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Nest site choice by the intertidal spider Desis formidabilis (Araneae: Desidae) and nest utilization by its hymenopteran egg parasitoid

Running title:

Intertidal spider and parasitoid

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ABSTRACT

1. Echthrodesis lamorali Masner 1968 is the only known parasitoid of the eggs of the intertidal rocky shore spider Desis formidabilis O.P. Cambridge 1890 and is endemic to a small area of South Africa.
2. The abundance of spider nests and parasitoid presence were assessed in relation to their in- and between-shore location at multiple sites within the distribution of E. lamorali along the Cape Peninsula (Western Cape, South Africa).
3. Desis formidabilis nests were more abundant in the mid-shore zone than higher or lower up the shore. Spider population sizes also differed between collection sites,

with higher numbers recorded on the cooler western coast of the peninsula.

4. Evidence of parasitoid activity was recorded in 43.31% of the 127 nests and 13.85% of the 592 egg sacs they contained.
5. Where parasitoids gained entry to a spider egg sac, oviposition took place into all of the eggs present.
6. Incidence of wasp activity was positively correlated with spider nest concentration, not height up the shore, suggesting that the host and parasitoid are tolerant of salt-water inundation.
7. These results should assist managers of the Table Mountain National Park, in which the full distribution of E. lamorali falls, to better understand this component of rocky shore community dynamics.

KEYWORDS: Density dependence, Echthrodesis lamorali, Platygastridae, Scelioninae, Rocky shore, Zonation

INTRODUCTION

Arthropods have repeatedly colonised intertidal rocky shore environments (Cheng, 1976; Barber, 2009). Crustaceans, a predominantly marine group, are the most conspicuous, but representatives of mainly terrestrial groups such as insects and spiders are also present. Dead and living plant and animal material provides resources for scavengers and predators, which in turn support other invertebrates, including parasitoids (Paetzold et al., 2008; Barber, 2009). Nonetheless, this is a harsh environment to colonise (Lubke, 1998), with each individual shore boasting different characteristics depending on the activity of the tides and currents (Tietz & Robinson, 1974; Lubke, 1998). Single shores alone are also a highly heterogeneous environment from a variety of abiotic aspects (Lubke, 1998). These abiotic factors in turn act as ‘stressors’ on biotic ones, leading to community structuring (Foster & Treherne, 1976; Sanford, 2002).

Spiders are a generally little-known inhabitant of the intertidal region. A total of eleven spider families have been recorded from intertidal zones globally, with Desis Walckenaer 1937 (Araneae: Desidae) the most common and cosmopolitan genus (McLay & Hayward, 1987). Individuals belonging to this genus also nest lower down the intertidal zone than any other maritime spiders

(McLay & Hayward, 1987). Desis formidabilis O.P. Cambridge 1890 (Araneae: Desidae) (Figure 1) is known only from southern Africa, where it occurs on rocky shores from Lüderitz (Namibia) in the north-west to East London (Eastern Cape, South Africa) in the east (Filmer, 1995; Dippenaar-Schoeman & Jocqué, 1997). This species is ecribellate, nesting in silk-lined crevices or empty shells found within the intertidal region (Lamoral, 1968; McLay & Hayward, 1987) (Figure 1), where it feeds nocturnally on isopods and amphipods (Day, 1974; Dippenaar-Schoeman & Jocqué, 1997, van Noort, 2009).

The intertidal habitat of D. formidabilis may allow the spider to avoid attack from predatory spider-hunting wasps (Pompilidae) (Lamoral, 1968), but in one part of its range, its eggs are host to a specialist egg parasitoid, Echthrodesis lamorali Masner 1968 (Hymenoptera: Scelioninae) (Lamoral, 1968; Masner, 1968; van Noort, 2009; Owen et al., 2014; van Noort et al., 2014; Owen, 2015; Owen et al., 2017) (Figure 2). The distribution of this wasp is restricted to a small area of the Cape Peninsula, south of Cape Town in the Western Cape Province of South Africa (Lamoral, 1968; Masner, 1968; van Noort, 2009; Owen et al., 2014; van Noort et al., 2014; Owen, 2015; Owen et al., 2017) and is fully encompassed in the Table Mountain National Park, a conservation region. Echthrodesis lamorali is one of only three species of parasitoid wasps worldwide that display unequivocal adaptations to rocky shore intertidal conditions and can be considered as a truly maritime species (van Noort et al., 2014).

A single D. formidabilis nest is built by one female only, and takes the form of several purse-like wedge-shaped egg sacs that fit together within a shell or crevice (van Noort, 2009; van Noort et al., 2014) (Figure 1). Not all egg sacs contain eggs, but where they are laid, one egg mass is produced per sac, and the number of eggs within each varies (van Noort, 2009; van Noort et al., 2014) (Figure 2). The empty egg sacs may act as ‘red herrings’ or ‘decoys’, that reduce the searching efficiency of the parasitoid (van Noort, 2009; van Noort et al., 2014). Decoy chambers with this apparent effect have been described in the galls of some species of gall wasps (Hymenoptera: Cynipidae) on Quercus spp. (Askew, 1984).

The intertidal zone represents a challenging and dangerous environment for both the spider and its associated parasitoid. Submersion by seawater is likely to be a particularly important structuring environmental variable and it is hypothesised here that spider nests would be distributed predominantly on the lower shore, which maintains a higher, less variable humidity than upper shore regions, as observed by McLay & Hayward (1987) for the genus. As the parasitoid is of more recent terrestrial origin (van Noort et al., 2014), it is hypothesized that E. lamorali would exhibit an opposing in-shore pattern by making use of more spider nests further away from the land-sea interface. This study assesses the factors influencing patterns in the distribution of spider population sizes and parasitism incidence in relation to both their in- and between-shore location at multiple sites within the distribution of E. lamorali along the Cape Peninsula (Western Cape, South Africa). Very little is currently known about the ecology of the spider and wasp, and their interactions, despite their unique nature. This study therefore also aimed to describe the within-habitat location and characteristics of the nests of D. formidabilis along the Cape Peninsula with emphasis on the nest size and composition, egg numbers and egg success. The full distribution of E. lamorali is encompassed in the SANParks Table Mountain National Park. To better manage the park, it is important for conservation officers and managers to understand the dynamics of this unique component of intertidal communities that exists nowhere else.

MATERIALS AND METHODS

<u>Localities</u>

Spider nests were collected from four sites located on either side of the Cape Peninsula (Western Cape Province, South Africa) where E. lamorali was known to be present: to the west, Kommetjie (34° 8' 22.7034" S, 18° 19' 17.5794" E) and Olifantsbos Point (Table Mountain National Park [TMNP]; 34° 15' 29.6274" S, 18° 22' 54.0474" E) and to the east, Buffels Bay (TMNP; 34° 19' 19.5594" S, 18° 27' 44.028" E) and Simon’s Town (34° 9' 43.7394" S, 18° 25' 55.5234" E) (Owen et al., 2014; Owen, 2015) (Figure 3).

The rocky shore at each site was separated into three zones: the sublittoral fringe, eulittoral range and littoral fringe (zones A, B and C respectively), following Lamoral (1968). Zones were demarcated using visual assessment of the coastline during the changing tides, in combination with patterns in encrusting materials on the shore, such as algal clusters.

