Ranging behaviour and home range size of smooth snakes inhabiting lowland heath in southern England

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Individually marked smooth snakes inhabiting a 10 ha area of lowland heath in southern England were studied between 1993–2011 and their movements estimated from capture data. During this period a total of 109 male and 82 female snakes were identified providing 177 inter-location distances from which to investigate overall, and seasonal, movements of adult and sub-adult males and females. The mean distances moved, between successive captures, by adult males was approximately 50% greater than that moved by adult females or sub-adult males and females. Monthly mean distances moved by adult females and sub-adult males and females were all very similar and, with the exception of May and July, were lower than those moved by adult males. During May, when mating occurs, the distance moved by adult males was almost identical to that of adult females suggesting a link with breeding.

The capture locations of 18 female and 18 male smooth snakes, whose range was assumed to be totally within the study area, also enabled home range areas to be estimated for these four categories of snake. The mean home range size of adult males (1.85 ha) was double that of adult females (0.87 ha), about four times larger than that of sub-adult males (0.46 ha) and approximately six times larger than that of sub-adult females (0.31 ha). The home range size of males increased sharply once sexual maturity was reached whilst that of females showed a more gradual increase as body length increased. The maximum home range sizes of adult male and female smooth snakes were 3.88 ha and 2.37 ha respectively. The movements and home range sizes of smooth snakes are compared with similar data found in other snake species

Key words: convex polygons, *Coronella austriaca*, home range, seasonal movements

INTRODUCTION

A major threat to the survival of many animal species, worldwide, is pernicious habitat loss occurring over large areas of the landscape e.g., loss of rainforest to palm oil plantations and/or timber extraction, and loss of natural landscapes to agriculture (Gibbons et al., 2000; Lindenmayer & Fischer, 2006; Gardner et al., 2007). Habitat loss may also occur through the piecemeal destruction of relatively small areas, within larger habitat types, resulting in a fragmented landscape consisting of a mosaic of small, disconnected areas that are potentially too small to sustain some species whose home ranges may usually be larger than the individual fragments (Lindenmayer & Fischer, 2006). The successful conservation of animal species within a habitat, subject to fragmentation, depends on an understanding of their precise habitat requirements, one of which is the size of their home range within a particular habitat type, so that sufficiently large areas can be conserved to allow them to survive.

In the UK the smooth snake, *Coronella austriaca*, is at the northern edge of its geographical range and is restricted to the dry lowland heaths of southern England (Frazer, 1983), a habitat that has declined significantly, as a result of fragmentation, from seven large fragments (>4 ha) with a total area of approximately 40,000 ha in 1759 to 151 smaller fragments (>4 ha), with a total area of 7,373 ha in 1996 (Rose et al., 2000). It is reasonable to assume that this reduction in the total area of dry lowland heath has also resulted in, at least, an equivalent decline in the overall size of the UK's smooth snake population, a species that is now protected under UK law (Wildlife and Countryside Act 1981 and Conservation of Natural Habitats and Species Regulations 2010).

Management protocols aimed at conserving this species depend on a sound knowledge of its behaviour and ecology. Unfortunately the smooth snake is a relatively small, secretive, long-lived animal with a restricted distribution in the UK making it difficult to study. Despite this its distribution (Braithwaite et al., 1989), habitat requirements (Spellerberg & Phelps, 1977), growth and breeding success (Goddard & Spellerberg, 1980; Reading, 2004a, b), hourly and daily movement rates (Gent & Spellerberg, 1993) have been investigated within the UK. There is also very limited published data on the home range of smooth snakes on lowland heath, though some information is provided in an *ad hoc* report by the Nature Conservancy Council (1983). As a consequence, the area of lowland heath that is required to support both individuals and sustain populations remains relatively unknown. The aim of the study reported here was to investigate seasonal ranging behaviour and home range size in both adult and sub-adult smooth snakes, occurring on heath land in southern England, with a view to improving the management protocols used in its conservation, and in particular in helping to define minimum areas of heath land required to support viable populations.

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Table 1. The total number of surveys completed each year (1993–2011), the total number of arrays and refuges used, inter-refuges distances within arrays and the total area covered by arrays (excluding areas between arrays). ** - 3 surveys in 2002.

