lowland heaths are also near to centres of human population and are used as recreational amenities (Underhill-Day & Liley, 2007; Cordingley *et al*., 2015). Consequently, they can support high numbers of predators of reptiles, including domestic animals (Phelps, 2004; Underhill-Day, 2005; Edgar *et al*., 2010).

The loss and degradation of lowland heathland has been implicated in historic population declines of adders *Vipera berus* in **the UK** (Baker, Suckling & Carey, 2004; Edgar *et al*., 2010; Gleed-Owens & Langham, 2012). Despite this, the impact of current heathlands management regimes for adders is poorly understood. Through the deployment of temperature loggers and adder models on heaths across lowland England, we quantify differences in thermal conditions and rates of adder predation, as well as the identity of predators, in areas with differing vegetation structure: either open, short swards or structurally complex vegetation.

Materials & Methods

Measuring the thermal environment

We quantified the thermal environment on heathlands by measuring operative environmental temperatures (T_e) using temperature loggers (Thermochron i-Button, Maxim Integrated) inside biophysical snake models (Bakken, 1992). The operative temperature is defined as the temperature of an inanimate object of zero heat capacity with the same shape, size and radiative capacity as the focal animal when exposed to the same microclimate (Bakken & Gates, 1975). Unlike simple measures of air or ground temperatures, operative temperatures integrate heat exchange across multiple pathways (radiation, convection and conduction), and thus reflect the thermal environment available to the study subject more effectively.

The biophysical models used here were constructed to represent adders, and consisted of 40-cm-long copper tubes (wall thickness 1.1 mm, diameter 22 mm) with sealed ends (tight-fitting rubber bungs). Each temperature logger was positioned at the centre of the model and wrapped in packaging foam so that it was not in contact with the walls of the copper tube. Comparison of the thermal behaviour of a model with that of a fresh snake carcass on a flat exposed concrete surface over a 24 h period revealed very similar temperature ranges (model = 6–33.5°C, snake = 5.3–34°C), very little thermal discrepancy (<0.1°C) and a highly significant correlation between simultaneous readings across this range ($r = 0.98$, $n = 96$, $p < 0.001$).

Estimating rates of snake predation

We used artificial model replicas of adders to measure predation rates on heaths. Each model was constructed using ~100 g of non-toxic sculpting clay (Newplast Plasticine; Animation Supplies Ltd, Worthing, UK) and measured ~35 cm in length and 2 cm in diameter. Grey-coloured clay was used for males and terracotta-coloured for females (Fig. 1). All models had a tapering tail end, a slightly enlarged head distinct from a thinner neck, with three bends in the body to replicate a typical S-shaped, resting posture. Using a black non-toxic water-based paint marker (Uni POSCA PC-5M; The SQL Workshop Ltd, Devon, UK), a mid-dorsal zigzag pattern and head markings similar to those of adders were painted onto all models. To reduce the risk of whole models being displaced or carried away by predators, each was secured to the ground using a small, black elastic band at the midpoint of the body attached to a concealed peg. Models were inspected for marks left by predators to aid identification of the animal responsible; (i) dog attack: identified by canine teeth or claw marks, (ii) avian attack: beak or claw marks of birds, or (iii) livestock trampling: hoof marks of ponies or cattle (Appendix 1). Predators of snakes often direct attacks towards the head, especially in venomous snakes **(Wüster *et al.*, 2004; Niskanen & Mappes, 2005)**, so the position of damage to models was also recorded.

Experimental design

The study took place on ten heathland sites in lowland England (Fig. 2; Table 1), all of which were open to public access and managed by modern scrub control regimes. At each site, a study area of ~1 ha comprising both cleared and structurally complex areas of vegetation (>40 m^2) separated by footpaths (Fig. 3a,b) was identified. Cleared areas were characterised by vegetation <10 cm in height (in any of five measurements using a ruler along a sampling transect) and contained no tall vegetation. Complex areas comprised mosaics of shrub species varying in height and patches of bare ground <1 m^2. Male and female adders were observed basking on or moving through cleared and complex areas at several of the sites (Fig. 3c).

To quantify operative temperatures during the period of adder activity, temperature loggers were deployed on all six Norfolk sites between 23-30 April (spring season) and 1-7 July (summer season) 2015. On each site, three loggers (programmed to record temperature every 30 minutes) were placed in each of three different microhabitats (i.e. 9 models per site, 54 models in total): 'cleared' (exposed and >20 m from shrubs and trees), ‘complex’ (exposed but <30 cm from vegetative cover) and ‘shelter’ (completely concealed beneath vegetation at a depth of 30 cm). The biophysical models containing loggers were in contact with the ground for their entire length and oriented on a north-south axis to maximise exposure to the midday sun, replicating adder behaviour.

