

Range expansion of the Common Dwarf Gecko, *Lygodactylus capensis*: South Africa's most successful reptile invader

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Here we describe the invasion history in South Africa of the Common Dwarf Gecko *Lygodactylus capensis* (Smith, 1849), particularly into areas distant from its native range. We provide maps that include detailed records of translocations dating as far back as the early 1980s, describing the spread of populations through time. We find that this gecko has rapidly increased its range, is persisting at invaded sites, and is continuously spreading across South Africa.

Amongst reptiles, lizards are the most frequently translocated and have the highest chance of establishing extralimital populations; and most records of invasive lizard translocations are members of the Gekkonidae (Kraus, 2009). While geckos have been translocated vast distances between continents (Daza et al., 2012), they have also been moved shorter distances overland (Davis, 1974), sometimes within their countries of origin and outside their natural ranges.

Lygodactylus capensis is a small diurnal lizard, slender in build, with grey to brown dorsal colouration and a white dorsolateral stripe (or series of whitish spots) which may be dark-edged and distinct (Figure 1). It has an extensive distribution range extending from Kenya southwards to southern Africa, and westwards into northern Namibia and southern Angola (Travers, 2012; Branch, 2014a; Spawls et al., 2018). Its native range within the greater South Africa region has been well documented (e.g. FitzSimons, 1943; De Waal, 1978; Visser, 1984; Jacobsen, 1989; Boycott, 1992; Bourquin, 2004). This gecko is largely restricted to mesic savannah and well-wooded areas in the north-eastern parts of South Africa, inclusive of Free State, North West, Gauteng, Limpopo, Mpumalanga and KwaZulu-Natal provinces, and in eSwatini (previously Swaziland).

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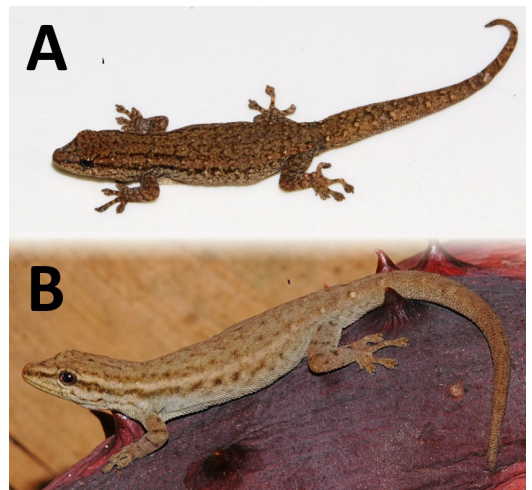


Figure 1. Adult specimens of *Lygodactylus capensis* from Giraffe House, about 7 km south-west of Klapmuts (1st Aug 2018; MBUR 08660), photograph by MB (A); and Port Elizabeth, photograph by WRB (B).

The recent *Atlas and Red List of the Reptiles of South Africa, Lesotho and Swaziland* (Bates *et al.*, 2014) plotted extralimital records for this species in four South African provinces, i.e. Eastern Cape, Western Cape, Northern Cape and Free State. However, an influx of new extralimital records prompted us to investigate the invasion history of *L. capensis* by considering all published (cited in text), museum, photographic and sight records (electronic supplementary table; Figures 2–3).

The genus *Lygodactylus* is distinctive and readily identifiable from other gecko genera in South Africa. However, identification is more problematic at species level, especially between *L. capensis* and *L. bradfieldi* Hewitt, 1936. Specimens in the Port Elizabeth Museum (PEM) collection from Rooipoort (PEM R18263) and even Kimberley (PEM R14601–3) all have two (not three) granules bordering the nostril, consistent with *L. bradfieldi* (see description in FitzSimons,