Period	Number of surveys	Number of arrays	Total number of refuges	Inter-refuge distance/ array - m	Area covered by arrays - ha
1993	28	6	174	(10.0, 17.5, 30.0) x 2	3.748
1994	25	6	330	(5.8, 15.0, 20.0) x 2	3.350
1995–1996	25	6	270	(7.5, 11.6, 25.0) x 2	2.990
1997	18	9	333	10.0	3.465
1998–2000	21	9	333	10.0	3.465
2001–2011	21**	11	407	10.0	4.235

MATERIALS AND METHODS

Study site

The study site was a 10 ha area of dry lowland heath (approximately 265m x 380m), located within a managed coniferous forest in southern England (50°44'N, 2°08'W). The area is surrounded on three sides by commercial conifer plantations and on the fourth by additional heath. The area comprises a mosaic of dry heath, dominated by a discontinuous expanse of Heather (*Calluna vulgaris*) and Gorse (*Ulex europeus* and *Ulex minor*), and wet heath, dominated by Purple moor grass (*Molinia caerulea*) and Cross-leaved heath (*Erica tetralix*). Small regenerated conifers (*Pinus sylvestris*) and Bristle bent (*Agrostis curtisii*) also occurred throughout the study area. Much of the ground surface, under the vegetation, was covered in moss. Small areas of open sandy ground were also present within the dry heath.

Field work

Over a period of 19 years (1993–2011) the study area was surveyed for smooth snakes annually, between March and October, using fixed hexagonal arrays of artificial refuges (Reading 1997, 2004a, b). The number of arrays within the study site, the total area covered by arrays, the total number of refuges used each year and the distance between refuges within each array all varied between 1993 and 2011 but remained constant between 2001 and 2011 (Table 1).

The location co-ordinates of each refuge, in relation to all the other refuges within the study area each year were triangulated, using known fixed points, enabling the precise location of captured smooth snakes (*C. austriaca*), usually found under refuges, to be determined and the distance between any two refuges calculated. The location co-ordinates of snakes found between refuges were determined by recording the capture location in relation to the nearest refuges. All captured smooth snakes were individually marked using Passive Integrated Transponder tags (PIT tags: ID 100), sexed, weighed (g) and their body length (SVL: snout-vent length: cm) measured (Reading, 1997).

The analyses of inter-location distances and home range sizes were based on four categories of snake, adult and sub-adult males and females. Since variation, between individuals, in the size at which they attain sexual maturity, is likely, and the aim of the analysis was to investigate movements and home range areas in adult and sub-adult snakes, individuals that occurred within the body length (SVL) range of 37.0–42.0 cm were excluded from the analysis as these may have exhibited behaviour of either sub-adult (sexually immature) or adult (sexually mature) snakes (Spellerberg & Phelps, 1977; Luiselli et al., 1996; Reading, 2004b).

The potential problem of autocorrelation between successive capture locations for individual snakes (Swihart & Slade, 1985) was considered to be insignificant given the known maximum published daily movement rates for radio-tracked smooth snakes of up to 166.8 m (Gent & Spellerberg, 1993), and the minimum sampling interval of two days between successive captures in this study (mean=8.2 days, SE=0.29, *n*=378, range=2–59 days). In this time an individual could potentially have traversed the study area and therefore its location at time, *t*, was considered to be independent of its previous capture location. In all the analyses of mean distances moved by snakes within each of the four age/size categories, either overall or by month, pseudo-replication of data was avoided (where some individuals were captured more than once) by using the mean distance moved by any individual within each category.

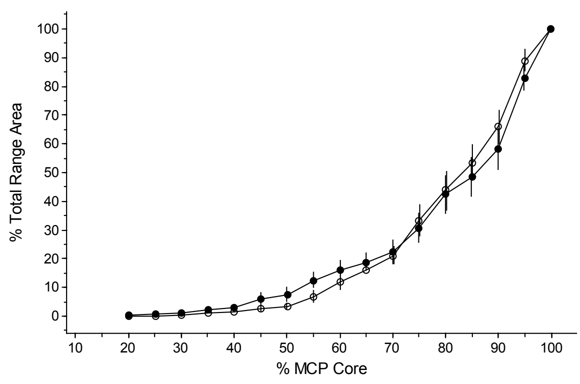

Fig. 1. Change in the proportion of the total Minimum Convex Polygon (MCP) home range areas (± SE) explained by an increasing proportion (% core) of total capture locations for individual male (solid circles) and female (open circles) snakes whose home ranges were assumed to be totally within the study area.

