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Evidence for displacement of a North American spider, *Steatoda borealis* (Hentz), by the European species *S. bipunctata* (Linnaeus) (Araneae: Theridiidae)

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The European spider *Steatoda bipunctata* has apparently been introduced into North America through human transport. The earliest American collections were made in Nova Scotia in 1913. Until about 1933, specimens were known only on the coast of the Atlantic provinces, Maine, and along the St. Lawrence River and Lake Ontario, but they are now found widely in the Atlantic Provinces, northernmost New England, and southern Québec and Ontario. Habitats include buildings, bridges, piles of lumber and firewood, and crevices on tree trunks or among rocks. Evidence indicates that *S. bipunctata*, which closely resembles the native *S. borealis* in size, colour, microhabitat, diel activity, prey selection and utilization, life history, and sexual behaviour, can displace *S. borealis*. Displacement is, however, only partial, as *S. borealis* persists in forest habitats, where human influence is minimal. Laboratory tests on reproductive potential and interspecific aggression failed to demonstrate the method by which displacement takes place.

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L'araignée européenne *Steatoda bipunctata* semble avoir été apportée en Amérique du Nord par des moyens de transport humains. Les premiers spécimens sont apparus en Nouvelle-Écosse en 1913. Jusqu'en 1933 environ, la répartition semble avoir été limitée aux côtes des provinces atlantiques et du Maine et le long du St-Laurent et du Lac Ontario, mais les araignées sont maintenant répandues partout dans les provinces maritimes, dans la partie nord de la Nouvelle-Angleterre ainsi que dans le sud du Québec et de l'Ontario. Elles se retrouvent dans les édifices, sur les ponts, dans les tas de bois de chauffage ou de bois de construction, les crevasses dans les troncs d'arbres ou les pierres. Il semble que *S. bipunctata*, qui s'apparente fortement à l'espèce indigène *S. borealis* par sa taille, sa coloration, son microhabitat, son activité journalière, son choix de proies et son utilisation des proies, son cycle biologique et son comportement sexuel, soit en mesure de remplacer *S. borealis*. Ce remplacement est cependant partiel, car *S. borealis* continue de vivre en forêt, où l'influence humaine est minimale. Les tests en laboratoire sur le potentiel reproducteur et sur l'agressivité interspécifique n'ont pas réussi à démontrer comment se fait le remplacement.

Introduction

Collections of spiders in North America commonly include representatives of 40 or more species that are regarded as introductions from abroad (Lindroth 1957). Some 25 of these are associated with houses, outbuildings, and greenhouses, and their principal means of transport is through human activity. Common examples of the latter group are the cross spider, *Araneus diadematus* Clerck, the zebra spider, *Salticus scenicus* (Clerck), the cellar spider, *Pholcus phalangioides* (Fuesslin), the cosmopolitan house spider, *Achaearanea tepidariorum* (C. L. Koch), and the European house spider, *Tegenaria domestica* (Clerck). All of these are well known in European buildings and, with the possible exception of *A. tepidariorum*, which may have come to both Europe and North America from the tropics (Bonnet 1935), probably originated there (Lindroth 1957; Gertsch 1979; Sacher 1983).

Among the presumed European immigrant spiders, though smaller and less conspicuous than those mentioned above, are four species of *Steatoda* (family Theridiidae), namely, *S. bipunctata* (Linnaeus), *S. grossa* (C. L. Koch), *S. triangulosa* (Walckenaer), and *S. castanea* (Clerck) (Levi 1957). It is *S. bipunctata* that particularly attracted our attention, for recent collections indicated that this spider could be found in areas not previously occupied, i.e., that it may be currently expanding its range in North America. Of even more interest was the close resemblance of this spider to a native North American relative, *S. borealis* (Hentz), in size, colour, and, more importantly, in

habitat requirements. The potential of displacement of the latter by the introduced species invited study.

Steatoda bipunctata is a small (6 or 7 mm long), short-legged web-building spider with a rounded, shiny black abdomen bearing white markings. Individuals build tangled webs over cracks in window or door frames, bricks and masonry, furniture, and outdoors on loose bark, lumber, firewood, and rubble. Daylight hours, at least in the outdoors, are usually spent in a retreat within a crack, but at evening the spider takes up its hunting posture in the web, where it alertly responds to the slightest touch of the threads. Several finds of both egg sacs and active stages in furniture in transit or newly arrived from other parts of the country attest to the potential for spread through passive transport.

Methods

The history of *S. bipunctata* and *S. borealis* in North America was investigated by a search of relevant literature, by examination of preserved specimens in public and private collections, by collecting trips to particular localities in eastern Canada and northeastern United States, and by more intensive collecting in an area where both species were, or had been, known to occur. Individual spiders were teased from their webs or retreats into vials; we recorded the habitat (house, barn, tree trunks, etc.), position in buildings (ceiling, wall, etc), and kinds of prey, if any, found in the webs.