1943). However, Jacobsen (2011) noted overlap in this character between *L. bradfieldi* and *L. capensis* in Limpopo Province; and 12 of the 14 National Museum (Bloemfontein) specimens of *L. capensis* (NMB R701, 724, 1678, 1713, 2079–80, 5451–3, 7506–7, 9218) from the species’ natural range in the north-western Free State also have only two granules bordering the nostril. A molecular assessment is needed to clarify the respective diagnostic morphological characters and distribution ranges of *L. bradfieldi* and *capensis*, especially in regions where the two taxa seem to occur close to each other. *Lygodactylus capensis* was considered a polytypic species with several subspecies (e.g. FitzSimons, 1943). Most of these taxa were subsequently raised to species level (e.g. see Branch, 1998), with *L. c. bradfieldi* and *L. c. grotei* Sternfield, 1911 now also considered full species (e.g. Roll *et al.*, 2010). This leaves only *L. c. pakenhami* Loveridge, 1941, a Pemba Island endemic morphologically and geographically most closely

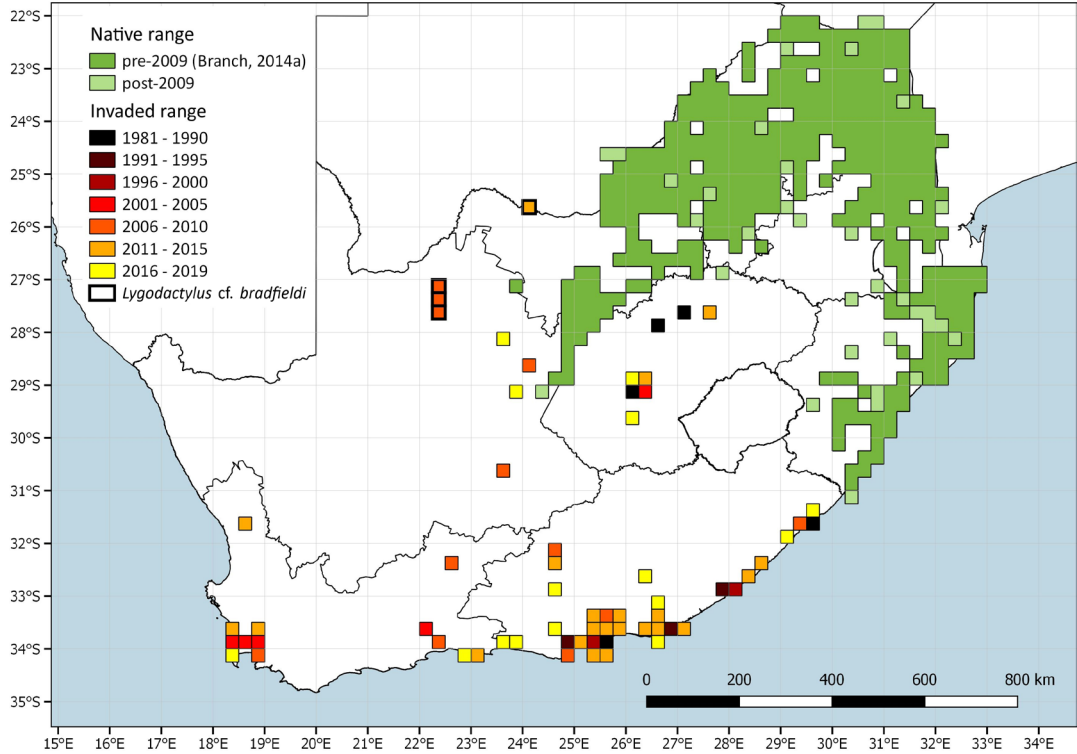


Figure 2. Quarter Degree Grid Cells (QDGCs) timescale map of *Lygodactylus capensis* distribution in South Africa. The colour shading represents the earliest record in each QDGC. The dark green QDGC represents the native range as presented in Branch (2014a), whereas light green QDGCs represent subsequent (post-2009) native records. Dark borders denote specimens close to the native range of *L. bradfieldi*. The use of QDGCs is explained in Bates *et al.* (2014).

