



Population dynamics of grass snakes (*Natrix natrix*) at a site restored for amphibian reintroduction

David Sewell¹, John M.R. Baker² & Richard A. Griffiths¹

¹Durrell Institute of Conservation and Ecology, School of Anthropology and Conservation, University of Kent, Marlowe Building, Canterbury, Kent, CT2 7NR, UK

²Halesworth, Suffolk, UK (johnhalesworth@aol.com)

Grass snakes (*Natrix natrix*) were monitored for nine years on a site in eastern England restored for an amphibian reintroduction. Counts of snakes increased between 2004 and 2012 from 1.25 to 3.83 snakes per survey visit. Grass snake counts were positively correlated with the number of common frog spawn clumps each year and peak counts of pool frogs. During surveys and incidental encounters 137 adult males, 161 adult females, 131 juveniles and 44 hatchlings were captured and individually photographically identified. Captures of hatchlings were erratic and recapture rates were low, so they were excluded from the analysis. Annualised capture data were analysed in the capture-recapture programme MARK, using the Cormack-Jolly-Seber model. The top ranked model gave an apparent annual survival rate of 0.66 (95% CI=0.543–0.755) and an individual detection rate of 0.17 (0.118–0.245). Population estimates based on this model ranged from 53 (95% CI=37–76) to 576 (95% CI=400–831) over the nine years of study. Grass snake population estimates were equivalent to densities of 4.8 to 52.4 individuals ha⁻¹. Nevertheless, it is unlikely that these snakes were permanently resident within the study area, and annual survival may therefore be underestimated. A more plausible explanation for the large population estimates is that the snakes were temporarily resident within a patch of high quality habitat and moved through home ranges that included the study site.

Key words: Cormack-Jolly-Seber, monitoring, *Natrix natrix*, population estimate

INTRODUCTION

Conservation interventions such as habitat management and reintroduction usually aim to enhance the population status of individual species. There are, inevitably, impacts on the system being managed that have implications for non-target species. Such impacts can be either positive or negative. Positive impacts are those that benefit a wider range of taxa, and thereby result in enhanced biodiversity. Negative impacts are those that benefit predators or pathogens which detrimentally impact the species of conservation focus (e.g., Walker et al., 2008). This means that any conservation intervention carries risks. Although assessment of these risks is becoming increasingly acknowledged within conservation practice guidelines (e.g., IUCN/SSC, 2013), there remains a dearth of evidence to support the notion that many conservation actions are effective in achieving their goals (Pullin & Knight, 2009; Sutherland et al., 2013). Fundamental to building this evidence base is the analysis and documentation of both direct and indirect effects of conservation interventions.

In this study, we examine the impact of interventions targeted at amphibian conservation on the grass snake (*Natrix natrix*), which is a predator of amphibians (Gregory & Isaac, 2004; Luiselli et al., 2005). The grass

snake is a vagile species, often found at low population densities (e.g., 3.6 ha⁻¹ [Mertens, 1995], 3 ha⁻¹ [Beebee & Griffiths, 2000]), with relatively low rates of recapture (Luiselli et al., 1997; Reading, 1997; Gregory & Isaac, 2004). Nevertheless, there can be strong relationships between the distribution of natricine snakes and their prey (e.g., Matthews et al., 2002; Moore et al., 2004). Despite the burgeoning interest in amphibian conservation and reintroductions (e.g., Griffiths & Pavajeau, 2008; Germano & Bishop, 2009) there are no studies that have examined the population dynamics of amphibian predators at sites that have been managed primarily for amphibians.

This study was one component of a programme of species and habitat monitoring being carried out in conjunction with the reintroduction of the northern clade pool frog (*Pelophylax lessonae*) to England (Buckley & Foster, 2005). Between 2005 and 2008 pool frogs were translocated from Sweden to a specially restored site in Norfolk, eastern England. Management for pool frogs entailed reversion of the site from former woodland to more open habitat. Consistent with international guidelines (IUCN/SSC, 2013) monitoring is integral to the reintroduction programme to measure the performance of the newly established pool frog population and to identify emergent threats. The study aimed to document

Correspondence: David Sewell (D.L.Sewell@kent.ac.uk)

the population dynamics of grass snakes at the site before, during and after the reintroduction of pool frogs.