Sample size for populations of either species was set at 16, based on the number of individuals estimated to provide 5% precision (Cochran 1963), though for practical reasons this number was not reached or was exceeded in some instances. Sample size when individuals of both species were present was determined by the proportions of individuals of the two species in the sample. The formula is

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$$n = \frac{\frac{t^2 PQ}{d^2}}{1 + \frac{1}{N} \left(\frac{t^2 PQ}{d^2} - 1 \right)}$$

where n = sample size; t = abscissa of the normal curve, here chosen at 5%, whence $t = 1.96$; P = proportion of adult spiders represented by *S. bipunctata*; Q = proportion of adult spiders represented by *S. borealis*; d = desired degree of precision, here set at 5%; and N = total number of adult spiders, here assumed to be a maximum of 1000.

Laboratory tests on ecological and behavioural responses of the two species were performed in clear plastic vials 10 cm in length by 4.5 cm in diameter, or in cubical screen cages 30 cm on each side. Living adults of either *Drosophila melanogaster* or *Musca domestica* were supplied as food. The spiders were reared in a chamber having an ambient temperature of 22°C, relative humidity of approximately 70%, and a photoperiod of 16 h per 24-h day.

Microhabitat relationships of the two species were examined in terms of the extent each utilized particular parts of the habitat. Observations of diel activity were made on 30 adult females of each species over 72 h during a 7-day period in September 1984; night counts were made with the use of diffuse (red) light. Overlap in space and time utilization was estimated by a formula given by Horn (1966) which provides an empirical measure of overlap between the observed proportions of individuals of two coexisting species utilizing one of these resource classes; values range from 0 (complete separation) to 1 (complete overlap). The formula is

$$\hat{C}_\lambda = \frac{2 \sum_{i=1}^s x_i y_i}{\sum_{i=1}^s x_i^2 + \sum_{i=1}^s y_i^2}$$

where \hat{C}_λ = overlap coefficient; s = total number of resource classes; x_i = occurrence of *S. bipunctata* in a resource class; and y_i = occurrence of *S. borealis* in the same resource class.

History of *Steatoda bipunctata* and *S. borealis* in North America

Steatoda bipunctata was originally described in Europe (Linnaeus 1758), and has been redescribed and illustrated by numerous European arachnologists. It ranges over Europe and Siberia to the Kamchatka Peninsula, and was early reported as an introduction in a number of South American countries (see Levi 1957, 1962). The first North American record is from the vicinity of Toronto (Blackwall 1846) (as *Theridion quadripunctatum* (Walckenaer)). Blackwall's specimens no longer exist, however, and he published neither description nor illustrations. The record is therefore equivocal, as it may actually pertain to *S. borealis*. The earliest available museum specimens of *S. bipunctata* from this continent are dated 1913 at Grand Pré, Nova Scotia. It is significant, however, that a collection of spiders, including house-dwelling species, made in 1912 in Nova Scotia did not include this spider, though specimens of the similar species *S. borealis* were found (Emerton 1918).

During the decade 1914–1923, specimens of *S. bipunctata* were collected at St. John's and Nicholsville, Newfoundland, on the southern coast of Labrador, in Ste-Anne des Monts and several other Gaspé coast towns in Québec, and in Toronto, as well as several coastal localities in Nova Scotia. Plant Quarantine officials found a specimen in a tree-importing nursery at Ottawa in 1925. The earliest specimens discovered in Maine are dated 1932–1933 (Bar Harbor), and finds have continued to the present year. New Brunswick has yielded specimens since 1947 (Grand Manan), and New Hampshire since 1946. Hackman

(1954) recorded *S. bipunctata* from both urban and rural places in Newfoundland. One of us (C.D.D.) collected numerous specimens in western Nova Scotia in the period 1954–1961, finding them in virtually every building searched and under objects on the ground; inland as well as coastal localities were included. Levi (1957) recorded two localities on the north shore of Lake Ontario dated 1942 (Toronto and Lakeport) and 1946 (Toronto).

Collections dated 1940 and later included localities more remote from the coastline and from Great Lakes harbours, e.g., central and northern New Brunswick; Breckenridge and Shawville, Québec; Ottawa, Chatterton, Aylen Lake, Iron Bridge, Aylmer, Orangeville, and St. Thomas, Ontario; and Gorham, Glen House, and Berlin, New Hampshire. In the present study, specimens of *S. bipunctata* were found as far inland as Burlington, Vermont, and Sault Ste. Marie, Ontario. Unsuccessful searches were made at Boston, Massachusetts; Rochester, New York; Vineland, Fort Erie, London, Windsor, and Thunder Bay, Ontario; Itasca State Park (Heimer *et al.* 1984) and Minneapolis—St. Paul, Minnesota; Winnipeg, Manitoba; Saskatoon, Saskatchewan; Edmonton, Alberta; Summerland and Victoria, British Columbia (West *et al.* 1984). Specimens of *S. borealis* were found at all of the above "unsuccessful" localities except Victoria, British Columbia, where no records exist for either species.