Nest collection

Nests were collected on six occasions at the lowest tides every two weeks in spring between 9 September and 22 November 2014. A single transect perpendicular to the shoreline was placed at random along the shoreline during each collection. The transects ran from the upper littoral (Zone C) to the lower sublittoral fringe (Zone A), encompassing all of the rocky shore in-between, and thus ranged in length depending on the shore sampled, the physical aspects of which were highly variable between sites due to the heterogeneous nature of the intertidal region. The area within a width of 2m of the line within each of the three zones was then visually searched for 30 minutes. Each collected D. formidabilis nest was stored individually in mesh-covered tubes and all nest characteristics, described below, were recorded.

Nest contents

In the laboratory, each nest was separated into its constituent egg sacs, and the number, condition and contents of each were recorded. Unhatched eggs were left within their individual egg sacs (to maintain adequate humidity levels for the eggs) in individual glass rearing chambers, the openings of which were sealed with netting. These chambers were kept at room temperature and moistened daily by adding a few drops of seawater to assist with the maintenance of humidity. The eggs were given three months to incubate and allow for the development and emergence of embryos therein. The state of the eggs at the time of collection were therefore referred to as 'pre-incubation', while those that had been maintained in the laboratory for an incubation period were thereafter referred to as 'post-incubation' eggs. Wasps and spiders that emerged from the eggs were counted and sexed (in the case of any E. lamorali emergence), while the contents of any eggs that did not hatch were subsequently assessed under a binocular dissecting microscope in an attempt to determine the species of the unsuccessful embryo where possible. Eggs that gave rise to wasps, or in which failed wasp embryos were identifiable were classed as being ‘parasitized’. All material was stored in 96% ethanol and accessioned into the entomology wet collection at the Iziko South African Museum (Cape Town, Western Cape, South Africa).

Statistical analyses

To explore the factors influencing patterns in the distribution of spider population sizes and parasitism incidence, they were assessed using two different sample size-corrected, Akaike Information Criterion (AICc, which are better suited to small datasets, such as those used here, than AICs) based, reverse model building processes (Symonds & Moussalli, 2011) in R version 3.1.3 (R Core Team, 2015) using the packages MuMIn (Barton, 2015) and car (Fox & Weisberg, 2011). An AICc analysis was chosen as it allows exploration of the system as a whole, and indicates what factors interact to define the ecological patterns that are evident. The most complex model using all possible predictor (independent) variables (those recorded for each nest during sample collection) was first constructed and co-linearity within the variables was determined for each outcome (spider population size or parasitism incidence). Where co-linearity was detected, the variable indicated (GVIF>5) was removed. Akaike Information Criterion values (AICcs) were then calculated for all possible models using the variables from the initial one. All models developed in this process with a delta value of less than 2 were considered and the variables used in the construction of these was assessed as in Symonds & Moussalli (2011). The most commonly occurring predictors that made the most biological sense were used in construction of the final model that outlined the effect that the remaining predictor variables had on the spider population size or parasitism incidence (Zuur et al., 2010; Symonds & Moussalli, 2011).

To answer specific questions on areas of interest, the following statistical tests were completed in Statistica 10 (StatSoft Inc., 2011). Differences in the number of egg sacs and the number of eggs laid per nest and egg sac collected from different sites and zones were analysed using a Kruskal Wallis test. Regression models tested for correlations between the total number of egg sacs and how many were left unused, and between the number of eggs and male wasp presence in the post-incubation emerged wasps. Generalized linear models revealed whether differences existed between sites and zones for hatching success, which is defined here as the full development and post-incubation hatching of either a spider or wasp from an egg, of parasitized and non-parasitized eggs.

RESULTS

All AICc results tables are presented as supplementary information in a supporting document. Only the patterns and interpretation of these results are presented here.

Nest numbers

A total of 127 nests comprising 592 egg sacs were collected from the four sites. The AICc model for spider population size (the number of nests collected) returned a total of eight plausible models with deltas of less than two. The final model illustrated that spider population sizes differed significantly between zones and sites. The most nests were collected in zone B, followed by A, and finally zone C, although zones A and B did not differ significantly (Figure 4A). The sites on the western shore of the Peninsula hosted the most spiders, with the highest population density (most number of nests collected) at Kommetjie, then Olifantsbos, followed by Buffels Bay and finally Simon’s Town (Figure 4B).

Nest contents

The number of egg sacs per nest ranged from one to 23 (mean ± SE = 4.0 ± 0.34), and differed between sites ($H_{(3, 127)} = 10.430$, $P = 0.015$), but not zones ($H_{(3, 127)} = 2.107$, $P = 0.349$). Larger nests were found at Olifantsbos than Kommetjie, but no differences existed between the other sites (Figure 5). Of the 127 nests collected, 28 (22.05%) consisted of only a single egg sac.

Among the 99 collected nests that had two or more egg sacs, 12 (12.12%) contained no eggs in any of the egg sacs, most (51.52%) had a mixture of used (with spider eggs) and unused (no contents) egg sacs, and 36 (36.36%) nests were collected where all egg sacs were used. Overall, in all of the collected nests, 42% of the egg sacs were left unused (Figure 6), 9% of which showed evidence of parasitoid action (holes chewed by wasps through the silk) (Figure 6A). The relationship between the total number of egg sacs in a nest and the number where no eggs had been laid was positively correlated ($F_{(1,125)} = 262.61$, $P < 0.0001$, $R^2 = 0.678$), indicating that bigger nests contained more unused egg sacs.

Thirty-three percent of pre-incubation egg sacs contained one or more eggs (Figure 6), of which 67% were still viable (“fresh” or “brown unhatched”) and were isolated for incubation (Figure 6B). The mean number of eggs per nest was 41.11 ± 4.439 (SE) (minimum = 1, maximum = 226), while the mean in egg sacs where at least one egg had been laid was 19.15 ± 0.803 (SE), with a minimum of one egg and a maximum of 54. The number of eggs per egg sac differed significantly between sites ($H_{(3, 85)}$ = 13.455, P = 0.004), but not zones ($H_{(2, 85)}$ = 1.218, P = 0.544), with spiders at Olifantsbos producing more eggs than at Buffels Bay (Figure 7). The remaining used egg sacs all contained spiderlings (21%) or wasps (4%) (Figure 6). Most of the former were alive (98%), with 60% darker and older, and 38% freshly hatched (Figure 6C), while the majority (88%) of the latter where the egg sacs contained wasps hosted live adult wasps (Figure 6D).

Parasitism of eggs, i.e. the number of eggs per egg sac from which wasps emerged or were visible as failed embryos, in a single egg sac ranged from 11.36% to 100%, with a mean of 60% ± 5.45 (SE). The parasitism incidence AICc returned zone as the only significant predictor as to whether an egg sac was parasitized or not. Following a similar trend to the spider population size modelled previously, most parasitism took place in the eulittoral zone (B), followed by the sublittoral fringe (A) and lastly the littoral fringe (C) (Figure 8).

