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Distributional range of the South African maritime spider-egg parasitoid wasp, *Echthrodesis lamorali* (Hymenoptera: Platygastridae: Scelioninae)

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ABSTRACT

The southern African coastline plays host to nine spider species. Two of these, namely *Desis formidabilis* (O. P.-Cambridge, 1890) (Araneae: Desidae) and *Amaurobioides africanus* Hewitt, 1917 (Araneae: Anyphaenidae), are recorded as hosts for an intertidal spider egg parasitoid, *Echthrodesis lamorali* Masner, 1968 (Hymenoptera: Platygastridae: Scelioninae). These two spider species occur from Lüderitz (Namibia) along the coast to East London (Eastern Cape Province, South Africa), while their parasitoid has been known from only a single locality on the Cape Peninsula. The South African coastline was surveyed from Jacobsbaai (Western Cape Province) to East London in an attempt to determine the full distribution of *E. lamorali*. The wasp was only reared from host eggs collected on the Cape Peninsula, confirming a high degree of endemism for this species.

KEY WORDS: Afrotropical Region, *Echthrodesis lamorali*, *Desis formidabilis*, *Amaurobioides africanus*, biogeography, intertidal.

INTRODUCTION

The intertidal region forms a narrow band along the interface of all land mass and oceanic bodies (Lubke & De Moor 1998), stretching for approximately 594 000 km globally, a total of 8% of the Earth's surface (Paetzold *et al.* 2008). The combined effects of terrestrial and oceanic conditions in this zone result in a unique environment, producing a distinctive community structure (Lubke & De Moor 1998). Organisms living here are immersed in seawater twice a day for varying periods of time and thus need to be able to cope with daily variations in humidity, temperature, salinity and pH conditions, as well as the physical action of crashing waves (Lubke 1998; Sanford 2002). This makes the intertidal environment particularly difficult to colonise (Cheng 1976; Lubke 1998).

Nonetheless, a variety of organisms have successfully established themselves in the intertidal zone (Cheng 1976; Barber 2009). Apart from the few fish, seaweeds, microorganisms, molluscs, fungi and algae found along the shore, a variety of arthropods have independently become established, invading a number of times throughout evolutionary history (Cheng 1976; Barber 2009). Crustacea dominate as predators (Cheng 1976), while a range of centipedes (Class Chilopoda), symphylids (Class Symphyla), pauropods (Class Pauropoda), millipedes (Class Diplopoda), scorpions (Order Scorpiones), microwhip scorpions (Order Palpigradi), pseudoscorpions (Order Pseudoscorpiones), mites and ticks (Order Acari) and spiders (Order Araneae) have also been recorded as living in the intertidal region worldwide (Roth & Brown 1976). The maritime spiders, representing 11 families globally (Roth & Brown 1976), are particularly relevant to this study.

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Fig. 1. Lateral view of the habitus of a female *Echthrodesis lamorali* Masner specimen.

In southern Africa, nine spider species have been recorded within the intertidal zone (Haddad & Dippenaar-Schoeman 2009). Of these, two are attacked by a small apterous maritime wasp, *Echthrodesis lamorali* Masner, 1968 (Hymenoptera: Platygastridae: Scelioninae) (Lamoral 1968; Masner 1968; Branch & Branch 1981; Van Noort 2009; Van Noort *et al.* 2014) (Fig. 1). One of these two species is the South African member of the best known maritime spider genus, *Desis* (see Roth & Brown 1976), namely *Desis formidabilis* (O. P.-Cambridge, 1890) (Araneae: Desidae), which has previously been found from Lüderitz in Namibia, down along the coast to East London (Eastern Cape, South Africa) (Day 1974; Dippenaar-Schoeman & Jocqué 1997). The other parasitised spider species is *Amaurobioides africanus* Hewitt, 1917 (Araneae: Anyphaenidae), which occupies a similar area to *D. formidabilis*, occurring from Namibia and throughout much of the Western (Dippenaar-Schoeman & Jocqué 1997) and Eastern Cape provinces as far as East London (Day 1974; Filmer 1995). To date, however, *E. lamorali* has only been found on the stretch of rocky shore at "The Island" (Kommetjie, Cape Peninsula, South Africa) (Lamoral 1968; Van Noort 2011; Van Noort *et al.* 2014). This study assessed the distribution of these two spiders and their associated parasitoid.