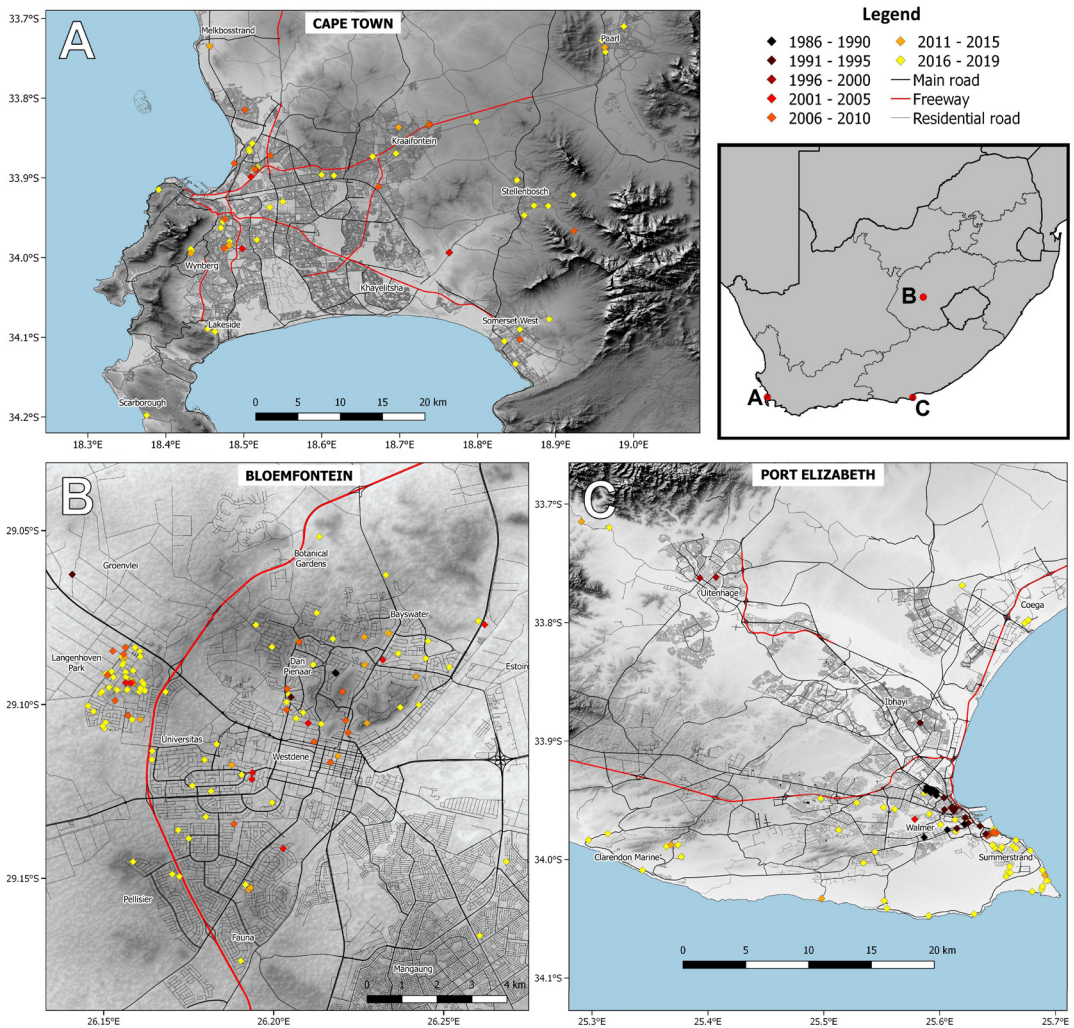


Figure 3. Point locality timescale map showing the extent of extralimital records of *Lygodactylus capensis* in: A – greater Cape Town region; B – Bloemfontein; C – greater Port Elizabeth region. A detailed list of all localities is provided in the electronic supplementary table.

allied to *L. grottei*, of which it should be considered a subspecies (i.e. *L. g. pakenhami*), and by which name combination it was originally described. We therefore consider *L. capensis* a monotypic species.