<u>Post-incubation figures and sex ratios of resultant wasps</u>

Isolated non-parasitized eggs exhibited a 47.99% ± 10.40 (SE) hatching success rate in the laboratory. Parasitized eggs (n=704 eggs) were less successful, with an average hatching rate of 24.13% ± 8.61 (SE). In most cases where parasitized eggs failed, the wasp embryo reached full development, but never eclosed. No significant differences were detected between either of these success rates at all sites (not parasitized: $F_{(3, 62)} = 0.291$, $P = 0.832$; parasitized $F_{(2, 45)} = 0.444$, $P = 0.644$) and zones (not parasitized $F_{(2, 62)} = 2.108$, $P = 0.130$; parasitized $F_{(2, 45)} = 1.138$, $P = 0.330$).

A total of 83 wasps were reared from the collected nests, 67 (80.72%) of which were female and only 16 (19.28%) male, indicating a strong female bias. A mean of 0.89 ± 0.29 (SE) male wasps were found per egg sac, while females averaged 3.72 ± 1.10 (SE) individuals per egg sac. The number of eggs in an egg sac and the number of males that emerged from them were marginally correlated ($R^2_{(16)} = 0.211$, $P = 0.055$), with a trend for larger broods to contain more male wasps.

DISCUSSION

This study has shown that D. formidabilis favours the western coastline of the Cape Peninsula, which is known to be much cooler than the east (Teske et al., 2006; Teske et al., 2011). It also favours the mid-shore zones, where twice a day salt-water inundation occurs, but for a shorter duration than below it, and longer duration than above it. Nests of the spiders varied greatly in terms of the numbers of egg sacs and eggs that they contained. Many egg sacs were empty and hatching success rates among the eggs was low. Within individual sites, parasitism of the eggs by E. lamorali followed a density-dependent pattern, with a concentration in the mid-shore zone where most hosts were located. The wasp population sex ratios were highly female-biased.

Significant differences in spider population sizes existed between intertidal zones and sites. In contrast to the original hypothesis that the spiders would prefer the lower regions of the shore closer to the water’s low tide edge, the intermediate eulittoral zone and highest sublittoral fringe hosted the largest spider populations and the fewest spider nests were found lowest down in the littoral fringe. This distribution pattern is likely to reflect the influence exerted by environmental conditions on a shore. Conditions become drier and hotter for longer periods of time up the intertidal region towards the terrestrial environment due to the movements of the tides (Sanford, 2002). Lower down the intertidal region, however, the physical force of wave action can be too stressful for certain species (Sanford, 2002). These abiotic changes across the intertidal range have large effects on the in-shore distributions of most of the organisms living in this environment, and this appears to include the spatial distribution of D. formidabilis.

The populations of the spider on the west coast are also significantly larger than those on the eastern side of the peninsula. A large variety of environmental and community-based parameters can have an effect on population sizes (Foster & Treherne, 1976; Sanford, 2002). This is often striking for intertidal regions, where the combination of varying biotic and abiotic conditions on different shores can lead to unique patterns (Tietz & Robinson, 1974; Lubke, 1998). As discussed in Owen et al. (2014) and Owen (2015), the spider populations fall within the ecotone between the warm temperate biogeographical region to the east and the cool temperate region to the west. The differences between these two biogeographical zones have strong influences on local conditions, and consequently modify community composition on the two shores (Tietz & Robinson, 1974; Foster & Treherne, 1976; Lubke, 1998; Sanford, 2002).

A significant outcome of the model on spider population sizes is that parasitism was not identified as a controlling factor. In many other systems, parasitoids exert a top-down controlling effect on spider populations, such as in spider populations affected by pompilid wasp abundances on islands in the Gulf of California (Polis & Strong, 1996), and the web building spiders attacked by Trypoxylon figulus von Linné 1758 (Hymenoptera: Crabronidae) in Switzerland (Coudrain et al., 2013). In contrast, the harsh environmental conditions and steep environmental gradients of the intertidal habitat of D. formidabilis result in dominance by bottom-up dynamics, which incorporate both biotic and abiotic factors (Chen & Wise, 1999; Denno et al., 2002; Menge et al., 2015). A bottom-up controlled system is defined as one where food sources and environmental conditions have a larger effect on a population than the effect of predators and parasitoids (Lynam et al., 2017). Such bottom-up control has previously been recorded in detritus-driven ecosystems such as the intertidal zone (Chen & Wise, 1999; Menge et al., 2015) and also among other arachnid species living in North American intertidal marshes (Denno et al., 2002).

Although differences existed in the average nest sizes (number of egg sacs) between some sites in this study, no clear difference between eastern and western shores of the Peninsula was discernible. However, the number of eggs produced per nest on the west coast of the Peninsula was higher than in the east.

The average D. formidabilis nest comprised around four egg sacs, which is comparable to the nests produced elsewhere by another maritime species in the same genus, Desis marina Hector 1877 (Araneae: Desidae), which contained an average of 3.4 egg sacs (McLay & Hayward, 1987). Almost half of all egg sacs in the D. formidabilis nests were unused. This contrasts with the results of McLay & Hawyard (1987), who recorded no unused egg sacs in the nests of D. marina. However, the number of eggs in utilised egg sacs were similar between the species, with the number of eggs in a single D. marina egg sac ranging from 11-61, compared with 1-54 eggs in Desis formidabilis.

Nine percent of the unused egg sacs exhibited signs of E. lamorali activity (chewed holes). The “red herring” hypothesis postulated by van Noort (2009) and van Noort et al. (2014) suggested that wasps may not have enough energy resources left to enter a second egg sac after having chewed into a first that contains no eggs. Austin (1984) showed that Ceratobaeus masneri Austin 1983 (Hymenoptera: Platygastridae) females usually die shortly after producing their first brood because dead individuals were often found on or in the host’s nests, though this may be the result of starvation during the brood guarding that is displayed by some platygastrids following oviposition (Matsuo et al., 2014). In contrast, none of the empty D. formidabilis egg sacs that exhibited signs of parasitoid entry contained dead adult wasps, which casts doubt on the ‘red herring’ theory as originally postulated, although any time ‘wasted’ by searching females is likely to reduce their lifetime reproductive success.

Parasitism incidences within a single egg sac averaged at 60%, in contrast to van Noort et al. (2014) on the same two species, who consistently recorded a parasitism incidence of 100% within a single egg sac. However, of the 566 egg sacs assessed in this study, only one contained both spiderlings and wasps and given that encapsulated and putrefied embryos were quite frequent, initial parasitism rates may often be close to 100% within those host egg batches utilised by the wasp. This parasitism frequency is not common for the Scelioninae (van Noort et al., 2014).

The zone in which a nest was built was the only factor identified as significantly influencing parasitism rates, with most parasitism recorded in the middle zone, the lowest in the upper zone and the lowest zone intermediate between the others. Parasitism incidence is likely to be affected by the wasp’s ability to find and recognise the host nest, a behaviour that is influenced by a variety of environmental factors (Fox et al., 1990; Austin et al., 2005). In this case, in contrast to the original hypothesis, the parasitism incidence followed density patterns displayed by the host spider rather than abiotic factors like water inundation.