MATERIAL AND METHODS

In March and November 2012, the intertidal zone of the South African coastline between Jacobsbaai (Western Cape, Republic of South Africa (RSA); 32°57'53.61"S 17°53'07.11"E) and Kidds Beach (Eastern Cape, RSA; 33°08'51.4674"S 27°42'10.5114"E) was searched for the presence of the two spiders, *D. formidabilis* and *A. africanus*, and the parasitoid *E. lamorali*. The intertidal region is here defined as "includ[ing] all rocky

TABLE 1

GPS co-ordinates of the fourteen sites surveyed (sites numbered from east to west) for the presence of *Desis formidabilis* and *Amaurobioides africanus* and their parasitoid, *Echthrodesis lamorali.*

Site number	Site Name	Latitude	Longitude
1	Kidds Beach	33°08'51.4674"S	27°42'10.5114"E
2	Kenton-On-Sea	33°41'31.999"S	26°40'23.9982"E
3	Summerstrand	33°58'47.892"S	25°39'31.0674"E
4	Cape St. Francis	34°10'06.348"S	24°49'59.3394"E
5	Nature's Valley	33°58'56.928"S	23°34'34.1394"E
6	Brenton-On-Sea	34°04'28.308"S	23°01'11.136"E
7	Mossel Bay	34°10'27.4434"S	22°08'08.9874"E
8	Jongensfontein	34°25'37.38"S	21°20'30.4794"E
9	Cape Agulhas	34°49'29.1"S	20°01'38.3514"E
10	Pearly Beach	34°40'13.7274"S	19°30'01.4754"E
11	Betty's Bay	34°22'17.1474"S	18°52'47.1"E
12	Simon's Town	34°09'43.7394"S	18°25'55.5234"E
13	Buffel's Bay (TMNP)	34°19'19.5594"S	18°27'44.028"E
14	Gifkommetjie (TMNP)	34°19'04.7994"S	18°24'56.7354"E
15	Olifantsbos Point (TMNP)	34°15'29.6274"S	18°22'54.0474"E
16	Kommetjie	34°08'22.7034"S	18°19'17.5794"E
17	Silwerstroomstrand	33°35'25.04"S	18°21'33.261"E
18	Jacobsbaai	32°57'53.61"S	17°53'07.11"E

shores ... and the vegetation immediately associated with the high tide breaker line" (Haddad & Dippenaar-Schoeman 2009).

Sites were surveyed every 100 km along the entire transect (Table 1). Thereafter, a local scale survey was conducted around the only known locality of occurrence of the wasp, namely Kommetjie, Western Cape, RSA (around 34°08'23"S 18°19'17"E). This survey covered an area 100 km below and above this beach, which was separated into 20 sites, each 10 km apart. Each location was actively searched from the water/air interface up to the inland edge of the rocks, commencing at least an hour before low tide (Lubke & De Moor 1998) in order to allow sufficient searching time. Where necessary, encrusted material such as mussels or tubeworm conglomerates was selectively dislodged to check for underlying nests.

The date, GPS co-ordinates, predominant habitat type, material collected, species collected, breeding state, shore exposure and nesting material/site were all documented for each sample. Also, all sites were photographed and a video providing a 360° view was recorded. At each site, at least two adults of any spider species and any egg masses found, were collected. All adult specimens were stored in 96% ethanol and deposited in the Iziko South African Museum (Cape Town) as voucher specimens. Collected egg-sacs were maintained in a moist, cool environment in the laboratory and reared through

