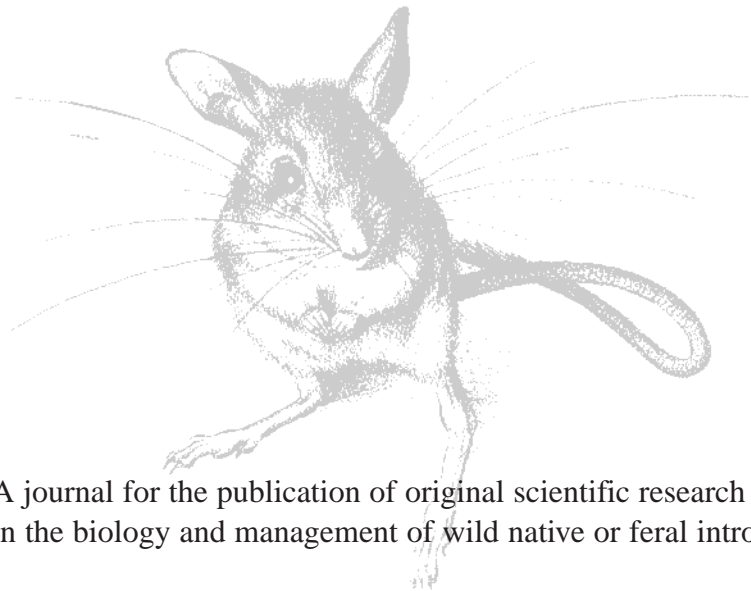

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Home-range characteristics of an alpine lizard, *Niveoscincus microlepidotus* (Scincidae), on Mt Wellington, southern Tasmania

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Abstract

We studied the home ranges of the alpine skink, *Niveoscincus microlepidotus*, in an alpine transition zone on Mt Wellington, Tasmania, over a 5-month period to examine seasonal patterns in the home-range characteristics of four male, four female and two sub-adult juvenile lizards. Home-range sizes and activity patterns within these were quantified. Adult males had significantly larger home ranges with more activity centres than adult females; most activity centres were clearly synonymous with basking sites and were defended by overt aggressive behaviour. Home ranges of males showed little overlap and no seasonal variation while those of females were unusual amongst reptiles in showing extensive overlap and seasonal change in size. Ranges were smallest in spring when all females were pregnant and were smallest in summer when only one female was pregnant. Range overlap ensured that all females studied had potential access to at least two males. Juveniles had no defined home ranges and appeared to be transients.

Introduction

An animal's home range is the entire area utilised in order to find the resources it requires (Burt 1943). For temperate-climate lizards these resources include food, retreats, mates and basking sites. Consequently, many factors can influence the size and location of an animal's home range (Ruby and Dunham 1987). For example, lizards may adjust the size and location of their home range in response to seasonal climatic changes (Christian *et al.* 1983), variation in habitat productivity (Simon 1975), hormonal status (DeNardo and Sinervo 1994a, 1994b), or reproductive activity (Ruby 1978; Stamps 1983). Numerous studies have shown a significant relationship between home-range size and body mass in lizards (e.g. Turner *et al.* 1969; Harestad and Bunnell 1979; Christian and Waldschmidt 1984). However, it is clear that home ranges are not simply determined by the interaction of food levels and energetic requirements alone. Social factors may also influence home-range size and home ranges of males can be much larger than those of females, despite similar body sizes (Ruby and Dunham 1987).

Most studies of lacertilian home ranges have centred on the size and overlap of home ranges, rather than on activity patterns within these ranges. Work has often focussed on easily observed species, such as those that inhabit relatively open country (e.g. Takeishi and Ono 1986; Dubas and Bull 1992; Avery 1993; Smith 1995), or arboreal species such as those in the *Anolis* complex (e.g. Stamps and Krishnan 1994a, 1994b). Less information is available for small, mobile lizards that occupy complex habitats where regular observation is often difficult. Data for Australian species are also limited and no information on home ranges and their usage is available for any alpine species.

