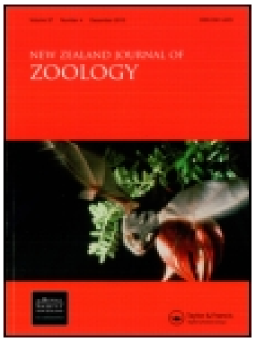

New Zealand Journal of Zoology

ISSN: 0301-4223 (Print) 1175-8821 (Online) Journal homepage: http://www.tandfonline.com/loi/tnzz20

Evidence for the displacement of an endemic New Zealand spider, Latrodectus katipo Powell by the South African species Steatoda capensis Hann (Araneae: Theridiidae)

S.W. Hann

To cite this article: S.W. Hann (1990) Evidence for the displacement of an endemic New Zealand spider, Latrodectus katipo Powell by the South African species Steatoda capensis Hann (Araneae: Theridiidae), New Zealand Journal of Zoology, 17:3, 295-307, DOI: 10.1080/03014223.1990.10422937

To link to this article: http://dx.doi.org/10.1080/03014223.1990.10422937

New Zealand Journal of Zoology, 1990, Vol. 17: 295–307
0301–4223/90/1703–0295$2.50/0 © Crown copyright 1990

Evidence for the displacement of an endemic New Zealand spider, *Latrodectus katipo* Powell by the South African species *Steatoda capensis* Hann (Araneae: Theridiidae)

S. W. HANN
Brooklyn RD3,
Motueka, Nelson, New Zealand

Abstract The competitive interactions between *Latrodectus katipo* and *Steatoda capensis* were studied under the hypothesis that *L. katipo* is being displaced from its natural habitat by competition from *S. capensis*. Use of trophic and spatial resources were studied. High overlap for both resources was found. Data on reproductive potential revealed that *S. capenisis* has a significantly higher reproductive output. Laboratory predation experiments indicated *L. katipo* adults are not inferior to *S. capensis*. Evidence suggesting displacement following *L. katipo* population crashes was obtained. Differences in reproductive potential and seasonal reproduction are proposed as the mechanism underlying the displacement.

Keywords *Latrodectus katipo; Steatoda capensis*; competition; reproductive potential; displacement

INTRODUCTION

Latrodectus katipo Powell 1870 is a theridiid spider endemic to New Zealand and restricted to coastal regions, mainly at sandy beaches (Forster & Forster 1973).

A decline in the abundance of *L. katipo* in some lower North Island regions in the last 10–15 years has been noted by various sources. Dr G. W. Gibbs (Victoria University of Wellington – pers. comm) has reported that *L. katipo* was common up to the late 1970s in the Cook Strait coast between Pencarrow and Fitzroy Bay, but was not found in this area during a search in 1983. He has also reported that *L. katipo* was present at "Wharekauhau" beach (Palliser Bay) in the late 1970s. I have made two extensive searches of this beach in consecutive years (1983–1984) and failed to reveal one *L. katipo*. In each of these situations a species of *Steatoda* was abundant.

R. Ordish (National Museum, Wellington—pers. comm) has reported that there was a dense population of *L. katipo* at Hokio beach in 1970 but that by 1983 the species had become very scarce, with a species of *Steatoda* previously not seen at this beach outnumbering *L. katipo* by at least 50 :1.

D. Laing (119 Creswick Tce, Wellington—pers. comm) in searches conducted in 1984 and 1985 from Paekakariki to Waikanae found no *L. katipo*. He did, however, find limited numbers of *L. katipo* along the coast netween Himitangi and Tangimoana. A species of *Steatoda* was abundant in both these areas. Searches I conducted in 1989 at Baring Head, Waikanae, Paraparaumu, Hokio beach, and Pukepuke Lagoon beach had similar results, i.e., either there were no *L. katipo* present (as with the first two sites named) or there were very few *L. katipo* but abundant specimens of one *Steatoda* species.

I have identified the *Steatoda* species which is now so common along the Wellington coast as a South African species described by O. P. Cambridge (1903) as *Teutana lepida*, and have given this species the new name of *Steatoda capensis* for reasons outlined elsewhere (Hann 1990). Identification was made initially using the description given by Cambridge (1903), and was confirmed by examining both male and female specimens on loan from the South African Museum. Cambridge described specimens from Cape Town but apparently *S. capensis* is fairly widely distributed throughout South Africa and is frequently recorded in and around houses (Dr Dippenaar-Schoeman, Plant Protection Research Institute, Pretoria—pers. comm.). I have observed *S. capensis* along the coast and associated with houses in Nelson, Blenheim, Wellington, and New Plymouth, with a wide range of web sites

Z89063
Received 10 November 1989; 10 May 1990

including the base of rose bushes and under corrugated iron, wooden planks, and concrete bricks. Examination of a *Steatoda* collection belonging to the Plant Protection Centre (Ministry of Agriculture and Fisheries, Auckland) revealed *S. capensis* to be a common species in the Auckland region. It is also widespread on the coast of the East Cape.

The recent disappearance of *L. katipo* from areas where it used to be common and the abundance of *S. capensis* in these areas, suggests the hypothesis that *L. katipo* is competitively inferior to *S. capensis* and as a consequence is being displaced from its natural habitat.

The existence of interspecific competition in spiders has been questioned (Wise 1984) as a result of a number of researchers finding no significant interspecific competition in their studies of spider communities (Wise 1981; Horton & Wise 1983; Riechert & Cady 1983). Alternatively, Brown (1981) concluded there was inferential evidence of interspecific competition among orb weavers and Spiller (1984) found interspecific competition between spiders was significant and appeared to play an important role in structuring their community. Nyffeler et al. (1986), in a study similar to the present one, concluded that competition was occurring between *Steatoda bipunctata* (Linnaeus) a European immigrant into North America, and *S. borealis* (Hentz) a native North American species, leading to the displacement of the latter. The two species are the same size, show a high level of micro-habitat and diel activity overlap, and both select the same prey species at the same rate (Nyffeler et al. 1986). Although Nyffeler et al. (1986) felt that displacement was occurring they were unable to identify the mechanism by which it was operating. *S. borealis* (the displaced species) actually appeared to be more likely to win an agonistic interaction with *S. bipunctata* in screen-cage laboratory experiments and *S. bipunctata* appeared to have no advantages in its reproductive potential or seasonal life history (Nyffeler et al. 1986).