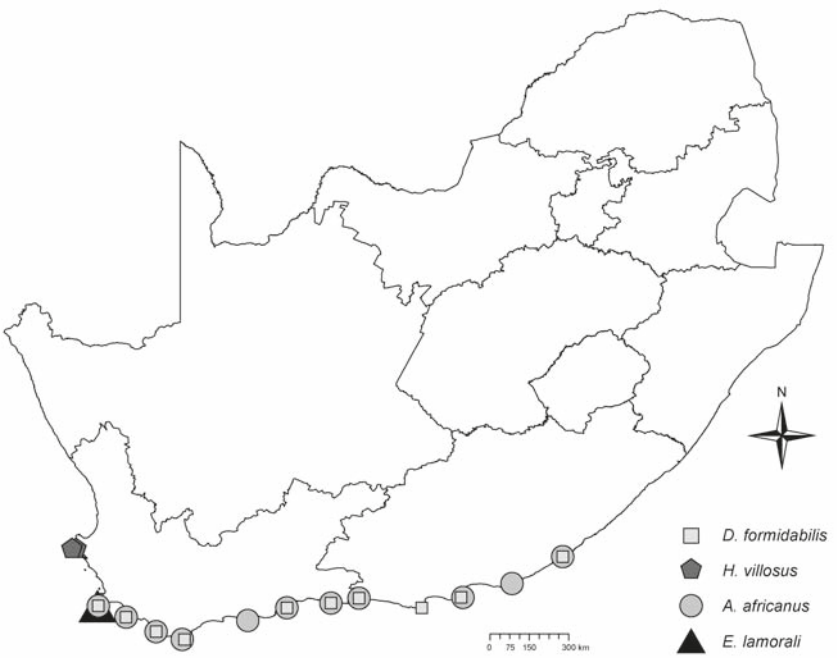

Fig. 2. Distribution of *Desis formidabilis, Amaurobioides africanus, Heliophanus villosus* and *Echthrodesis lamorali* along the transect spanning Jacobsbaai to Kidds Beach, surveyed during this study in March 2012.

to confirm potential parasitism. Distribution data were mapped using ArcCatalog and ArcMap (ArcGIS) 10 (ESRI 2011).

RESULTS

Of the 14 sites sampled during the broad scale survey in March, *D. formidabilis* was found at 10 (all except Kenton-on-Sea, Jongensfontein, Silwerstroomstrand and Jacobsbaai) and *A. africanus* at 11 (all except Cape St. Francis, Silwerstroomstrand and Jacobsbaai) (Fig. 2). *Echthrodesis lamorali* was only seen emerging from *D. formidabilis* egg-sacs collected at Kommetjie (Fig. 2). These data support the recorded distribution of both spider species along the coastline from Kommetjie, east to East London.

Other than the two previously mentioned spider species, a salticid, *Heliophanus villosus* Wesołowska, 1986 (Araneae: Salticidae), was collected at Jacobsbaai (32°57'53.61"S 17°53'07.11"E) (Fig. 2; Table 2). Individuals were found nesting in a similar manner to *A. africanus*, whereby crevices or holes in rocks above the high tide mark are covered and lined with stiff white silk and there is a single entrance/exit hole. Most nests contained two adult spiders.

Neither spider species was found at as many sites in November as in March, with *D. formidabilis* located only along the Cape Peninsula and at Betty's Bay (34°22'17.1474"S 18°52'47.1"E) and *A. africanus* not as prevalent in areas east of the Peninsula (Figs 2 & 3). The vast majority of these last-mentioned (eastern) sites were distinctively visually

