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Future climate may limit the spread of the Australian house spider *Badumna longinqua* (Araneae: Desidae) in South Africa

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Abstract. Badumna longinqua (L. Koch, 1867) (Araneae: Desidae) is a web-building spider indigenous to eastern and southern Australia; it has been introduced to several countries in North and South America, as well as New Zealand, Japan and Germany. In South Africa, where it was formally recorded for the first time a decade ago, B. longinqua has been sampled from the southern coastal areas (Eastern and Western Cape provinces) and central Free State Province, with almost all of the records associated with synanthropic urban habitats. We present a brief account of its invasion history in the country. Predictive ecological niche models suggest that only the southern coastal areas represent suitable habitat. This suggests that samples from the Free State (only in horticultural nurseries) can be attributed to regular translocations from the southern coastal areas, but that an unsuitable climate there prevents long-term establishment. Future climate change may further restrict this species, which prefers year-round warm, humid areas with low seasonal variability, climatic conditions that are predicted to become increasingly rare in South Africa.

Keywords: Cribellate webs, garden, house, transport

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South Africa is one of the seventeen most biodiverse countries globally (e.g., Myers et al. 2000; Algotsson 2009; Paknia et al. 2015), otherwise known as megadiverse countries. Although it is one of the countries with a relatively low number of established alien invasive species (Seebens et al. 2017), those that have invaded successfully have had significant impacts on terrestrial ecosystems, their biodiversity, and the services they deliver (Van Wilgen et al. 2008).

Of the 2170 species of spiders recorded from South Africa so far (Dippenaar-Schoeman et al. 2015), 74 species are cosmopolitan or introduced (Dippenaar et al. 2011; Foord et al. 2011; Haddad et al. 2013; Dippenaar-Schoeman et al. 2015). Some of these species have a naturally broad distribution extending beyond the Afrotropical Region, while others have clearly been introduced from other continents.

Badumna longinqua (L. Koch, 1867) (Araneae: Desidae) is indigenous to eastern and southern Australia and is one of several Australian web-building spiders that has benefited favorably from the human impacts of urbanization (Main 2001), which has seen its abundance increase significantly in synanthropic environments. This has created source populations that have facilitated its human-mediated dispersal to other continents and islands.

The first country that *B. longinqua* invaded was New Zealand, where it was first recorded in 1896 from French Pass at the northern end of the South Island (Simon 1899). It would have been introduced accidentally from Australia and is likely to have established in New Zealand during the European colonial period (1830–1880). It is found throughout New Zealand in all habitats except native forest, and is especially common around human habitations (Forster 1970; Paquin et al. 2010). Since then, *B. longinqua* has been recorded from the western U.S.A. (Gertsch 1937) and Hawaii (Roth & Nishida 1997), Mexico (Leech 1972), Argentina (Pompozzi et al. 2013), Brazil (Simó et al. 2015), Uruguay (Capocasale & Pereira 2003; Simó et al. 2011), Japan (Okumura et al. 2009), Germany

(Kielhorn & Rödel 2011) and South Africa (Haddad et al. 2013), with early specimen records from the U.S.A. dating back to 1918 (Leech 1971). As such, this species provides an excellent example among arachnids of the effects of expansion in global trade during the past century in facilitating accidental species introductions (Seebens et al. 2017).

Badumna longinqua can be easily distinguished from other South African cribellate web-building spiders, particularly amaurobiids (Almeida-Silva 2013) and phyxelidids (Griswold 1990), by the distinctive abdominal markings (Figs. 1a, 2a, c) and unique structure of their cribellate webs, usually comprising a two-dimensional sheet-like capture web with zig-zagging threads accompanied by a retreat to one side (Figs. 1b–d, S1a, c, d, f). Among desids, Badumna can be recognized (e.g., Gray 1983; Paquin et al. 2010) by the distinct transverse ridge at the posterior edge of the epigynal atrium (Fig. 2c), the S-shaped embolus of the male palp (Fig. 2d) and the comparatively stout median apophysis (Fig. 2e), with B. longinqua being distinguished from congeners by details of the form of the epigynal ridges, the male palpal structure, and structure of the tarsal organs and trichobothrial bases (e.g., Gray 1983).