METHODS

The study site is located in Norfolk, in eastern England. Its core comprises 10 ha of an open mosaic of grassland, bracken, scattered scrub and trees and many ponds. It is located within an area of approximately 130 ha of forestry plantation, comprising mostly coniferous, but also some broad-leaved, woodland. The plantation also includes some areas of reed fen, grassland and scrub. It is located within a landscape of agricultural and forestry land.

Grass snakes were surveyed using artificial cover objects (sheets of weathered corrugated iron, measuring approximately 80x70 cm) and by visual survey. In 2004 cover objects were placed on site in May, in subsequent years they were put in place in March. They were removed at the end of each survey season and replaced in different locations the following year to ensure that any effects of the refuges 'bedding in' or snakes learning where refuges were located were constant between years. The survey used a relatively low density of cover objects. Twenty cover objects were distributed to give even coverage of the core survey area (density 2 ha⁻¹) and a further two were placed in open areas alongside an unpaved forestry road linked to this, adding almost another hectare to the area surveyed, giving approximately 11 ha in total. Cover objects were placed in microhabitat judged likely to be used by grass snakes, i.e. sunny, sheltered locations adjacent to cover.

Between 7 and 17 surveys were made each year from 2004 to 2012 during the snakes' active season, from March to September. Each survey involved walking a directed transect (approximately 3 km), defined by the locations of cover objects, looking for snakes underneath the corrugated iron sheets and in the open in likely habitat along the transect. Attempts were made to capture all grass snakes observed, either under cover objects or in the open. Captured snakes were placed in cloth bags and processed either immediately after capture (within approximately five minutes) or, in a few cases, held for several hours as other survey work determined. Each captured snake was weighed to the nearest 1 g using a Pesola balance. Patterns on the anterior ventral scales were recorded using compact digital cameras to allow recognition of individual snakes (Carlström & Edelstam, 1946). Snakes weighing 30 g or more were sexed by external appearance (relative length and shape of the tail). Although grass snakes are sexually dimorphic at all ages (Gregory, 2004) the current study did not attempt to sex

younger (small) snakes. Snakes under 30 g were recorded as a single category and were treated separately in data analysis because young grass snakes may have a different mortality rate to adults (e.g., Madsen, 1987). Although hatchlings were noted in most years, recaptures were too few to treat this group separately. After examination and data collection snakes were released at the location of capture.

The number of snakes (excluding hatchlings) captured or just observed during each survey was recorded as a count. Additional snakes captured, for example, during other survey work on site, were not included in survey counts but were used in the annualised analysis of individual capture data.

A sample of fourteen ponds was targeted for surveys of amphibian species recorded as present prior to the reintroduction programme (Nick Gibbons, pers. comm.); these included smooth newt (*Lissotriton vulgaris*), great crested newt (*Triturus cristatus*), common frog (*Rana temporaria*) and common toad (*Bufo bufo*). Surveys for the newt species and common toads provided presence/likely absence information but insufficient data to provide standardised counts. Common frogs were monitored by spawn clump counts (Griffiths & Raper, 1994) made over three to four survey visits each year from late March to early April. Pool frogs were surveyed by making counts of adult frogs in ponds over 5 to 18 survey visits per year from April to August. The greatest number of adults counted on a single survey visit was used to obtain a peak count for each year. As the relationships between grass snake counts and common frog and pool frog counts were non-linear, Pearson correlations on log-transformed amphibian counts were used to explore these.

The capture histories of individual snakes were annualised, pooling those encountered incidentally as well as during dedicated surveys, recording each snake as either captured or not captured for each year of the study. Between year adult survival and detection rates, based on capture-mark-recapture data, were estimated using the Cormack-Jolly-Seber model in Program MARK (White & Burnham, 1999). Pre-defined models were used, allowing models that were both time and group dependent to be run. 'Groups' in this context represented analysis by sex and life stage, i.e. males, females and juveniles. Model fit was determined using the quasi-likelihood Akaike Information Criterion, corrected for small sample sizes (QAICc). We followed Burnham & Anderson (2002) in using Δ QAICc to determine the best model and took a Δ QAICc of <2 as evidence of no substantial difference from the best-fitting model, values between 3 and 7 as indicating less support and a Δ QAICc of >10 as having little or no support. Models with a Δ QAICc of over 10

Table 1. Captures of individual grass snakes by sex and year.