Niveoscincus is a genus of small to medium-sized lygosomine skinks (Hutchinson *et al.* 1990). *Niveoscincus microlepidotus*, one of the larger species in the genus (50–69 mm adult snout–vent length, SVL, 3.5–5.0 g), occurs in disjunct populations on mountain tops above 1000 m in southern Tasmania (Hutchinson and Schwaner 1991). It is a small, highly mobile, and exclusively alpine species endemic to Tasmania (Hutchinson *et al.* 1990). The species is sexually dimorphic, which greatly simplifies observations of behaviour in the field: males are significantly larger than females and have wider heads in relation to their snout–vent lengths (Melville 1994). Preliminary field observations indicated that home ranges are generally stable,

and this, coupled with the preference in this species for relatively open habitat (Melville and Swain 1997a) and high abundance, provided an opportunity to add to our knowledge of home-range characteristics in small Australian lizards. Our objectives were to quantify intraspecific differences in home-range size, variation in the size of ranges over an activity season, and patterns of usage within ranges.

Methods

The study site was at an altitude of 1080 m, immediately above the tree-line on the eastern face of Mt Wellington, near Hobart, Tasmania. For three days in each of November, January and March (1993/94 activity season) fixes were recorded for a home-range study. These observation periods represent the mid-points of spring, summer and autumn, respectively. Low winter temperatures result in obligatory hibernation. A 10×10 m grid was mapped out in a boulder field, allowing the precise location of individual lizards to be recorded (Fig. 1). The grid contained large boulders (1–2 m diameter) with alpine heath vegetation concentrated mostly around the perimeter. Our choice of location was based on our previous research (Melville and Swain 1997a), which identified boulder fields as the preferred habitat of *N. microlepidotus*. The decision to base our observations on a small study area was influenced by the apparently small home ranges suggested by a preliminary study, our desire to observe individual lizards over an entire activity season, and by Rose (1982), who argued that it is better to concentrate on a small number of animals in a limited area than to make fewer sightings of more lizards in a large study area (at least 1 ha) because this reduces sample-size bias and increases the probability of resighting a subject. Our subjects comprised 4 adult males, 4 adult females, and 2 sub-adult juveniles that a preliminary trial had indicated were the sole residents in the area and could be observed consistently. Lizards were captured and sexed by eversion of the hemipenes in males. The reproductive status of females was determined by gentle palpation to locate developing eggs or embryos. Each lizard was tagged dorsally with a 4×4 mm square of yellow tape, numbered so that individuals could be identified from a distance throughout the study. Observations were made at 0900, 1100, 1300, 1500 and 1600 hours (Local Summer Time) on each observation day. Adequate sampling is particularly important in range analysis because areas tend to increase as the number of fixes increases (Rose 1982). *Niveoscincus microlepidotus* is an active forager so a target of at least 15 sightings per individual on each sampling occasion was set in order to identify at least 80% of an individual's range. A fix of all 10 individuals could usually be collected within about 30 min. A preliminary plot of the number of fixes versus the home-range size confirmed that 15 fixes adequately estimated the home-range size of *N. microlepidotus*. Particular care was given to selecting observation days in which similar weather conditions prevailed; warm sunny days with little cloud cover were chosen in order to minimise differences in behaviour associated with heavy cloud, rain squalls or snow showers.

Convex polygons were calculated to describe individual home ranges for November, January and March, and for the entire season; harmonic means were used to define activity centres within ranges. Calculations were made using the RANGES IV program in MS-DOS format (Kenward 1990). Convex polygons, drawn around all the fixes, often reflect the presence of a few outlying fixes and may overestimate the range in which an animal spends most of its time (Schoener 1981). Consequently, we attempted to exclude outliers by using only those fixes that made up 90% of the activity range.