Plasticine adder models were deployed during the adder mating season (Norfolk: 1-14 May; Surrey: 18-31 May). In total, 770 models (385 of each sex) were deployed. At each site, the number of models ranged from 60 to 90, and equal numbers were deployed in cleared and complex areas. Models were deployed singly at ground-level and at 15 m intervals (alternating between male and female models) along one transect in each study area. Transects ranged from 5 m to 30-50 m from footpaths, with the range of distances being equal in cleared and complex areas at each site. In complex areas, all models were positioned close to (<30 cm) vegetative cover (e.g. gorse or heather stands). On one of the sites (Headley Heath), in addition to cleared and complex areas, 20 models were deployed in each of two ‘wildlife havens’ (areas of approximately 50 m^2 enclosed by gorse).

At each site **and in each treatment**, all models were deployed on the same day and subsequently relocated and checked for damage five times in 48 hr intervals (i.e. deployed for 10 days in total). For each damaged model, the location (cleared or complex area), distance to the nearest footpath, animal responsible for damage, and the most intensively damaged body section (the full body length was divided into equal thirds: head and neck, mid-body, tail-end) were recorded. Damaged models were removed and not replaced.

Estimating levels of recreational activity

During each of the five spring (May) surveys of adder models on each site, the number of visitors was also recorded. Each survey took place between 08:00 and 18:00 and one of the five surveys on each site was undertaken on a weekend. At each site, one 200 to 400 m-long transect was established along existing footpaths, providing good visibility and coverage of the entire study area containing adder models. Surveys consisted of walking the transect for 0.5 h recording each person entering the study area, along with their activity: walking (W), dog walking (DW), running (R), cycling (C), or horse riding (HR). Each dog was recorded as either on or off the lead (L/NL), and each individual was recorded only once per survey. These counts were used to generate ‘human activity indices’ for each site by dividing total count (of each category and all categories combined) by the number of surveys.

Analysis

Variation in the operative temperatures recorded by temperature loggers every 30 minutes was explored using a generalised linear mixed model (GLMM using the R package ‘lme4’ (Bates et al. 2013)) with time of day (hour), treatment (cleared, complex or sheltered), season (spring or summer), and their interactions, as predictor variables, and day, site and logger ID as random factors (Table 2). **A post-hoc test (using R package ‘multcomp’ (Hothorn et al. 2017)) was used to examine temperature variation within treatment.** The effects of habitat structure on adder model attacks was explored in a GLMM with a binomial error structure and model fate (attacked or not attacked) as the response variable, treatment (cleared or complex) and distance to footpath and their interaction as predictor variables, and site as a random effect (Table 2). Separate models with this structure were then used to examine attacks by (1) all predators, (2) dogs, and (3) livestock (too few attacks by avian predators were recorded to allow analysis). We examined the relationship between the index of human activity ($\log_{10}$ transformed people survey^{-1}) and model attack rate (mean proportion of models damaged in the two survey periods) across the 10 sites using linear regression. Variation in recreational activity was explored using a general linear model (GLM) with a Poisson error structure and log link function, with number of people as the response variable, and day, site and activity as predictor variables (Table 2). To test the overall effects of factors, we used Chi-squared tests to compute analysis of deviance tables for model fit.

In all models, non-significant ($P > 0.05$) variables were removed by sequential backwards deletion (although for completeness, their estimates and associated probabilities in maximal models are also reported). All analyses were carried out in R 3.4.2 (R Core Team 2017).

Results

Thermal variation across heathland sites

Operative temperatures (T_e) on heaths varied significantly throughout the day and with habitat structure (Table 3; Fig. 4). Temperature loggers in shelter beneath vegetation had mean temperatures up to 20°C cooler than those exposed within structurally complex and cleared areas and, although the difference in temperatures between treatments was similar across the seasons, overall temperatures were significantly higher in summer (July) than spring (April) (Table 3). Consequently, while mean spring temperatures in sheltered areas remained well below adders' preferred range **(T_{set}: measured in a laboratory thermal gradient by Herczeg *et al*., 2007 & Lourdais *et al*., 2013)**, temperatures in structurally complex and cleared areas approached T_{set} (deviation < 5°C) for 5.5 hours of the day

(Figure 4). In the summer period, T_e in both cleared and complex areas greatly exceeded adders' critical thermal maximum temperature **(CT_{max}: Brattstrom, 1965; Spellerberg, 1972)** for the majority of adders' activity period (Fig. 4), while those in sheltered areas remained well below CT_{max} and only approached T_{set} (deviation < 5°C) for four hours of the day (Fig. 4).