	2004	2005	2006	2007	2008	2009	2010	2011	2012
Female	2	11	18	22	21	22	23	26	16
Male	5	6	13	17	12	15	27	22	20
Juveniles	2	2	13	16	19	14	32	12	21
Hatchlings	0	1	5	1	2	5	16	7	7
Total:	9	20	49	56	54	56	98	67	64

Table 2. CJS model selection based on ΔQAICc in Program MARK of <10 from the best-ranked model, where ϕ =survival and p =detectability. Other model notation is (g)=group (sex), (t)=time and (.)=constant parameter.

Model	QAICc	Delta QAICc	QAICc Weights	Model Likelihood	Number of Parameters
<i>Phi(.) p(.)</i>	491.74	0.00	0.45	1.00	2
<i>Phi(.) p(g)</i>	492.94	1.20	0.24	0.55	4
<i>Phi(g) p(.)</i>	495.02	3.29	0.09	0.19	4
<i>Phi(.) p(t)</i>	495.36	3.62	0.07	0.16	9
<i>Phi(t) p(.)</i>	495.51	3.77	0.07	0.15	9
<i>Phi(g) p(g)</i>	496.68	4.94	0.04	0.08	6
<i>Phi(t) p(g)</i>	497.35	5.62	0.03	0.06	11
<i>Phi(g) p(t)</i>	498.85	7.12	0.01	0.03	11
<i>Phi(t) p(t)</i>	500.50	8.77	0.01	0.01	15

were therefore discounted as unimportant. Goodness-of-fit was tested by means of 1000 bootstrap iterations of the best-fitting model, and these were used to estimate the variance inflation factor (\hat{C}) for comparing models. Model assumptions followed Williams et al. (2002), and included the assumptions (i) that every marked animal had the same probability of recapture; (ii) that every marked animal had the same probability of survival until the next sampling period; (iii) that marks were not lost or overlooked, and were recorded correctly and (iv) that all emigration was permanent. The extent to which a grass snake population is likely to meet these assumptions is considered further below. Model notation followed Lebreton et al. (1992), viz: ϕ_i =survival probability from time i to $i+1$; p_i =probability of detection (i.e. capture or recapture) at time i ; (g)=group (sex) dependent survival or recapture; (t)=time dependent survival or recapture; (g*t)=both group dependent and time dependent survival or recapture; (.)=constant survival or capture rate. The estimated population for each year was calculated by multiplying the number of individuals caught by $1/\text{detection probability}$.

Because grass snakes range widely and animals may temporarily leave the population, goodness-of-fit was also tested using U-CARE, as component 3.SR of this programme tests for transience (Madon et al., 2013). However, the results of this test were not significant and are therefore not reported here.

RESULTS

Hatchlings were excluded from counts of grass snakes made during surveys because their occurrence appeared to be dependent on whether eggs hatched near to a cover object rather than reflecting the numbers of snakes frequenting the site. Removing hatchlings from the count data was also consistent with the treatment of individual capture data below. The mean counts of grass snakes (excluding hatchlings) ranged from 1.25 to 3.83 (Fig. 1), increasing over the nine years of the study, indicated by a significant positive correlation between year and annual mean count (Pearson's $r=0.891$, $p=0.001$).

Counts of common frog spawn clumps between 2004 and 2012 varied between 0 to 44 (mean=22.8 SD=16.92).

Peak counts of pool frogs from 2005 (the year of the first reintroductions) to 2013 ranged from 0 to 31 (mean=20.6 SD=12.03). Grass snake counts were positively correlated with both log-transformed common frog spawn clump counts ($r=0.90$, $p<0.001$, $df=7$) and log transformed pool frog peak counts ($r=0.77$, $p<0.05$, $df=6$).

A total of 396 captures (137 male, 161 female, 131 juvenile and 44 hatchlings) took place over nine seasons 2004–2012. These comprised 117 individual males, 126 females and 112 juveniles and 41 hatchlings (excluded from analysis). In most years more females were caught than males (Table 1), but overall the sex ratio did not differ from unity ($\chi^2=1.93$, $df=1$, $p>0.05$).

The 1000 bootstrap iterations suggested that the data were marginally over-dispersed, and an alteration was therefore made to \hat{C} to adjust this to 1.06. Analysis of adult captures using the Cormack-Jolly-Seber (CJS) model in MARK showed that 7 of the 16 predefined models had a ΔQAICc of >10 , and these were therefore discarded. The remaining models primarily suggest that the parameters of survival and detection are either constants or vary between the groups (Table 2), or over time.