For D. marina eggs, McLay & Hayward (1987) reported a high hatching success rate of 89.99%. In this study, most sites experienced an approximate 50% success rate of juvenile spider emergence from eggs that had not been parasitized. A low hatching success rate of eggs is common for species with high reproductive outputs (Deevey, Jr., 1947; Murdoch, 1966; Gadgil & Bossert, 1970), such as D. formidabilis.

Echthrodesis lamorali have strongly female-biased broods (83% female) in this study, similar to the 87.29% female brood recorded by van Noort et al. (2014). Female dominated sex ratios are common for platygastrids (Austin, 1984; Strand, 1988; Fox et al., 1990; Austin et al., 2005). As overall clutch size increases, Green et al. (1982) showed that the number of males follows the same trend for other parasitoid wasps, which was also demonstrated here, although only weakly.

In conclusion, D. formidabilis displays a preference for mid-shore elevations along cooler rocky coastlines. Its egg parasitoid, which has a very restricted distribution within the wider range of its host, is able to utilise spider nests from the lower to upper shores, but concentrates its activities in the mid-shore, where its hosts are most abundant. These results should assist managers of the Table Mountain National Park in better understanding the intertidal community dynamics within the reserve.

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CONTRIBUTIONS OF AUTHORS

Candice Owen, Julie Coetzee and Simon van Noort were responsible for study design, while Candice Owen carried out all of the fieldwork, data collection and manuscript preparation. Stephen Compton assisted with manuscript content and data analysis.

REFERENCES

Askew, R.R. (1984) The biology of gall wasps. The Biology of Galling Insects (ed. by T. N. Ananthakrishnan), pp. 223-271. Oxford & IBH Publishers, New Delhi.

Austin, A.D. (1984) The fecundity, development and host relationships of Ceratobaeus spp. (Hymenoptera: Scelionidae), parasites of spider eggs. Ecological Entomology, **9**, 125-138.

Austin, A.D., Johnson, N.F. & Dowton, M. (2005) Systematics, evolution, and biology of scelionid and platygastrid wasps. Annual Review of Entomology, **50**, 553-582.

Barber, A.D. (2009) Littoral myriapods: a review. Soil organisms, **81**(3), 735-760.

Barton, K. 2015. MuMIn: Multi-Model Inference. R package version 1.13.4. [Online] Available at: http://CRAN.R-project.org/package=MuMIn. Accessed: 17/06/2015.

Chen, B. & Wise D.H. (1999) Bottom-up limitation of predaceous arthropods in a detritus-based terrestrial food web. Ecology, **80**(3), 761-772.

Cheng, L. (1976) Insects in marine environments. Marine Insects, pp. 1-4. North-Holland Publishing Company, Amsterdam.

Coudrain, V., Herzog, F. & Entling, M.H. (2013) Effects of habitat fragmentation on abundance, larval food and parasitism of a spider-hunting wasp. PLoS ONE, **8**(3), 1-7.

Day, J.H. (1974) A guide to marine life on South African shores, pp. 122. A. A. Balkema, Cape Town.

Deevey, Jr., E.S. (1947) Life tables for natural populations of animals. The Quarterly Review of Biology, **22**(4), 283-314.

Denno, R.F., Gratton, C., Peterson, M.A., Langellotto, G.A., Finke, D.L. & Huberty, A.F. (2002) Bottom-up forces mediate natural-enemy impact in a phytophagous insect community. Ecology, **83**(5), 1443-1458.

Dippenaar-Schoeman, A.S. & Jocqué, R. (1997) African spiders: an identification manual, pp. 101-103; 145-147. Agricultural Research Council, Pretoria.

Filmer, M.R. (1995) Southern African spiders: an identification guide, pp. 74-45; 79-80. Struik Publishers, Cape Town.

Foster, W.A. & Treherne, J.E. (1976) Insects of marine saltmarshes: problems and adaptations. Marine insects (Cheng L.), pp. 5-42. North-Holland Publishing Company, Amsterdam.

Fox, J. & Weisberg, S. (2011) An {R} Companion to Applied Regression, Second Edition. Thousand Oaks CA: Sage. [Online] Available at: http://socserv.socsci.mcmaster.ca/jfox/Books/Companion. Accessed: 17/06/2015.

Fox, L.R., Letourneau, D.K., Eisenbach, J. & van Nouhuys, S. (1990) Parasitism rates and sex ratios of a parasitoid wasp: effects of herbivore and plant quality. Oecologia, **83**, 414-419.

Gadgil, M. & Bossert, W.H. (1970) Life historical consequences of natural selection. The American Naturalist, **104**(935): 1-24.

Green, R.F., Gordh, G. & Hawkins, B.A. (1982) Precise sex ratios in highly inbred parasitic wasps. The American Naturalist, **120**(5), 653-665.

Lamoral, B.H. (1968) On the ecology and habitat adaptations of two intertidal spiders, Desis formidabilis (O.P. Cambridge) and Amaurobioides africanus Hewitt, at "The Island" (Kommetjie, Cape Peninsula), with notes on the occurrence of two other spiders. Annals of the Natal Museum, **20**(1), 151-193.

Lubke, R.A. (1998) Chapter 11: Marine ecology. Field guide to the Eastern and Southern Cape coasts (ed. by R.A. Lubke & I. de Moor), pp. 170-179. University of Cape Town Press, Cape Town.

Lynam, C.P., Llope, M., Möllmann, C., Helaouët, P., Bayliss-Brown, G.A. & Stenseth, N.C. (2017) Interaction between top-down and bottom-up control in marine food webs. PNAS, **114**(8): 1952-1957.

Masner, L. (1968) A new Scelionid wasp from the intertidal zone of South Africa (Hymenoptera: Scelionidae). Annals of the Natal Museum, **20**(1), 195-198.

Matsuo, K., Hirose, Y. & Johnson, N.F. (2014) A taxonomic issue of two species of Trissolcus (Hymenoptera: Platygastridae) parasitic on eggs of the brown-winged green bug, Plautia stali (Hemiptera: Pentatomidae): resurrection of T. plautiae, a cryptic species of T. japonicus revealed by morphology, reproductive isolation and molecular evidence. Applied Entomology and Zoology, **49**(3), 385-394.

McLay, C.L. & Hayward, T.L. (1987) Reproductive biology of the intertidal spider Desis marina (Araneae: Desidae) on a New Zealand rocky shore. Journal of Zoology, **211**, 357-372.

Menge, B.A., Gouhier, T.C., Hacker, S.D., Chan, F. & Nielsen, K.J. (2015) Are meta-ecosystems organized hierarchically? A model and test in rocky intertidal habitats. Ecological Monographs, **85**(2), 213-233.

Murdoch, W.W. (1966) Population stability and life history phenomena. The American Naturalist, **100**(910), 5-11.

Owen, C.A. (2015) Life history of the maritime platygastrid Echthrodesis lamorali Masner 1968. PHD Thesis. Rhodes University (Grahamstown).

Owen, C.A., Coetzee, J.A. & van Noort, S. (2014) Distributional range of the South African maritime spider-egg parasitoid wasp, Echthrodesis lamorali (Hymenoptera: Platygastridae: Scelioninae). African Invertebrates, **55**(2), 323-332.