The current paper presents the first comprehensive review of the South African records of *B. longinqua*, which was recently reported for the first time from the Grassland Biome (Haddad et al. 2013). Further, we used various predictive ecological (bioclimatic) niche models and analytical methods to determine potentially suitable areas for *B. longinqua* in South Africa and the factors that explain its current distribution. We also determine its possible future range expansion and potential distribution based on hypothetical future climate scenarios.

METHODS

Distribution data.—Distribution data on the occurrence of *B. longinqua* was gathered from South Africa based on



Figure 1.—Habitus and web photographs of *Badumna longinqua* in South Africa: (a) Female with retreat in a leaf, Lorraine, Port Elizabeth. (b) Web constructed in a fence post, Kamma Park, Port Elizabeth. (c) Web amongst cycads in a garden, Thornhill. (d) Webs constructed on the roof of a house, Lorraine, Port Elizabeth.

specimens collected in the field by the first author and a few donated specimens, which were identified using illustrations from several taxonomic publications (Forster 1970; Gray 1983; Paquin et al. 2010). Following confirmation of the species' identity, photographic records were sourced from several public resources, including the South African National Survey of Arachnida Virtual Museum (online at http://www. arc.agric.za:8080/), the iSpot website (online at http://www. ispotnature.org/communities/southern-africa), and through circulation of e-mails to colleagues at various academic, conservation and public institutions nationwide. Although the majority of records relate to field-collected specimens (20 point localities; see Appendix 1), photographic records were sourced from another five localities (Appendix 2; see Supplemental Figure S1, online at https://doi.org/10.1636/JoA-S-20-069.s1), which were suspected to belong to B. longingua through comparisons with photographs of the spiders and their webs taken by the author (Fig. 1), whose corresponding specimens were sampled. This gives a total of 23 point localities from which B. longingua has been recorded in South Africa. The whole of Australia was used for the native range of B. longingua, and a total of 202 native records were sourced from GBIF (28 July 2020).

Distribution modeling.—An initial model describing the distribution of B. longinqua in its native range was developed using all 19 bioclimatic variables in WorldClim (available online at http://www.worldclim.org/). This initial model was refined by including a subset of five environmental variables that together explained more than 90% of the native distribution (Table 1). Environmental variables (global climate data) were at $15 \times 15'$ arc minutes resolution. The political borders of the species' native range (Australia) were used as a mask (Phillips 2008) to avoid over-predicting and generating low specificity. The models were then projected onto the same environmental variables for South Africa. This was done to determine whether the same conditions (environmental variables, and their ranges) characteristic of B. longinqua's native range exist in South Africa. Colinearity of the 19 bioclimatic variables were accounted for through a step-wise procedure of calculating the variance inflation factor (VIF) for all the variables, removing the variable with the highest VIF, and repeating the procedure until all the variables had a VIF

Model evaluations were done through cross-validation and bootstrapping. The K-fold cross-validation consisted of splitting the data into five equal parts and then fitting the model five times. Each time, one part is used as the test data

Table 1.—Model performance of four modeling algorithms, namely BRT, GLM, MAXENT and RFT, using AUC, COR, TSS and Deviance statistics to assess accuracy. Mean performance of models were evaluated using K-fold cross-validation and Bootstrapping. Abbreviations: AUC – area under curve; BRT – boosted regression trees; COR – point-biserial correlation; GLM – Generalized Linear Models; MAXENT – Maximum Entropy Species Distribution Modeling; RFT – random forest trees; TSS – true skill statistic.