In addition to the top ranked model in Table 2 there is also considerable support for models that show variation between the groups in either survival or detection. However, the model that allows for variation between the sexes in both survival and detection has a higher ΔQAICc than either of the models where variation by sex

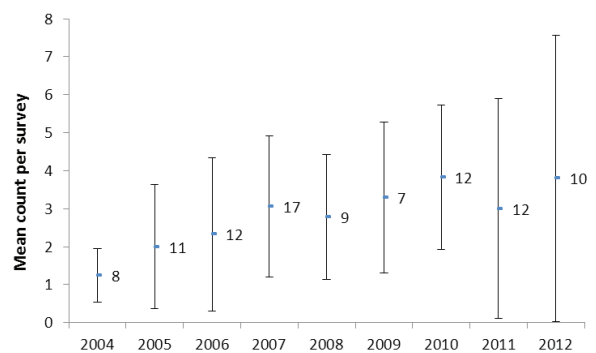


Fig. 1. Mean survey counts of grass snakes by year. The number of surveys each year is indicated and error bars represent 1 SD.

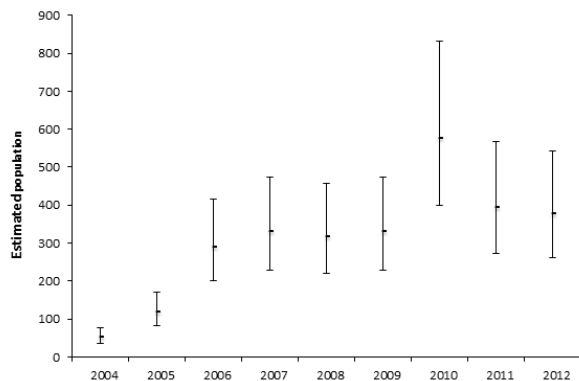


Fig. 2. Population estimates of grass snakes by year based on model $\Phi(\cdot) p(\cdot)$ in Table 2. Error bars represent 95% confidence intervals.

only counts for one parameter. For this reason we prefer to accept the top ranked general model, $\Phi(\cdot) p(\cdot)$, which provides an overall estimate of inter-year survival of 0.66 (95% CI 0.543–0.755) and an individual detection rate of 0.17 (0.118–0.245). The population estimates in Fig. 2 are based on this detection rate.

The second and third ranked models in Table 2 provide evidence of some differences in both inter-year survival and detection rates between the groups. The second ranked model, $\Phi(\cdot) p(g)$, suggests that whilst detection rates for both males and juveniles are very similar at 0.15 (0.084–0.244) and 0.14 (0.081–0.238) respectively, those for females are higher at 0.22 (0.138–0.331). The confidence intervals do, however, show a wide overlap. The third ranked model, $\Phi(g) p(\cdot)$ shows a similar pattern, with female inter-year survival at 0.69 (0.547–0.807) being slightly higher than either that of males at 0.62 (0.462–0.763) or juveniles at 0.63 (0.466–0.770). Variation in survival over time only accounts for 0.04 of model weighting, whilst for detection the figure is 0.08. Support for variation in either survival or detectability over time is therefore low. The high overlap between the groups in both survival and detection rates as well as the bulk of QAICc weighting being in favour of models with constant survival and detectability means that we have chosen the top ranked model in producing population estimates.

Using the top ranked model, annual population estimates range from 53 (95% CI=37–76) to 576 (95% CI=400–831) (Fig. 2) increasing over time ($r=0.806$, $p=0.009$). These estimates are equivalent to densities within the survey area (11 ha) ranging from 4.8 to 52.4 snakes ha^{-1} .