Table 2. Comparison of the mean inter-location distances (m) of adult (SVL=42+ cm) and sub-adult (SVL=0–37 cm) males and females using Student's *t*-test. Significant differences (*p*<0.05) are shown in *italic*s.

	Adult Male Mean=64.48m *SE*=4.76; *n*=35 Range: 0–135.34m	Sub-Adult Male Mean=43.37m *SE*=7.20; *n*=61 Range: 0–371.99m	Adult Female Mean=41.93m *SE*=5.35; *n*=37 Range: 0–127.17m
Sub-Adult Male Mean=43.37m	*t*=-2.44 *p=0.016* df=92	-	-
Adult Female Mean=41.93m	*t*=-3.15 *p=0.002* df=69	*t*=-0.16 *p*=0.872 df=95	-
Sub-Adult Female Mean=47.01m *SE*=6.74; *n*=44 Range: 0-197.46m	*t*=-2.12 *p=0.038* df=73	*t*=-0.37 *p*=0.713 df=101	*t*=0.59 *p*=0.556 df=77

In this study, permanent arrays of refuges were used within an area of lowland heath to obtain capture locations for individual snakes rather than using locations obtained from free-ranging radio-tracked individuals. As a consequence, the capture location data of individual snakes were constrained by the overall area covered by the refuges (including areas between the different arrays) and inevitably included location data for snakes that may have had home ranges occurring mainly outside the study area. Including location data for these individuals may have resulted in an under-estimate of the overall mean home range size of smooth snakes. This problem was addressed by using data for only those snakes whose capture locations all occurred within the study area and that did not also include refuges located around the periphery of the study area, thereby increasing the likelihood that the home range of these individuals fell totally within the study area.

There are various methods for estimating home range size in animals including ellipses, concave polygons, minimum convex polygons, harmonic mean and kernel contours (Kenward, 2001). Minimum convex polygons were used in this study as they are suggested to be more appropriate than kernels for estimating home range size in herpetological studies (Row & Blouin-Demers, 2006). They also resulted in an apparently more realistic home range area (when plotted on a map of the study area) than the other methods, given the relatively homogeneous structure of the habitat in which the snakes occurred.

Table 3. Monthly mean inter-location distances (m), standard errors (SE) and *n*, for adult (Ad: SVL=42+ cm) and sub-adult (Sub: SVL=0–37cm) male and female smooth snakes.

		Month						
Category		Apr	May	June	July	Aug	Sept	Oct
Ad Male	*Mean*	95.52	49.72	53.93	46.096	60.93	85.79	92.09
	SE	20.285	6.303	6.030	6.074	7.948	11.593	13.198
	n	13	25	25	25	21	19	15
Sub Male	*Mean*	36.13	38.54	44.04	42.33	24.05	40.70	58.38
	SE	24.232	5.462	7.724	15.076	5.547	7.409	10.752
	n	7	39	41	26	26	28	14
Ad Female	*Mean*	53.45	52.93	31.79	47.19	32.91	35.48	57.03
	SE	11.328	11.836	7.427	11.296	11.372	9.917	13.481
	n	5	22	30	23	15	16	6
Sub Female	*Mean*	-	47.88	37.48	52.46	31.02	50.98	46.07
	SE	-	9.922	8.787	12.323	12.822	12.155	16.405
	n	-	22	27	26	11	18	11

Table 4. Comparison of the mean minimum convex polygon home range areas (100% cores), using Student's *t*-test, for adult (SVL=42+ cm) and sub-adult (SVL=0–37cm) male and female smooth snakes whose capture locations did not include refuges located along the boundaries of the study area. Significant differences ($p<0.05$) are shown in *italics*.