					Cross-validation		Bootstrap		
Modeling methods	AUC	COR	TSS	Deviance	AUC (training)	AUC (test)	AUC (training)	AUC (test)	
BRT	0.96	0.77	0.86	0.43	0.97	0.96	0.98	0.97	
GLM	0.96	0.74	0.85	0.39	0.96	0.95	0.96	0.96	
MAXENT	0.96	0.77	0.86	0.35	0.97	0.96	0.98	0.97	
RFT	0.97	0.81	0.88	0.28	1	0.97	1	0.99	

and the other four parts as training data. Model evaluation by Bootstrapping involves sampling with replacement until the database is the same size as the original database. Observations not selected are used for the evaluation. Models were evaluated for accuracy (i.e., goodness of fit) by using the area

under the receiver operator curve (AUC) values, with an AUC value of 1.0 indicating a near perfect prediction and a value of 0.5 a prediction that is no better than random (Fielding & Bell 1997). Models with an AUC of >0.9 can be considered very good, with AUC of 0.7–0.9 as good, and <0.7 as uninforma-

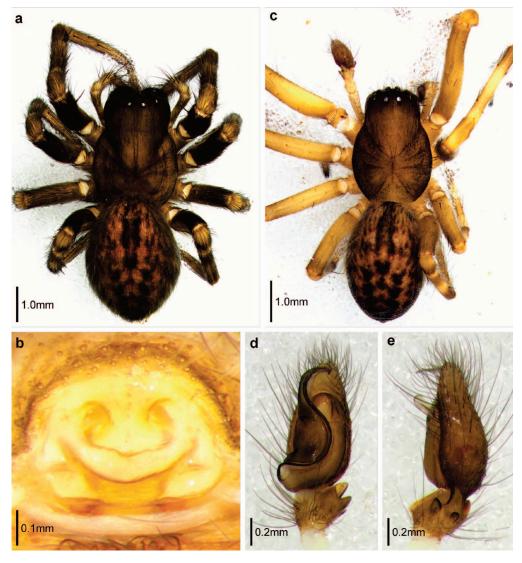


Figure 2.—Habitus and genitalic structure of *Badumna longinqua*, female (a, b) and male (c–e) from Port Elizabeth. (a), (c) Dorsal habitus. (b) Ventral epigyne. (d) Palp, ventral view. (e) Same, retrolateral view.

tive (Swets 1988; Baldwin 2009). In addition to AUC, true skill statistic (TSS), point-biserial correlation (COR), and Deviance were used to evaluate models (Naimi & Araújo 2016).

Four modeling methods were used, namely Generalized Linear Models (GLM), Maximum Entropy Species Distribution Modeling (MAXENT) (Phillips et al. 2006; Phillips & Dudík 2008), random forest trees (RFT) and boosted regression trees (BRT). Model predictions were done based on ensemble output that was weighted by the Deviance for each model (Naimi & Araújo 2016).

Species response curves were modeled using the methods proposed by Elith et al. (2005). The relative importance of variables was assessed by correlating the predicted values to values predicted when a variable is randomly permuted. Permutations of important variables will lead to lower correlation, and correlation of 1 would therefore give an indication of variable importance (Thuiller et al. 2009).

RESULTS

Invasion history.—Badumna longinqua specimens were first collected in South Africa in January 2010 in Lovemore Park, Port Elizabeth (now Gqeberha) in the Eastern Cape, and initially misidentified by the first author as a species of Amaurobiidae. Subsequently, specimens were collected in the vicinity of Bloemfontein (Free State Province) and elsewhere in Port Elizabeth (Appendix 1). It was only during a collection event in Bloemfontein in 2011 that visiting researcher Dr Charles Griswold (California Academy of Sciences, San Francisco) recognized specimens of this species as belonging to Badumna, which was the first confirmation of the occurrence of this genus on the African continent.

During the following years, the species was collected at several additional sites in the Eastern and Western Cape Provinces (Appendix 1). Circulation of photos of *B. longinqua* in September 2015 led to several photographic records of spiders and webs being provided by members of the public (Appendix 2; Supplemental Figure S1), which confirmed quite a wide distribution of the species along the southern coast of South Africa. Although *B. longinqua* was only formally recorded in 2010, it is likely that it was introduced to South Africa several decades ago, evidenced by its wide distribution in the southern parts of the country—particularly its almost ubiquitous occurrence in synanthropic habitats in this area—and by the high population densities observed in many cities and towns in this area, e.g., more than 50 individuals per square meter on flat surfaces (See supplemental Figure S1a).

