CONSERVATION OF THE SAND LIZARD, *LACERTA AGILIS*, BY HABITAT MANAGEMENT

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INTRODUCTION AND BACKGROUND

The sand lizard (*Lacerta agilis agilis* L.) is one of the seven large species in the "green" *Lacerta* Part 1 taxon (Arnold, 1973) and is widely distributed in Europe where it exploits a variety of habitats from open steppe to fields, hedgerows and woodland. It reaches its north-westerly range limits in Britain where it occurs only in open, sandy country (Smith, 1951), principally within the lowland dry (*Calluneta*-dominated) heaths of southern England, but also in the remnants of a less extensive habitat-type among the south-west Lancashire coastal dunes where, nevertheless, the species was once abundant. Similar habitat restriction is known elsewhere in north-west continental Europe.

This paper describes the work of one of the authors (K.F.C.) and, since 1971, of the Conservation Committee of the British Herpetological Society in the conservation of *L. agilis* by habitat management.

Habitat requirements of the sand lizard in southern England

Corbett's investigations since 1968 (summarised in Prestt, Cooke & Corbett, 1974) of this species' detailed distribution in southern England has shown that their typical habitat is based on mature Callunetum (Fig. 1), which is dominated by deep ling (*Calluna vulgaris*), with local co-dominance of bell heather (*Erica cinerea*) and dwarf gorse (*Ulex minor*). Historical data confirmed that sand lizard concentrations/colonies had been associated almost exclusively with this dwarf shrub habitat; whereas, in contrast, individual lizards are always few and colonies absent in short heath—apparently because of the relative paucity of invertebrate prey and the lack of cover against predators. Although comparable heights (50+ cm) may be attained by Calluneta of only ten years duration, stands of 15–30+ years old are those which would support that structure of cover more indicative of sand lizard habitat, and are best described as large bushy plants with deep litter, often with overlapping procumbent stems and central "pads" of mosses.

Most temperate basking reptiles tend to become concentrated on south facing (sunny) open areas; the English sand lizard also has an affinity toward local variation in topography, e.g. banks, tumuli, gullies, ridges, steep slopes and bluffs, etc., and where from stable populations have been recorded at density equivalents of 230–340 adults per ha (Fig. 2).

Fire is now one of the most immediate threats to sand lizard colony habitat, and observation at 63 colony sites burnt in 1975 and 1976, showed that whilst many

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lizards survived the conflagration, and some the observed increased attentions of avian predators and scavengers such as crows (*Corvus corone*) and gulls (*Larus* spp.) they rarely persisted for more than one season.

Exceptionally, survival is enhanced, and even breeding re-established, when the slow regeneration of *Calluna* is offset by the rapid growth of competitors such as gorse (*Ulex europeus* or *U. minor*) or heathland grasses such as *Molinia*. However, the resulting population never becomes so large, nor so vigorous, as that preceding it and ultimately disappears wherever bracken, *Molinia*, or *U. europeus* remains dominant.

Continuous deep heath is also incompatible with colony status, regularly successful breeding being local or peripheral and dependent on the availability of unshaded bare sand (as provided by erosion on steep slopes, spoils from fox, badger or rabbit excavations, sides of tracks etc. Indeed, *breeding populations were never found anywhere in Britain in habitat lacking this feature.* Observations in large, open-air, heath vivaria confirmed this requirement; although many alternative media were available, eggs were almost always laid in bare sand, and clutches hatched successfully only when bare sand was used. The use of bare sand was first recognised by Allen (1896). Egg-laying in bare sand was also witnessed in the field by Monro (1967); many of our field-workers have reported unearthing of egg-clutches in the field, always from bare sand, as have C. Simms (personal communication, and 1971) and R. V. Skinner (pers. comm.). Finally, in the wild, concentrations of hatchlings (i.e. before dispersal of the clutch) are invariably found close to bare sand, in contrast to concentrations of newborn *L. vivipara* which are found on many substrates, including continuous deep heather on the same sand lizard sites.

Unlike *L. vivipara*, *L. agilis* is usually absent, and certainly never breeding on the localised clay outcrops on the Dorset heaths.

It should be noted that areas lacking bare sand, or with shading, overgrowth, and even replacement of the deep heather habitat (as above), can still support *L. agilis*, whether colonisers from, or remnants of, breeding populations, but do not satisfy the requirements for a colony in that egg-laying sites are absent or populations too sparse for regular breeding. For example, many of the *L. agilis* populations recorded from peripheral habitats (gardens, fields, hedgerows etc.) in Dorset, before 1970, soon became extinct after loss of adjacent heath, i.e. after loss of the colonisation source.

These findings, derived from investigations over eight seasons, at all recorded, and may previously unrecorded, *L. agilis* localities in southern England, suggest reasons for the decline and loss of colonies following habitat change. Essentially, *L. agilis* needs open habitat with dense ground vegetation as provided by mature Callunetum. Tree or scrub undergrowth, whether "natural" or through afforestation, not only suppresses the heather, but, more rapidly, causes failure of breeding. In overgrown habitats, *L. agilis* shows breeding failure leading to extinction. That this failure is caused by shading of the eggs is suggested by the longer persistence of breeding populations of non-egg-laying reptiles, and confirmed by the observations reported in this paper, when clearance of overgrowth normally resulted in immediate resumption of *L. agilis* breeding. It is significant that apart from the sparse duneland populations, *no L. agilis colonies were ever found in areas which were not, or had not recently been, open, dry heath.*

The decline of the English sand lizard

The past twenty years have seen a steep and accelerating decline in both numbers and distribution of *L. agilis* in Britain following widespread loss and fragmentation of

habitat, principally by afforestation, urbanisation, agricultural reclamation and mineral extraction (Moore, 1962; Prestt *et al.*, 1974; Tamarind, 1975). Degradation of much of the remaining habitat has been caused by the spread of pine (*Pinus*) (Figs. 4a and 5a) spreading from plantations, and by fire-induced encroachment of birch (*Betula*; see Robinson, 1972) (Fig. 3a), bracken (*Pteridium*; see Tubbs, 1974) (Fig. 3b) and similar local spreading of *U. europeus, Molinia* and *Rhododendron*.