Spiller (1984) suggests predators or abiotic factors of mortality may have reduced spider abundance in some of the above studies, thus reducing competition. This suggestion is supported by Enders' explanation of the coexistence of two species of orb weavers (Enders 1974) and by Gertsch & Riecherts' explanation of the coexistence of congeneric species in the absence of niche partitioning (Gertsch & Riechert 1976). Other researchers (Uetz 1977; Turner & Polis 1979; Kessler et al. 1984) reported temporal, spatial, or trophic specialisation as means of reducing niche overlap between spider species. As pointed out by Colwell & Futuyma (1971), niche overlap values can be used as evidence for or against interspecific competition. Thus, the low overlap values of these researchers may be evidence of no competition or could equally well be the result of intense competition which lead to segregation along a resource dimension. However, niche overlap values are valuable as indicators of the degree to which the species examined jointly use a resource.

The following study examines the assumptions that interspecific competition does occur in spiders, and that the distribution of one species may be limited by the presence of another species through competition (Krebs 1978). The study involved: (1) assessing species distribution patterns in relation to habitat and to each other; (2) assessing spatial and trophic niche overlaps; (3) a small population manipulation experiment; (4) assessing reproductive potential; and (5) conducting laboratory predation experiments.

STUDY SITE

The study site is an area of sand dune beach (173°02′E, 41°06′S lat) in Motueka, (Nelson, New Zealand), in the form of a flat spit bounded by the sea and tidal mudflats. In 1984 it was clearly divided into: a densely vegetated zone (habitat A)made up mainly of tree lupin (*Lupinus arboreus*) with marram grass (*Ammophilia arenaria*) on the outer edges of the lupin and large patches of iceplant (*Carpobrotus edulis*) among the lupin; and a sparsely vegetated zone (habitat B) made up of clumps of marram grass and isolated tree lupin plants. Habitat A extended approximately 274 m along the study area, with habitat B comprising the last 140 m. In subsequent years, the lupin and marram spread throughout habitat B and by 1987 there was no clear separation of the habitats.

METHODS

Logs occupied by *L. katipo* or *S. capensis* were located by a systematic search of the study area. All logs and areas of congregated small driftwood in the study area were searched as were areas of iceplant and marram grass. For each occupied site, i.e., isolated log or clump of marram, the number of spider occupants and their species was recorded. To determine species habitat distribution pattern, the spider's location was recorded as either habitat A or habitat B. χ^2 analysis was used to determine whether

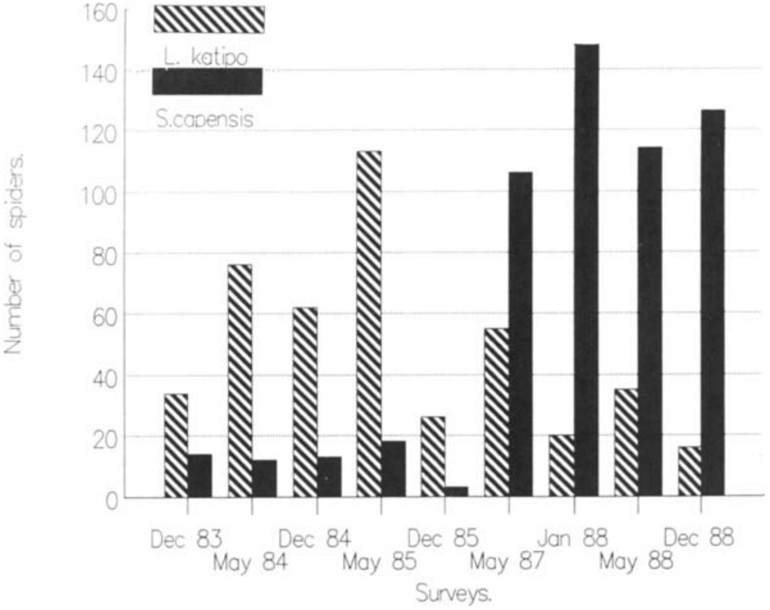

Fig. 1 Changing abundance of species over time (Habitat A).

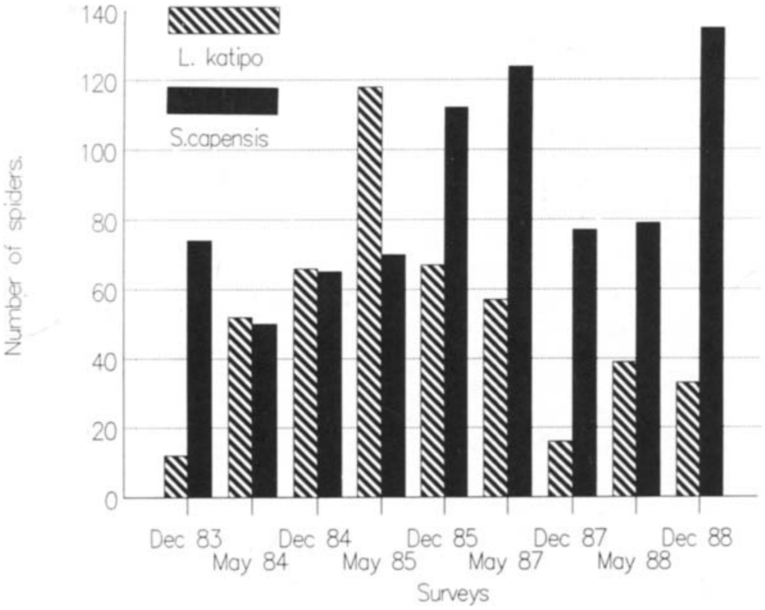

Fig. 2 Changing abundance of species over time (Habitat B).

the two species were distributed independently of habitat. A coefficient of association *V* was calculated for each species, where *V* varies from –1 (negative association) to +1 (positive association) and is 0 when there is no association (Krebs 1978).