	Adult Male Mean=1.850 ha SE=0.299; *n*=13 Range: 0.537–3.879	Sub-Adult Male Mean=0.458 ha SE=0.050; *n*=5 Range: 0.325–0.619	Adult Female Mean=0.871 ha SE=0.200; *n*=14 Range: 0.115–2.374
Sub-Adult Male Mean=0.458 ha	*t*=4.58 *p=0.001* df=12	-	-
Adult Female Mean=0.871 ha	*t*=2.72 *p=0.013* df=21	*t*=-2.01 *p*=0.064 df=14	-
Sub-Adult Female Mean=0.307 ha *SE*=0.180; *n*=4 Range: 0.031–0.827	*t*=4.42 *p=0.001* df=14	*t*=0.81 *p*=0.476 df=3	*t*=2.11 *p*=0.059 df=11

When estimating the size of an animal's home range outlying capture locations are often excluded from any analysis as they may represent 'exploratory excursions' outside the usual home range of an individual (Kenward, 2001), and their inclusion would result in an over-estimation of an individual's home range size. However, in the analysis reported here no justified reasons were found to exclude any capture locations from the analysis, based on distances moved, as the relationship between the proportion of capture locations, for any individual, whose home range was assumed to have been totally within the study area (see Table 4), and the mean proportion of an individual's total home range area that this proportion of captures estimated, showed no clearly defined 'step change' in slope that might indicate such 'exploratory excursions' had occurred (Fig. 1). Despite this, however, the data did not exclude the possibility that such 'excursions' may have occurred. The use of all (100% cores) of the capture locations for those snakes assumed to be living totally within the study area may, therefore, still have over-estimated the home range size of some individuals resulting in an over-estimate of the mean home range size for smooth snakes generally.

Increases in home range area with increase in body size (SVL) were achieved after first calculating the maximum home range area for each individual snake that was captured more than once at a particular SVL.

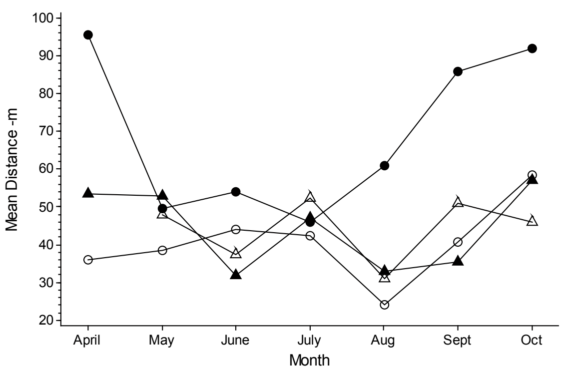

Fig. 2. Change in the monthly mean inter-location distance for adult and sub-adult male and female smooth snakes. Adult males: solid circles; Adult females: solid triangles; Sub-adult males: open circles; Sub-adult females: open triangles. Standard errors and n for each data point are given in Table 3.

Data analysis

Home range areas and the distance between consecutive captures (inter-location distance) of each individual snake were analysed using Ranges8 v2.5 software (Kenward, et al,, 2009). Minimum convex polygons (MCP), derived using all of the capture data (100% cores), were used in the determination of individual home range areas. Home range areas and inter-location distances were compared using Students *t*-test and one-way ANOVA within Minitab 16 (Minitab, 2010).

RESULTS

Inter-location distances

Between April 1993 and October 2011 a total of 191 smooth snakes (109 males and 82 females) were captured and individually marked with a pit-tag. Over this period a total of 177 mean inter-location distances for individual snakes within the four age/SVL size categories (males=96; females=81) were obtained from those individuals that were captured more than once (Table 2). Overall, the mean distance moved by adult males between consecutive captures (64.48 m) was 37–54% greater than that moved by adult females (41.93 m), sub-adult males (43.37 m) or sub-adult females (47.01 m). There were no significant differences between the inter-location distances moved by adult females and sub-adult males and females (Table 2).

The differences in the extent of the movement between consecutive captures of adult males and females suggest