Microhabitat preferences.—To date, almost all records are associated with synanthropic habitats, notably fences, gardens, buildings (walls, gutters and roofs), and horticultural nurseries (Figs. 1b–d; Supplemental Figure S1a, c, d, f), a pattern consistent with other parts of the world where it has been introduced (e.g., Simó et al. 2011), as well as in its native Australia (Main 2001). Webs are also regularly constructed on a variety of automobiles, which may have contributed to its dispersal. At only one locality (Oyster Bay) has *B. longinqua* been collected from farm outbuildings and farming implements. In South Africa, the species has not yet been encountered in undisturbed natural habitats. Although regularly collected from *Eucalyptus* bark in South America and its native Australia, the species has not been collected

from plantations or isolated *Eucalyptus* trees in synanthropic environments in South Africa.

Current distribution and potential range of *Badumna long-inqua* in South Africa.—Model performance averaged at 0.96 for AUC, 0.78 for COR, 0.86 for TSS and 0.36 for deviance (Table 1). Random forest models performed the best, with an AUC of 0.98, COR of 0.81, TSS (0.88) and deviance (0.28). Both cross-validation and bootstrapping suggest that models based on training data performed equally well in predicting test data (Table 1).

Based on projections from Australian records (Fig. 3a), suitable habitat is mainly restricted to the southern coast of South Africa, extending to the east, with the entire interior of the country (including central Free State records) indicated as extremely unsuitable for *B. longinqua* (Fig. 3b). The southwestern parts of the country were considered to be of very low suitability. Only a single record has been collected in Cape Town and the surrounding areas (Appendix 1), despite information on this species being passed on to a number of invasion biologists and the amateur arachnologists working in this part of South Africa.

The records and modeled native distribution range of *B. longinqua* in Australia (Fig. 3a) suggest that it prefers consistently humid, warm climates, with warm summers (Kottek et al. 2006). Projected distributions of *B. longinqua* point to suitable climatic conditions along the southern coast of South Africa in particular, but also along the east coast (Fig. 3b), and were mainly associated with the Cfb climate category (Fig. 4) of the Köppen-Geiger climate classification (Beck et al. 2018).

Four bioclimatic variables were consistently the most important for all modeling approaches and evaluation criteria: Bio15 – Precipitation seasonality; Bio18 – Precipitation of the warmest quarter; Bio19 – precipitation of the driest quarter; and Bio2 – Mean diurnal range in temperature (see Supplemental Figure S2, online at https://doi.org/10.1636/JoA-S-20-069.s2). The species seems to be particularly sensitive to increases in seasonality of precipitation (Supplemental Figure S3, online at https://doi.org/10.1636/JoA-S-20-069.s3), while increases in precipitation in both the warmest quarter and the driest quarter increased the probability of observing *B. longinqua*. Increased ranges in diurnal temperature also decreased the likelihood of occurrence in an area (Supplemental Figure S3).

DISCUSSION

In California, Burger et al. (2001) found that the proportion of non-native species in spider assemblages declined with distance inland from the coast. In South Africa, *B. longinqua* is more common and widespread in its coastal range, notably at altitudes less than 300 m. The milder climatic conditions along the southern coast, where rainfall occurs all year round, temperatures are generally warm and summers are warm but not extremely hot, contrast greatly with those in central South Africa, characterized by distinctive wet-dry seasons, very low winter rainfall, hot summer days frequently above 35°C, and cold winters with regular subzero minimum temperatures.

However, suitable climatic conditions are found at higher elevations to the east of its current range, in the eastern parts of the Eastern Cape and parts of KwaZulu-Natal (Fig. 4a).