The New Forest heaths have become unsuitable for *L. agilis* from management regimes based on regular burning, this in the mistaken belief that burning of the dry heath component improves the grazing for cattle and ponies (Tubbs, 1974).

The secondary effects of widespread "fragmentation" of heathland (Moore, 1963) act via fires, collection by children, predation from urban cats, and the winter gassing of rabbit burrows (often used by reptiles as hibernacula), and so cause local declines and even extinction of *L. agilis* which can no longer be reversed by natural recolonisation from adjacent undisturbed habitat. The magnitude of these declines can be gauged by comparing 1970 estimates (Prestt *et al.*, 1974) of under 200 adults remaining in Surrey, where the species was previously abundant (Leighton, 1903; Smith, 1951), with the population densities recorded from optimum habitat of 230–340 adults/ha. Local decreases are illustrated in Table I, while none of the twenty-two breeding populations known in the mid-1950s from the large area of the New Forest now remains, and no new populations have been discovered, despite surveys.

TABLE I. Loss of known sand lizard colonies from two prominent areas of their distribution

Zone	Locality	Approx. area (km²)	Approx. time scale (yr)	Colony loss (from–to)	% Loss	% Causes of decline		
						Site loss	Habitat change	Other/ unknown
II	Frensham (Surrey)	110	20 to 1975	56–2	96.5	66.7	27.8	5.6
III	Bournemouth/ Poole (Dorset)	160	15 to 1975	169–24	85.8	43.5	56.5	0.0

Significantly, in the majority of cases the causes of colony decline are known (Table I), and those few tabulated under "Other" have implications for collection and rabbit gassing. The causes all appear man-made, and are collectively more than enough to account for this species' overall decline; there is no reason to postulate, nor any evidence for, climatic change or ecological factors other than habitat alteration. Even "natural succession" (overgrowth) on lowland dry heath can be seen to result almost entirely from human agency—firstly in (re)introducing pine (Figs. 4 and 5) and secondly in causing fires which allow competitors (birch, bracken, gorse) to attain dominance (Fig. 3).

The historical preoccupation of the natural history movement with "attractive" fauna and flora resulted in a general neglect of the herpetofauna, even though our twelve indigenous species represent two of the four classes of terrestrial vertebrate which, as carnivores near the top of their food chains, may act as major control factors within their respective ecosystems. It is not surprising therefore that the decline of the

more restricted species continued unchecked until they became endangered. Even as general conservation activity has grown, interest in dry heath has been greatly over-shadowed by concern for the botanical richness of damp and wet heath and associated bogs. Before the present programme was started in 1969 there had been no habitat management for reptiles in Britain, not even on national and local nature reserves.

Sand lizard conservation policy

In a series of internal papers to the Working Group set up by the Nature Conservancy to look into this problem, Corbett defined four geographical "zones" for the distribution of *L. agilis* in Britain. Zone I comprises the coastal dunes of south-west Lancashire, zone II, the Wealden and associated heaths of south and west Surrey, south-east Berkshire, north-east Hampshire and north-west Sussex; zone III, the New Forest and Avon Valley heaths from Ringwood to Bournemouth; zone IV, the Dorset heaths westwards from Poole. The last two had only recently become separated by growth of the Poole–Bournemouth–Christchurch conurbation.

As an interim measure to offset declines in southern England, and to maintain a reasonable semblance of its natural distribution in zones II, III, and IV, a number of "Key Sites" were proposed as a basis for conservation. However, most of these were also recognised as in need for protection and/or management—a more empirical and logical selection from those sites already representing a high status for sand lizard population and habitat condition proved too often impractical, for by 1971 much heathland was already irreversibly assigned to development or change. Initially, seventy-four "Key Sites" were agreed with the Nature Conservancy as meriting action; since when, other sites have been added to replace some of those failing at the stage of negotiation with the owner. Unfortunately, by 1976, another twenty sites had been destroyed by fires. The "Key Sites" varied from 1 to 50 ha, although they were usually less than 5 ha.

The restricted choice of sites, coupled with the backlog of neglect of dry heath in favour of wet heath, and the resultant degeneration and overgrowth dictated immediate management to rejuvenate or upgrade the habitat. Indeed, *L. agilis* had already become extinct at some of the sites it was possible to secure, prompting experimental re-introduction using stock from actual or incipient development sites; these experiments have all proved successful (Corbett, in preparation).

The Key Site strategy was adopted by the British Herpetological Society's Conservation Committee as a major part of its policy (1973). Protection was to be achieved by negotiations with landlords and lessees, normally in collaboration with the relevant Nature Conservancy Region and County Naturalists' Trust; habitat management was based empirically on the above knowledge of *L. agilis* ecology from which it was predicted that clearance of invading pine, birch etc., together with provision of bare sand either by direct excavation or by removing shade from existing tracks etc., would increase *L. agilis* populations and their breeding potential on parts or all of the sites. Experiments in Surrey (see Tamarind, 1975) had already shown restoration of breeding by just such management.