Two methods were used to investigate distribution of *L. katipo* in relation to *S. capensis*. The first involved recording the presence/absence of each species at each site. Data were analysed using Sorensen's test which gives a value from 0–1, 0 indicating no association and 1 indicating perfect association, i.e., where one species occurs the other will always occur. The second method involved recording the species of the nearest neighbour for each spider. χ^2 analysis was used to indicate whether the number of times one species was the nearest neighbour of the other was different from that expected assuming random distribution. A measure of segregation *S* (Pielou 1961) was calculated, where *S* varies from –1 (negative segregation, i.e., the nearest neighbour is always the other species), to +1 (positive segregation i.e., the nearest neighbour is always a conspecific), and 0 if the two species are mixed.

Data were gathered on the spiders' use of spatial and trophic resources. Web presence in marram was recorded, whereas size (surface area) of inhabited logs was recorded and logs grouped into four size categories: <1200 cm^2, 1200–2400 cm^2, 2400–3600 cm^2, and >3600 cm^2. These data were analysed to see if species had preferred web sites and if they overlapped in this resource component.

Nine surveys were conducted spanning 5 years. The month and year of each survey are given in Fig. 1 and 2. In survey 1, food use was determined by collection of prey from webs of a randomly selected sample of spiders (35% total population). All webs were collected and examined for the presence of food items and rebuilt webs were collected at the end of each of the following 2 weeks. In survey 3, old webs were collected from all sites still occupied (some spiders had left their webs since the initial observation), this being 83% of *L. katipo* webs and 75% of *S. capensis* webs. All rebuilt webs were collected 3 weeks later as part of survey 3. Availability of prey in each habitat was estimated in 1984 by pitfall trapping, which also provided intact specimens for identification of prey taken from webs. A χ^2 test for heterogeneity was conducted on pitfall-trap data to establish whether different prey species were available in the two habitats. χ^2 tests were also carried out where possible to test for differences between the two species in their use of prey within habitats.

Niche overlap values were calculated from data on the spiders' use of four resource dimensions, namely habitat used, food species habitat A, food species habitat B, and web site preference. The equation used to calculate unidimensional niche overlap was

$$\text{alpha jk} = \frac{\sum \text{pij} \cdot \text{Pik}}{\sqrt{\sum \text{pij}^2 \cdot \sum \text{Pik}^2}}$$

where Pij and Pik represent the proportions of the ith resource used by the j and k th species (Pianka 1974).

At the end of survey 1, a population manipulation experiment was begun. This involved releasing 12 *L. katipo* among the resident *S. capensis* in habitat B and 24 *S. capensis* among the resident *L. katipo* in habitat A. The introduced spiders were monitored for 3 weeks after release. All spiders were introduced into an area where conspecifics were scarce (i.e., <3 conspecifics within 10 m of the release site) so marking was not considered necessary.

In surveys 6–9 the number of egg sacs per spider and the number of immatures and males were recorded.

Laboratory predation experiments were conducted in 1984. These involved placing one *L. katipo* and one *S. capensis* female into a wooden enclosure measuring 200 mm long × 150 mm wide × 15 mm deep, with a 10 mm lip under which the spiders could live, a removable median partition, and a glass top. Spiders were weighed before the experiment using a Mettler H10 to ±0.0005 g with paired spiders matched on weight equality. At the start of a trial the two spiders were set into the enclosure one either side of the partition. After webs were established the partition was removed. A trial was judged complete either when one spider was killed or died naturally.

RESULTS

Distribution

Distribution of spiders between the two habitats is shown in Fig. 1 and 2.

Table 1 Habitat overlap values.

Survey								
1	2	3	4	5	6	7	8	9
0.49	0.74	0.85	0.87	0.94	1.0	0.98	0.97	0.95

The salient features are: (1) the distribution of *L. katipo* between habitat A and B has changed from being predominantly habitat A at Survey 1 (73.9%) to an even distribution by surveys 3–4 and 6–9. By survey 5, *L. katipo* numbers in habitat A decreased dramatically due to severe storm damage; (2) *S. capensis* distribution has changed from predominantly habitat B (90–97%) in surveys 1–5, to a more even distribution in surveys 6–9; (3) *L. katipo* numbers increase during summer with a maximum in late autumn (May), followed by a decrease over winter; whereas (4) in general, *S. capensis* numbers are greatest in mid-summer (December) and decrease slightly through the autumn; and (5) *L. katipo* dominated all surveys except one up to 1985, whereas *S. capensis* dominated at all surveys after May 1987.

Habitat association

The habitat overlap values indicate a high degree of overlap for all surveys except survey 1 (Table 1). These results reflect the fact that *L. katipo* spread into habitat B after survey 1 and *S. capensis* spread into habitat A after survey 5.

The χ^2 analysis of habitat association indicates that for surveys 1–5 *L. katipo* occurred more often in habitat A and less often in habitat B than expected if one assumed a random distribution across habitats (Table 2). The coefficients of association all indicate negative association with habitat B.

Conversely, in surveys 1–5, *S. capensis* occurred more often in habitat B and less often in habitat A than expected and the *V* values indicate positive association with habitat B (Table 2). However, the situation changes in surveys 6–9 when both species occur as often as expected in each habitat given random distribution. All *V* values for both species for surveys 6–9 indicate no association with either habitat, i.e., *V* values all approach zero. This change is mainly because before survey 6 *S. capensis* was found almost exclusively in habitat B, but in surveys 6–9 it is also found throughout habitat A. *L. katipo* distribution had already spread over the two habitats by survey 3.

Species association at web sites

All Sorensen values for species association at web sites were low (Table 3) indicating *L. katipo* and *S. capensis* rarely occur at the same site.