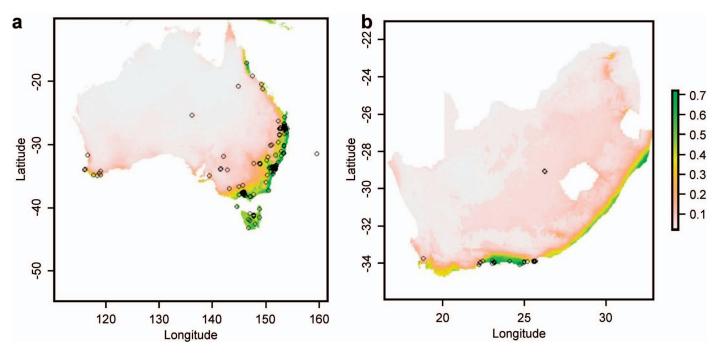


Figure 3.—(a) Predicted native distribution of *Badumna longinqua* in Australia. (b) Projected introduced distribution in South Africa. Circles represent actual observations of *Badumna longinqua*. Key indicates habitat suitability on a scale of 0 (least suitable) to 1 (optimum).

Their absence here so far could be related to low sampling intensity in this part of the country, but might also be linked to the larger diurnal range in temperature and the rainfall seasonality of these regions. So, although these regions experience warm summers and rainfall tends to be year-round, the climate is more variable. The 'Bedford gap' (Lawes 1990), a semi-desert intrusion between Port Elizabeth and East London that divides the eastern and south-eastern parts of the Cape Floristic Region, might act as a further barrier to dispersal. This gap has played an important role in the biogeography of a range of taxa (e.g., Kulenkampff et al.

2019; Taylor et al. 2020). Predicted future climate (Beck et al. 2018) suggests that this gap will become larger (Fig. 4b), further limiting the dispersal of this species. Although garden irrigation is a common practice in central South Africa, particularly during summer, this does not seem to have facilitated the spread of *B. longinqua* in this area.

Considering its currently known distribution in South Africa, the most plausible point of introduction and subsequent spread of *B. longinqua* was through Port Elizabeth harbor, which has approximately 7% of the shipping market share amongst southern African ports (Fraser & Notteboom

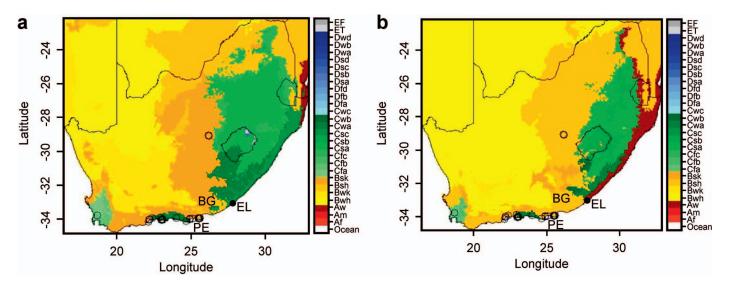


Figure 4.—Koppen-Geiger climate classification (a) for present day (1980–2016) and (b) into the future (2071–2100). Circles represent actual observations of *Badumna longinqua* in South Africa. Key indicates global climate zones according to the classification of Kottek et al. (2006). PE, Port Elizabeth/Gqeberha; EL, East London; BG, Bedford Gap.

2012). It is likely that populations spread to central South Africa through transportation of imported or transported goods (particularly plants, flowerpots and other gardening infrastructure) from the southern coastal parts of its range, particularly Port Elizabeth.

In considering these factors, it is clear that the two populations (i.e., southern vs central South Africa) have displayed contrasting levels of establishment, according to the classification system of Van Wilgen et al. (2014). The southern population has passed through Phase 2 (incursion), Phase 3 (spread), and can now be considered as a Phase 4 species (dominant), as, through competitive exclusion, B. longinqua has displaced most web-building spiders typically found in synanthropic habitats in southern South Africa (Haddad, pers. obs.), e.g., Theridion purcelli O. Pickard-Cambridge, 1904 and Latrodectus geometricus C.L. Koch, 1841 (Theridiidae), Neoscona spp. (Araneidae), and the cosmopolitan Uloborus plumipes Lucas, 1846 (Uloboridae). This aspect of competitive exclusion needs to be more thoroughly investigated and quantified in the future to determine which species are most susceptible to displacement by B. longingua.