DISCUSSION

Capture-mark-recapture analysis using Program MARK has provided valuable insights into grass snake use of a site of particular significance to wildlife conservation. A protocol established to monitor this potential predator of the pool frog, which is the subject of an international conservation translocation, has revealed a high level of site use by grass snakes. On average between 1.25 and 3.83 snakes (excluding hatchlings) were found on each

survey visit with an increasing trend over time (2004–2012). Photo-identification established the presence of between 9 and 98 individual snakes (including hatchlings) in any year while capture-mark-recapture analysis provides population estimates ranging, annually, from 53 to as high as 576. The large difference between population estimates and the numbers of snakes encountered during surveys reflects low detectability, which is common in snakes (Steen, 2010). In the current study individual detection rate was 0.17, which is relatively high for this species. Kéry (2002) found detection rates in the range 0.11–0.25 for grass snakes, but was examining the presence/absence of the species rather than individual animals. The individual detection rate of 0.17 is, of course, a mean rate across the surveying season. The species may be easier to detect in spring, when temperatures are cooler and there is less vegetation, than later in the year when higher temperatures and the rampant growth of vegetation make detection harder. Within-season variation in detection rate has not been investigated as part of this study.

The population estimates obtained here are in excess of any likely grass snake carrying capacity for the sampling site. Gentilli & Zuffi (1995) found a carrying capacity of 12–18 ha^{-1} . As their study site was in northwestern Italy where conditions are warmer and presumably more suitable for grass snakes, the current site would support only up to 198 individuals, even if capacity was at the high end of their estimate. Our population estimates, however, greatly exceed this for most of the study period (2006–2012).

There are two, not mutually exclusive, possible explanations of the high population estimates of grass snakes in the current study: mobility of the species and habitat quality. The grass snake is a relatively mobile snake, sometimes moving more than 100 m per day (Madsen, 1984; Mertens, 1994). Home range sizes are variable but can cover large areas. Madsen (1984) found an average home range size of 21.2 ha, Reading & Jofré (2009) found individual ranges between 0.18 and 9.41 ha while Wisler et al. (2008) found they varied from 15.1 to 120.5 ha (mean 39.7 $\text{SD}\pm 34.5$ ha). The large numbers of grass snakes estimated here may represent individuals temporarily using the site in the course of annual movements through home ranges that include part, or all, of the study site. Hence our estimates are likely to represent a population covering a much larger area than that of the study site. Whilst the test carried out for transience was not significant, this could be a sampling issue resulting in low statistical power rather than the absence of transient individuals within the population. The wide confidence intervals for the population estimates (Fig. 2) are to be expected for such a mobile species. Steen (2010) suggests that population estimates are of little value without an associated unit of area, and that the boundaries of the area being sampled are difficult to define for terrestrial animals. The study serves to illustrate that sampling area and the area occupied by a population are not synonymous, especially with a wide-ranging species such as the grass snake. If, as we suspect, transience does occur, the survival estimate

given above must be re-examined. Apparent survival does not distinguish between emigration and mortality, and thus can underestimate survival estimates (Pradel et al., 1997). For example, Sasso et al. (2006) found that taking transience into account increased the survival estimates for loggerhead turtles.

Such issues may raise questions as to whether the other assumptions of Capture-Mark-Recapture models have been met. Of the other model assumptions given above, the most problematic is that of all emigration being permanent, in some respects a similar problem to transience. With such a mobile species, it is possible that some individuals could leave the population, and return at a later date. These individuals would therefore not be available for recapture whilst absent, thus violating the model assumption about all captured animals being available for recapture. The effect of this would be to create lower estimates of detectability, which in turn drives population estimates up.

Gregory (2013) noted that grass snakes that had been captured previously were more likely to flee when first detected in subsequent observations than first-time captures. It is therefore possible that repeated capture could cause some individual snakes to move elsewhere. However, this merely serves as one explanation why the estimate for detection (p) is relatively low. Certainly, the practice of annualising the data from 7–17 visits per year into annual totals would serve to reduce any differences between 'catch-prone' and 'catch-shy' individuals if such differences existed.

A further factor that may contribute to the high population estimates is habitat quality. In this case the survey site has been managed to benefit pool frogs, which require networks of warm, sunny, breeding ponds. To achieve this, the extent of tree cover has been reduced, creating a less shaded site, which is likely to favour grass snakes. Management has also increased the suitability of the ponds for amphibians, increasing the numbers of prey available. For example, in 2004 no common frogs were found, but the number of spawn clumps has steadily increased over the years. Likewise, pool frog counts have increased since the start of the reintroduction in 2005. Less reliable data are available for newts, but it is possible that the two species present (great crested newt and smooth newt) may also have increased in response to the pond management. So, in addition to the importation of the project focal species, the pool frog, the study site has provided increasing numbers of amphibians of other species, which presumably attract grass snakes. The effect of sympathetic management can be dramatic on snake population levels. In a study of the giant garter snake, Wylie et al. (2010) found that in optimal wetland conditions, the population at one natural site was an order of magnitude higher than that at a restored site with seasonal drying, managed for multiple species.