The two species occur together at only 5.80% of all sites observed over the nine surveys. This result may be because of the spiders' tendency to occur alone (*L. katipo* in particular—Table 4) or it may reflect interspecies avoidance. As Table 4 shows, *L. katipo* normally occurs alone whereas *S. capensis* occurs mainly alone or with one or more conspecific, i.e., least often with *L. katipo*.

Analysis of nearest neighbour data revealed *L. katipo* and *S. capensis* were associated in a significantly non-random manner (Table 5), with the measures of segregation indicating positive segregation, i.e., the nearest neighbour is usually a member of the same species.

These results support the idea that the two species avoid each other.

Web site

Analysis of web site data revealed that both species used the two smaller classes of log most often. Use by *L. katipo* varied from 91.3% of spiders at survey

Table 2 Results of χ^2 analysis of habitat association data. Coefficients are *V* values and indicate the degree of association of the species with habitat B.

	L. katipo			*S. capensis*		
Survey	Coeff. assoc.	χ^2	*P*	Coeff. assoc.	χ^2	*P*
1	–0.56	33.58	<0.00001	+0.57	35.35	<0.00001
2	–0.36	21.42	0.00001	+0.40	26.91	<0.00001
3	–0.30	15.64	0.00008	+0.41	29.24	<0.00001
4	–0.22	11.33	0.0008	+0.27	16.47	0.00005
5	–0.29	11.40	0.0008	+0.37	19.20	0.00001
6	–0.04	0.51	0.48 NS	+0.06	0.93	0.33 NS
7	+0.07	1.32	0.25 NS	–0.05	0.04	0.84 NS
8	+0.15	5.06	0.024 NS	–0.10	2.29	0.13 NS
9	+0.10	2.89	0.089 NS	–0.12	3.6	0.058 NS

Table 3 Results of analysis of species association at sites.

	Survey								
	1	2	3	4	5	6	7	8	9
Sorensen's value	0.10	0.07	0.13	0.23	0.18	0.14	0.03	0.10	0.008

N.B. Values of 0 indicate no association i.e., the two species never occur together. Values of 1 indicate complete association i.e., the two species always occur together

Table 4 Percentages of each species population occurring alone, with conspecifics or with other species at a site (i.e., isolated log or clump of marram).

	L. katipo			*S. capensis*		
Survey	Alone	+Consp.	+*S. capensis*	Alone	+Consp.	+*L.katipo*
1	89.1	0	10.9	54.5	37.5	8.0
2	84.4	6.2	9.4	61.3	21.0	17.7
3	83.6	6.3	10.1	56.4	21.8	21.8
4	55.0	27.7	17.3	40.9	12.5	46.6
5	78.5	6.4	15.1	22.6	57.4	20.0
6	62.5	17.0	20.5	64.4	25.6	10.0
7	91.7	0	8.3	69.7	28.1	2.2
8	63.5	18.9	17.6	72.5	19.7	7.8
9	98.0	0	2.0	61.3	38.3	0.4

Table 5 Results of nearest neighbour analysis. *S* values are measures of segregation and vary from –1 (the NN is always the other species) to +1 (the NN is always a conspecific).

	Survey							
	1	3	4	5	6	7	8	9
χ^2	38.6	12.7	11.8	30.8	27.2	5.2	14.0	6.4
Measure of segregation	+0.55	+0.25	+0.19	+0.38	+0.28	+0.10	+0.23	+0.14

Note: All χ^2 values significant at $P < 0.001$, except for survey 7 and 9 where P is between 0.025 and 0.01.

Table 6 Web site overlap values.

Survey								
1	2	3	4	5	6	7	8	9
0.77	–	0.76	0.96	–	0.97	0.98	0.99	0.99

Table 7 Percentage of each species using marram or small logs in surveys 4 and 6.

	Web site	*L. katipo*	*S. capensis*
Survey 4	Small logs*	54.5%	67.0%
	Marram	42.0%	31.8%
Survey 6	Small logs*	54.6 %	60.9%
	Marram	36.6%	24.8%

*Small logs indicates < 1200 cm^2 and 1200–2400 cm^2 categories.

1 to 54.5% at survey 4, whereas *S. capensis* use varied from 53.8% at survey 1 to 85.5% at survey 7. This accounts for the high overlap values gained for web site use (Table 6).

Use of marram grass for web sites was normally low, i.e., less than 15% of sites used by both species in surveys 1–3 and 7–9, but during surveys 4 and 6 when the total spider population was over 300 the percentage of spiders using marram increased notably (Table 7). Smith (1971) found 89% of 187 *L. katipo* in marram grass at South Brighton beach in Christchurch, and the other 11% mainly in Pingao (*Desmoschoenus spiralis*). However, as Smith (1971) points out, *L. katipo* at this beach did not have the opportunity to inhabit driftwood which is removed by inhabitants of New Brighton.

Table 8 Pit-fall trap data from 155 pit-fall traps and actual prey data for surveys 1 and 3.

