

How Fast Can You Crawl? Mobility and the Distribution of Snakes in Southeast Australia

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Abstract

The observed distribution of snakes in southeast Australia is assessed on the basis of the climate tolerance of all relevant taxa, inferred distributions at the time of the end of the last glacial period (about 12,500 YBP) and that of the present (taken as being from 1985 to 2008). While many authors have given many reasons or alleged factors for the observed distributions of snakes in southeast Australia, this paper suggests that perhaps another overlooked and critically important factor determining distribution of snakes in Australia's southeast is the *relative mobility of the taxa combined with snake/snake interactions*. This is as opposed to factors such as habitat preference, climate/cold tolerance, food availability or others previously invoked as paramount in determining modern distribution patterns.

Introduction

Southeast Australia (taken here as including most of New South Wales, all of Victoria, Tasmania, and nearby parts of South Australia), has been heavily collected by herpetologists over the last 200 years (since settlement by Europeans starting in the 1770s). Texts such as Cogger (2000), based on a summary of data from earlier literature and museum records give a fairly accurate picture of snake species and genera found in this region as well as broad distributional data.

Notwithstanding this, Cogger's text is based primarily on data sourced from his home state of New South Wales. In fact, excluding Wilson and Knowles (1988) (two Queensland-based authors), all major texts on Australian reptiles (including mine from 1989) have been written and published by Sydney (New South Wales) based authors.

More recently I have been based in Victoria, and while I can say that all the aforementioned texts are broadly accurate in their distribution information, none of these texts have given particularly accurate information in terms of Victorian taxa.

Another book on Victorian snakes, Coventry and Robertson (1991), is perhaps the most accurate in terms of distributional records for the snakes from Victoria, being written by persons from Melbourne, but on inspection, for even the most common taxa, is riddled with errors. Despite inaccuracies relating to death adders, red-bellied black snakes, and brown snakes (see below), the distribution records and southernmost limits for most snake taxa in Victoria as given in that book do not alter the arguments of this paper and conclusions drawn, in terms of southern migration of species.

By and large Coventry and Robertson (1991) overstate the southern limits of distribution of taxa, including the black and brown snakes, but the relativity between taxa in terms of southern limits remains in line with the real picture, albeit exaggerated. For the first time, these distribution limits are assessed against the known limitations of the taxa themselves to show that all species but three were until settlement advancing south and their distributions advancing beyond that seen.

Black snakes and brown snakes

Coventry and Robertson (1991) state that both black and brown snakes are common throughout metropolitan Melbourne and environs, including all parts of the Mornington Peninsula. In fact, black snakes are absent from all areas within 35 km of the Melbourne Central Business District (CBD), including all areas south of the CBD, which includes the Mornington Peninsula and running further south to the Victorian south coast. Brown snakes are found north and west and very slightly southwest of the CBD, but not south of the CBD or on the Mornington Peninsula or environs as stated in the book by Coventry and Robertson.

The basis of the distribution maps in the text are so-called dot maps with "confirmed records" followed by a lighter shading of "probable distribution," which generally overlaps and joins up the dots. The authors say that the "confirmed records" are derived from reliable records held by the wildlife department in a computer database. However this in turn is based largely on identifications by field workers who may or may not have herpetological training.

The database is unreliable, with all attributed reports of black and brown snakes from south of Melbourne being readily corrected to be copperheads, which occur in two (and other) color phases, even within a single locality and are routinely confused by people as being of the wrong taxon. A record of the same department for a death adder on the Murray River at Walhalla Island, northwest Victoria, by Peter Menkhorst (a mammal expert), based on an illustration in a book by Hal Cogger and quoted as accurate for many years was later ascertained to be a record for a DeVis's banded snake (*Denisonia devisi*), previously unknown from Victoria, but since found to be common in the relevant region.

Further unreliability of the distribution information in the Coventry and Robertson text is seen in their treatment of copperheads (genus *Austrelaps*), which gives broadly overlapping ranges for the two identified forms, "lowland" (*A. superbus*) and "highland" (*A. ramsayi*). The alleged diagnostic feature be-

tween the taxa in this book and in the original paper separating them is the definition of the white markings on the labial scales (the “highland” copperhead having more distinct markings). As it happens, this characteristic is more fluid than originally thought and varies between specimens, the result being that field workers often can’t assign a specimen to either the highland (*ramsayi*) or lowland (*superbus*) “species.”

As there is no gap in the known ranges of either taxon and the only alleged diagnostic character separating the forms (the labials) varies, even between specimens of the same litter, and all obviously interbreed in the wild, there remains no firm basis for attempting to split the southeast Australian copperheads into two species. At best the variation is clinal, rather than based on specific separation. Hence for the purposes of this paper (and in reflection of my own considered views), all copperheads are referred to the species *Austrelaps superbus*.