Preliminary studies by Corbett (Prestt *et al.*, 1974), including investigation of its historical distribution, had shown that the smooth snake (*Coronella austriaca*) was also rare and primarily an inhabitant of mature dry heath in Britain, and that it too had declined severely; thus it was anticipated that the same management might well benefit this species.

METHODS

Habitat management

Work was carried out between October and March to minimise disturbance to the fauna, since reptiles and amphibians are mainly hibernating, and birds are not nesting, in this period. Because of the limitations of funds and labour, management of individual sites was rarely completed within a single season, but several were part-managed each year, usually to re-establish or maintain a breeding nucleus from which animals could colonise the managed areas as it was subsequently extended. Priority was given to heavily overgrown habitat before the heather became irrecoverable.

(i) *Scrub clearance*

Clearance was rarely total; from ornithological and aesthetic considerations, some gorse was left, as well as selected trees, always with their lower branches removed ("brashed") to minimise shading and leaf fall on to the heather below (Fig. 5). Clearance was principally in mature heath areas, with some removal of peripheral trees where these shaded the heather, and particularly where this shade was encouraging bracken invasion. Although the pines cleared were usually self-seeded, some planted pine were removed (with the kind co-operation of the Forestry Commission and of Tillhill Forestry Ltd.) in areas where this was dictated by overall loss of habitat (Fig. 4). Birch, gorse and rhododendron stumps were "painted" with growth inhibitors to reduce coppicing.

(ii) *Sand exposure*

The aim was primarily to provide egg-laying areas which would remain viable for several seasons, and which might also act as territorial foci, and sometimes also to aid access and protect against fire (provision of exposed sand was not intended to provide basking areas, and observations showed they were very rarely used as such). It was recognized as impractical and uneconomical to attempt to recreate the large amount of exposed sand (up to 15% of the site area) or the variation in local topography (banks, gullies, tumuli etc.), both typically associated with the densest natural colonies. Overall, therefore, a compromise was adopted based on conditions known from colonies with ca. 125 adults/ha.—with locally 5%, overall 1 to 20%, of the site area so exposed (Fig. 7). Inevitably, no two sites were treated alike because of local topographical differences, fire-breaking considerations and, often, the landowner's preferences.

Sand "patches" and paths were orientated roughly east–west to present the largest area of sand to the south and thus to the sun. On flat land and gentle slopes, a width of 1 m (much greater than that needed for egg-laying alone) was used to minimise shading and delay overgrowth by the peripheral heather. On steeper slopes narrower patches were practicable and were shelved into the hillside to prevent erosion. Patches were of maximum size 2×1 m thus barely exceeding the natural spoils at the entrances to fox or badger excavations (Fig. 6).

Most patches and even some paths were excavated by hand, by first cutting the heather with the back of the spade and then "turfing" down to about 10 cm to expose the sand. The inverted turves were piled on the north side of the excavation (Fig. 6d), following Corbett's early observation that adult *L. agilis* tended to colonise these artifical "banks". The Forestry Commission kindly used a tractor and plough to create wider tracts of sand (serving also as fire-breaks) on two of the larger sites.

Provision of additional sand exposure for existing breeding populations (whether

native or produced by habitat management) was carried out between mid-April and mid-May to minimise the risk of digging up either hibernating lizards or eggs—alternatives made possible by the vagaries of the English climate.

Monitoring of L. agilis populations

To minimise disturbance and for other reasons (see Discussion) complete reliance was placed on visual survey. In the smaller sites (<2 ha.), all the habitat could be searched, but "sampling" was often necessary on the larger sites. Purely objective sampling by "transects" had been well tested by Corbett in his original work and later (Corbett, 1974), but proved totally impractical for these small, territorial animals in such densely vegetated terrains (Fig. 2); unlike more subjective searching of the same areas, it frequently failed to reveal lizards. Further, rigid adherence to straight-line transects damages the heather.

Use was made of the fact that reptiles show definite preference in their choice of basking spots, during which activity they are most readily found, and potential basking places were searched throughout the sites. As well as those observed basking, many lizards were initially located by the characteristic sounds of their rustling through the vegetation or by slight movement at the periphery of the observer's vision; therefore several return visits were often needed to record size, sex and species (Fig. 1). The collective field experience of the participants confirmed that choice of weather, time of day and season were important in timing site visits.

L. agilis were assigned to one of three age-maturity groups according to size and appearance, and with regard to time of year, as:

"juvenile"—hatchlings between birth and first hibernation;

"immature"—lizards between their first and second hibernations; 7 to 14 months old;

"mature"—adult, sexually mature lizards after their second hibernation; from 18 months of age.

Wide individual variation in subsequent growth rates (Corbett, unpublished) forbade systematic assignment of adults to specific ages, however, "young" adults (18 to 24 months old) were normally distinguished in field records from very large, i.e. very old, ones—a category predominant on degraded, non-breeding habitat before management.

The locations of L. agilis sightings were recorded on site maps bearing a reference grid in order to follow detailed changes in distribution.

For *quantitative assessment* a sightings frequency technique was adopted as the only practicable method for routine monitoring, since Lincoln Index-type sampling techniques are inapplicable (see Discussion). Sightings of lizards of each age-maturity group were expressed as "numbers per man-hour" (i.e. "sightings frequency"). Mean sightings frequency values from individual sites were taken as indices of population density to permit (a) assessment of age-maturity group composition and (b) detection of the direction and approximate magnitude of changes in adult population density from year to year.