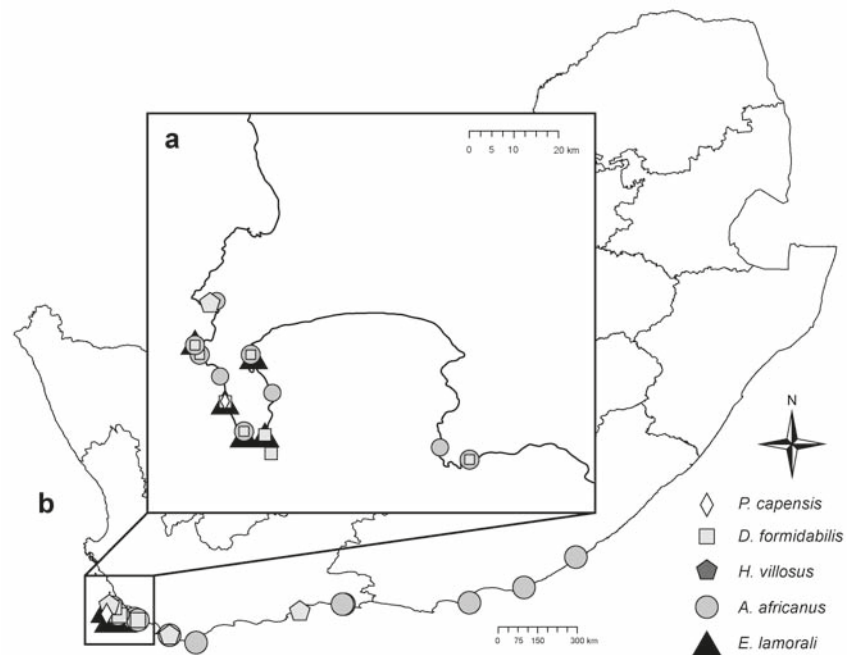

Fig. 3. Distribution of *Palpimanus capensis*, *Desis formidabilis*, *Amaurobioides africanus*, *Heliophanus villosus* and *Echthrodesis lamorali* along the coastline surveyed during this study in November 2012 (a – Cape Peninsula; b – Entire survey area).

different to when they had been searched in March. In particular, there was a marked reduction in rock covering (algae, molluscs and other encrusting intertidal organisms) (Fig. 4). The local scale survey showed the distributional range of *D. formidabilis* to end only 200 m north of "The Point", Kommetjie (Fig. 3). *A. africanus* was located 10 km above that, but none were found any further north.

The salticid *H. villosus*, previously only known from north of Kommetjie (Fig. 3), was found in two other areas (Pearly Beach [34°40'13.7274"S 19°30'01.4754"E] and Mossel Bay [34°10'27.4434"S 22°08'08.9874"E]) during the second survey (Fig. 4). Furthermore, another species new to the study, *Palpimanus capensis* Simon, 1893 (Araneae: Palpimanidae), was collected just above the high-water mark at Olifantsbos Point (34°15'31"S 18°22'52"E) (Table Mountain National Park, Cape Peninsula, Western Cape) (Fig. 4; Table 2). Nests resembled those of *A. africanus*, taking the form of a white silk-lined crevice with a single individual inside.

Prior to this study, *E. lamorali* had been recorded from a single shore at Kommetjie. The first large scale survey confirmed its occurrence there. However, the second, finer-scaled search in November expanded the wasp's known distribution significantly (Figs 3 & 4), revealing that it is present throughout much of the Peninsula extending south of Kommetjie on the western side, and as far north as Simonstown on the eastern side. Thus, the species appears to be a Cape Peninsula endemic under protection by the Table Mountain National Park. No *E. lamorali* or any other parasitoids were reared from *A. africanus* eggs at any point during the investigation.

TABLE 2

All arachnid species recorded in the intertidal region in southern Africa by Haddad and Dippenaar-Schoeman (2009) and Larsen (2012) (white cells) as well as additional records resulting from this study (grey cells).

Recorded by	Family	Species
Haddad & Dippenaar-Schoeman (2009) and present study	Anyphaenidae	*Amaurobioides africanus* (Hewitt, 1917)
Haddad & Dippenaar-Schoeman (2009)	Araneidae	*Larinia natalensis* (Grasshoff, 1971)
Haddad & Dippenaar-Schoeman (2009) and present study	Desidae	*Desis formidabilis* (O. P.-Cambridge, 1890)
Haddad & Dippenaar-Schoeman (2009)	Salticidae	*Heliophanus* sp. 4
Present study	Salticidae	*Heliophanus villosus* (Wesołowska, 1986)
Haddad & Dippenaar-Schoeman (2009)	Salticidae	*Massagris regina* (Wesołowska, 1993)
Haddad & Dippenaar-Schoeman (2009)	Theridiidae	*Steatoda capensis* (Hann, 1990)
Haddad & Dippenaar-Schoeman (2009)	Zoropsidae	*Griswoldia robusta* (Simon, 1898)
Haddad & Dippenaar-Schoeman (2009)	Atemnidae	*Cyclatemnus* sp.
Haddad & Dippenaar-Schoeman (2009)	Geogarypidae	*Geogarypus purcelli* (Ellingsen, 1912)
Larsen (2012) and present study	Palpimanidae	*Palpimanus capensis* (Simon, 1893)