The harmonic mean model (Dixon and Chapman 1980) estimates the density distribution by the inverse mean reciprocal distance from each grid intersection to all the fixes. Fixes are then ranked according to the density at each cell centre, and contours interpolated across the notional grid so that the resulting isopleths contain the required percentage of fixes. Since isopleths are fitted most accurately when there are many grid cells, the RANGES IV default option of a 40×40 grid was used. The harmonic mean was used to describe the range use of individual lizards and to locate their range centres.

All other statistical analyses were carried out using the program SYSTAT for the Macintosh (Wilkinson *et al.* 1992). ANOVA assumptions were checked by examining plots of standardised residuals against estimated values and the normal probability curve of the residuals.

Results

The mean range areas of all adults, and for each season, are shown in Table 1. A two-way ANOVA was used to examine the changes in home-range size over the seasons for each sex. There was no significant interaction between the sex of a lizard and the season in which home range was measured (ANOVA: $F_{2,18} = 2.772$; $P = 0.089$). However, males had significantly larger

Table 1. Core activity ranges of adult male and female *Niveoscincus microlepidotus*
Values are mean area (m²) ± s.e. *N* = 4 in all cases

	Spring	Summer	Autumn
Female	6.2 (0.02)	10.5 (0.25)	14.0 (0.11)
Male	14.5 (0.99)	13.9 (0.98)	13.5 (0.67)

home ranges than females (ANOVA: $F_{1,18} = 44.643$; $P < 0.001$). Average range size of females increased progressively from spring to autumn (Table 1). In spring all females were pregnant, two were still pregnant in summer (animals 'N' and 'Q'), and a single animal remained pregnant in autumn (animal 'N'). Animals 'O', 'P' and 'Q' had therefore overwintered as pregnant females while animal 'N' presumably ovulated shortly before capture in spring. A Tukey's test indicated that home ranges of females in spring differed significantly from those in summer or autumn ($P < 0.001$). There were no significant seasonal differences in average home-range size in the males.

The home ranges of all the study animals had multiple activity centres, most of which were on rocks and were clearly synonymous with basking sites. Males had many more of these sites than females (8–11 cf. 3–7; Figs 2, 3). All lizards were observed to utilise the vegetation around the perimeter of the study grid at least once a day. This activity was associated with foraging.

The total home ranges of the male lizards are shown in Fig. 2. Male *N. microlepidotus* utilised a number of basking sites spread throughout the home range. The male with the largest spread of basking sites (Fig. 2, animal 'A') was the largest lizard observed in the grid area (SVL 63.2 mm). This individual was sighted most frequently and was often observed displacing other subjects, including juveniles, females and other males, from basking sites. These displacements