Monitoring grass snakes at this pool frog reintroduction site has determined very high levels of site use by this amphibian predator. While this situation is a potential concern during the establishment stages of the reintroduced frog population, the continued presence of the latter indicates a degree of resilience to grass snake

predation. Although grass snakes have preyed upon reintroduced pool frogs (Baker, 2012), the impacts of predation on the newly established population may be diluted by increases in alternative prey species.

The results demonstrate large numbers of grass snakes using a patch of high quality habitat. This is consistent with radiotelemetric studies showing that grass snakes often have large home ranges, but within these are confined to specific areas of favourable habitat (Madsen, 1984; Reading & Jofré, 2009; Wisler et al., 2008) and genetic studies that show movement of individuals between patches (Meister et al., 2010, 2012). Data from a heathland site in Dorset, southern England, also suggest that grass snakes move through an area much larger than the sampling site (Reading, 1997).

The top ranked model in Table 2 gives an annual survival rate of 0.66 (95% CI=0.543–0.755), i.e. any captured individual has an average 0.66 chance of survival for a further year. Where models in Table 2 did indicate a difference in inter-year survival between the sexes, differences were slight. These results are comparable to the Swedish study of Madsen (1987), where adult mortality was given as 50%, which is within the 95% confidence interval given here. Gravid females have previously been assumed to be at higher risk of predation than males due to the greater amount of time they spend basking, and their burden of eggs (Madsen, 1987). However, we found only limited support for higher detection rates in adult females, whilst the third ranked model in Table 2 offered some support for females actually having a higher survival rate than either males or juvenile snakes. We emphasise that these variations in detection and survival both have limited support, and that the main weight of evidence in our study suggests both parameters are similar between the three groups examined here.

There have been relatively few capture-mark-recapture studies of snakes in temperate regions other than that of Madsen (1987). Flatt et al. (1997) examined two populations of the asp viper (*Vipera aspis aspis*) in Switzerland, and found that the likelihood of annual survival was 0.75 (0.55–0.90). Most other studies have been on garter snakes (*Thamnophis* spp. in North America, and as the garter snakes are also natricines may be of greater relevance. In a six-year study, Stanford & King (2004) found that female plains garter snakes had a higher survival rate than males, and Lind et al. (2005) found similar results. Halstead et al. (2012) found that female giant garter snakes (*Thamnophis gigas*) had a mean annual survival of 0.61 (0.41–0.79). These survival rates are broadly in line with those for grass snakes reported above. The highest annual survival estimate we are aware of is that of Koons et al. (2009), with an estimate of 0.79 (0.69–0.88) for the cottonmouth (*Agkistrodon piscivorus*). However, this species (family Viperidae) is less closely related to the grass snake, and may therefore be less comparable.

The current results emphasise several points relevant to surveying for, and monitoring, grass snakes. Photo-identification of individuals and capture-mark-recapture analysis of subsequent data greatly enhance the quality

and quantity of the information gained, and can highlight issues with survey protocols. For example, more intensive survey protocols may have allowed the application of robust models, from which temporary emigration can be estimated (Rodda, 2012). Nevertheless, without capture-mark-recapture analysis the survey protocol used here would have established that the numbers of snakes using the site increased over time but the counts of snakes encountered during surveys (rising from approximately one to four snakes per survey visit) give no indication that in most years much larger numbers of snakes may be using the site. It would be interesting to determine population densities of grass snakes at other locations to establish whether this species is equally abundant in other areas. The current results reinforce the importance of evaluating detectability because the numbers of grass snakes observed may be an order of magnitude lower than the actual local population size.

ACKNOWLEDGEMENTS

The authors thank Rachel McCrea, NERC Research Fellow at the National Centre for Statistical Ecology for her helpful comments and assistance with the data analysis. The authors are also grateful to Amphibian and Reptile Conservation, Anglian Water, and Natural England for funding field work and to Nick Gibbons and Neal Armour-Chelu (Forestry Commission) for site access and vehicle permits.

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Accepted: 12 September 2014