Owen, C.A., Coetzee, J.A., van Noort, S. & Austin, A.D. (2017) Assessing the morphological and physiological adaptations of the parasitoid wasp Echthrodesis lamorali for survival in an intertidal environment. Physiological Entomology, **42**, 173-180.

Paetzold, A., Lee, M. & Post, D.M. (2008) Marine resource flows to terrestrial arthropod predators on a temperate island: the role of subsidies between systems of similar productivity. Oecologia, **157**, 653-659.

Polis, G.A. & Strong, D.R. (1996) Food web complexity and community dynamics. The American Naturalist, **147**(5), 813-846.

R Core Team (2015) R: A language and environment for statistical computing. R Foundation for Statistical Computing. Austria. Available at: http://www.R-project.org/. Accessed: 17/06/2015.

Sanford, E. (2002) Water temperature, predation, and the neglected role of physiological rate effects in rocky intertidal communities. Integrative and Comparative Biology, **42**, 881-891.

Statsoft, Inc. (2011) Statistica 10. Oklahoma, United States of America.

Strand, M.R. (1988) Variable sex ratio strategy of Telenomus heliothidis (Hymenoptera: Scelionidae): adaptation to host and conspecific density. Oecologia, **77**, 219-224.

Symonds, M.R.E. & Moussalli, A. (2011) A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. Behavioural and Ecological Sociobiology, **65**, 13-21.

Teske, P.R., McQuaid, C.D., Froneman, P.W. & Barker, N.P. (2006) Impacts of marine biogeographic boundaries on phylogeographic patterns of three South African estuarine crustaceans. Marine Ecology Progress Series, **314**, 283-293.

Teske, P.R., von der Heyden, S., McQuaid, C.D. & Barker, N.P. (2011) A review of marine phylogeography in southern Africa. South African Journal of Science, **107**(5/6), 43-53.

Tietz, R.M. & Robinson, G.A. (1974) Tsitsikama shore. Wallachs Printing Co., Pretoria.

van Noort, S. (2009) The maritime platygastrid Echthrodesis lamorali Masner. Skaphion, **3**(40), 1-3.

van Noort, S., Masner, L., Popovici, O., Valerio, A.A., Taekul, C., Johnson, N., Murphy, N.P. & Austin, A.D. (2014) Systematics and biology of the aberrant intertidal parasitoid wasp Echthrodesis lamorali Masner (Hymenoptera: Platygastridae s.l.): a parasitoid of spider eggs. Invertebrate Systematics, **28**, 1-16.

Zuur, A.F., Ieno, E.N. & Elphick, C.S. (2010) A protocol for data exploration to avoid common statistical problems. Methods in Ecology and Evolution, **1**, 3-14.

FIGURE LEGENDS

Figure 1: Desis formidabilis lives solely in the intertidal habitat. (A) The shore at Kommetjie where Echthrodesis lamorali was first discovered. The different rock colours visible in this photograph indicate the three zones. (B) The typical habitat in which both D. formidabilis and E. lamorali live. (C and D) Desis formidabilis constructs its nests in gaps between rocks and under empty limpet shells, which are usually concealed beneath the boulders shown in the previous photo, using silk to form a waterproof lining between the substrate and nest. (E) Desis formidabilis individuals within a nest. Pale pink egg sacs are visible to the bottom and right of the nest. (F) A close-up photograph of the egg sacs showing the purse-like shape that opens when spiderlings exit the egg sac. The entry or exit holes made by E. lamorali are visible on the two left-most egg sacs.

Figure 2: (A) Desis formidabilis eggs within two opened egg sacs showing freshly laid white eggs and mature parasitized brown eggs. Egg colour was shown to correlate with parasitism status, with the brown colour of the eggs on the left a good

indicator of parasitism. (B) Freshly hatched D. formidabilis spiderlings are pale and emerge through the opened edge of the egg sac. (C and D) Echthrodesis lamorali oviposits one egg into each D. formidabilis egg in an egg sac. (E) Echthrodesis lamorali males eclose first and guard an egg containing a female. On her emergence, the two immediately mate. (F) The full habitus of an E. lamorali female.

Figure 3: The four sites that were actively searched for Desis formidabilis and Echthrodesis lamorali presence, Kommetjie (A), Olifantsbos Point (B), Buffels Bay (C) and Simon's Town (D).

Figure 4: The mean number (± SE) of Desis formidabilis nests collected from different zones (A) and sites (B) throughout all of the collection trips (letters indicate significant differences).

Figure 5: The mean number (± SE) of egg sacs recorded in Desis formidabilis nests collected from different sites (letters indicate significant differences).

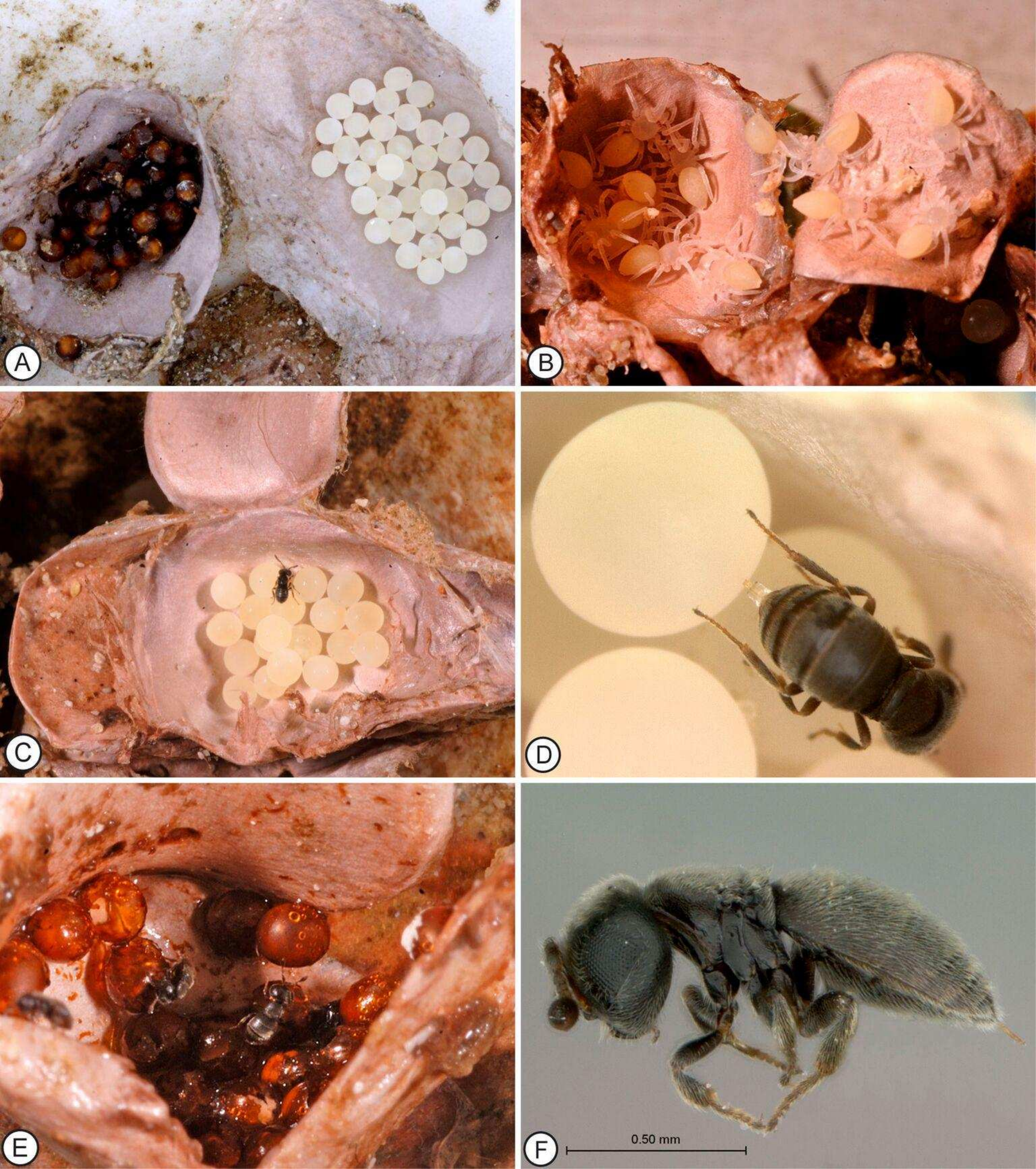
Figure 6: The pre-incubation contents of 592 collected Desis formidabilis egg sacs. Egg sacs with no contents (A) were either intact, or had holes chewed by adult Echthrodesis lamorali. Eggs (B) found in egg sacs at the time of collection exhibited the greatest variety of states, with the majority comprising of freshly laid, live eggs, followed by older, brown unhatched eggs, batches inflicted with mould, hatched eggs and finally putrefied