A separate and geographically isolated form of *Austrelaps* from the Adelaide Hills (South Australia) and southwest of there, referred by authors to the taxon *A. labialis* is not relevant to this paper, save to say that as a cold-climate species, its distribution is disjunct, reflecting a retraction in range over the past 12,500 years.

They were here already

During the last glacial period, Tasmania was attached to the Australian mainland. As the world warmed about 12,500 years ago and sea levels rose, Tasmania was cut off from Victoria. It is reasonable to infer that the herpetofauna in both places was the much the same. Observed in Tasmania now are three snake taxa, namely tiger snakes (*Notechis scutatus*), copperheads (*Austrelaps superbus*) and white-lipped snakes (*Drysdalia coronoides*).

All three taxa remain common in the southern half of Victoria, including all areas south of and including the colder parts of the Great Dividing Range. That includes the region of Melbourne (the state capital of Victoria), and at least 100 km north of Melbourne. The three taxa are also found in colder parts of New South Wales including areas as far north as Sydney. Hence none of these taxa are regarded as northern invaders of Victoria (which for *N. scutatus* is contrary to a view by Rawlinson [1991]).

Those not originally from Melbourne

After temperatures rose, northern taxa were able to migrate south to invade new areas.

Melbourne is situated on a large bay in the south of Victoria, Australia (with coast stretching about 100 km further south on both sides), making Melbourne and its southern environs a logical southern point for northern species to be migrating towards in terms of this paper. These migrating snakes included species within the main groups of Australian snakes, namely pythons, small elapids (skink feeders as adults) and large elapids (usually just over a meter as adults).

Taxa included in these categories would be: pythons — Murray/Darling carpet snakes (*Morelia metcalfei*) and diamond

pythons (*Morelia spilota*); small elapids — small-eyed snakes (*Cryptophis nigrescens*) and little whip snakes (*Suta flagellum*); large elapids — eastern brown snakes (*Pseudonaja textilis*), red-bellied black snakes (*Pseudechis porphyriacus*) and death adders (*Acanthophis antarcticus*).

That the species are recent arrivals is inferred from the facts that:

- 1 – They are not in Tasmania.
- 2 – Their distributions are effectively continuous to their southernmost points and there are no outlier populations beyond this. That is they are not relictual populations.

This means that these species have invaded Victoria (and/or Australia’s southeast) from further north and at the time of settlement by Europeans (when habitat was unbroken by farms, roads and the like), their ranges were probably still expanding.

Inaccurate records

Before continuing, it is worth noting some inaccuracies that have crept into the records, which if taken at face value may confuse the picture given here of snakes invading from further north.

The Snakes of Victoria by John Coventry and Peter Robertson (1991) is based on records and specimens at the Museum of Victoria, which while as good as for any other state museum, have been shown to have defects in terms of reptiles sourced from Melbourne. Some reptiles lodged as coming from Melbourne may in fact have been stowaways from elsewhere. This situation has arisen as for considerable periods, curators of reptiles at this Museum have either not been herpetologists, or had a primary interest in reptiles, or alternatively have been appointed from elsewhere, with no immediate knowledge of the local herpetofauna, other than what they have read in the popular literature or identification manuals such as Cogger (2000).

This is mentioned in the context of the red-bellied black snake, a snake that occasionally turns up in Melbourne and hence shows up on the Museum’s own database, but is not native here. Another species here, the copperhead (*Austrelaps superbus*), commonly looks identical to the red-bellied black snake and can be distinguished only by the subcaudal scales being all single as opposed to being single and divided in the red-bellied black. Lay persons see copperheads that are black with a red belly and then mistakenly identify it as the better known red-bellied black snake.

Even reptile hobbyists and alleged “experts” whom I’d assume would know better routinely confuse the two species on a regular basis. As recently as June 2008, a Melbourne Zoo reptile keeper Jon Birkitt told a local newspaper that a snake killed in the northern suburb of Roxburgh Park by a resident was a red-bellied black snake (Brown, 2008). I later ascertained that in fact it was a copperhead. The journalist said to me “surely the man from the zoo would know?”

Add to that the small number of “genuine” red-bellied black snakes lodged in the museum and there becomes a general perception that red-bellied black snakes are native to Melbourne. This is perpetuated among local herpetologists so that

when I arrived in Melbourne in 1985 (after 18 years in Sydney), I was led to believe that red-bellied black snakes were a common species here. This is also what most books and literature report, including my own book (Hoser, 1989), which was based on reports I'd erroneously believed as coming from reliable sources.

It is only after catching snakes in all suburbs of Melbourne for many years that it's become apparent that red-bellied black snakes are not a part of Melbourne's fauna. It's that simple!

The species is, however, common in areas about 125 km east of Melbourne, starting just east of Traralgon, and about 70 km north of Melbourne (starting north of the Great Dividing Range). Beyond either point it is a common species. Specimens commonly turn up in Melbourne after climbing into parked cars that are then driven from the relevant areas back to Melbourne, or alternatively in boxes of fruit and vegetables shipped from the growing regions in northern Victoria where these snakes dominate.