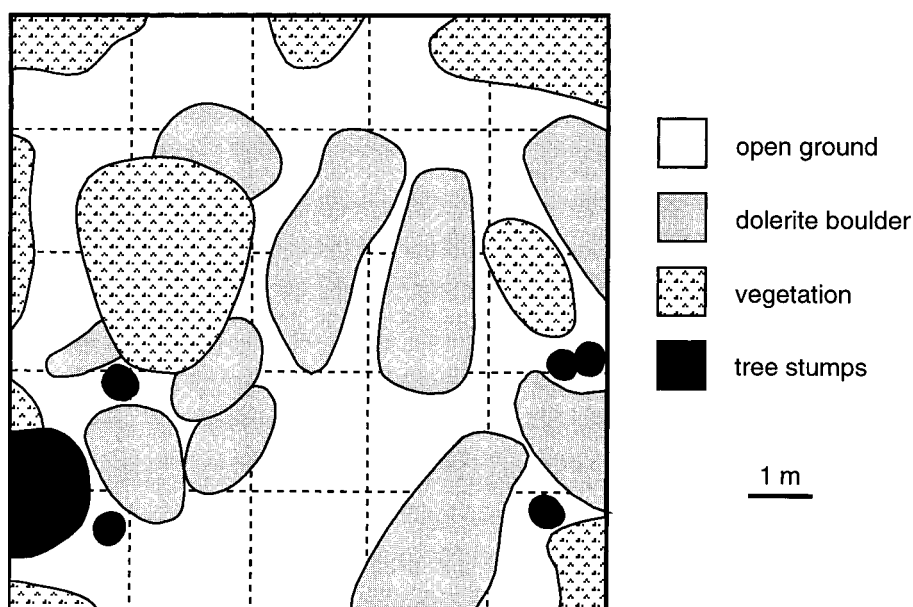


Fig. 1. Map of the study area used to investigate home ranges in *Niveoscincus microlepidotus*.

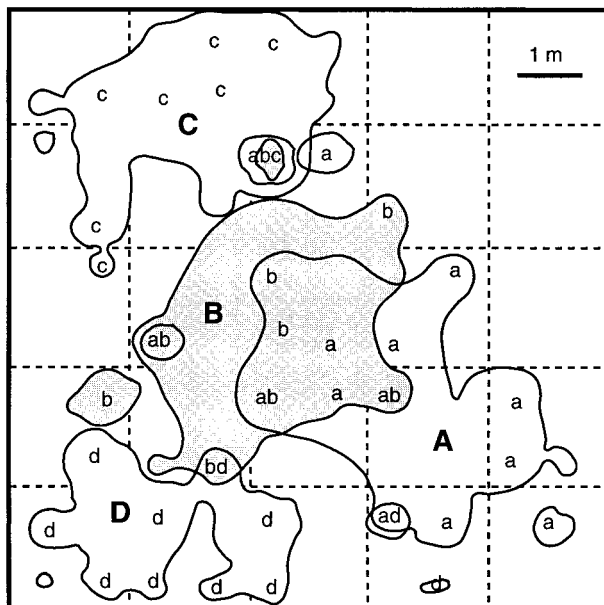


Fig. 2. Total home-range area (based on 90% isopleths) for adult male *Niveoscincus microlepidotus* studied through spring, summer and autumn. Upper-case letters identify the ranges of individual lizards; corresponding lower-case letters identify their activity centres.

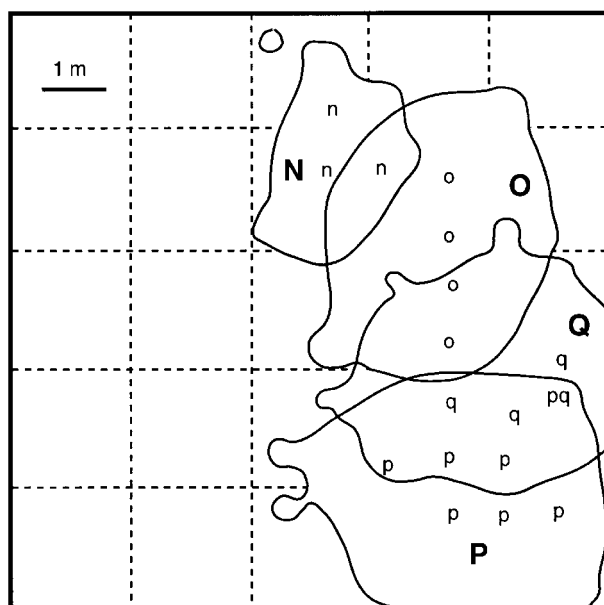


Fig. 3. Total home-range area (based on 90% isopleths) for adult female *Niveoscincus microlepidotus* studied through spring, summer and autumn. Upper-case letters identify the ranges of individual lizards; corresponding lower-case letters identify their activity centres.

were achieved through threats or overt aggressive behaviour, including head and tail biting. Despite this evidence of aggressive interaction, there was quite extensive overlap in the areas occupied by males 'A' and 'B' and all males showed some degree of intrasexual overlap in home ranges; several instances of common basking sites occurred, although these were never shared simultaneously (Fig. 2).