eggs. Spiders (C) present in egg sacs at the time of collection were classed as either live, freshly hatched individuals; live, older spiderlings; or mouldy dead adults. Where egg sacs contained wasps at the time of collection (D), they were either dead or alive.

Figure 7: The mean number (± SE) of eggs in egg sacs of Desis formidabilis nests collected from different sites (letters indicate significant differences).

Figure 8: Percentage parasitism of Desis formidabilis eggs in different egg sacs by Echthrodesis lamorali differed significantly between zones (letters indicate significant differences).


A
B
C
D
E
F


A
B
C
D
E
F
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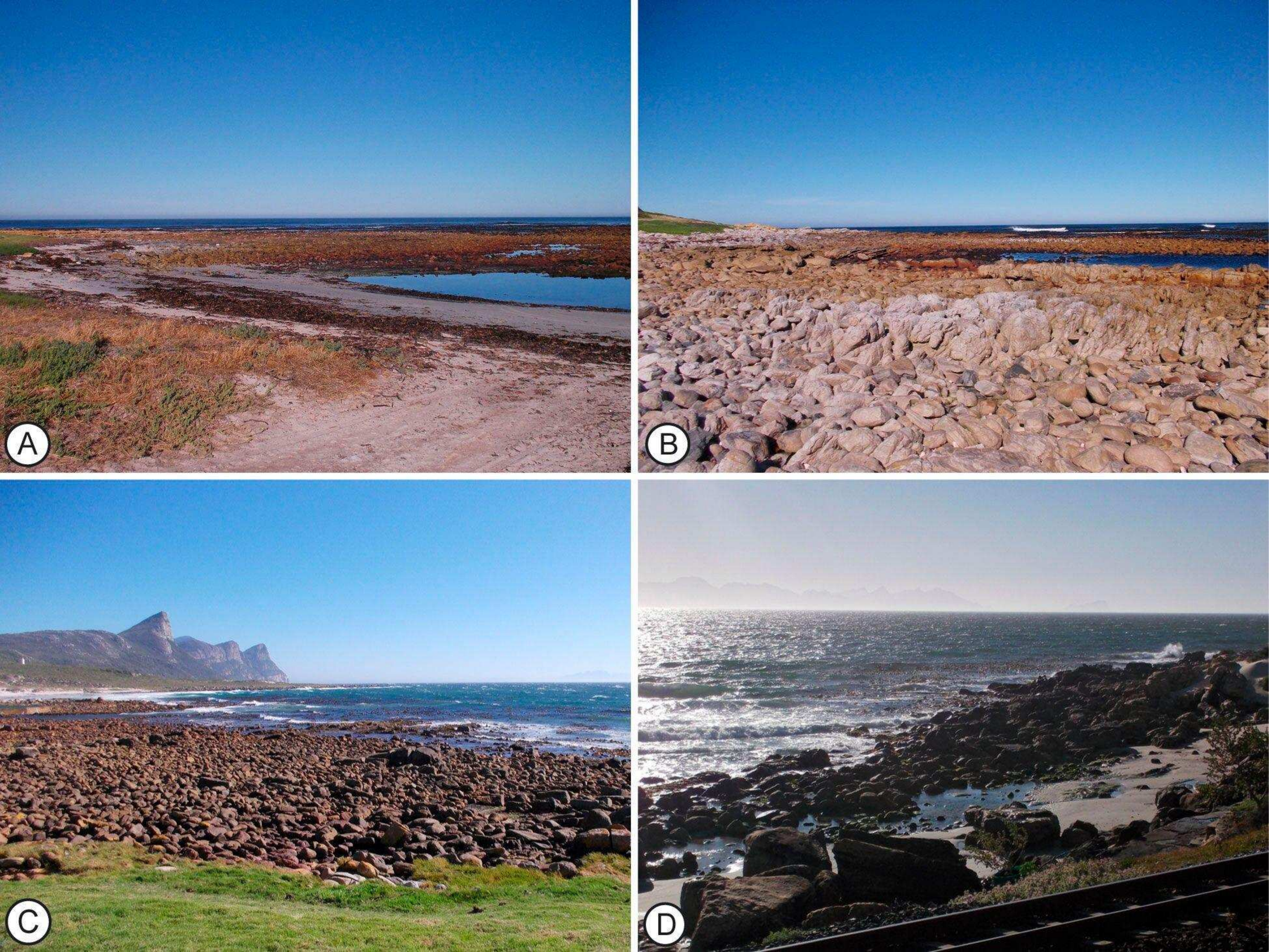
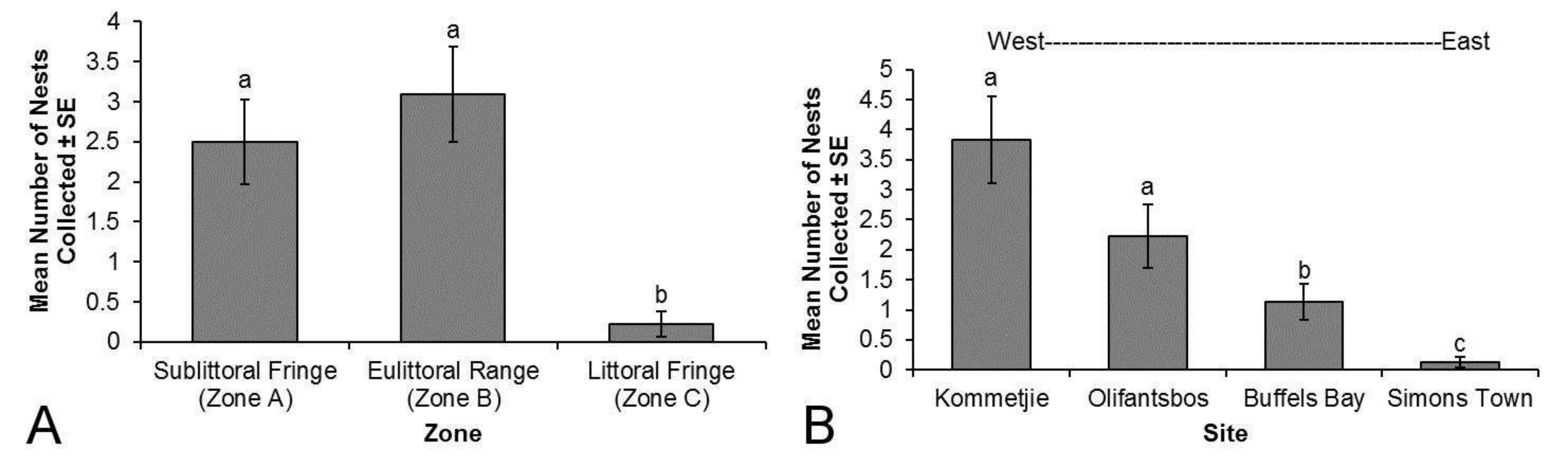
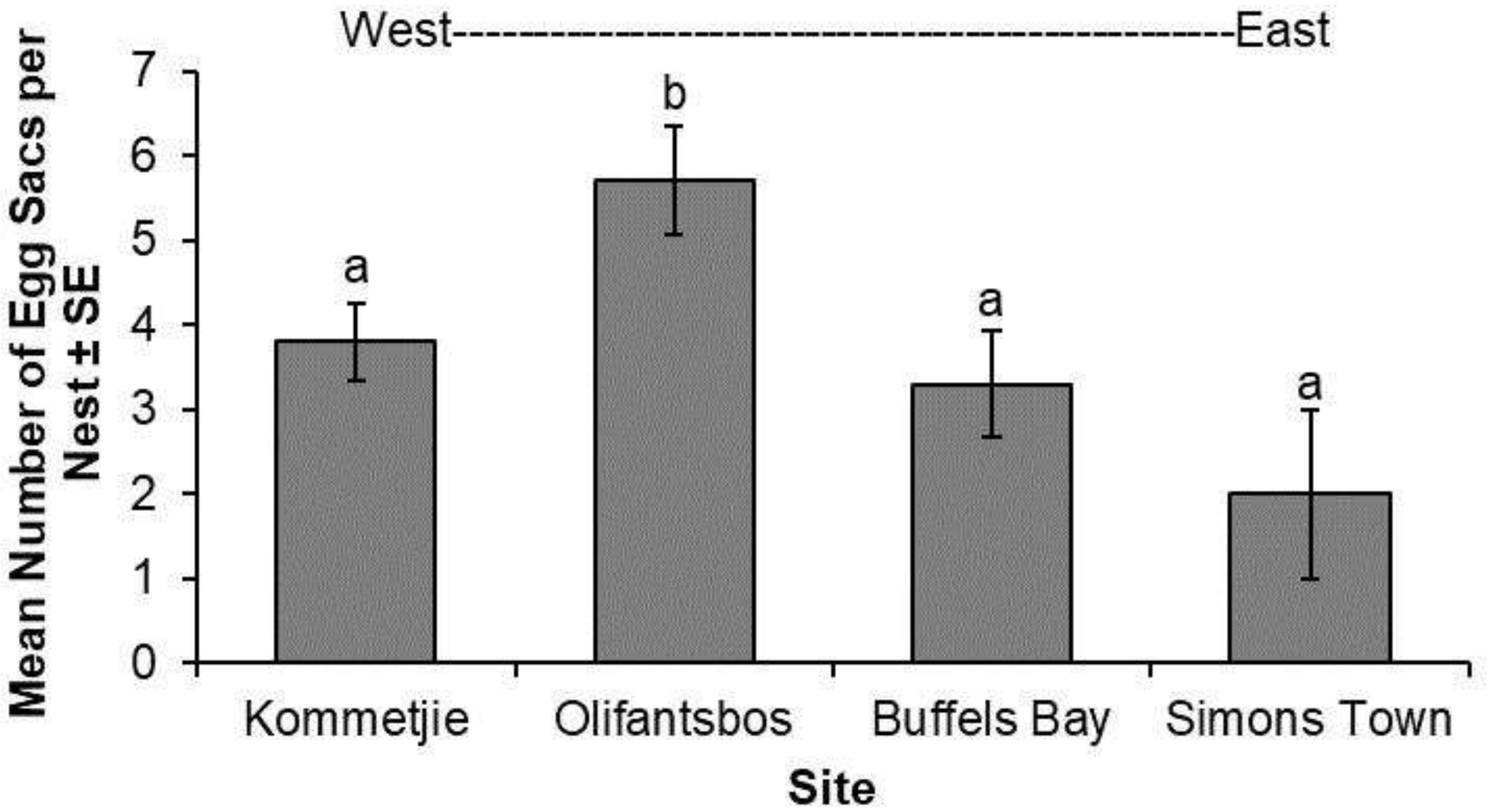