Attack rates between sites

Of the 770 model adders, 203 (26.4%) were damaged. The rate of damage to models ranged from 6.3% at Buxton Heath to 68.6% of models at Marley Common (Table 4; Fig. 5).

Effects of habitat complexity and distance to footpaths on attack rates

Significantly more models were damaged in cleared than in structurally complex areas on heaths (Fig. 6a) and attacks were significantly more frequent closer to footpaths (Table 4). Overall, damage rates were ~3 times more frequent in cleared areas but the relative impact of different predators varied with habitat structure; the few recorded bird attacks occurred in both cleared and complex areas and similar numbers of models were trampled by livestock in cleared and complex areas (Fig. 6b, Table 4). However, the risk of dog attack was significantly greater in cleared than complex areas, with 79% of dog attacks occurring in cleared areas (Fig. 6b), and in areas closer to footpaths (Table 4). The risk of dog attack close to footpaths (<20 m) was significantly greater, and attacks occurred over a greater range of distances (up to 40 m) from footpaths, in cleared than complex areas (Fig. 7).

Recreational activity and attack rates

The human activity index varied significantly between sites, as did the relative amounts of the five recreational activities (Fig. 8; Table 5). Dog walking was the most frequently recorded recreational activity at most sites and virtually all dogs seen were off the lead (Fig. 8).

Animals responsible for damage to models

While five bird attacks were recorded across three sites, dog attacks and trampling by grazing livestock constituted the great majority of damage to models (Fig. 5). The most heavily damaged part of the model varied among animals responsible ($x^2 = 9.11$, d.f. = 2, $P = 0.01$; Fig. 9). In models attacked by dogs, significantly more damage was sustained to the head and neck ($x^2 = 32.70$, d.f. = 2, $P < 0.001$), while trampling by livestock caused similar damage among body sections ($x^2 = 8.14$, d.f. = 2, $P = 0.54$).

Discussion

While scrub control is an important component of heathland management and conservation, large-scale reduction in complex vegetation can have potentially important consequences for adder thermoregulation and survival. In cleared areas in which management has reduced vegetation height and structural complexity over large areas, thermal conditions were harsher and adder models were subject to an increased risk of predation. Our study suggests the greatest direct threat to survival on open-access heaths is posed by domestic dogs, and attack rates were greater in sites with more recreational activity and in areas closer to footpaths. Although maintaining adder populations is often an aim of this type of heathland management, these findings suggest that the scale at which these operations take place may have unintended impacts on adder populations in the short and long-term (Martin & Lopez, 1999; Webb & Whiting, 2005). Efforts to retain habitat structural complexity and moderate the impact of recreational activity on open access heaths are likely to be of great importance to the conservation of adders on heathlands.

In thermally suboptimal conditions, structurally complex vegetation can facilitate adder thermoregulation by enabling effective energy assimilation (Huey, 1974; Huey & Slatkin, 1976), and our biophysical models showed that temperatures deviated least from adders' preferred range in complex areas. The effect is especially important during spring when, following emergence from hibernation, adders must bask in direct sunlight for long periods to achieve preferred body temperatures. However, on hot summer days the effect of habitat structural complexity is more immediate, as ground temperatures in areas without shelter exceeded adders' critical thermal maximum for much of the day, reaching over 50^{o}C. While reptiles are well adapted behaviourally and physiologically to cope with thermal variability (Huey, Losos & Moritz, 2010), extreme high ground temperatures on heaths in summer months represent a potentially lethal risk to adders of overheating, particularly while mate-seeking, foraging or dispersing. Where vegetation on heaths is reduced to large areas of short vegetation, adders are unable to thermoregulate by seeking refuge from the sun (Huey, 1974).

Structurally simplified areas of heaths also produced significantly higher attack rates of adder models than in complex areas. The detection of snakes by other animals is likely to be primarily visual, and habitat simplification could reduce concealment of adders (Isbell, 2006; Stevens, 2009; Allen *et al.,* 2013), in addition to facilitating mammalian movement across heathlands (e.g. Murison *et al.*, 2007). Although not measurable in our experiments, adders may also be less able to escape from predators in cleared areas, and thus be less likely to survive an attack.