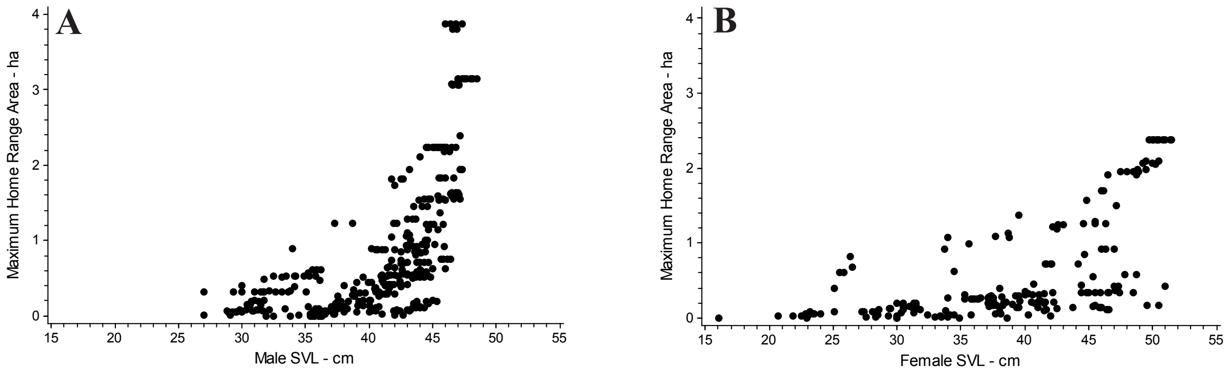

Fig. 3. Plot of minimum convex polygon home range areas (ha) against body length (SVL) for 18 male (A) and 18 female (B) smooth snakes whose home ranges were assumed to be totally within the study area.

that this may be related to breeding behaviour and so the inter-location distances for both sub-adult and adult, males and females, were analysed by month (Fig. 2; Table 3). There were no significant differences (p>0.05) between the inter-location distances moved by adult females, sub-adult females and sub-adult males in all months between April and October. Although the inter-location distances moved by adult males were not significantly different from those moved by adult females in May (t=-0.24; p=0.812; df=32), July (t=-0.09; p=0.933; df=33) and October (t=1.86; p=0.084; df=14) the similarity in the distances moved was, nevertheless, most marked in May and July.

Similarly, there were no significant differences in distances moved, between months, within adult females (April–October: $F_{6,116}$=0.80; p=0.572; r^2=4.18%), sub-adult males (April–October: $F_{6,180}$=0.90; p=0.494; r^2=3.02%) and sub-adult females (May–October: $F_{5,114}$=0.45; p=0.815; r^2=2.01%). Between month differences were found, however, in adult males (April–October: $F_{6,142}$=4.66; p<0.001; r^2=17.04%) showing that distances moved in April, September and October were significantly greater than in May, June and July with those in August not differing from those in either July or September (Fig. 2).

Home range areas (Minimum Convex Polygons)

A total of 367 capture locations from 18 individual male smooth snakes and 231 capture locations from 18 individual female smooth snakes, whose home ranges were all assumed to be totally within the study area, were obtained enabling home range areas to be estimated. The minimum and maximum number of capture locations for individual males and females ranged between 5–45 and 5–29 respectively.

Despite the size of male home range areas increasing with increasing male SVL it did not do so uniformly (Fig 3A). Male home range areas showed a steady, but relatively slow increase up to about 1.1 ha, at an SVL of approximately 42–43cm, after which it increased sharply to reach a maximum size of 3.88 ha at an SVL of approximately 46–47cm. Conversely, the change in the size of female home range areas increased relatively uniformly, across the size range of females, reaching a maximum size of 2.37 ha (approximately 61% of that for males) at an SVL of approximately 50–52cm (Fig 3B).

The mean home range size of the adult males (1.85 ha) was approximately double that of adult females (0.87 ha), approximately four times that of sub-adult males (0.46 ha) and approximately six times that of sub-adult females (0.31 ha; Table 4). There was no significant difference (p>0.05) between the mean home range sizes of adult females, sub-adult females and sub-adult males. The greatest similarity in mean home range size was found between sub-adult males and females.

DISCUSSION

Seasonal movements

The pattern of change in the mean monthly inter-location distances of sub-adult and adult males and females showed that in early spring (April) and late summer (September and October) adult males moved significantly more than adult females, and sub-adult males and females, a trend not observed in a previous radio-telemetric study of smooth snakes in southern England (Gent & Spellerberg, 1993), probably due to the relatively short period of time (<10 days) over which each snake was radio tracked. This trend was also absent from eastern kingsnakes (*Lampropeltis getula getula*) in New Jersey, USA (Wund et al., 2007) and northern watersnakes (*Nerodia sipedon*) in Missouri, USA (Roth & Greene, 2006) but was found in brownsnakes (*Pseudonaja textiles*) in Australia (Whitaker & Shine, 2003), a racer (*Coluber constrictor*) in Illinois, USA (Carfagno & Weatherhead, 2008) and northern pinesnakes (*Pituophis melanoleucus melanoleucus*) in Tennessee, USA (Gerald et al., 2006).