Female lizards occupied a more restricted region of the study site than males and exhibited much more overlap in their home ranges (Fig. 3). They had fewer activity centres and these centres tended to be located on the same rock. For example, the range of individual 'O' in Fig. 3 was concentrated around one large boulder and contained four distinct basking locations. The smallest activity range recorded was for one female ('N') that was pregnant throughout the study period (Fig. 3). Subjects ('O' and 'P') that were pregnant only in spring had overall activity ranges similar to those exhibited by two of the four males (Fig. 3). Despite the considerable overlap in home ranges of females, shared basking sites were rare (Fig. 3).

Juveniles foraged throughout the study site and had many activity centres, even though the least number of fixes were obtained for these animals. Activity centres were not maintained between observation periods and no distinct home ranges could be identified.

Discussion

The importance of an adequate number of fixes for the reliable estimation of home-range size is widely acknowledged. A small number of observations is likely to lead to underestimation (Schoener 1981), whereas the use of correction factors (e.g. Jennrich and Turner 1969) is now discouraged because of the danger of overestimation (Rose 1982). Although practicalities have sometimes necessitated use of a low minimum number [e.g. Swallow and Castilla (1996) set their minimum at 5], published estimates based on regressions of home-range size against number of observations suggest that our minimum threshold of 15 is a better choice that should produce reliable data in small lizards. Thus, 13 was identified as the minimum number of resightings for valid analysis in *Uta stansburiana*, which is similar in size to our species (Christian and Waldschmidt 1984), and, for the slightly larger *Sceloporus virgatus*, Rose (1982) and Smith (1995) identified the need for 18 and 8 observations respectively.

Fixes also need to be closely spaced in time if estimates of home range are to be reliable, otherwise shifts in range may be missed and lizards without fixed ranges cannot be distinguished from residents (Rose 1982). This danger is illustrated by our observations on juvenile *N. microlepidotus*: calculation of home ranges for these animals, based on the data-set for the entire study period, would have yielded areas vastly larger than those for adults, when in fact our observations clearly indicated that juveniles were transients, without fixed ranges. However, the advantages arising from detailed observations of a small number of lizards are accompanied by the danger that resulting generalisations may be biased in some way. Consequently, we have taken a deliberately conservative approach in the interpretation of our results.

We can be confident that, at least in our study area, there are undoubted similarities between males and females in home range characteristics, although there are also some important differences that presumably relate to differences in behaviour and habitat usage. Thus, home-range areas in *N. microlepidotus* are small compared with those of other lizard species that have been studied (e.g. Stamps 1983; Christian and Waldschmidt 1984) and are clearly focussed around the boulders that dominate their habitat. Lizards are frequently associated with key structural features within their home range (Jones and Droge 1980) and tend to occupy some areas more than others (Dixon and Chapman 1980). The point of greatest activity is often associated with a home site. However, in *N. microlepidotus* distinct home sites were not identified but all animals possessed multiple activity centres that were largely synonymous with basking sites; *N. microlepidotus* employs both heliothermy and thigmothermy for thermoregulation, and basking almost invariably occurs on rocks (Melville and Swain 1997b).

As well as distinct basking sites, all home ranges included extensive areas of open ground and heath shrubbery. *Niveoscincus microlepidotus* is an active forager, feeding mostly on insects, although some plant material is also eaten (M. Olsson, personal communication), and animals do most of their foraging away from the boulders. Thus, it is probable that individual home ranges incorporate both some minimum number of basking sites and some minimum foraging area from which adequate food supplies can be obtained. In an alpine species such as *N. microlepidotus* availability of a range of basking sites to accommodate changes in the angle of solar radiation may be essential for effective thermoregulation.