As a licensed snake catcher (Hoser, 2007) who catches many snakes a year, I catch an average of one red-bellied black snake a year in Melbourne, all of which so far have had their original (non-Melbourne) source identified.

As another note of interest, I catch an average of two Queensland carpet pythons (*Morelia mcdowelli*) a species not found within 1,000 km of Melbourne, per year, all obviously being either escaped pets or "stowaways." I mention this as no one has yet claimed these to be native to Melbourne, even though they turn up here.

In line with other large elapids, red-bellied black snakes are as a rule, very common where they occur naturally. There are no such sites in Melbourne, again indicating they are not from here. However at the southern and eastern limits of the range of these snakes, this is the very case. The snakes are common. The same applies for other taxa "invading" from the north, be they death adders, carpet snakes or eastern brown snakes.

Notwithstanding the fact that the specimens of red-bellied black snakes that are caught on "call outs" tend to come from the most heavily urbanized areas or otherwise settled areas lacking snakes, the fact is that in the last decade it's become apparent to me and all the other licensed snake catchers in Melbourne that the species is not native to Melbourne and that there is no place or suburb that the snakes can be found and caught.

All other elapids native to Melbourne (six species), are common where they occur and easily found. With rare exceptions as noted above, regular "call outs" for red-bellied black snakes invariably turn out to be copperheads.

Red-bellied black snakes—they have never been native to Melbourne

For all taxa moving south in Australia there is a pattern whereby at the leading edge of their southernmost limits they are very common, readily found and readily caught. This is seen for green tree snakes (*Dendrelaphis punctulatus*) south of Sydney, brown tree snakes (*Boiga irregularis*) north of Sydney

Harbour, death adders (*Acanthophis antarcticus*) around Bega in southern New South Wales, Murray/Darling carpet pythons in the Warby Ranges 10 km south of Wangaratta, brown snakes on Melbourne's northern fringe and so on. The same is seen for the red-bellied black snakes around Tallarook at about the southernmost limit of their known distribution, about 70 km north of Melbourne.

For black snakes this abundance is not seen in Melbourne. It's simply not possible to go anywhere in Melbourne to find a black snake on demand. Hence it's unlikely the species has ever been native to Melbourne (except as stowaways or similar) since at least the beginning of the last glacial period! The sometimes mooted idea that the species may be rare and cryptic in Melbourne is also laughable, based on what is well-known about the species. The fact is that they are large and hard to miss where they occur.

Further misinformation on red-bellied black snakes

On the Museum Victoria website (Anonymous, 2008) is an account for red-bellied black snakes. Under the heading "Distribution and habitat" it reads:

"It is widespread in eastern Victoria; north of the Dividing Range it is often associated with water courses. It is also relatively common in Melbourne's east and has been recorded around Bacchus Marsh, Park Orchards, Bayswater, along the Plenty River in the South Morang area and around the Merri Creek in the Campbellfield to Somerton area."

The Bacchus Marsh record is credible in that the Lederderle Gorge north of there, broadly equates with the known southwest limit for the species, but also happens to be well outside of the suburban Melbourne boundary.

The other records, all well within the Melbourne metropolitan area (broadly along the 25 km line from the CBD running from the north (Somerton) to the east (Bayswater)) are clearly erroneous and based on copperheads of identical color, which are the dominant species in all these areas. I regularly catch such specimens (black with red belly) in all these areas. And invariably they are misidentified by others as "red-bellied black snakes."

The mention of Park Orchards as a location for red-bellied black snakes is perhaps the best evidence of a general misidentification of copperheads. This is the suburb I have lived in over the last 7 years. It is semi-rural and in that time of hundreds of snakes I have seen here, none have been red-bellied black snakes.

However again copperheads of the same color are common here and even more so along the ridgeline running from the Maroondah Highway ridge, along North Ringwood, Warranwood and Wonga Park. Beyond that area, to the upper Yarra Valley (north or east) melanistic copperheads become the more common color phase for the species.

As of 2008 and in the years immediately prior, the reptile curator at the Museum Victoria was Jane Melville, a professional herpetologist. Not resident of Melbourne before she took up the position, her own actual collecting experience of Melbourne's snakes was effectively nil, which is a situation she happily concedes. Her herpetological experience and training is

extensive, but not in terms of Melbourne's snakes. Hence her only real knowledge of snakes in Melbourne is what others have told her, including the general view that red-bellied black snakes are native to Melbourne.

Her predecessor, Diane Bray, had her main interest in fish and managed the reptile collection in the absence of a "dedicated" curator, the position being vacant on the retirement of John Coventry some years prior. Her main role was to catalogue and file specimens as lodged by the public and to respond to public requests to examine specimens and the like. This of course was in addition to her main line of work which was studying and classifying fish.