RESULTS

QUALITATIVE

Intersite variations in the status of the population before management and in the extent and time-course of management make comparison difficult between individual sites, although the following generalisations can be made:

(a) Sites with a low *L. agilis* population, little or no evidence of recent breeding and with no nearby colony (typical of zone II in 1970): from being scattered, lizards gathered in the cleared areas in the first season after the start of management and definite concentrations became apparent, associated with the ridges and turves of freshly exposed sand and/or in the vicinity of natural bare sand from which shade had been removed. These concentrations were localised to a small proportion of the sand areas and the lizards were predominantly very large; their sizes corresponded to those of *L. agilis* known from mark-recapture studies as at least 5 years old. Subsequently, the number of sightings fell, but rose again by the third season, when young (18 to 24 months old) adults predominated. In contrast to the localised distribution shown by the old adults of the first season, these young lizards were distributed throughout the sites, according with Corbett's findings on naturally viable sites in which immature lizards dispersed widely from their birthplaces. The new distribution was maintained in subsequent years.

Use of freshly-exposed sand for breeding was recorded during the first full season after its provision, but on average only about 10% of the potential egg-laying areas were used. Utilisation, as revealed by the number and distribution of associated broods, increased markedly in the third and later seasons. However, at one zone II site the patches rapidly became overgrown by bracken and although the initial concentration of old adults was recorded, sightings subsequently declined to below pre-management levels, followed by presumed local extinction.

(b) Sites with a low *L. agilis* population, but with local (often peripheral) breeding, and/or breeding populations in adjacent heath (a typical 1970 zone III/IV situation). This group showed similar concentrations of adults close to freshly-exposed sand; however, these were more widely distributed and although large adults tended to predominate (particularly where the breeding nuclei were small or distant) they were not the only age-class represented. These sites did not show a comparable fall in sightings between the first and third seasons, and the transition from old to young adult predominance, although observed, was less marked.

The number of clutches of young lizards, and the extent and dispersion of exposed sand usage, was initially much greater than in the first group of sites, with up to 70% being exploited in the first season.

The evidence was consistent with continuous recruitment of lizards from the existing breeding areas, but until management these colonists did not breed. Similar patterns were seen whether the existing breeding population was "natural" or produced by earlier management.

In summary, successful use of exposed sand for breeding was recorded in the first full season after its provision, the degree and rate of utilisation being directly related to the original population density; the rate of increase and dispersion of sightings were similarly dependent on the premanagement population level, with formerly non-breeding and low-density sites usually exhibiting a trough in sightings during the second season after management.

A further conclusion was that tree and scrub clearance alone did not promote breeding, unless of itself it removed shade from existing bare sand. This was seen strikingly at those sites where clearance preceded sand exposure by up to two seasons. In contrast, provision of unshaded bare sand in continuous deep heath, even when short or sparse overgrowth had not been cleared, resulted in immediate lizard concentration and breeding. Of the twenty-six sites studied in detail, this occurred at all fourteen where clearance was accompanied by sand exposure and at all five where

sand was exposed in continuous deep heather (despite the continued presence of light tree growth at two of them). However, colonisation and breeding were not recorded at any of the seven cleared sites without bare sand, until after sand had been exposed a season or more after the initial clearance.

The experiment of providing exposed sand in shaded locations was not tried as this was already a natural feature of many unmanaged areas at which *L. agilis* was failing to breed.

QUANTITATIVE

Age-maturity group composition of L. agilis *populations*

For this and succeeding analyses, sites were classified as:

Unmanaged—at which examination of the habitat showed that immediate management was needed to reverse degradation (Fig. 4a and 5a).

Viable unmanaged—where the habitat was consistent with a stable breeding population (large or small), and potential management was only to extend the breeding area.

Managed—(sites cleared of overgrowth, but lacking bare sand were classed as unmanaged).

Natural recovery—sites with good habitat at which the population was recovering from the effects of known collection, or of partial habitat destruction by fire.

Results from all types of site cover the period 1969 to 1976, with the widest coverage from 1972 to 1975. Sightings frequencies of adult and immature lizards were averaged for all surveys throughout the active season. As hatching can occur at any time between the beginning of August and mid-September (sometimes even in October), depending on the weather during the incubation period, juvenile sightings frequencies were averaged for all surveys after the first was seen on the site in question. If no juveniles were seen, but surveys did not extend to mid-September, it was taken that the site had received no post-hatch surveys; if surveys continued beyond mid-September still failed to reveal juveniles, a zero "birthrate" was assumed for statistical purposes. Juvenile:mature ("observed birthrate") and immature:mature ratios were calculated (for individual sites) from these data.

It should be noted that owing to differences in behaviour and mortality patterns in the three groups, these ratios provide only a reflection of the age-maturity composition and not an absolute value which would include more juveniles and immatures than are locatable by comparative observation.

The results are summarised in Tables II and III.

Mean birthrates were higher in all groups of managed sites than in unmanaged sites, significantly so ($P < 0.001$) for all combined and for all separate groups ($P < 0.01$), save the first season value which was based on observations from very few sites.

None of the managed site values differed significantly from one another.

The mean immature: mature ratio from the first season of management was almost identical with that from unmanaged sites, confirming similar poor breeding success before management, but in each subsequent season was elevated significantly ($P < 0.01$ or better), reflecting improved breeding and confirming a "real" birthrate increase in the first season.