In many lizard species males have been found to have larger home ranges than females (e.g. Ruby and Dunham 1987; Jansson *et al.* 1989; Rand *et al.* 1989; Brown *et al.* 1995; Smith 1995; Swallow and Castilla 1996) although similar-sized ranges do occur in some species (e.g. Takeisho and Ono 1986; Lewis and Saliva 1987; Dubas and Bull 1992; Schell *et al.* 1993). *Niveoscincus microlepidotus* clearly follows the former, and more common, pattern although, in contrast to the iguanid *Sceloporus jarrovi* (Simon 1975; Simon and Middendorf 1976), these gender-based differences are unlikely to be driven by a need for additional food resources. Males are significantly larger than females in *N. microlepidotus* but the differences are not great (~5 mm in SVL: Melville 1994) and it seems unlikely that differences in home-range area as great as those observed would be necessary simply to account for any additional food requirements in males. The increased number of basking centres exhibited by males implies an increased level of activity on their part, and this, together with their larger home-range area, is presumably related to mate-acquisition strategies in this species.

Mating activity in *N. microlepidotus* extends throughout much of the active season, largely because females become progressively available over a long period. Females of this species are biennial breeders and are unusual because, although embryonic development is completed before hibernation, they overwinter their young and do not give birth until the next spring, sometimes not until early summer (Olsson and Shine 1998). Presumably, therefore, males must maintain relatively large home ranges throughout the activity season in order to be sure of access to females whenever they become available; increasing home-range size before mating to overlap with more female ranges, as occurs, for example, in *Sceloporus jarrovi* (Ruby 1978), is consequently not an option for *N. microlepidotus*. Males are quite aggressive towards each other and only one of the males in our study (the largest and most aggressive) showed significant overlap in range area with any other male. As a result of this overlap the two males involved ('A' and 'B') each had access to the ranges of at least three females. The remaining males ('C' and 'D') had access to only a single female each.

Overlap in home ranges of females appears to vary among different lizard species. Stamps (1983) reviewed the literature then available and concluded that, in iguanids and agamids, females generally show little overlap in home ranges; this generalisation was supported by Smith (1985) who reported that female *Sceloporus virgatus* have distinct, non-overlapping home ranges. However, other studies on iguanids (Waldschmidt and Tracy 1983), lacertids (Takeisho and Ono 1986), and teiids (Lewis and Saliva 1987; Schell *et al.* 1993) have all demonstrated extensive overlap within females, as well as between sexes, so it is probable that this occurs fairly commonly. Overlap in *N. microlepidotus* may be unusual because it appears to be more extensive in females than in males. We suggest that it may provide a mechanism to ensure access to several males in a relatively immobile species characterised by very small home ranges centred on basking sites. The ranges of each of the females we studied overlapped with those of at least two males.

Average home-range size in female *N. microlepidotus* also increased from spring to summer, apparently correlated with reproductive status; unfortunately, because no non-breeding females were included in our study area we cannot draw firm conclusions about this relationship. However, females spend significantly more time basking and less time foraging when pregnant (Melville and Swain 1997b), so may not require as large a range as they do when non-pregnant. Average range areas were small in spring when all females were pregnant and increased

progressively through the seasons until only one female ('N') was pregnant in summer; this animal had the smallest home range over the activity period. Seasonal adjustment in home range area of females appears to be unusual in lizards and we have been unable to find other records of it. Presumably, it is a consequence of interactions between the resources available within an alpine habitat (both food and thermal), mate-acquisition strategies, and a viviparous lifestyle characterised by the unusual habit of deferring birth until after hibernation. In particular, relationships between mate-acquisition strategies and use of time and space by *N. microlepidotus* present important avenues for future research. More data on food intake would also be valuable since a reduction in feeding activity could be associated with a smaller foraging area. *Niveoscincus microlepidotus* feeds throughout pregnancy but we have not investigated whether prepartum females reduce food intake, as does *Eulamprus tympanum* (Schwarzkopf 1996).

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