	Potential prey (Pit-fall trap data)		**Actual prey**			
Prey			*L. katipo*		*S. capensis*	
Order/species:	Habitat A	B	A	B	A	B
ISOPODA						
Talorchestia quoyana	79.98	74.75	36.11	70.26	33.33	72.76
COLEOPTERA						
Cecyropa lucunda	5.53	4.32	43.01	16.92	33.33	9.70
Mimopeus elongatus	NA	NA	8.63	0.51	11.76	NA
Ceratognathus irroratus	NA	NA	1.26	2.22	NA	3.36
Costelytra zealandica	NA	NA	0.94	1.54	1.96	1.49
Pericoptus truncatus	NA	NA	0.47	0.34	NA	NA
P. truncatus larvae	<.01	0.10	0.94	0.34	NA	NA
Xyloteles griseus	1.00	0.10	0.63	NA	NA	NA
Thelyphassa diaphana	1.28	1.08	0.31	0.85	1.96	4.85
Cafius quadri–impressus	NA	NA	0.16	0.17	1.96	NA
Lagrioda brouni	1.06	3.53	0.16	1.71	NA	NA
Laemostenus complanatus	0.44	NA	0.16	NA	NA	NA
Conoderus exsul	NA	NA	NA	NA	7.84	1.49
Prionoplus reticularis	NA	NA	NA	0.17	NA	NA
DERMAPTERA						
Forficula sp.	1.40	0.10	3.92	0.17	3.92	NA
Anisolabis littorea	NA	NA	0.16	NA	NA	NA
HYMENOPTERA						
Apis mellifera	NA	NA	0.78	0.34	1.96	1.12
Vespula germanica	NA	NA	NA	NA	NA	0.37
HEMIPTERA						
Hahnia australis	NA	NA	1.10	NA	NA	NA
LEPIDOPTERA						
Uresipheta polygonalis#	0.73	0.98	0.47	NA	NA	NA
Agrotis ipsilon aneituma	0.28	0.69	0.16	0.34	NA	1.87
A. i. aneituma larvae	NA	NA	0.31	2.91	NA	0.37
ARANEAE						
Dolomedes minor	0.39	NA	NA	0.51	1.96	NA
Dysdera crocata	<.01	NA	0.16	NA	NA	0.37
Amaurobid unidentified	NA	NA	0.16	NA	NA	NA
Lycosid unidentified	0.44	1.47	NA	0.17	NA	NA
Theridiid unidentified	NA	NA	NA	0.51	NA	2.23
Non–prey species	8.28	12.87				
ACTUAL NUMBERS	1789	1018	708	608	86	342

#U. polygonalis larvae

NA = Not Applicable, meaning never observed.

Note: data from the first "old webs" collected at survey 1 are not included in the table as this early data was not kept seperate by habitat. This data is given in Hann (1984).

This increased use of marram during times of high population suggests a limited number of suitable log sites. During survey 9 there was an abundance of small driftwood and the number of spiders using marram grass was again low, even though the spider population was over 300.

Prey

All pitfall trap items are listed in Table 8 along with actual prey for surveys 1 and 3. χ^2 analysis of pitfall trap data for items which contributed greater than 1.0% of either species diet revealed a significant difference in prey available in the two habitats ($\chi^2 = 41.7, P < 0.001$). The main contributors to the difference were *Lagrioda brouni* and *Forficula* sp. Web analysis supports this conclusion and also shows that *Cecyropa lucunda* and *Mimopeus elongatus* were much more common prey items in habitat A than habitat B. This difference makes separate analysis of web contents necessary for the two habitats.

Analysis of web contents revealed these spiders to be euryphagous predators. From the 2048 prey items collected overall there were 30 taxonomic groups. The major prey items were *Talorchestia quoyana* (51.72% survey 1, 55.32% survey 3) and *C. lucunda* (23.15% survey 1, 27.0% survey 3). A detailed breakdown of web contents for survey 1 is given in Hann (1984).

For habitat A the two species use of five prey species (*T. quoyana, C. lucunda, Forficula* sp., *M. elongatus*, and *Ceratognathus irroratus*) was χ^2 tested using data from survey 3 and "rebuilt web" data from survey 1. These five species combined represent 93% and 86% of the diet of *L. katipo* and *S. capensis*, respectively, in habitat A. The results indicate prey use is significantly different from expected ($\chi^2 = 12.5, 0.005 < P < 0.01$) reflecting that *L. katipo* eat proportionally more *C. lucunda* and less *T. quoyana* than expected, whereas *S. capensis* does the reverse.

For habitat B the two species use of six prey species (*T. quoyana, C. lucunda, C. irroratus, Agrotis ipsilon aneituma* larvae, *Thelyphassa diaphana*, and *Costelytra zealandica*) were χ^2 tested. These six prey species combined represent 94% and 89% of the diet of *L. katipo* and *S. capensis*, respectively, in habitat B. The result indicates prey use is significantly different from expected ($\chi^2 = 23.4, P < 0.001$) reflecting the fact that *L. katipo* eat proportionally more *C. lucunda* and less *T. diaphana* than expected, whereas *S. capensis* does the reverse.

Overlap values indicate a high degree of prey-use overlap.

Population manipulation

The introduction of 24 *S. capensis* to habitat A had no apparent effect. None of the released spiders could be found 3 weeks after release and *S. capensis* numbers at the next survey were not higher as might have been expected. The 12 *L. katipo* released in habitat B were all located after release, 10 of them occupying small logs. At the end of 3 weeks nine were still present, one having been eaten by another *L. katipo* and two disappearing after a spring tide flooded their logs. As the *L. katipo* numbers increased dramatically in habitat B by survey 2 it seems likely that most of the remaining *L. katipo* introductions survived and reproduced.

Predation experiments

Of 28 trials which yielded results, *L. katipo* killed *S. capensis* in 19 trials whereas *S. capensis* killed *L. katipo* in 9 trials. These results indicate that an adult female *L. katipo* is more likely to win an agonistic interaction with an adult female *S. capensis* ($z = 1.89$, $P = 0.0588$) There was no significant difference between the weight of the surviving spiders (mean = 0.1017 g, =0.0284 g) and those that were killed (mean =0.1044 g, SD = 0.0345 g; $t = 0.31, P > 0.10$)

Reproductive potential

The ability to produce offspring may provide an advantage to one species or the other (Nyffeler et al. 1986). Although Nyffeler et al. (1986) found that *S. bipunctata* and *S. borealis* have a very similar life history and sexual behaviour, the present study indicates two major and important differences in reproductive biology between *L. katipo* and *S. capensis*. Firstly *S. capensis* egg sacs contain, on average, a little less than three times the number of eggs that *L. katipo* sacs contain (Table 10). However, as *S. capensis* spiderlings emerge from the sac as first instars, their mortality rate may be much higher than that of *L. katipo* spiderlings, which emerge as larger second instars.

Table 9 Overlap values for prey use.