Eastern Cape Province: The southern-most limit of this gecko's natural distribution range is considered to be the coastal region of southern KwaZulu-Natal around Margate, about 30 km north of the border with the Eastern Cape (Branch, 2014a). However, Smith's (1849) vague type locality description includes 'Kaffirland' which suggests that it also occurred as far south as the Kei River

in the Eastern Cape. The first published extralimital records of *L. capensis* in this province were of specimens observed in 1986 in Port Elizabeth's Kensington and South End suburbs (Branch, 1987; Branch and Haagner, 1993). A Kensington resident claimed that the species was first observed in this neighbourhood about 30 years earlier (i.e. 1956), and by 1986 it was already common there. Additionally, it was reported that about 20 adult geckos had been deliberately introduced to Walmer suburb in 1986, where the population became well established in subsequent years. This prompted one of the authors (WRB) to initiate a public outreach program

in Port Elizabeth and surrounding areas. Subsequent public sightings in and around Port Elizabeth included Central suburb and Kwazakele in 1992, Humewood in 1994, Uitenhage in 1996 and Linkside in 2005 (Figure 3C). The species was also recorded at several localities between the KwaZulu-Natal border and Port Elizabeth: Port St. Johns in 1989; Mtumbane in 1990; East London in 1992; Port Alfred in 1995 (Haagner and Branch, 1996); Chintsa in 1998; Mgazana in 2006; near Butterworth in 2013; Kenton-on-Sea, Grahamstown and Kleinemonde in 2014; Woody Cape Nature Reserve and Colchester in 2015; Morgans Bay, Great Fish River Nature Reserve, Mboyti, Coega, Coffee Bay and Kowie River in 2016; Kei Mouth in 2017; and Adelaide in 2018. It was also observed to the west of Port Elizabeth at Kabeljous River near Jeffreys Bay in 1992 (Haagner and Branch, 1996); Loerie region, Island Nature Reserve and Sardinia Bay Nature Reserve in 2015; Seaview Lion Park in 2016; Hankey and Gamtoos River Mouth in 2017; and Baviaanskloof in 2018. A few records were also obtained from localities in the Great Karoo to the north-west of Port Elizabeth: Graaff-Reinet in 2008, Kirkwood in 2015, and Jansenville in 2017.

Western Cape Province: The first Western Cape records are of specimens observed on palm trees and walls of the snake park at Ratanga Junction amusement park at Century City, Cape Town in 2001. Thereafter the species was recorded from several localities within the City of Cape Town municipal area: Lynedoch in 2004 (De Villiers, 2006); Lansdowne in 2005; Somerset West in 2006 (De Villiers, 2006); Joostenbergvlakte in 2007 (Witberg and Van Zyl, 2008); Intaka Island, Bellville, Rosebank, Parklands and Bothasig in 2008; Harfield Village in 2010; Bonny Brook and Melkbosstrand in 2013; Kirstenbosch National Botanical Garden in 2014; Claremont and Paarl in 2015; Athlone, Klappmuts, Rozendal and Stellenbosch in 2016; Avondale, Lakeside and Vergelegen in 2017; Boston, Kylemore, Milnerton, Welgevonden Estate and Wynberg in 2018; and Brackenfell, Goodwood, Rondebosch, Rusthof, Scarborough and Seapoint in 2019 (Figure 3A). A few observations were also made in other areas of the province, including localities within the Great Karoo: Oudtshoorn in 2005 and Karoo National Park in 2006; localities along the Garden Route in a few suburbs of George (2009–2015; see also Jacobsen, 2012) and Knysna in 2012; a record along the west coast in the Vredendal region in 2013 (Heinicke and Bauer, 2018); and an abundance of individuals at Vanrhynsdorp in 2016. At some of the localities where extralimital

L. capensis specimens were first observed in the Western Cape, the species has formed seemingly viable populations that have persisted for over a decade. For example, the localities in Lynedoch (2004), Lansdowne (2005) and Joostenbergvlakte (2007) still had thriving populations in 2018.

Northern Cape Province: Apart from *L. capensis*, the very similar *L. bradfieldi* also occurs in the (north-western) Northern Cape, extending as far east as Grootdrink near Upington (Branch, 2014a; Figure 2). *Lygodactylus capensis* records for this province include Britstown in 2006, Tswalu Nature Reserve (in both natural habitat and on buildings; L. Verburgt pers. comm.) in 2008, Rooipoort in 2009 (Conradie *et al.*, 2011), Danielskuil in 2016 and a farm near Douglas in 2018. However, the records from Tswalu (and the isolated North West Province record) are situated close to the range of the morphologically similar *L. bradfieldi* (see above) and have been marked as *L. cf. bradfieldi* in Figure 2.