A
B
C
D

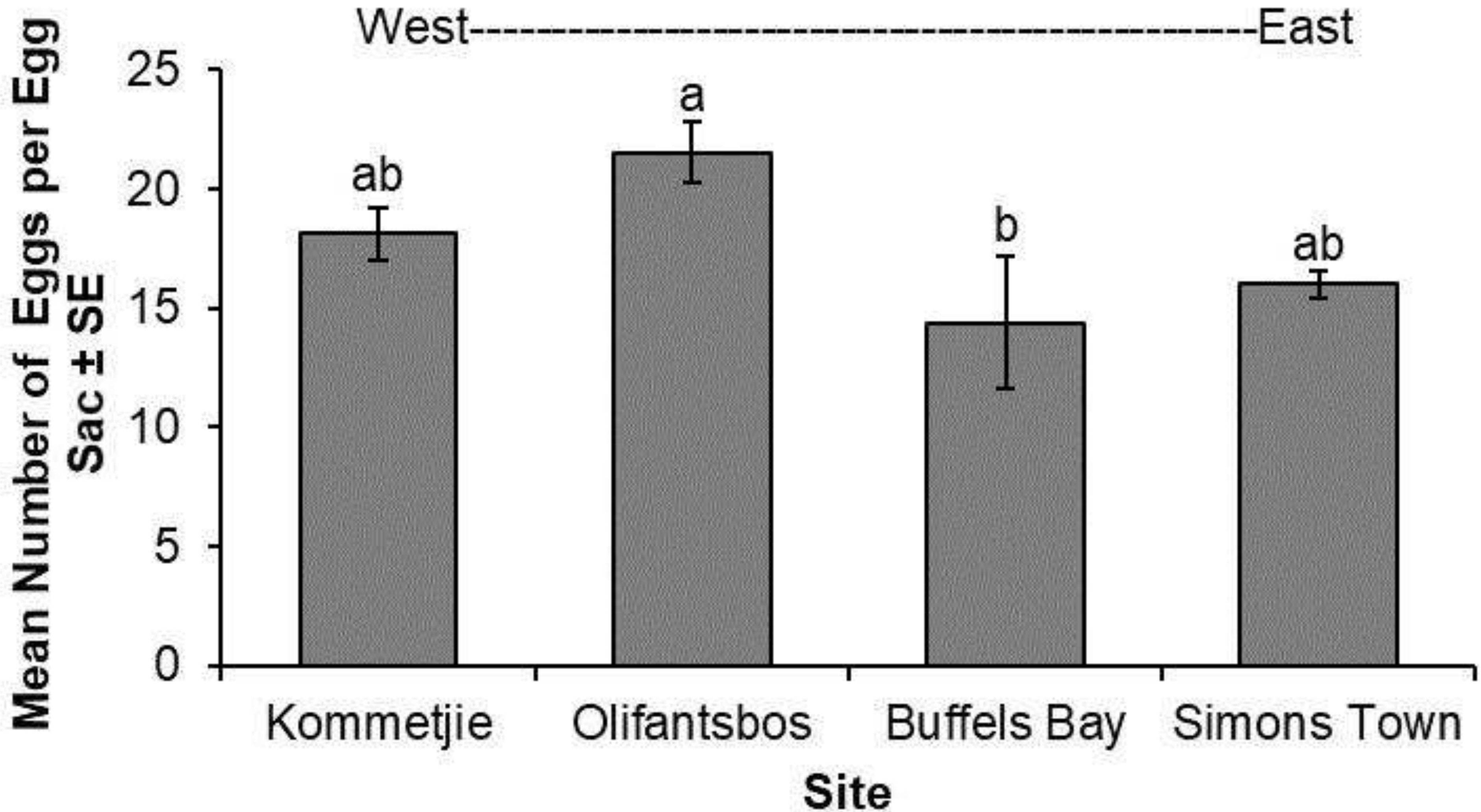


Mean Number of Nests Collected ± SE
4
3.5
3
2.5
2
1.5
1
0.5
0
a
a
b
Sublittoral Fringe (Zone A)
Eulittoral Range (Zone B)
Littoral Fringe (Zone C)
Zone
A
West--East
Mean Number of Nests Collected ± SE
5
4.5
4
3.5
3
2.5
2
1.5
1
0.5
0
a
a
b
c
Kommetjie
Olifantsbos
Buffels Bay
Simons Town
Site
B

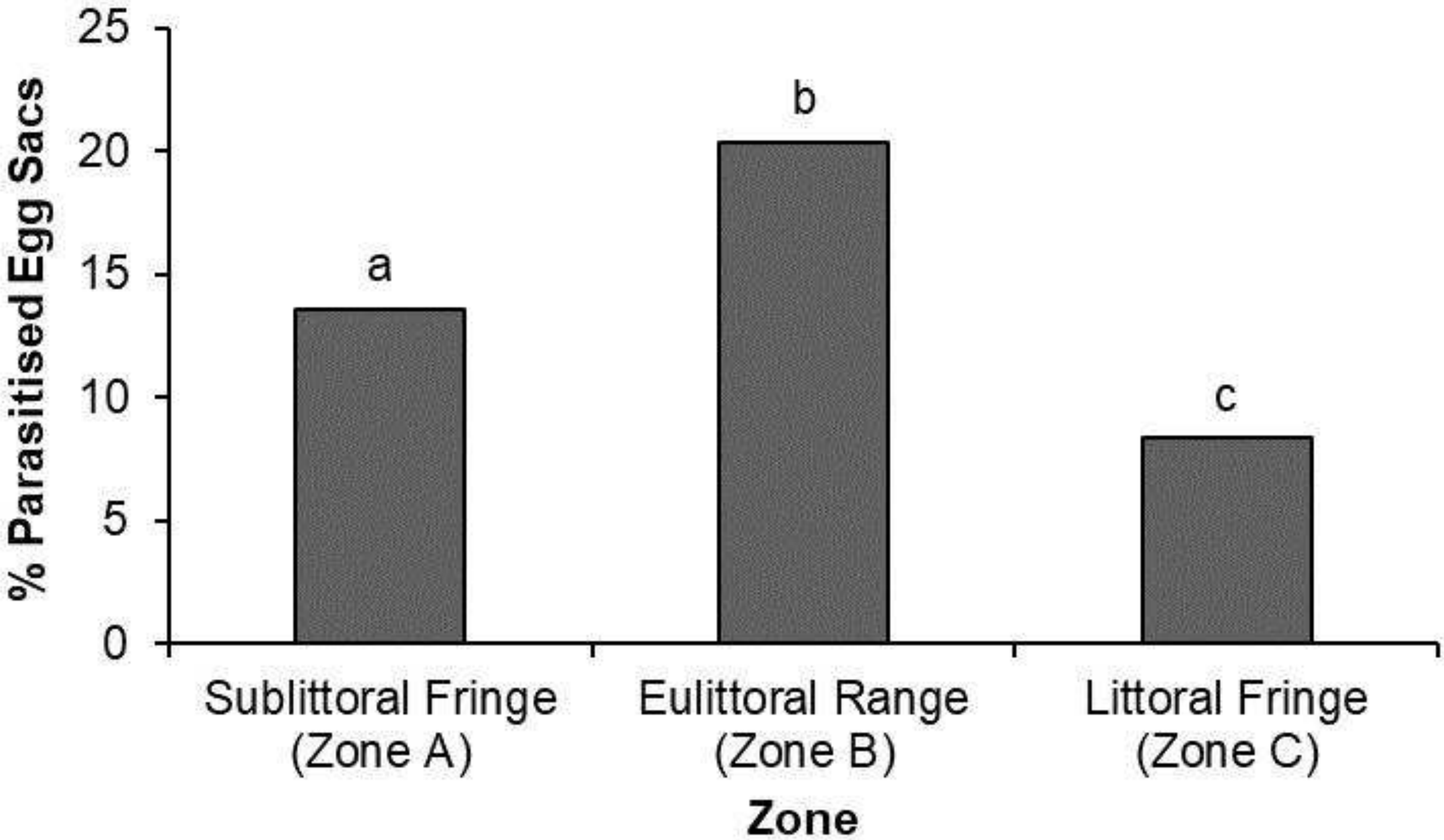


West--East
Mean Number of Egg Sacs per Nest ± SE
7
6
5
4
3
2
1
0
a
b
a
a
Kommetjie
Olifantsbos
Buffels Bay
Simons Town
Site

Wasp hole
Intact
9%
91%
A
Putrefied
Mouldy
Brown Unhatched
Fresh
Hatched
4%
13%
16%
15%
52%
B
No contents 42%
Eggs 33%
Spiders 21%
Wasps 4%
D
Dead
Live
12%
88%
C
Fresh
Mouldy
Older
38%
60%
2%



West--East
Mean Number of Eggs per Egg Sac ± SE
25
20
15
10
5
0
ab
a
b
ab
Kommetjie
Olifantsbos
Buffels Bay
Simons Town
Site


% Parasitised Egg Sacs
25
20
15
10
5
0
a
b
c
Sublittoral Fringe (Zone A)
Eulittoral Range (Zone B)
Littoral Fringe (Zone C)
Zone