	Habitat A	Habitat B
Survey 1	0.68	0.93
Survey 3	0.92	0.96

Secondly, *S. capensis* reproductive output during winter is much higher than that of *L. katipo* (Table 11). During winter the mean number of egg sacs per spider is significantly greater for *S. capensis* and the proportion of the *S. capensis* population with egg sacs is much higher. Although the mean number of egg sacs per spider is greater for *L. katipo* in the summer surveys this point is overshadowed at surveys 7 and 9 by the fact that for each reproductive *L. katipo* there are at least five reproductive *S. capensis*, thus the total output is in favour of *S. capensis*. The mean number of egg sacs per spider has increased significantly for *S. capensis* from survey 3 to survey 7 ($z = 3.28, P = 0.001$)

S. capensis immatures and males were more abundant than for *L. katipo* at all times of year (Table 12). The majority of the *S. capensis* immatures observed at these surveys occurred at web sites occupied by *S. capensis* adults (i.e., 60% immatures seen with adults at survey 6, 87.9% at survey 7, 67.5% at survey 8, and 96.1% at survey 9) The small number of *L. katipo* immatures makes identifying a similar trend difficult.

DISCUSSION

What caused the initial division of species over habitats? The preference of *L. katipo* for habitat A may be linked to its preference for *C. lucunda* which occurs more commonly in the dense lupin area. Spiders are known to respond to such variations in habitat quality, e.g., Riechert & Tracy (1975) found choice of web site in *Agelenopsis aperta* was influenced by temperature and the presence/absence of ground depressions. The absence of *S. capensis* from habitat A cannot be attributed to choice of habitat B as preferred habitat because by survey 6 *S. capensis* has become abundant in habitat A with no change in the characteristics of this habitat. It is possible that the dominance of *L. katipo* in habitat A at surveys 2–4 prevented expansion of *S. capensis* into this area.

Table 10 Eggsac data from field collected sacs.

	Number of sacs	Mean No. of eggs/sac	Standard deviation	Range
S. capensis	37	183.6	53.9	92–309
L. katipo	23	68.3	21.0	34–115

Note: As the sacs were field collected it is not known whether each sac represents the 1 st, 2nd, or 3rd egg sac produced by the spider for that summer. The mean is thus a mean for all egg sacs.

Why did the distributions change?

There are two possible causes for the increase of *L. katipo* in habitat B from survey 1 to survey 4: (1) the 12 introduced *L. katipo* from the population manipulation experiment gave *L. katipo* a more stable breeding population or (2) the increase of *L. katipo* was a consequence of the spread of the dense lupin into and right through habitat B. *L. katipo* also increased in habitat A over this period but from Fig. 1 it can be seen that this is part of a seasonal fluctuation pattern.

The distribution of *S. capensis* remained stable until survey 6 which was conducted 17 months after habitat A was destroyed by a combination of severe storms and high tides. These storms in late 1985 caused lupin to die off, flattened the marram grass and swept away driftwood. The *L. katipo* population declined from 113 in May 1985 to 26 in December 1985. While a seasonal decline over this period is expected the decline was magnified by the destruction of habitat. This conclusion is supported by the fact that in habitat B *L. katipo* only declined from 118 to 67. Seventeen months later, in May 1987, *L. katipo* numbers have increased but to nowhere near the level of May 1985, whereas *S. capensis* numbers had exploded from 18 (May 1985) to 106 (May 1987). This population explosion following the reduction of *L. katipo* numbers supports the idea that *S. capensis* was previously limited to habitat B by the dominance of *L. katipo* in habitat A. In the months after the storms of late 1985 there would have been many vacant potential web sites into which *S. capensis* could migrate either from habitat B or more likely from the fields behind habitat A, without encountering interference from *L. katipo*. It seems more likely that migration of *S. capensis* into such vacant sites lead to the establishment of this species in habitat A by May 1987 rather than direct displacement of *L. katipo* adults from web sites by *S. capensis* adults. The latter is unlikely for a number of reasons: (1) an established species has a competitive advantage over an immigrating species (Riechert & Cady 1985); (2) *L. katipo* consumes other spiders so the probability of a web takeover by another spider species is probably low (Riechert & Cady 1983); and (3) laboratory trials have shown that an adult *L. katipo* is more likely to kill an adult *S. capensis* than be killed in a conflict at a web site (Hann 1984).

Are limited resources causing interspecific competition?

By survey 6 the two species show total overlap in habitat use and the question arises of whether they can coexist in this distribution or will interspecific competition lead to the displacement of one species.

The two species show a high degree of overlap in all resource dimensions examined. The overlap values for prey use were particularly high. The proportion of each species diet which appeared as exclusive to that species was very small, and given further data would probably disappear altogether. However, there is no evidence that prey is a limited resource so even though the diet of the two species overlap almost completely this should not be used as an indication of interspecific competition (Riechert & Cady 1983). Also the fact that the two species show significant differences in the proportions in which they consume certain prey species would suggest that coexistence is possible in this resource dimension. High overlap values were obtained for preferred web site. Both species appeared to prefer to build webs under the smaller-sized logs. One difference which did separate the two species was that *S. capensis* would occupy logs located among damp depressions which *L. katipo* appeared to avoid. This last observation supports Forster's hypothesis (1984) that *Latrodectus* species prefer habitats of low relative humidity. However, even with *S. capensis* using these damp sites there is a finite and relatively small number of suitable logs or suitable marram sites. Webs were only located in older dense marram clumps and most of the marram was young and open. Smith's (1971) observations also indicate *L. katipo* prefer medium to dense marram. Thus, although prey may not be limiting it seems likely that availability of suitable log sites will be a limiting factor. Riechert & Cady (1983) found space affording suitable characteristics for web construction to be limiting to spiders in their study. That log sites are limited is supported by the increase of use of marram grass during high total population numbers. Interspecific competition for web sites therefore seems likely. In interactions at web sites between *L. katipo* and *S. capensis* in laboratory trials, the most common result was the predation of *S. capensis* by *L. katipo* (Hann 1984). This was so for spiders showing no significant size (weight) difference; however, where *L. katipo* is likely to be disadvantaged by competition for web sites is in the establishment of immature spiders at web sites. Results show that *L. katipo* normally occurs alone whereas *S. capensis* is much more likely to tolerate the presence of conspecifics, with instances of four to six adult *S. capensis* occurring at one site, plus immatures. *S. capensis* and *L. katipo* adults, however, consistently showed no association at sites. In terms of immatures seeking web sites this suggests that *L. katipo* immatures would be rejected by both established *L. katipo* and *S. capensis* web owners, whereas *S. capensis* immatures are less likely to be rejected by established *S. capensis* web owners, resulting in a higher than usual mortality rate for *L. katipo* immatures. This theory is supported by immature numbers recorded during surveys 6–9

Table 11 Species egg sac production in summer (surveys 3, 7, and 9) and winter (surveys 6 and 8) showing the number of spiders with sacs, total number of egg sacs, the percentage of the population with egg sacs, and the mean number of egg sacs per spider.