In contrast, the populations from central South Africa may have been introduced to the Bloemfontein area on multiple occasions (Phase 2) but have failed to establish and spread beyond the horticultural nurseries where they were collected, suggesting that unsuitable climatic conditions could cause repeated annual mortality of populations during the very cold winters. It is plausible that the Port Elizabeth population of *B. longinqua* serves as a bridgehead invasive population (see Guillemaud et al. 2011), from which introductions to other areas such as Bloemfontein have occurred through ground transport. Considering that Bloemfontein populations have to date been exclusively collected from nurseries, it is likely that new individuals are introduced annually with the transportation of ornamental pots and plants from southern South Africa.

The lack of collection data of B. longingua prior to 2010 could be explained by two factors: (1) the southern parts of the country have historically been poorly sampled for spiders, and as a result, collecting records for these degree-square grids are generally at a much lower level here than many other parts of the country (Foord et al. 2011, 2020); (2) although there is a spider collection housed in the Albany Museum in Grahamstown, approximately 150 km east of Port Elizabeth, the lack of an arachnological curator and researcher there for several decades has contributed greatly to the undersampling of spiders, particularly in the coastal parts of the Eastern Cape. This has resulted in a paucity of identified spider material that could potentially contribute taxonomic data to ecological studies, including the current one. It is quite plausible that there are some B. longinqua specimens amongst this unidentified material that could vastly improve our knowledge of the invasion history of the species in South Africa. However, predicted future climatic conditions in South Africa may probably not be favorable for this species' continued spread in the country.

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SUPPLEMENTAL MATERIALS

Supplemental Figure S1.—Photographic records of *Badumna longinqua* in South Africa submitted to the first author, with locality details (see Appendix 2). Online at https://doi.org/10.1636/JoA-S-20-069.s1

Supplemental Figure S2.— Relative importance of climatic variables in modeling approaches and evaluation criteria. Online at https://doi.org/10.1636/JoA-S-20-069.s2

Supplemental Figure S3.— Response curves of bioclimatic variables. Online at https://doi.org/10.1636/JoA-S-20-069.s3

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Appendix 1.—Collection data of *Badumna longinqua* specimens sampled to date in South Africa. Province abbreviations: EC – Eastern Cape; FS – Free State; WC – Western Cape. Depository abbreviations: LUNZ – Entomology Research Collection, Lincoln University; NCA – National Collection of Arachnida, Pretoria.