Ratios at viable unmanaged sites were intermediate between those from managed and unmanaged sites. This might suggest that managed habitat was even better than the naturally good habitat on which it was modelled, but there is another inter-

TABLE II. Age/maturity-group composition of *L. agilis* populations

Site group	Number of sites	Sightings frequency ratios Immature : mature	(Mean ± Standard error) Juvenile : mature
Unmanaged	16	0.0723 ± 0.0259 (22)*	0.423 ± 0.214 (9)†
Managed—			
1st season	9	0.0753 ± 0.0371 (9)	1.758 ± 0.985 (5)
2nd season	15	0.3515 ± 0.0877 (15)	1.939 ± 0.479 (9)
3rd season	15	0.2523 ± 0.0488 (15)	2.436 ± 0.627 (11)
4th and later seasons	17	0.324 ± 0.0791 (17)	1.945 ± 0.368 (10)
All managed	24	0.3095 ± 0.0425 (47)‡	2.079 ± 0.273 (36)
Viable unmanaged	11	0.1606 ± 0.0589 (19)	1.181 ± 0.312 (11)
1st season "extension" management	5	0.396 ± 0.085 (5)	2.240
Unmanaged + viable unmanaged	27	0.1132 ± 0.0031 (41)	0.8398 ± 0.2105 (20)
Natural recovery	6	0.3000 ± 0.142 (8)	3.030 ± 0.230 (2)

* Number of observations. Differs from number of sites as sites can fall into the same group (other than a specific season after the start of management) for more than one year.

† Number of observations. Less than (*) since not all sites were surveyed after hatching time.

‡ Excludes the immature : mature ratio for the 1st season as this reflects breeding in the season before management.

Mean number of surveys per site per year = 7.8.

TABLE III. Statistical comparison of age/maturity-group compositions

Site group	Compared with	Immature : mature ratio "t"	P	Juvenile : mature ratio "t"	P
Unmanaged	1st season managed	Inapplicable		n.s.†	
	2nd season managed	2.94	<0.01	2.90	<0.01
	3rd season managed	3.26	<0.005	3.04	<0.01
	4th and later season managed	3.19	<0.005	3.65	<0.005
	All managed*	4.65	<0.001	5.88	<0.001
	Viable unmanaged	1.37	n.s.†	2.16	<0.05
Viable unmanaged	1st season extension management	2.27	<0.05	Inapplicable	
	All managed*	2.045	<0.05	2.15	<0.05
Unmanaged + viable unmanaged	All managed*	3.73	<0.001	3.60	<0.001

* Excludes 1st season immature : mature ratios.

† n.s. = not significant ($P > 0.05$).

pretation. Predation of young *L. agilis* by their elders occurs in the wild (see Discussion) and would naturally be more intense where adult density was high, as at stable, naturally viable sites, than where it was relatively low as in the first few years after the start of management work. Cannibalism would thus tend to depress the *observed* ratios more at viable unmanaged than at managed sites. In these circumstances, extension of the habitat available to an already thriving colony should

enable an increased proportion of young lizards to escape adult predation, thus increasing the immature:mature ratio in the first post-management season; there is evidence for this in Tables II and III.

Ratios in "natural recovery" sites were similar to those in managed sites, presumably because in both classes a small population was growing to fill a large area of suitable habitat, and confirming the similarity between managed and naturally good habitats.

"Absolute" incidence of breeding

Evidence for successful breeding in any given year can arise from records of juveniles in that year, of immatures the next year, or of young (newly mature) adults the spring following. Using these as criteria, it is clear from Table IV that successful breeding was both more frequent and more regular on managed than on unmanaged sites, with viable unmanaged sites again occupying an intermediate position.

TABLE IV. Absolute incidence of breeding in *L. agilis* populations

	Unmanaged	Viable unmanaged	Managed
Sites with any breeding	5/10 = 50%	16/17 = 94%	25/25 = 100%
Site-years with breeding	8/27 = 30%*	38/44 = 86%†	70/71 = 98%
Breeding every year for which there is evidence	0/10 = 0%	11/17 = 65%	24/25 = 96%
Breeding in 2 consecutive years	1/9 = 11%	10/13 = 62%	19/19 = 100%

* By X^2 test: significantly different from viable unmanaged ($P < 0.001$) and from managed ($P < 0.001$).

† Significant different from managed sites ($P < 0.005$).

Annual changes in adult population density

Increases in adult density resulting from management cannot be expected before the third season, when the first season progeny reach maturity; earlier changes can only be the result of movements or of natural wastage of the original stock. However, where management is aimed to extend the habitat of an already viable colony, increased numbers of immatures escaping adult predation should yield an increase in adult population in the second post-management season (before this, outward diffusion of adults from the original nucleus may well reduce population density).

For Table V, annual mean adult sightings frequencies are calculated as proportions of the previous years' values for individual sites monitored in consecutive years (paired results); the managed site group includes observations only where one of the years was the third, or later, after the start of management, save for one—an initially viable colony whose habitat had been extended by management—where the second season value is compared with the first.

Unmanaged sites showed a mean, significant ($P < 0.001$) fall of over 50% *per annum* in sightings frequency; viable unmanaged sites showed no significant annual change, but managed sites showed a significant ($P < 0.001$) annual doubling.

Statistically, these sightings frequency observations show clear trends, and it is of value to compare the mean annual changes from managed and unmanaged sites. The ratio is $2.173/0.436 \simeq 4.98$, indicating that managed sites were nearly five times as "productive" of adult lizards as were unmanaged sites. The ratio between the mean

TABLE V. Proportional annual changes in sightings frequencies of adult *L. agilis*.
Mean ± S.E.

Site group	Sites	Number of Paired observations	Mean proportional sightings frequency change
Unmanaged	5	9	0.436 ± 0.123*
Viable unmanaged	3	7	1.200 ± 0.250†
Managed	13 ·	23	2.173 ± 0.375‡

* Significantly less than unity ($P < 0.001$); less than viable unmanaged ($P < 0.01$); less than managed ($P < 0.001$).
† Not significantly different from unity (i.e. no change).
‡ Significantly greater than unity ($P < 0.001$); greater than viable unmanaged ($P < 0.05$).