Survey		Number spiders with sacs	Total sacs	% popn	Mean no. of sacs/spider	SD	z value	Signif. level
3	*L. katipo*	89	155	69.5	1.21	1.12		
	S. capensis	30	40	38.4	0.51	0.75	5.37	<0.0001
7	*L. katipo*	23	49	63.9	1.36	1.30		
	S. capensis	157	184	70.1	0.82	0.62	2.45	0.014
9	*L. katipo*	39	90	79.6	1.84	1.37		
	S. capensis	194	257	74.3	0.99	0.74	4.22	<0.0001
6	*L. katipo*	2	2	1.8	0.02	0.13		
	S. capensis	61	64	26.5	0.28	0.47	7.7	<0.0001
8	*L. katipo*	5	5	6.8	0.07	0.25		
	S. capensis	37	38	19.2	0.20	0.41	3.13	0.0018

Note: the mean number of egg sacs per spider was calculated from all observations i.e., including observations of zero.

which greatly favours *S. capensis* (Table 12). Spiller (1984) has shown that interspecific exploitative competition for a resource can become a limiting factor for a spider species. As well as being rejected from suitable web sites it is likely that many immature *L. katipo* are predated upon during their attempts to occupy web sites already occupied by *S. capensis* which have matured during the winter/spring months. Spiller (1984) found such interspecific interference significant between spiders which showed seasonal differences in size.

Is displacement of *L. katipo* occuring?

Since the destruction of habitat A in late 1985 and the consequent decimation of the *L. katipo* population, *S. capensis* appears to have undergone competitive release in this habitat. After conducting removal experiments Riechert & Cady (1983) sought three kinds of evidence for competitive release: (1) changes in densities of juveniles and adult spiders; (2) changes in level of egg production; and (3) shifts in microhabitat use. The first criterion is clearly satisfied for adults and juvenile densities have also increased (Table 12).

The second criterion also appears to be satisfied. The average number of egg sacs per spider for *S. capensis* has increased significantly from survey 3 to survey 7, as has the proportion of the *S. capensis* population producing egg sacs (Table 11). Comparing the same period the egg sac production for *L. katipo* has not changed significantly (Table 11).

As no food data was collected at survey 6 or survey 8 it is not possible to say whether *S. capensis* has changed its use in prey species, for example in increasing its consumption of *C. lucunda*. There has been no apparent change in web site use by *S. capensis* since survey 5. Thus, only two of the three forms of evidence for competitive release have been satisfied.

Competitive release of *S. capensis* following natural or accidental human-related reduction of the *L. katipo* population is one explanation for the colonisation of *L. katipo* habitat by *S. capensis*. The alternative is that *S. capensis* is a relatively recent introduction into New Zealand and it is only now reaching the *L. katipo* habitat where it is displacing *L. katipo* by direct competition. Although it seems likely that *S. capensis* is a recent immigrant, I do not believe it is displacing *L. katipo* by direct competition. Evidence suggests the former explanation is more likely.

Table 12 Comparison of numbers of immatures and males seen for each species at surveys 6–9.

Survey	6	7	8	9	6	7	8	9
	Number of immatures				Number of males			
L. katipo	2	9	4	5	4	4	1	1
S. capensis	85	33	126	26	40	6	39	15

After natural destruction of a segment of its habitat, *L. katipo* could recolonise in one of two ways, either by lateral migration of spiders from adjacent undamaged habitat, or by replacement with new spiders from summer reproduction. Given low *L. katipo* numbers either method is likely to be a slow process. Colonisation of the damaged habitat by *S. capensis* could be much more rapid, either by large-scale immigration of spiders from adjacent inland habitat where *S. capensis* occur with no competition from *L. katipo*, or by new spiders from reproduction by *S. capensis* already in the area. *S. capensis* continue to reproduce year round and produce significantly more eggs per sac than *L. katipo*, two features which would aid it in rapid colonisation of vacant habitat. If *S. capensis* can recolonise more quickly than *L. katipo* then it would gain the competitive advantage of being the established species and *L. katipo* immatures would find it difficult to locate free web sites. Given this situation it is likely that *L. katipo* would be permanently displaced from this area.

CONCLUSION

The displacement of *L. katipo* by *S. capensis* at the study site was triggered by a dramatic decline in the *L. katipo* population size after storm damage to the *L. katipo* habitat. Displacement at other sites, such as Hokio Beach (Wellington) may also have been triggered by natural acts or by human interference with the habitat. Nyffeler et al. (1986) found that the permanent displacement of *S. borealis* by *S. bipunctata* was restricted to those parts of the habitat range most influenced by human activity. L. Forster (100 Norfolk St, Dunedin—pers. comm.) has suggested that the lack of *L. katipo* along the Otaki-Wanganui coast may be related to the substantial modification of the sand dunes by construction of parking lots, barbeque areas, etc, and a consequent change in vegetation. The destruction or modification of habitat may lead to the habitat becoming totally unsuitable for the narrow-niched *L. katipo*, in which instance the effect of *S. capensis* would be irrelevant. However, if the habitat is not rendered entirely unsuitable for *L. katipo* then the population should slowly recover in the absence of *S. capensis*. In my view the presence of *S. capensis* can have a significant effect and lead to permanent displacement of *L. katipo* because *S. capensis* can colonise the newly vacant web sites faster than *L. katipo* can recolonise them. *S. capensis* can colonise a vacant habitat quickly because: (1) *S. capensis* immigrants are available from inland which is not true for *L. katipo*; (2) the reproductive rate of *S. capensis* is higher than that of *L. katipo*; and (3) *S. capensis* reproduce year round whereas *L. katipo* produce very few egg sacs in the winter months.