Locality	Co-ordinates	Alt.	Date	Microhabitat	Juv	♂	9	Depository
EC: Jeffrey's Bay, Kabeljauws	34°00.413′S, 24°55.796′E	10 m	8.I.2015	in house on curtain at night	-	-	1	NCA 2015/1789
EC: Jeffrey's Bay, Kabeljauws	34°00.413′S, 24°55.796′E	10 m	22.XII.2012	_	-	-	1	LUNZ 00012878
EC: Jeffrey's Bay, Wavecrest	34°01.678′S, 24°55.485′E	60 m	27.XII.2015	hand collecting in garden	2	-		NCA 2015/2331
EC: Kareedouw, Tsitsikamma	33°58.983′S, 24°01.832′E	240 m	8.I.2015	webs on wall of building	2	2	3	NCA 2015/1791
Gardens Restaurant								
EC: Port Elizabeth*, Kamma	33°59.089′S, 25°29.240′E	180 m	14.IX.2012	on walls of building	2	-	-	NCA 2015/1792
Park								
EC: Port Elizabeth*, Lorraine	33°57.928′S, 25°29.144′E	160 m	13.IX.2012	night collecting around house	8	3	2	NCA 2015/1793
EC: Port Elizabeth*, Lorraine	33°57.928′S, 25°29.144′E	160 m	31.XII.2012		2	1	3	LUNZ 00012879
EC: Port Elizabeth*, Lovemore	34°00.282′S, 25°31.597′E	170 m	1.I.2010	night collecting, bark and	1	1	-	NCA 2009/3674
Park				foliage in garden				
EC: Port Elizabeth*, Walmer	33°59.490′S, 25°33.392′E	120 m	9.XI.2011	on outer walls of house	4	-	1	LUNZ 00012883
Park, Kings Court								
EC: Port Elizabeth*, Walmer	33°59.498′S, 25°33.395′E	120 m	27.IV.2012	on outer walls on building	3	5	2	LUNZ 00012884
Park, Kings Court				in webs				
EC: Port Elizabeth*, 17 on 5 th	33°58.802′S, 25°36.016′E	60 m	28.IV.2012	on outer walls on building	9	1	5	LUNZ 00012885
Avenue Guest House				in webs				
EC: Thornhill, African Dawn	33°55.048′S, 25°06.610′E	95 m	22.XII.2015	hand collecting in shrubs	2	-	2	NCA 2015/2322
Bird and Wildlife Sanctuary								
FS: Bloemfontein, Builders	29°08.376′S, 26°12.164′E	1425 m	28.VIII.2012	webs in wooden trellises	2	-	2	LUNZ 00012880
Warehouse								
FS: Bloemfontein, Builders	29°08.381′S, 26°12.152′E	1430 m	30.V.2016	on frames of display shelves	2	-	1	NCA 2016/2042
Warehouse								
FS: Bloemfontein, Greenside	29°05.096′S, 26°09.169′E	1405 m	5.IX.2012	webs in wooden trellises	2	2	1	LUNZ 00012881
nursery								
FS: Bloemfontein, Pretty	29°05.029′S, 26°09.369′E	1410 m	5.IX.2012	webs constructed in border	7	-	1	LUNZ 00012882
Gardens Centre				fence				
FS: Bloemfontein, Pretty	29°05.026′S, 26°09.368′E	1410 m	30.V.2016	on border fence of property	3	1	1	NCA 2016/2043
Gardens Centre								
WC: Cape Town, Kraaifontein	33°50′S, 18°42′E	105 m	19.XI.2018	on frame of fence	-	-	1	NCA 2019/516
WC: Garden Route National	33°55.729′S, 22°57.349′E	280 m	4.IX.2015	off fence at gatehouse	2	-	-	NCA 2015/2374
Park, Goudveld								
WC: George, Redberry Farm	33°57.491′S, 22°22.915′E		7.I.2015	web on wall of building	1	-		NCA 2015/1790
WC: Knysna, Knysna Animal	34°02.951′S, 23°04.571′E	20 m	24.IV.2016	from webs on trees	1	-	-	NCA 2015/2375
Welfare								
WC: Knysna, Leisure Island	34°04.099′S, 23°03.895′E	10 m	24.IV.2016	found dead in web	-	-	1	NCA 2015/2376
picnic site								
WC: Knysna, Marlin Road	34°02.943′S, 23°04.254′E			off palisade fencing	4	-	-	NCA 2015/2377
WC: Mossel Bay, Harbour	34°10.864′S, 22°08.893′E	10 m	4.I.2018	on walls of building	-	-	1	NCA 2019/521
WC: Mossel Bay, Rhebok	34°04.489′S, 22°10.311′E	55 m	8.I.2018	on walls of building	_	_	3	NCA 2019/520

^{*} Port Elizabeth renamed Gqeberha in 2021

Appendix 2.—Details of photographic records of the invasive Australian spider *Badumna longinqua* from the Eastern Cape (EC) and Western Cape (WC) provinces, South Africa. See Supplementary File S1 for images.

Locality	Co-ordinates	Alt.	Photographer	Supplementary File S1 figure
EC: Oyster Bay	34°09.509′S, 24°38.825′E	10 m	R. Dreyer	a, b
WC: Buffelsbaai	34°05.388′S, 22°58.550′E	10 m	J. Spies	e
WC: Groot-Brak	34°02.436′S, 22°13.373′E	10 m	C. Haddad	c
WC: Knysna	34°02.951′S, 23°04.571′E	20 m	J. Hayes	d
WC: Mossel Bay, Reebok	34°04.498′S, 22°10.315′E	55 m	G. de Jager	f