As both relevant taxa (copperheads and black snakes) are common in the southeast Australian region, get moved about by people often and as a result turn up all over the place, it isn't surprising that until now, no one has ever actually tried to resolve the southernmost distribution limits of the black snake taxon.

I also plead guilty to aiding the misinformation about red-bellied black snakes in Melbourne until recent years. I was advised by herpetologists and others of the fact and repeated it in good faith, including in printed material. I now know this information to be erroneous and generally based on misidentified copperheads, aided at times by the occasional "stowaway" red-bellied black snake, giving apparently credible evidence of the concept of red-bellied black snakes in Melbourne.

Genuine red-bellied black snake call outs

For the record I shall identify here where I or fellow licensed snake catchers have found (genuine) red-bellied black snakes in Melbourne on reptile call outs in the period 2003–8 and their original source:

- Alphington, came in with shipment of paper (myself).
- Broadmeadows, found next to railway yard where goods from northern Victoria are shipped in (myself).
- Toorak Road, Glen Iris, on footpath, apparently having alighted from a car that had recently traveled to northeast Victoria (Scott Eipper).
- Langwarrin (2), both snakes having alighted from cars driven to the Omeo region of northeast Victoria. Both snakes in the same street came from cars driven to the region on a weekly basis over several years and had lodged in the two houses either side of the man who did the trips, with both snakes taking up residence in "compost bins" (both caught by me).
- Mount Martha shopping strip, for two specimens apparently imported with fruit and found in a fruit shop (Barry Goldsmith).
- Montmorency, where snake was removed from a car that had been driven back from a fishing trip at Barmah Forest, northern Victoria (myself).

Notable is that none of the above locations were near any bushland or likely refuges for the species, indicating all had been brought into the localities by human means.

As to how often snakes get into cars and then get driven to other locations, as seen from my own capture records, I get about two calls a year for such snakes. However in northern and

eastern Victoria, where black snakes are common, this species is clearly the one most commonly seen entering cars or engines, with snake catchers in these regions reporting a much higher incidence of this.

By way of example, twice when doing snake shows at agricultural shows (Swan Hill and Orbost), I have had to adjourn proceedings to remove a red-bellied black snake that had lodged underneath a car's bonnet on top of the engine. Please note that in these situations, I have literally been passing through these towns for one or two days only and not been employed as the local snake catcher.

No death adders in Victoria

For death adders, the situation is that there are no known extant populations of death adders in Victoria. There are old (1800s) records of death adders along the Murray River of Victoria, in the vicinity of Swan Hill in northwest Victoria. There are no known museum specimens to back up these records, only notes! Bearing in mind that locations given for specimens in the 1800s were often inaccurate in that the locations given often related to point of shipping, rather than point of capture, it is possible that the specimens referred to may have come from some distance north of that given.

The region has long been degraded for agriculture to such an extent that the snakes are likely to be extinct from the exact localities given. Nearby areas of suitable habitat (including for example Sunset Country), lack death adders (ascertained from extensive searching by herpetologists for the species in the areas), leading to a general view that the old records may be inaccurate due to the fact that otherwise it would make sense for death adders to be in areas such as Sunset Country, Victoria (northwest of the state), where they are not.

What the above also means, is that any death adders in northwest Victoria (alive or recently extinct) derive from stock from northeast of here (in New South Wales) as opposed to being of the South Australian/west Australian stock (a different subspecies).

The historically recorded sites along the New South Wales-Victoria border do broadly correlate with the expected southern limit for the death adder taxon based on known migration rates (extant distributions) for other snake taxa in terms of the New South Wales coast and inland New South Wales-Victoria.

However, for the purposes of this article it makes little difference whether or not the northwest Victorian records are accurate, as death adders have also migrated south along the New South Wales coast and ranges to within about 100 km of the Victorian border, where they are very common. However none have been recorded on the Victorian side of the border in identical bushland and in spite of extensive collecting by herpetologists.

Southern limits for the other taxa

In terms of their southward migration, the eastern brown snakes have a continuous distribution from Melbourne's northern outskirts (where they are very common) right through Aus-

tralia and into New Guinea (also cut off from Australia during the last interglacial).

However, no brown snakes are found south of the Melbourne CBD or beyond into areas such as the Mornington Peninsula, Wonthaggi or West Gippsland. This is spite of the distance being small and habitat perfectly suitable for these snakes, with the species being found in identical habitat (and climate) elsewhere in Australia.

The distribution of the little whip snake (*Suta flagellum*) mirrors that of the brown snake to the north and west of Melbourne, although at the southern limits west of Melbourne (and up to 200 km west) in some areas one or the other taxon may be found up to 20 km further south than the other.