Free State Province: The natural distribution of *L. capensis* in the Free State comprises thornveld areas on the north-western edge of the province. Extralimital records of Common Dwarf Geckos are now available for four areas in the Free State, namely Welkom, Bloemfontein, Kroonstad and Reddersburg (electronic supplementary table). The earliest known records refer to sightings in a garden in Flamingo Park suburb in Welkom in 1981. Three specimens were later collected in Naudesville in 1989, and another sighted in Jim Fouche Park, both suburbs of Welkom (Douglas, 1990). An additional six specimens were collected at unspecified localities in Welkom in 1990 (Bates, 1996), and two collected in the nearby town of Odendaalsrus in 1995 (and again in 2006). Two individuals were collected in Kroonstad in 1989 (Yeadon, 1991), and in 2014 specimens were photographed at Doornkloof Voortrekker Farm south of Edenville in Kroonstad district. One of the authors (MFB) has been collecting distribution records of this species in Bloemfontein since 2004, and all records collected to date are presented here. Sometime between mid-1985 and 1990, a specimen was found on a motor vehicle that had travelled between Ladybrand and Bloemfontein, but the first confirmed record for the latter city dates to 1988 when a hatchling was found on the wall of a house in Dan Pienaar suburb (Douglas, 1990). In 1993 a specimen was collected at a nursery in Groenvlei to the west of the city (Bates, 1996), and a specimen was also sighted in Westdene suburb. A gecko was also seen on a car parked at a petrol station in Universitas suburb (circa

2001–2005), but it may have travelled from elsewhere. The earliest records for other Bloemfontein suburbs are: General de Wet in 2002/3; Bayswater, Universitas and Langenhoven Park in 2004; Arboretum and Waverley in 2006; Fichardt Park, City and Spitskop Small Holdings in 2010; Baysvalley in 2012, Fleurdal and Naval Hill in 2014; The Kloof in 2017; Grasslands in Heidedal area, Heuwelsig, Bayswater Rural, Pellissier, Fauna and Wilgehof in 2018; and Gardenia Park, Peter Swart Phase 2B and Navalsig in 2019 (Figure 3B). The comparatively large number of localities in Langenhoven Park reflects the fact that MFB resides in this area and conducts regular searches there. The numerous observations from a large part of the city indicate that this species is now well established in Bloemfontein. This is supported by at least three populations known to be present for several years: 22 Dickie Clark Street in Dan Pienaar, 1988–2005 (Bates, 2005; according to Douglas, 1997, the latter population originated from Mpumalanga); 16 Borckenhausen Crescent, Westdene, 1993–2019 (MFB unpubl. data); and Artemis Townhouse in Langenhoven Park 2004–2019 (MFB unpubl. data). At the latter locality specimens have been observed virtually every month from 2004 to the present, and hatchlings (mostly brown with orange tails) are often seen. *Lygodactylus capensis* is also known from three localities north of Bloemfontein: in 2012 the species was observed at Karee Kloof Private Game Farm, in 2015 a specimen was recovered from the stomach of a Common Duiker (Bates & Du Preez, 2018) found on the farm Daskop in Brandfort district, and in 2017 one was photographed ‘30 km north of Bloemfontein’. In 2019 a specimen was photographed in Reddersburg, about 65 km south of Bloemfontein.

Discussion

With regard to the extralimital range of *L. capensis* as indicated in Figure 2, we exclude the following records obtained through the FitzPatrick Institute of African Ornithology (2018): TM1985–8 from Farm Peover (772) which were incorrectly geo-referenced in the Northern Cape (2923CC) instead of Limpopo; John Ellerman Museum record no. 978 from “Kaffirskraal” in 1957 which was geo-referenced in the Northern Cape (3122CC), but is likely from North West province based on data for other specimens collected by A. Els in the Rustenberg area; and NMB 5534, a 1986 record from the farm Cecilia near Bloemfontein (2926AA) which refers to a different species according to the National

Museum’s records (but note that other valid records exist within this Quarter Degree Grid Cell).