"birthrates" of the two groups is $2.079/0.423 \simeq 4.91$, a remarkably close agreement. Similarly, the managed sites appeared about twice as productive of adults as viable unmanaged sites, and had about twice the mean birthrate.

Correlation of the immature:mature ratio of one year with the birthrate of the previous year and the proportional change in adult sightings frequency by the next year

The preceding analyses consider groups of, rather than individual, sites. Although the intrinsic sampling errors of the field observations preclude a rigorous analysis, the values should, however, show some degree of correlation at individual sites.

From the observations at viable unmanaged sites, a juvenile:mature ratio of ca. 1.2, and an immature:mature ratio of ca. 0.16, are associated with stable populations. Juvenile:mature ratios were therefore categorised: 0 to 0.499 as 0; 0.5 to 0.999 as 1... > 3.0 as 6. Immature:mature ratios were categorised: 0 to 0.059 as 0; 0.06 to 0.119 as 1 . . . > 0.36 as 6. Proportional changes in mean adult sightings frequency were categorised: 0 to 0.399 as 0; 0.4 to 0.799 as 1 . . . > 2.4 as 6. Significant correlations were found between the juvenile:mature ratio of one year and the immature:mature ratio of the next ($r = 0.516$; N = number of observations = 38; n = number of sites = 22; $P < 0.01$), between the immature:mature ratio of one year and the proportional change in adult sightings frequency by the next ($r = 0.531$; $N = 50$; $n = 26$; $P < 0.001$) and even between the juvenile:mature ratio of one year and the proportional change in adult sightings frequency over the next two years ($r = 0.551$; $N = 18$; $n = 11$; $P < 0.02$) for individual sites surveyed in consecutive years irrespective of the stage of management, if any.

These findings accord with the more general conclusions drawn from the preceding analyses and further confirm that a habitat in which *L. agilis* shows a high level of breeding success is one consistent with a high survival rate so that the species will maintain or increase its adult population density.

Other rarities

Most important amongst our reptiles, because of its extreme rarity in Britain, is the smooth snake (*Coronella austriaca*). This too is a specialised dry heathland species and, although the complete habitat requirements are as yet unknown, its historical

distribution closely parallels that of *L. agilis* in zones II, III and IV (Corbett in Prestt *et al.*, 1974). By 1970, it was virtually extinct in zone II, with reliable, but rare, records from only three sites, two of which have since been destroyed by fire. However, a number of different specimens (all significantly large adults) were initially recorded from a very isolated site without previous *C. austriaca* records, and which was being managed to receive an experimental re-introduction of *L. agilis*. Immature snakes were then found there during the 1978 season.

C. austriaca is now found on most of our zone III and IV sites; a number of sites managed to promote colonisation from adjacent *L. agilis* populations have also been colonised by breeding *C. austriaca*. It is particularly interesting that the sole management for two of these, and the main management for another, was provision of sand patches in continuous mature heather.

TABLE VI. Proportional annual changes in sightings frequencies of adult *C. austriaca*. Mean ± S.E.

Site group	Sites	Number of Paired observations	Mean proportional sightings frequency change
Unmanaged	3	7	0.477 ± 0.179*
Viable unmanaged	2	5	1.144 ± 0.210†
Managed	6	11	2.324 ± 0.653‡

* Significantly less than unity ($P < 0.01$); less than viable unmanaged ($P < 0.025$); less than managed ($P < 0.05$).

† Not significantly different from unit.

‡ Significantly greater than unity ($P < 0.05$).

Few sites receive the intensive study needed to yield useful quantitative results on this species and a detailed statistical analysis as for *L. agilis* is not yet feasible. However, comparison of mean adult sightings frequencies year by year (Table VI cf. Table V), indicates that population changes in *C. austriaca* parallel those of *L. agilis* in the different groups of sites.

In addition to reptiles, most sites have developed breeding populations of one or more of the rare or restricted heathland bird species: Dartford warbler (*Sylvia undata*), nightjar (*Caprimulgus europeus*) and stonechat (*Saxicola torquata*). Increases in numbers and species of sand wasps (Hymenoptera) have also been recorded from many sites, apparently in direct response to sand excavations.

DISCUSSION

It is of interest that the preferred habitat-type resembles that described by Peters (1970) for the closely related *L. viridis* at its own northern European range limits in E. Germany. Recent study of *L. agilis* in the Lancashire dunes (Corbett, 1974) showed that an essentially similar habitat was exploited there, but based on mature, tangled marram (*Ammophila arenaria*) in place of mature *Calluna*.

Methods

As all British reptiles favour densely vegetated habitat, and populations are usually disperse, population estimation demands intensive, prolonged mark-recapture study;

Corbett found that one season's full-time work sufficed to mark only 70% of the adults on his two intensive study sites, which is clearly impractical for routine use on our more numerous and generally larger Key Sites.

Trapping is similarly restrictive, inefficient, and appears irresponsible on both academic and conservational grounds. The restraint must distort the trapped animals' behaviour, notably interfering with basking patterns and hence physiology, so threatening modifications of the populations structure. Traps in sunny places present risk of heat-deaths; pitfall-type traps can fill with rainwater and cause drowning. They give the lizards no opportunity to escape predators, and may reduce food availability. As they can catch only those individuals with whose ranges they coincide, many traps are needed to capture a useful sample of the population, with a consequent increase of the hazards. Frequent inspection every day could reduce these, but the attendant disturbance would also distort the observations. Further, and particularly in dry weather, mature *Calluna* is very vulnerable to destruction by trampling (Burden & Randerson, 1972; Bibby & Tubbs, 1975), an inevitable consequence of frequent inspection.