As noted earlier, the red-bellied black snakes have a similar distribution to that of the browns in southeast Australia, the only obvious difference being that they are not quite as far south. East of Melbourne the main ridge of the Great Dividing Range is high (often capped with snow). Due north of Melbourne the height of the ranges is lower and this remains the case further west. This is mentioned because for blacks, browns and little whip snakes, all seem to have had more success in crossing the Great Dividing Range west of Melbourne than from the east. In fact the red-bellied black snakes are only found south of the Great Dividing range in a small area about 80–100 km northwest of Melbourne in the general vicinity of Castlemaine with reliable reports of the species from the nearby Lederderle Gorge, northwest of Bacchus Marsh. That river in turn runs into the Werribee River (on Port Phillip Bay), giving the species a long-term route into Melbourne and environs.

Carpet pythons never got as far south as the Great Dividing Range. If one draws a horizontal line through the Warby Range 10 km south of Wangaratta, in turn about 200 km north of Melbourne and runs it across Victoria to include regions north of this line, you find the Murray/Darling carpet pythons (*Morelia metcalfei*). Further north again and on the New South Wales side of the Murray River, you find death adders.

While the highest and coldest mountains of the Great Dividing Range are northeast of Melbourne, and for one reason or other have formed a largely impenetrable barrier to invading snakes from further north, a second invasion front has been along the coastal strip running from New South Wales and into Victoria, with most species getting to the eastern edge of the Latrobe Valley at around Rosedale. Here we find the western limit (on that front) for brown and black snakes.

Diamond pythons (*Morelia spilota*) the coastal equivalent of the Murray/Darling carpet (*Morelia mcdowelli*) made similar progress to the carpets and also crossed the border to Victoria (here being further south), but only made it about 50 km (at best) over the border) giving it similar penetration south. Death adders, as already mentioned never quite got as far as the Victorian border.

All the taxa referred to so far reflect a suite of species with current ranges centered on about the latitude of mid New South Wales, about 800 km straight line north of Melbourne. That is the faunal suite characteristic of the modern day Murray/Darling

basins and New South Wales coastal plains and ranges, each invading south via the logical lowland routes.

Other taxa whose ranges come from further north (as the center of distribution) have also migrated towards Victoria, either just crossing the border, or not quite. Included here, but not considered in the context of this paper are taxa such as the southern form of western brown snake (*Pseudonaja nuchalis*), the coral snake (*Simoselaps australis*), DeVis's banded snake (*Denisonia devisi*) and mulga (king brown) snake (*Cannia australis*), all of which have a center of distribution about 800 km straight line north of the other suite of species.

Distributions expanding

While 200 years of European settlement is a split second in geological time, and in that time a lot of movement of reptiles has been arrested due to the building of broad acre farms, major highways, towns and the like, some southern migration of the above taxa has continued.

Brown snakes were in the 1980s confined to Melbourne's north, northwest and Maribynong Valley, although also common due west of Melbourne at Melton, Bacchus Marsh and nearby. Few if any were seen south of the Yarra River. By 2000, records south of the river were increasingly common and in areas of the city of Manningham formerly only known to have tiger snakes (including Westerfolds Park), brown snakes started to become common. Likewise for parts of Ivanhoe that previously never had snakes other than tigers. These are all heavily urbanized suburbs at the limit of the known range of brown snakes.

In 2007, a brown snake was caught in the You Yangs about 60 km southwest of Melbourne, about 20 km straight line from Bacchus Marsh. Collectors from the area expressed surprise that a brown snake had turned up so far south.

South of the You Yangs are Lara and Geelong, with brown snakes unknown from these areas or south of there. However there are no physical barriers preventing the snakes invading these regions.

The Colac area in southwest Victoria is also of interest in terms of the southward spread of brown snakes. Historically the region was covered in fairly dense forest and the local snake fauna consisted of tiger, copperhead and little whip. (White-lipped snakes occurred in pockets, mainly south of there.) North of Colac, brown snakes occurred, but south they didn't. Put simply, the brown snakes have turned up further and further south and in the invaded areas, the relative numbers have consistently risen.

The "new" habitat of most of the region is open farmland, which both reduces the underlying densities of all snake species (including cannibalistic copperheads) and enables the brown snakes to breach what was previously impenetrable habitat. In terms of the thermal requirements for egg-laying, the new habitat also enables the mobile brown snakes to readily find and use suitable ground-level laying sites with ready access to sunlight to heat and hatch the eggs, none of which would have been widely available in the original forested habitat.

Distributions explained—it's not too cold

That these taxa moved south during the recent interglacial is not really in dispute. A perusal of any relevant reptile book sets out the distribution maps for each taxon and for each there is a distinctly southern limit. With temperature being an obvious limiting factor on reptile's distributions, there has until now been no questioning of the doctrine that temperature alone has been the main limiting factor for the distributions of these taxa. Surely as you go south it gets colder?