In its native range, *L. capensis* is an active diurnal gecko that inhabits trees and rocks where it also finds refuge (Fitzsimons, 1943; Branch, 1998). The species is absent from neighbouring Grassland, Nama-Karoo and arid Savanna biomes (Mucina & Rutherford, 2006), which may act as barriers that prevent range expansion, possibly because trees and rocks are mostly lacking. Humans have undoubtedly facilitated the breaching of these barriers by long distance transport of goods along road networks, with cargo and nursery trades being two of the main agents of inadvertent reptile introductions (Kraus, 2009). Similar pathways for extralimital movement of amphibians within southern Africa have also been noted (Measey et al., 2017). Indeed, many of the first extralimital *L. capensis* records were at plant nurseries, campsites and travel lodging facilities (Bates, 1996; De Villiers, 2006; Witberg and Van Zyl, 2008; Venter and Conradie, 2015), which suggests that these geckos have been hitch-hiking to new locations for several decades now. The increased volume of transport has provided numerous opportunities for introductions, and the expansion of urban areas has increased the chances of introduced populations becoming established. Established alien populations in cities and towns may contribute to the rate of range expansion by serving as additional sources for dispersal to other urban areas.

The greater Port Elizabeth area has also experienced the introduction of the Tropical House Gecko, *Hemidactylus mabouia* (Moreau de Jonnès, 1818), which was first observed at the harbour in 1980 (PEM R1881; and remains common in the area) and then at Addo Elephant Park in 1986 (PEM R4388); as well as the Marbled African Leaf-Toed Gecko, *Afrogecko porphyreus* (Daudin 1802), in the suburb of Humewood in 1981 (PEMR2686; WRB pers. obs.). In Bloemfontein, a small population of *H. mabouia* became established in Dan Pienaar suburb in the late 1980s (Douglas, 1990) and persisted for at least nine years (Douglas, 1997), although its current status is unknown. Douglas (1997) also noted that *Chondrodactylus bibronii* (Smith 1846) became established in Bloemfontein, possibly a reference to specimens which have been observed on buildings at the National Museum. In Port Elizabeth, specimens of the Angulated Dwarf Gecko (*Lygodactylus angularis* Günther, 1893) and Spotted House Gecko (*Gekko monarchus* [Schlegel, 1836], of tropical Asian origin) were detected at Walmer in 1991 (PEM R7337) and at Deal Party in 2002 (PEM R5412; Bauer and

Branch, 2004), respectively, but are not known to have established populations there. It appears that expansion into the south-western winter rainfall region of South Africa has been facilitated by human alteration of the environment, a pattern that is shared with *Hemidactylus mabouia* (Branch, 2014b; Weterings and Vetter, 2017) and *Hyperolius marmoratus* Rap, 1842 (Tolley *et al.*, 2008). According to records on the citizen science platforms ReptileMAP and iNaturalist (both accessed in October 2018), *L. capensis* is by far the most widespread and commonly sighted invasive reptile in South Africa. The tallies are 210 *L. capensis*, 32 *H. mabouia* and six *A. porphyreus*.

The invasion success of gekkonids when compared to other squamates is due to the ease with which they are translocated (Kraus, 2009), especially where species colonise man-made structures (Davis, 1974; Hoogmoed and Avila-Pires, 2015). Indeed, the world's most invasive geckos spread rapidly along road networks (Davis, 1974) and via cargo ports (Daza *et al.*, 2012). Human-mediated dispersal enables these species to spread much faster than would otherwise be possible through natural dispersal (Bourquin, 1987; Locey and Stone, 2006). For example, *Hemidactylus turcicus* (Linnaeus, 1758) was known from a single location in Texas, but within five years had established populations approximately 400 km away, and after 20 years the species was found throughout south Texas (Davis, 1974); and it expanded from four to 30 parishes across Louisiana (up to 400 km apart) in 17 years (Meshaka *et al.*, 2006). *Hemidactylus mabouia* has invaded the Americas, and the fact that populations across Florida lack genetic structuring is due to the frequency of human-assisted dispersal (Short and Petren, 2011). *Lepidodactylus lugubris* (Duméril & Bibron, 1836) has invaded nine Central/South American countries and is widespread and dominant in six of these, with a reported spread rate of up to 8.63 km/year (Hoogmoed and Avila-Pires, 2015).