There is no evidence to suggest that adult *L. katipo* spiders are competitively inferior to adult *S. capensis* spiders; on the contrary, *L. katipo* adults appear to be superior in instances of direct agonistic interactions. Similarly, in limited laboratory trials Nyffeler et al. (1986) found *S. borealis* to be the consistent winner in antagonistic interactions against *S. bipunctata*, even though in the wild it is being displaced by *S. bipunctata*. Where *S. capensis* is likely to gain an advantage once it has become established is in competition for web sites between homeless immature *L. katipo* and web-occupying mature *S. capensis*. In this situation, the immature *L. katipo* would be inferior and be chased from the web site or predated. So, by its ability to rapidly colonise vacant habitat and become the dominant established species, *S. capensis* displaces *L. katipo* from its previous habitat.

As *S. capensis* is an introduced species this phenomenon may be relatively new, but combined with increasing human interference along coastal areas it is likely that *L. katipo* will continue to decline in areas in which it was once common, and finally be totally displaced by *S. capensis*.

ACKNOWLEDGMENTS

I would like to thank Dr G. W. Gibbs (School of Biological Science, Victoria University, Wellington) for his help in reading drafts of this paper and Shirley Pledger (Statistics and Operations Research, Victoria University, Wellington) for her help with statistical considerations.

REFERENCES

Brown, K. M. 1981: Foraging ecology and niche partitioning in orb weaving spiders. *Oecologia (Berlin) 50*: 380–385.

Cambridge, O. P. 1903: Descriptions of some new species, and characteristics of three new genera, of Araneidea from South Africa. *Annals of the South African Museum 5 (3)*: 143–166.

Colwell, R. K.; Futuyma, D. J. 1971: On the measurement of niche breadth and overlap. *Ecology 52*: 565–576.

Enders, F. 1974: Vertical stratification in orb-web spiders (Araneae, Araneidae) and a consideration of other methods of coexistence. *Ecology 55*: 317–328.

Forster, L. 1984: The Australian redback spider (*Latrodectus hasselti*): Its introduction and potential for establishment and distribution in New Zealand. *In*: Laird, M. *ed.*, Commerce and the spread of pest and disease vectors. New York, Praeger. pp. 274–289.

Forster, R. R.; Forster, L. M. 1973: New Zealand spiders: an introduction. Auckland, Collins.

Gertsch, W. J.; Riechert, S. E. 1976: The spatial and temporal partitioning of a desert spider community with descriptions of new species. *American Museum novitates 2604*: 1–25.

Hann, S. W. 1984: Competitive interactions between *Latrodectus katipo* Powell 1871 and two *Steatoda* species (Araneae: Theridiidae). Unpublished. B.Sc. Hons. Project, Victoria University of Wellington, New Zealand.

———1990: A new combination involving *Lithyphantes lepidus* Cambridge 1897 and a new name for *Teutana lepida* Cambridge 1903 (Araneae, Theridiidae) *New Zealand journal of zoology 17:* 283.

Horton, C. C.; Wise, D. H. 1983: The experimental analysis of competition between two syntopic species of orb-web spiders (Araneae, Araneidae). *Ecology 64 (4)*: 929–944.

Kessler, A.; Vermeulen, J. W. C.; Wapenaar, P. 1984: Partitioning of the space in tussocks of the sedge, *Carex distans*, during winter, by a spider community. *Journal of zoology, London 204*, 259–269.

Krebs, C. J. 1978: Ecology: the experimental analysis of distribution and abundance. 2nd edition. Harper & Row, U.S.A.

Nyffeler, M.; Dondale, C. D.; Redner, J. H. 1986: Evidence for displacement of a North American spider, *Steatoda borealis* (Hentz) by the European species *S. bipunctata* (Linnaeus) (Araneae: Theridiidae). *Canadian journal of zoology 64*: 867–874.

Pianka, E. R. 1974: Niche overlap and diffuse competition. *Proceedings of the National Academy of Sciences of the United States of America 71 (5)*: 2141–2145.

Pielou, E. C. 1961: Segregation and symmetry in two-species populations as studied by nearest neighbour relationships. *Journal of ecology 49*: 255–269.

Riechert, S. E.; Cady, A. B. 1983: Patterns of resource use and tests for competitive release in a spider community. *Ecology 64 (4)*: 899–913.

Riechert, S. E.; Tracy, C. R. 1975: Thermal balance and prey availability: bases for a model relating web-site characteristics to spider reproductive success. *Ecology 56*: 265–284.

Smith, D. J. 1971: The habitat and distribution of the katipo spider at South Brighton beach, Christchurch, New Zealand. *New Zealand entomologist 5*: 96–100.

Spiller, D. A. 1984: Competition between two spider species: experimental field study. *Ecology 65 (3)*: 909–919.

Turner, M.; Polis, G. A. 1979: Patterns of coexistence in a guild of raptorial spiders. *Journal of animal ecology 48*: 509–520.

Uetz, G. W. 1977: Coexistence in a guild of wandering spiders. *Journal of animal ecology 46*: 531–541.

Wise, D. H. 1981: Inter- and intraspecific effects of density manipulations upon females of two orb-weaving spiders (Araneae, Araneidae). *Oecologia (Berlin) 48*: 252–256.

————1984: The role of competition in spider communities. Insights from field experiments with a model organism. *In*: Strong, D. R.; Simberloff, D.; Abele, L. G.; Thistle, A. B. *ed*., Ecological communities: conceptual issues and evidence. Princeton, New Jersey. Princeton University Press. pp. 42–53.