However, examination of these species' distribution reveals a starkly different picture. With the exception of *Suta flagellum*, all the invading taxa are found in the vicinity of Sydney, New South Wales. And other species in the genus *Suta* are found around Sydney, including for example *Suta dwyeri*. All the invading taxa, including *Suta dwyeri*, are found in the Blue Mountains and/or nearby hilly regions that are higher in altitude and significantly colder than either Melbourne, coastal Victoria south of Melbourne or the plains and ranges north of Melbourne, and anywhere else between where they are found and these co-joined regions.

Furthermore, in the case of Victoria, it is not as one moves south that it gets colder. In the materially relevant respects, the reverse is true. North of Melbourne where many of these invading taxa occur, the elevation is higher and hence the temperatures cooler. Heading south, temperatures rise (as elevation declines) and so lack of heat cannot be a limiting factor in terms of these species moving south.

While northern areas away from the coast get warmer in summer, this heat (often excessive and well over 30°C, is well above preferred temperatures for the relevant snakes, giving no major advantage to them over southern areas. More important, the potentially hostile extremes of heat and cold are actually avoided as one moves south and towards the coast. In other words it is not cold that prevented any of the invading taxa from getting to Melbourne or beyond.

While all the invading taxa have certain habitat requirements or preferences, observation of these taxa in their known ranges shows that they are adaptable and invasive of habitats and can apparently tolerate habitats beyond their known distribution limits.

While it may be possible to argue that taxa like death adders require virgin bushland and that perhaps aboriginals in years past burnt and degraded too much bush to prevent their southern migrations, this argument cannot possibly be used to explain failure of wide-ranging habitat liberal taxa like black, brown or carpet snakes to get further south. The large elapid taxa in particular live in all kinds of habitat, including severely degraded, as seen by their abundance in the most intensively farmed regions and in all other habitats in their known distribution ranges.

With climate or "cold" being eliminated as a factor stopping the spread of these species south, one must look at other possible factors.

The most obvious thing seen by comparing the invading taxa and where their southernmost limits of distribution are, is that

the more mobile taxa got further south. Brown snakes, the most mobile of the large elapids, got furthest south. Black snakes also quite mobile, broadly shadowed the brown snakes, except in western Victoria, where the brown snakes got about 50 km further south (on average). Less mobile, the carpet snakes, crossed the Victorian border, but only just, making it an average of about 100 km north of the black snakes, while the death adders, (based on known distributions along the New South Wales coast), didn't quite get as far as the Victorian border.

As a well-established rule, snakes consistently managed to get further south when migrating east of the Great Dividing Range, as opposed to the same taxa migrating to the west of it, as seen by the known limits of black, brown, death adders and carpet/diamond snakes.

As for whether or not these taxa can survive in Melbourne, the result is already known. They can! Escapees thrive here! All the black snakes, carpet snakes and diamond snakes that I catch in Melbourne tend to be well-fed on local food and in good general health.

Another factor—other snakes

However, how fast a snake can crawl can't be the whole explanation. Studies of invasive species, such as cane toads (*Bufo marinus*) in Northern Australia have shown traveling speeds of several km a year for the invasion front. Now these feral toads are radically different to taxa that have evolved in this continent and so it'd be expected that factors may be wildly different for them as opposed to taxa that have co-evolved over millions of years.

Assuming the last glacial period to have ended about 12,500 years BP, it would appear that short of some unknown calamity, even at just 1 km a year, any of the invading taxa could have covered all habitable parts of Victoria by now, if invading a new area was as simple as moving in.

I have of course omitted "mini-ice ages" that may have impacted on migrations and for good reason. The small elapid species, namely *Suta flagellum* and *Cryptophis nigrescens*, have in sharp contrast to the large species managed to successfully colonize almost all possible areas of suitable habitat that can support them, or at least all that which they obviously prefer. That these invaders haven't been knocked out by a calamity, would indicate that none has been big enough to affect the overall picture.

Also the speed and success of the invasion of the smaller elapids (as opposed to the larger ones) would indicate that what has slowed the invasions of the larger species hasn't affected the smaller elapids in the same way. Hoser (2005) detailed a well-defined pecking order in terms of snakes. That paper showed that a major determinant of snakes distributions in given localities was other snakes.

Since that paper was published, further research here has shown that the key factors indicating likely dominance of taxa (between snakes and/or lizards) identified here are in order of importance listed as:

- Egg-laying versus live-bearing

- Ambush versus stalking (in feeding)
- Lack of cold tolerance
- Potential mobility of snake

Habitat partitions and adaptations are also important in the real world situation, but were excluded from testing at our facilities for several reasons, including difficulties in standardizing tests for this.

Another, perhaps critically important factor not tested, was competition between species in the form of potential cannibalism. This factor gives copperheads (*Austrelaps*) a major advantage over competitors where it is numerous (see later).