In comparison, *L. capensis* has dispersed to major cities across South Africa, where the first Cape Town records were noted 15 years after the first Port Elizabeth records, over 800 km away. We postulate that translocation of *L. capensis* has been aided by its small size and habit of seeking refuge under bark and in rock cracks, together with the fact that it lays eggs in such places (FitzSimons, 1943; Branch, 1998). In addition, human-modified habitats provide ample refugia with a multitude of microhabitats, resembling natural wood and rock, which may also liberate these geckos from most predators and allow them to thrive (Bates, 2005). Despite falling prey

to domestic cats (MFB pers. obs., Artemis Townhouse in Bloemfontein), Fiscal Shrikes (iNaturalist 18873363) and smaller birds (iNaturalist 20991364) in urban areas, populations are able to persist.

Branch (2014a) noted that *L. capensis* was rapidly expanding its range in South Africa, but seemingly not into areas of natural vegetation. Outside their native range, *L. capensis* individuals are most often observed on walls and fences, especially those with plants growing on or against them, often on metal electric boxes, and occasionally on trees and (in Port Elizabeth gardens) on specific plants such as agaves, aloes and strelitzias (see electronic supplementary table). However, extralimital records of this species are also known from areas some distance away from human habitation, e.g. at the Kabeljous River in the Eastern Cape (1992). It has also invaded areas of the Wild Coast where, in 2016, specimens were found on wooden posts of cattle fences; and in 2017 an established population was observed in native vegetation near Grahamstown (L. Kemp pers. comm.) and on the outskirts of Port Elizabeth at Cape Recife (ADR). In 2018, eggs (confirmed to be *L. capensis* after hatching) were found to be abundant under loose rocks in coastal thicket around Port Elizabeth, some distance from human habitation (iNaturalist 16385704). In Bloemfontein, individuals were sighted on natural rocks at the top of Spitskop Hill in 2005 and at the top of a smaller hill nearby between Elias Motsoaledi and Boerneef Streets in Langenhoven Park in 2009, both sites at least partly surrounded by townhouse complexes and/or houses (MFB); a specimen was also seen in an area of natural trees and rocks at the edge of a hiking trail at Oliewenhuis Art Museum (in the period 2006–2010), several hundred meters from the nearest building (MFB); and the species was twice sighted, over 1 km apart, in the game reserve on Naval Hill (one specimen on rocks in 2014, MFB; the other on a tree in 2016, W.R. Schmidt pers. comm.). Given enough time, it appears as though *L. capensis* may spread into natural habitats with rocks or woody vegetation, although some of the current sightings of individuals may merely reflect short-term presence in such areas.

In conclusion, *L. capensis* has rapidly expanded its range, with recent isolated records suggesting that this species is still spreading within South Africa. This small diurnal gekkonid appears particularly adept at hitching rides on transported goods in motor vehicles and establishing populations in human-transformed habitats (Bates, 1996, 2005; Jacobsen, 2012). This is likely to have been encouraged by the lack of niche

competition, as was suggested to explain the patterns of global house gecko invasions, *Hemidactylus* spp. (Rödder *et al.*, 2008), especially given the fact that no other diurnal gekkonids occur in the invaded range of *L. capensis* in South Africa, and other lizards are seldom spotted utilising the same habitat. The proliferation of this species in Port Elizabeth and Bloemfontein, versus its relatively subdued occurrence in Cape Town, is of interest. This may be due to several factors, such as time since introduction and differences in climate (e.g. summer vs winter rainfall regions). The impact of these invasive geckos on the native ecology in South Africa should also be investigated.

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Electronic supplementary table. Extralimital records of *Lygodactylus capensis* in South Africa. Provinces (Prov.) include Eastern Cape (EC), Free State (FS), KwaZulu-Natal (KZN), Northern Cape (NC) and Western Cape (WC). PEM = Port Elizabeth Museum; NMB = National Museum, Bloemfontein; TM = Ditsong National Museum of Natural History, Pretoria.