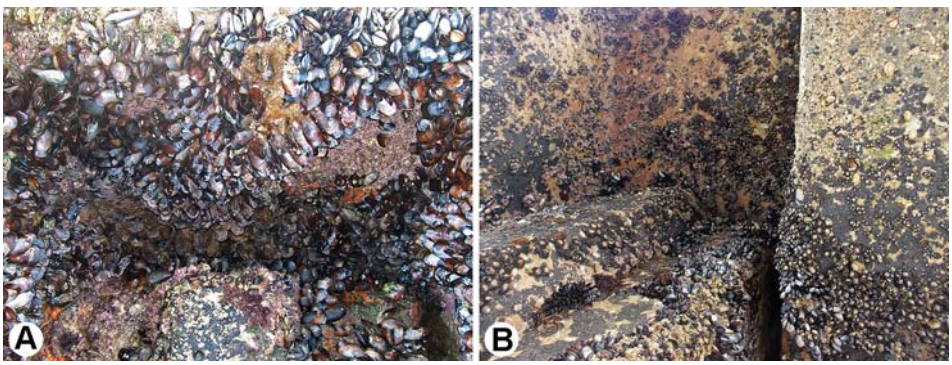

Fig. 4. Locality in Summerstrand (33°58'47.892"S 25°39'31.0674"E) during (A) March 2012 and (B) November 2012, showing marked visual differences, with a great reduction in invertebrate covering of the intertidal rocks.