The distances moved by adult male smooth snakes in May, when mating occurs (Spellerberg & Phelps, 1977; Frazer, 1983), was virtually identical to that moved by adult females suggesting that they may have been 'shadowing' females in order to pair and mate with them. The reduction in the movements of adult males during May–July may indicate that they may be establishing breeding territories at this time of year though more data are required to support this hypothesis. After May the distances moved by adult females declined to a minimum in June, August and September, the latter two months coinciding with the timing of parturition (Smith, 1951; Goddard & Spellerberg, 1980; Frazer, 1983; Braithwaite et al., 1989). It is likely that, in late summer (August/ early September), gestating females are less able to hunt or ingest prey due to the mass of relatively large embryos they contain, a trend also reported for grass snakes (*Natrix natrix*) which ceased feeding for about 45 days prior to oviposition (Reading & Davies, 1996). A similar reduction in distances moved was observed in gravid grass snakes (*N. natrix*) just prior to oviposition (Madsen, 1984) and in gravid garter snakes (*Thamnophis sirtalis* and *T. elegans*) during gestation (Charland & Gregory, 1995). Following parturition, in late August/early September, the mean inter-location distances moved by adult females appeared to increase perhaps reflecting their need to hunt and feed prior to entering hibernation in late October (Frazer, 1983).

Home range

The increase in home range size in relation to SVL in males is a reflection of the increase in their inter-location distances with increasing SVL. Male home range area increased rapidly following sexual maturity at an SVL of approximately 42.0 cm (Reading, 2004b). Although female smooth snakes are sometimes capable of breeding in successive years many do so in alternate years (Spellerberg & Phelps, 1977; Luiselli et al., 1996; Reading, 2004a) and thus the larger home range size exhibited by adult males, compared to sub-adult males, is consistent with them moving around the habitat in search of mature females that were in breeding condition, behaviour that has also been found in *Vipera lataste* (Brito, 2003).

Although the home range size of females was significantly smaller than that of adult males it did, nevertheless, also increase relatively steadily with increasing SVL up to the attainment of sexual maturity at an SVL of approximately 43.5 cm (Spellerberg & Phelps, 1977; Luiselli et al., 1996; Reading, 2004b), after which no further significant increase was apparent. This suggests that once females have developed a particular home range size, perhaps depending on its ability to provide sufficient resources e.g., prey and cover, they remain within it and depend on the more vagile males to find them when they become able to breed.

Using fixed arrays of refuges has both disadvantages and advantages when compared with using radio telemetry to obtain location fixes for individual smooth snakes. The disadvantages are that snakes can only be found within the array area and usually only under refuges whereas the location fixes of radio-tagged snakes are unconstrained. In addition, little data can be obtained about the use of areas not covered by refuge arrays. The advantage of fixed arrays are that snakes occurring within them can potentially be captured many times, over many years, compared to over just a few days/weeks when using radio-tagged individuals (Gent & Spellerberg, 1993). Radio-tagging snakes may also affect the behaviour of snakes with internal tags (ingested or surgically implanted), potentially affecting their ability to feed and breed, whilst externally attached tags can hinder movement through dense vegetation (Tozetti & Martins, 2007). Estimating the home range size of individual smooth snakes requires data to be collected over relatively long periods of time and this favours the use of refuges over that of radio-tags.

The study reported here represents a first step in understanding vagility and home range size in smooth snakes inhabiting lowland heath in southern England and gives an initial insight into their minimum home range requirements thereby providing information essential for the formulation of sound conservation strategies for this species. However, evidence from mammals suggests that home range size is likely to vary between different sites depending on the availability of resources (e.g., cover and prey availability) resulting in smaller home ranges where resources are abundant than where they are scarce (South, 1999). To this end, essential future analyses will investigate within, and between, year differences in individual home range size, the correlation between home range size and habitat parameters, e.g., prey availability and habitat structure, and whether individual home range size is correlated with smooth snake population density as a result of territoriality.

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