A sampling method was clearly essential, but Lincoln Index-type techniques are inapplicable, notably because of the difficulty of catching adequate population samples in single surveys (cf. Avery, 1975); the limited mobility of many reptiles (e.g. *L. agilis*; Simms, 1971; Corbett, unpublished observations), such that marked animals do not mix randomly with the general population; wide individual variation in habits and longevity, such that survival of a batch of marked animals is unknown at any given time without accurate knowledge of mortality patterns throughout life and possibly for each individual site (for the small proportion of *L. agilis* reaching maturity, Corbett estimated an average total life expectancy of 4–5 years, but some marked individuals attained 8 years in the wild; 10 years has been recorded in captivity—Walters, 1971). Thus the sightings frequency technique was the only practicable method for routine use. It has the enormous advantage of causing minimal disturbance, hence minimal distortion of the results. The results show great internal consistency providing strong evidence that the technique yields valid results when analysed statistically. The observations have a built-in control against observer bias in that sites of all types were surveyed throughout the period of investigation by a diversity of fieldworkers.

All the results depend upon visual observation and it is worth considering whether a secondary effect of management was to render the animals more easily visible. However, this view is contradicted by:

(*a*) In overgrown habitat, reptiles are observed mainly during basking. By increasing the number of basking places, management actually *reduced* the probability of seeing reptiles in a given time, tending to reduce sightings frequency for a constant population.

(b) Increased visibility would cause only a once-and-for-all increase in sightings, not the progressive increases obtained.

(c) Increased visibility to the human observer implies increased visibility to predators, so were this a factor, the increased sightings should be short-lived.

(d) Short heath, where visibility is high, yields fewer observations than deep heath, where visibility is low.

(e) The differing patterns of sand-patch utilisation also confirm that the observed responses were not an artifact of increased visibility.

In practice, the available data showed no overall mean change in adult sightings frequency between the immediate premanagement and the second post-management

seasons. Most individual sites showed decreases, but a few showed increases, considered attributable to incursions from surrounding unmanaged habitat.

Implications of the observations: population control and colonisation

The qualitative and quantitative observations, effectively four independent modes of assessment, agree in confirming that the method of management provides a habitat in which *L. agilis* can thrive, and even rebuild from relict populations. That the increased density is not an artificial concentration of lizards is suggested by the high stable populations found naturally in similar habitat, supported by the sequence of events observed and by the absence of increase before the third season after the start of management—when the first post-management hatchlings reach maturity but many of the original adult stock have died.

Similarly, the increased populations are not temporary, artificial peaks. A single female may lay up to 13 eggs, with a 100% hatch in a good summer, therefore potentially, without controlling factors, any breeding population of *L. agilis* should quickly peak, and presumably crash. On the contrary, stable populations are the rule once the optimum colony level is reached, and no evidence has been obtained to suggest any fluctuation.

One of the most important and logical factors for the natural control of colony population size is cannibalism, by the adults on their young, and particularly on the juveniles and young immatures. Corbett (in preparation) has found field evidence from the results of faecal pellet analyses, and has also observed avid cannibalism in large outdoor heath vivaria—even from well-fed adult populations. Field observations of adults eating their young have recently been made from various Dorset sites (Nature Conservancy Staff personal communication; British Herpetological Society, 1975). Such habits have also been noted from the wild in Germany (Peters, 1970) and in Holland (Van de Bund, 1957, 1964). Clearly, pressure of adults on young would tend to increase natural colonisation rates into habitat with lower density, or entirely lacking, adult populations. Corroborative evidence may be seen above, when extension of the habitat available to viable unmanaged colonies produced an immediate increase in the immature:mature ratio.

The evidence indicates that further declines in *C. austriaca* can also be prevented, and probably be reversed, by the same management, giving time to determine the exact optimum habitat, home range and thereby minimal viable areas. The managed sites have also proved viable for Britain's four other reptile species. The essential aim was to restore areas of a rapidly disappearing form of habitat, lowland mature dry heath, by removal of invading vegetation, on the assumption that restoration of an open, heather-dominated habitat would lead to natural regeneration of the whole ecosystem. The response of the reptiles, and the recolonisation by specific heathland birds, for example, suggests that the approach was sound.

Significance of exposed sand

It is important to note that the policy was simple and empirical, being based on descriptive investigation of the habitat in which *L. agilis* was found to thrive best. A crucial factor was identification of the particular habitat features required for breeding, as opposed to those needed by the animals for all other aspects of their lives. The distinction between the "living" and "breeding" facets of occupied habitat does not appear to be generally recognised, despite the obvious (and significant) example of Britain's only other oviparous reptile, *Natrix n. helvetica*. This species probably owes

its wide distribution in Britain to use of the warmth of rotting vegetation to incubate its eggs (Howes, 1972), although rarely having such features as part of its normal home range. The evidence from artificially introduced reptiles in Britain (Fitter, 1957; Frazer, 1964), and from *L. agilis* itself, suggest that the northerly range of oviparous reptiles is limited by the availability of suitable conditions for egg incubation; the free-living animals can survive for an apparently normal life-span of many years under conditions that do not permit breeding. Strictly, the limitation is that "breeding" habitat must occur within the species normal range of movement; where this is small, as in *Lacerta* spp., "living" and "breeding" habitat must occur side by side, for more mobile animals such as *Natrix n. helvetica* (Prestt *et al.*, 1974; Prestt, pers. comm.) the two may be widely separated, providing the intervening terrain is one which the animals can cross.