Perhaps a major impediment to the successful colonization of regions south was other snakes of other species, as in those already there. Two of three were large elapids. This may mean that in terms of the invading snakes and in a world devoid of modern human influences, unless and until the invading snake taxon gets sufficient numbers in the region of the invading front, then they cannot push their species to new regions. The end-point of the argument being that competition for already occupied habitat by invading taxa may greatly slow the migration of these taxa.

As an alternative explanation, most snakes being forced to new habitat (by whatever means) do, for a variety of factors (but mainly due to already resident snakes) fail to survive. A similar scenario is seen for translocated reptiles and other animals (see Hoser, 1995). This is particularly so for sedentary and less mobile taxa like the death adders and pythons.

In the case of the high mountain barriers north and east of Melbourne referred to earlier, one part of this barrier starts at about Kinglake and runs around through just east of Healesville, through the Dandenong Ranges, Warragul and into the Stresleki Ranges. Another runs through the high country and into Victoria. In the high country of New South Wales and into Victoria, black and brown snakes have made progress but not in terms of the high mountain barriers skirting the northeast of Melbourne. These mountains are (naturally) covered in dense forests and the dominant species here are copperheads. Copperheads are strong predators of other snakes, and when numerous literally eat out all competing snakes! Hence, where copperheads are strongest forward migration of other snakes would seem to be slowest.

In the case of Melbourne this is readily seen. Running due east of Melbourne from Kew (about 5 km east of the CBD) is a long ridge running along the Maroondah Highway to the Dandenongs. Except around the Yarra River at Kew (the start of the ridge), where there are tiger snakes associated with the Yarra Valley, the only snake native to the ridge-line is the copperhead.

The same pattern repeats in the region south of here, although further south along major waterways and the Port Phillip Bay where the Yarra drains, tiger snakes are again found. North of this ridgeline is the Yarra Valley, where tiger snakes dominate and as mentioned earlier, brown snakes are found as far south as here.

Historically it seems that this ridge of dense forest, with its copperheads was a sufficient barrier to prevent southward

movement of brown snakes. However with the urbanization of the area and a general drop in snake numbers overall, this ridge is now open to movement of other snakes, the result being that for the first time, in 2008, a young brown snake was found at the summit of the ridge in Ringwood.

Areas formerly only with copperheads have also had tiger snakes turn up. This is significant as in the backdrop of urbanization, copperhead numbers usually increase relative to browns and tigers, where all three taxa occur.

Because black snakes aren't native to Melbourne, no comparisons can be made. However in Sydney, the black snakes dominate urban areas and nearby rural areas as well, with their relative position improving against the competing taxa—browns and tigers.

The “copperhead” barrier

In terms of the cold-climate/copperhead barrier, it appears that the higher parts of the Great Dividing Range in Victoria, running from the Dandenong Ranges and east of there into New South Wales have formed a barrier to other snakes' movements to new areas, the only obvious exception being the small-eyed snakes (*Cryptophis*) a distinctly smaller species, which appears able to bypass severe competition with copperheads in marginal and hilly habitats.

This barrier also runs south of the Dandenongs (and the ranges near the Latrobe Valley, south of here, through west Gippsland and includes west Gippsland, broadly west of Wilson's Promontory. While in terms of physical or habitat obstacles, there does not seem to be (historically) any major impediment stopping southern movement of taxa through Melbourne, other than the fact that the main Great Dividing Range barrier north of Melbourne was only breached in recent geological time and hence the relevant taxa, never got further.

Thus there is a section of Victoria starting roughly at the Melbourne CBD, running roughly east to about Wilson's Promontory, where the only large elapids to occur are the original inhabitants, namely tiger and copperhead.

Testing the copperhead barrier hypothesis

Testing the theory isn't something that can be done in a lab. However using Australia as a giant-sized lab, the hypothesis can be assessed.

In southwestern Australia, similar genera of snakes occur to the southeast. These are of course, *Pseudechis/Cannina*, *Notechis*, *Pseudonaja* and *Acanthophis*. All have penetrated considerably further south (or cooler climates) than is seen in Victoria, including across the south Australian parts of the Great Australian Bight and beyond. The only notable absence in the large elapid fauna of the southwest as compared to the southeast is the genus *Austrelaps*. In the absence of other obvious factors, it seems populations of copperheads have limited the southward movement of similar-sized elapids.

Southern limits of genera to the east and west

Noting that the same genera have migrated south via two

routes, these being along the east coast and secondly south, through the Murray/Darling basin and across the slopes and ranges northwest of Melbourne, the trend of different taxa getting further south via the eastern corridor is consistent.