Overall, attack rates on our models were high, with 26% being damaged during their 10 day deployment. While live adders may be likely to seek cover when dogs are nearby, high numbers of adder bites of dogs have been documented in the UK (Reading *et al*., 1995; Sutton, Bates & Campbell, 2011) and elsewhere in Europe (Kangstrom, 1989; Lervik, Lilliehöök & Frendin, 2010), and there are numerous reports of adder bites to the legs of cattle, ponies and sheep (Luckham, 1944; Prestt, 1971; Arbuckle & Theakston, 1992). Conversations with dog walkers during fieldwork revealed accounts of dogs attacking and killing adders and JWH has previously found the carcases of adders showing injuries apparently consistent with dog attack and trampling by livestock (Appendix 2). While the immobility of Plasticine models may have led to overestimation of the true frequency of predation, our estimate of avian predation rates is similar to that reported on heathlands by Wüster *et al*. (2004), and the fact that dogs attacked predominantly the head or tail regions of models [reflecting predator behaviour in other studies (Smith, 1973; Brodie, 1993; Wüster *et al*., 2004)] suggests they were treated as if they were real snakes, and were not merely 'tasting' the Plasticine as some rodents do (Madsen, 1987).

Hostile conditions could result in cleared areas on heaths being actively avoided by adders, which may further reduce habitat availability for this declining species. The movement of adders into remaining patches of complex vegetation or adjacent land could, in turn, lead to increased predation risk if there is an immediate increase in adder density in these areas. In addition, scrub clearance can cause significant habitat fragmentation on heaths, and simplified areas that are large relative to the size of the site, or represent a high proportion of the site, have the potential to seriously inhibit adder movement (Fahrig, 2007; Croak, Webb & Shine, 2013).

Implications for heathland management

The findings of this study suggest that, where heathland management is necessary to maintain mid-successional stage habitat, strategies that retain some habitat structural complexity within managed areas should be included to reduce detrimental effects on adders. **Ideally, the simultaneous removal of all vegetation cover across a site, or substantial areas of it, should be avoided, and the selection of sections of a site to be cut should target areas where scrub encroachment is most severe, and avoid important habitat features for adders, such as hibernacula and foraging areas. Cutting and clearing of vegetation should ideally be conducted in narrow strips, and/or in phased cutting of many small (rather than fewer, large) management plots, as this is likely to have less severe impacts on adders, and the resulting more connected mosaic of different vegetation types and age classes can provide a greater spectrum of discrete resources for adders and other important heathland taxa. Where mechanised cutting makes such small-scale management more difficult to achieve, opportunities for hand cutting of vegetation may be important to consider, where feasible. Finally, where the conservation of adders is a primary objective, avoiding the use of livestock grazing as the means of habitat management will likely reduce the risk of disturbance and trampling.** Our findings add to evidence that the generic, landscape-scale policy of grazing management on heathland can be harmful to many species of conservation concern (Lindenmayer & Fischer, 2006; Newton *et al*., 2009; Reading & Jofré, 2015; Reading &

Jofré, 2016). The apparent threat to adders posed by dogs on heathlands highlights a management issue for reconciling the recreational needs of visitors with the requirements of species of conservation interest. The Countryside Rights of Way Act 2000 (CRoW Act) is based on the notion of responsible access, with a provision for dogs to be kept on a fixed lead during the ground nesting bird season (generally 1 March to 31 July). This period coincides with the adders' breeding season, and our findings strongly support the need for such a provision. However, alternative options to manage, or manipulate, recreational activity may be more beneficial, **and could include diverting footpaths and strategic placement of impenetrable barriers (e.g. gorse *Ulex europaeus*) to protect sensitive areas, as already occurs on some heaths (JWH, pers. obs.). Targeted vegetation clearance may help to dissuade adders from specific areas, such as access points, car parks, or dedicated off-lead areas for dogs.** However, this should be weighed against the value of public engagement on peri-urban or urban green spaces, which has produced tangible conservation benefits even for venomous snakes (Bonnet *et al*., 2016). For people and adders, and towards the broader aim of coexisting with wildlife, educational activities, informative (rather than warning) sign boards, and other initiatives to raise awareness and understanding of adders, may also be a component of management plans on heathland sites.

Acknowledgements

We are grateful to Norfolk Wildlife Trust, Surrey Wildlife Trust, the Forestry Commission and the National Trust for allowing access onto their nature reserves. Thanks to Tom Biddulph for assistance in the field, to all who helped with making adder models and to two anonymous reviewers for helpful comments on the manuscript. Funding was provided by the Sir Philip Reckitt Educational Trust (SPRET).

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Image of study species to be considered for the publication cover.

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