The importance to *L. agilis* of sand, which is sterile (heath) or wind-disturbed (dunes), is thought to be linked with its poor colonisation by plants. In a preliminary experiment, Corbett transplanted mixed clutches of eggs into bare sand, loam and chalk soils; hatching occurred of all the eggs in sand (which showed little plant colonisation during the incubation period), but of only a few of those in loam and chalk, which were rapidly vegetated. All the unhatched eggs were found to be enmeshed in developing root systems, which presumably altered the temperature and humidity of their immediate environment. All eggs placed in clay failed to hatch, irrespective of vegetation, presumably because of mechanical damage from the physical changes of clay with wetting and desiccation.

The dependence on bare sand probably arose with the fall of about 2°C in average summer temperatures accompanying the close of the sub-Boreal period about 2000 years ago. During the sub-Boreal period, it is probable that a wide range of habitats were exploited, as in central Europe today, where eggs hatch successfully under logs, stones, leaf litter etc. Significantly, only in the cooler climates of Britain, Netherlands and Sweden is *L. agilis* known as the "sand lizard".

One interpretation of the observed increase in *C. austriaca* populations following sand exposure is that they are secondary to the concentration, and population increases, in *L. agilis*. *C. austriaca* feeds predominantly on lizards (see Bruno, 1970, and apparently preferentially on *L. agilis* (Andren and Nilsen, 1976).

Other species

Most temperature climate reptiles are "shuttling heliotherms" which depend on basking, and would therefore be expected to benefit from reduction of shade by tree and scrub clearance. Certainly, thriving populations of adders (*Vipera berus*) and viviparous lizards (*Lacerta vivipara*) now occur on all of our managed Key Sites. *L. vivipara* often became restricted to areas not favoured by *L. agilis*, probably because of dampness or distance from exposed sand, and at least partly because of their predation by the latter, which has been observed in the field and confirmed by the occurrence of lizard remains in *L. agilis* faecal pellets (Corbett, in preparation). Slow-worms (*Anguis fragilis*) occur widely on our managed sites; their secretive habits tend to obscure population densities, but where assessment was possible, they were usually found to be abundant.

The grass snake (*Natrix n. helvetica*), primarily a predator of amphibians and fish, has not previously been recorded as being regularly associated with a dry heath habitat (Appleby, 1971; Smith, 1951; Spellerberg, 1975), yet the species is common on our managed sites. Overall, sightings have doubled since 1972, and recapture records from

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marked snakes confirm that they are residents on the sites, not transients. Regurgitated stomach contents show that the main food in dry heathland is the toad, *Bufo b. bufo* (more surprisingly, our heathland adders have also regurgitated toads!). In this context it is interesting to note how often *B. bufo* is found in dry heath; it is not unusual to find sites over 1 km from the nearest breeding pools reliably having newly-metamorphosed toads by late summer.

Conclusions

The qualitative and breeding incidence observations showed that management, to reproduce the natural habitat conditions in which stable *L. agilis* populations occurred, led to restoration and/or enhancement of breeding and to colonisation of recreated habitat by breeding lizards. This produced population increases manifested by sightings at increasing numbers of locations within sites. The quantitative observations confirmed this, with significantly higher proportions of juvenile and immature lizards on managed compared with unmanaged sites. This led to increases in overall adult sightings frequency, whilst monitored unmanaged sites, by contrast, showed progressive falls in sightings frequency.

Management achieved its original aim of offsetting the continuing decline of both species and habitat and in establishing practical techniques for their conservation. However, the Key Site strategy must be seen as a short-term measure filling an urgent need; in the long term, conservation of dry heath *per se* is essential. Apart from persistent pressures for various forms of development, the habitat is exceptionally vulnerable to fires, which are increasing in frequency with increasing public pressure. Thousands of hectares, including many vital Key Sites, have burnt even as this paper was being prepared (Bibby, 1976; DNT/RSPB, 1976; SNT/RSPB, 1977). These fires have again had a noted and disproportionate effect on the all important mature dry heath—such that only an estimated 5% of Dorset heaths are thought to have survived unburnt for 20 or more years (DNT/RSPB, 1976).

Dry heath reserves are urgently needed, ideally large in order to allow effective fire-breaking and the containment of local, accidental fires; this in turn necessitates an acceptance of "compartmentation" from primary and secondary ploughed breaks, both of which can twist and follow contours aesthetically. Intermittent management seems likely to be needed in perpetuity, although this is not in the experience of our field-workers considered to be an over-demanding commitment, once the initial back-log of clearance is complete. It should only involve periodic clearance of young pine scrub and maintenance of exposed sand, every 5 to 10 years. Local control of bracken by summer spraying of new fronds with Asulam (Cadbury, 1976) is also strongly recommended to prevent further encroachment, and to recover Calluneta so degraded.

The National Nature Reserves should provide the required security, but in practice occupy only a small fraction of even the little dry heath which remains. The hazards of relying on such reserves alone are illustrated by the recent total loss, by fire, of one of the three relevant reserves. Another dry year could mean loss of all. However, as yet, there is no national policy for the conservation of lowland dry heath either from the Nature Conservancy Council or the Society for the Promotion of Nature Reserves, although the loss of comparable areas in continental Europe led Bibby (1975) to report on the international importance of conserving our own dry heath.

Recent action

Recognition of the overall problem has led the Nature Conservancy Council

to set up in January 1977 a representative Advisory Group on Herpetofauna, and whose main responsibility is to undertake the drafting of a detailed National Policy for the Conservation of Endangered Herpetofauna and their Habitat. At the same time, the publication of the Nature Conservation Review (1977) may be seen as justification for the acquisition of more lowland heath reserves, hopefully with the accent on dry heath.

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Extended versions of Tables II, IV, V and VI are held in the library of the British Herpetological Society.

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