Known southern limits for the said taxa are thus as follows:

- Carpet/diamond python 37.6°S (east of ranges), 36.8°S (west of ranges)
- Death adder 37.1°S (east of ranges), 35.5°S (west of ranges)(Lake Boga record only)
- Red-bellied black snake 38.5°S (east of ranges), 37.5°S (west of ranges)
- Brown snake 38.5°S (east of ranges), 38.4°S (west of ranges)(Colac/Warrnambool regions)

Little whip snakes

Coventry and Robertson (1991) state that little whip snakes are found in all Melbourne suburbs. They are not. Broadly the distribution of the taxon mirrors that of the eastern brown snake in the region north and west of Melbourne. However, they appear to have penetrated all of southwest Victoria where suitable habitat exists in the form of stony plains and similar nearby environments, including granite hills and the like. They are not found in the heavily forested regions east and south of Melbourne, meaning that in Melbourne the eastern limit for the taxon is about the Plenty River Valley with none naturally occurring at any time in the region running south of the same line that limits the modern distribution of eastern brown snakes.

In other words, this taxon does not occur in any of the wetter eastern suburbs or anywhere south or southeast of Melbourne in any area beyond the eastern shoreline of Port Phillip Bay. North of the Yarra River, little whip snakes appear to be found no further east than the Plenty River Valley. Beyond that point, small-eyed snakes appear to take over the ecological position of the species. This indicates that both taxa compete directly and may limit one another's (or one or the other's) distributions. Brown snakes by contrast are found east of the Plenty Valley to the very edge of the colder parts of the main Great Dividing Range, within a few kilometers of Yarra Glen Healesville.

Small-eyed snakes

I have caught small-eyed snakes in hilly areas north and east of Melbourne. There are also records from hilly areas on all sides of Melbourne in National Parks, but I have no direct experience of the taxon at locations west or south of Melbourne. They have migrated into Victoria using the eastern side of the Great Dividing Range as their main line of movement into the region. They are cold tolerant and able to invade areas devoid of numbers of other taxa.

Dale Gibbons of Bendigo has never seen the taxon in his area (about 150 km northwest of Melbourne), and in areas of suitable habitat closer (e.g., Kyneton/Castlemaine) in spite of

extensive collecting over many years. This indicates that the taxon is either rare or nonexistent west of Melbourne, with Melbourne and/or western environs being the western limit of the distribution.

White-lipped snakes

The distribution of the white-lipped snakes broadly mirrors that of copperheads in Victoria. Hence it is found in cooler regions on all sides of Melbourne. It typically occurs in "pockets," where they are very abundant and easily found. Other areas of apparently similar habitat often lack the species. As is the case for copperheads, numerous color morphs may occur at the same locality.

Different starting points

A counter-argument to the proposition put here in terms of southward migrating taxa is that perhaps the relevant species of snake (or lizard) were either in the southern Victorian region before the others in the same faunal assemblage arrived, or alternatively had a further south starting point. This may be the case for a number of species with a more northern center of distribution as mentioned earlier in this paper. However in terms of the relevant taxa to this paper as named at the outset, these arguments do not appear to hold. All appear to have similar climate tolerances and a similar adaptability to all relevant habitats, as evidenced by their modern day distributions, particularly further north in New South Wales where in high altitude regions the taxa survive in areas cooler than those presently occupied in Victoria.

Conclusion

In light of the above, the only remaining conclusion to be drawn in terms of modern day distributions of invading snakes in southern Victoria as named, is that what's seen is a direct result of the relative mobility of the relevant taxa. This means the more mobile taxa were able to colonize further south faster and not as a result of any added pre-adaptation to the invaded habitat or innate ability to survive there.

Due to the apparently slow speed of the invasion fronts of all snake taxa as compared to feral invasive species introduced to Australia within the last 200 years, it appears that there are one or more factors at play greatly slowing the forward invasions. The most obvious factor worthy of investigation appears to include snake/snake interactions and how resident and/or dominant snakes are able to block successful colonization by invaders, which may themselves be mainly individuals forced out of their habitat by others of the same or similar species.

In the context of southern Victoria, it seems that copperheads in particular, have slowed the spread southwards of the three locally occurring elapids of similar size, namely the genera *Pseudechis*, *Notechis* and *Pseudonaja*.

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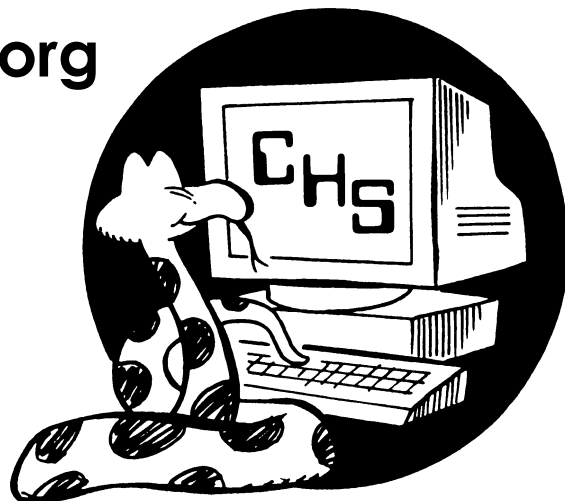
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