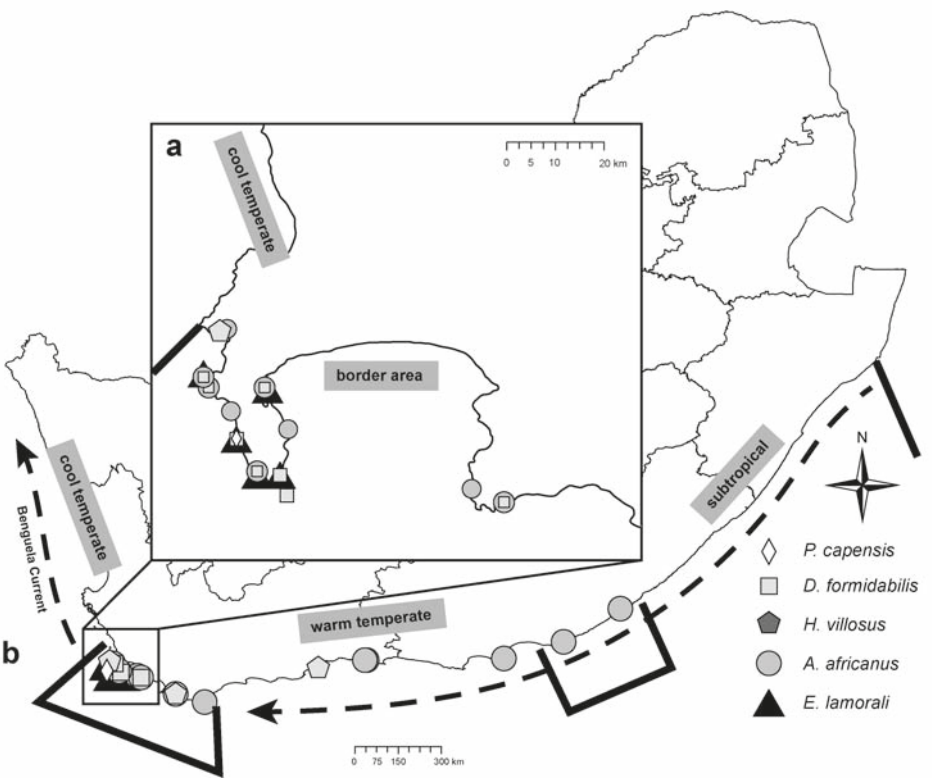

Fig. 5. Main biogeographical zones bordering the South African coast [Brackets: Regions in which the border between zones could fall; Stippled arrows: Current direction and name; Grey Textboxes: Zone name] (After Teske *et al.* 2011).

DISCUSSION

Amaurobioides africanus and *D. formidabilis* are reported by Day (1974) and Dippenaar-Schoeman & Jocqué (1997) as occurring from Lüderitz in Namibia to East London in the Eastern Cape of South Africa, yet no individuals were found during the course of this study at either of the two surveyed sites situated north of Kommetjie. This being so, further surveys along the west coast are required. The absence of *D. formidabilis* at Kenton-on-Sea and Jongensfontein could be explained by the lack of appropriate nesting niches at those two sites. In both areas, the lower shore region that *D. formidabilis* would usually inhabit was exposed to high wave action, a characteristic that appears to have driven the spider to nest behind tubeworm conglomerates, mussel beds or barnacles at other sites. On these two shores, this covering was not present, leaving *D. formidabilis* with no suitable habitat in which to nest. This may also be the reason why *D. formidabilis* was not recorded east of the Peninsula in November, where stochastic oceanographic events lead to marked reduction in the extent of encrusting by invertebrate organisms. Similarly, *A. africanus*, a species that inhabits the upper intertidal zone, preferring areas only inundated with water every spring tide, was not found at Cape St. Francis, where all rocks are covered by water during both spring and neap high tides.

The records for *H. villosus* and *P. capensis* are interesting, as both are species that are not usually found within the intertidal region (Haddad & Dippenaar-Schoeman 2009). Haddad and Dippenaar-Schoeman (2009) include an unknown *Heliophanus* species in their checklist, but it is unclear whether this is *H. villosus* or not. Therefore, the only confirmed instance of occurrence of the species in the Western Cape is on Signal Hill (part of Table Mountain, Cape Town) (Wesołowska pers. comm.). The first mention of *P. capensis* inhabiting the intertidal region is made in Larsen (2012): an individual was seen attacking and eating *A. africanus* adults within their own nests at Kommetjie. The results of the present study accordingly extend both spiders' known distributions.

Parasitoids may not be spatially connected to a host by the presence of the latter alone —they may be linked to only certain characteristics of the host's living environment (Laing 1937) because of the parasitoid's specific physical capabilities (Atkins 1980). Laing (1937) showed that certain parasitoids search for the particular habitat in which their host is found before searching for the host itself, a behavioural phenomenon called a 'fixed action pattern' (Atkins 1980). This search for a particular stimulus, which in this case is of an environmental nature, is known as orthokinesis (Atkins 1980). As a result, the parasitoid may not be exploring the entirety of its host's range (Laing 1937). While many scenarios exist that might explain the distribution of *E. lamorali*, if the spiders living outside of the Peninsula have taken up occupancy in areas with different habitat conditions—which they appear to have done by settling on small cliff-like rock faces or under other marine organisms on highly exposed shores—the wasp may not be driven to look for its host there, and perhaps for this reason has remained restricted to its current habitat. Lack of stimuli in a different area may inhibit movement, thereby resulting in congregation in one locality (Atkins 1980). Furthermore, while aptery has likely evolved as a mechanism to maintain a presence within a locally restricted area of distribution of the host spiders, the apterous condition in both sexes of *E. lamorali* restricts their host-finding ability, thus selecting for restricted local population distributions.

Dispersal of *E. lamorali* from one area to another could take place in a variety of ways, not all of which may be mutually exclusive (Barber 2009). Biologically, transport by birds or other animals (zoochory), humans (anthropochory) (Barber 2009) or the host itself (phoresy) (Strand 1986; Austin *et al.* 2005) could all result in dispersal. *E. lamorali* could also easily be blown around by the strong coastal winds in the Cape Peninsula (Barber 2009; Van Noort 2009; Van Noort *et al.* 2014). However, this is one mechanism that is thought to be driving selection for aptery (Van Noort 2009; Van Noort *et al.* 2014) so it is unlikely to be a means of dispersal. Finally, rafting on plant or other floating material could lead to transportation of individuals by oceanic currents or even of small populations of wasps far from their original location, only to become settled on another shore (Barber 2009). Floating material carrying live insects has previously been found up to 16 km offshore (Barber 2009).

The oceans and coastal areas bordering South Africa can be divided into three biogeographical regions based on different species assemblages and hydrological characteristics (Fig. 5) (Turpie *et al.* 2000; Teske *et al.* 2006, 2011; Allanson & Baird 2008). These areas include a 'cool temperate South-West coast' region; a 'warm temperate South coast' region; and a 'subtropical East coast' region (which may include a 'tropical East coast' region) (Fig. 5) (Turpie *et al.* 2000; Teske *et al.* 2006, 2011; Allanson & Baird 2008). The last-mentioned two regions are affected by the warmer

Agulhas current, while the first one is kept cool through action of the cold Benguela current (Allanson & Baird 2008). With respect to the present study, the location of the boundary between the first two zones appears to be the most important determinant in keeping *E. lamorali* solely within the western region of the distributional range of *D. formidabilis*. Although the exact positioning of the boundary line is disputed and appears to change temporally and spatially (Allanson & Baird 2008) (with increased distance outwards from the coast (Teske *et al.* 2011)), it is generally found to lie somewhere between Kommetjie and Cape Agulhas (Turpie *et al.* 2000; Teske *et al.* 2006, 2011).

Teske *et al.* (2011) cite factors such as upwelling cells, coastal currents, eddies and coastal dunefields as posing potentially significant barriers to dispersal. All of these factors combine to define biogeographical zones. The effects that they may have on organisms appear to be species-specific (Teske *et al.* 2006).

The Cape Peninsula is situated in a region of high upwelling, which results in a lowering of coastal sea temperatures (Allanson & Baird 2008). These cells may prevent dispersal due to differing environmental conditions, such as temperature and eutrophication of the water along the coast (Teske *et al.* 2011). Furthermore, specifically if the wasp is using rafting for dispersal, upwelling cells may cause eddies that then remain within the vicinity of their location of origin, thereby hindering dispersal to other areas (Teske *et al.* 2011).

On a wider scale, the Benguela current runs from the Cape Peninsula upwards towards central Africa, diverging from the land mass as it proceeds (Allanson & Baird 2008). Rafting wasps would therefore be swept northwards out to sea and thus could possibly have become established only north of Kommetjie. In the present study, neither *D. formidabilis* nor *A. africanus* were found along this stretch of coastline. Mixing of the Benguela and Agulhas currents also occurs offshore from the Peninsula (Teske *et al.* 2011). With the Benguela flowing to the north (Allanson & Baird 2008), it is unlikely that any individuals enter the Agulhas and disperse eastwards.

Finally, a paucity or absence of rocks and, therefore, insufficient availability of potential nesting sites on coastal dunefields may prevent establishment of the spiders and, consequently, wasp populations in these areas. Considering the highly varied nature of the South African coast, where dunefields are often widely separated from rocky shores (Teske *et al.* 2011), dispersal of such a small organism could be limited to between rocky shores that are spaced close together (Emanuel *et al.* 1992; Barber 2009; Teske *et al.* 2011), such as are found along the Peninsula. The area east of the Peninsula is an extensive sandy coastline, possibly preventing dispersal from taking place in that direction.

Perhaps because of a variety of physiological factors, coastal structure, and host ecology in other areas, *E. lamorali* appears to be limited to the temperate South-West biogeographical region, and specifically to the Cape Peninsula. The distribution of the species falls within the Table Mountain National Park, thereby ensuring its effective conservation.

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