The foregoing observations led us to formulate the hypothesis that *S. bipunctata* is, as supposed by Hackman (1954), Lindroth (1957), and Levi (1957), a true introduction to eastern Canada and the northeastern United States. The spider's earlier restriction to coastal localities and later occurrence in many inland places (Fig. 1), its affinity for buildings and other habitats influenced by humans, and its widespread and common occurrence in and on buildings in Europe constitute strong circumstantial evidence that the spider is not only introduced but is continuing to spread. The collections led to a second hypothesis regarding this spider, namely, that its appearance in an area marks the coincident disappearance of the native *S. borealis*, at least in some of the habitats suitable for occupation by individuals of either species.

Evidence for the partial displacement hypothesis was obtained in the Ottawa–Hull area, in Cape Breton Island, and in Maine. Our searches in the urban and suburban area of Ottawa–Hull in 1983–1984 showed that buildings and tree trunks in the city core yielded specimens of only *S. bipunctata*, whereas crevices on tree trunks and limestone quarries at the periphery yielded specimens of both *S. bipunctata* and *S. borealis*, or of the latter alone (Fig. 2). Still farther from the city core, in a farm district 10–50 km to the southwest, searches of buildings on 18 farms revealed the presence of *S. bipunctata* alone on 7 of the farms and of both species or of *S. borealis* alone on the remainder (Table 1). On the Paul farm, the main barn, which was occupied by a large dairy herd, yielded specimens of only *S. bipunctata*, whereas a dilapidated house and shed, used for lumber storage, yielded nine specimens of *S. borealis*. Crevices in stone piles and under tree bark in a nearby pasture yielded no specimens of *S. bipunctata* but 16 of *S. borealis*.

Five barns or cottages in Cape Breton Island were found, in 1984, to be occupied by individuals of *S. bipunctata* alone (4 to 22 individuals each). Two other buildings, one a doorless shed attached to a cottage in contact with forest trees and the other an emergency shelter for hikers in the forest, yielded specimens of *S. borealis* alone (seven individuals each). The

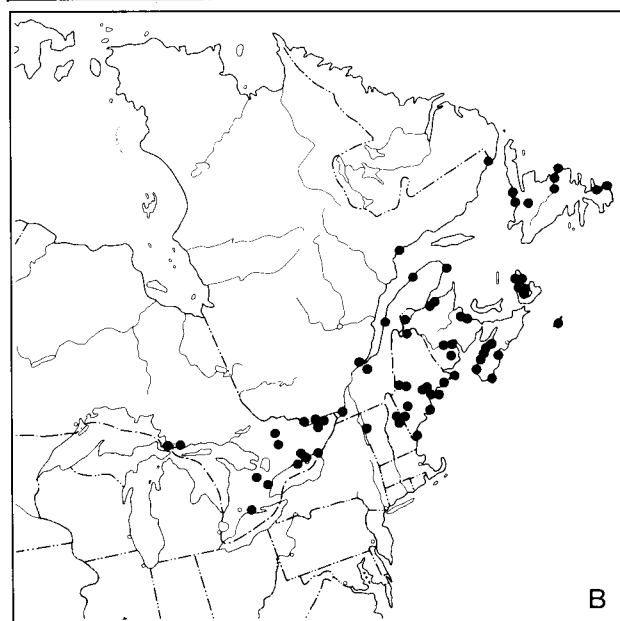
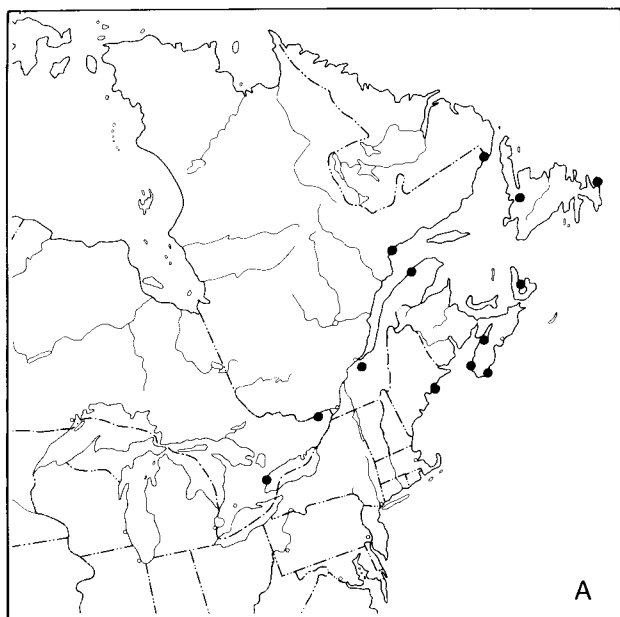


FIG. 1. Collection localities of *Steatoda bipunctata* in North America. (A) 1913–1940. (B) 1913–1984.

same relationship appears to exist in Maine, where all of the 46 specimens of *S. bipunctata* captured since 1980 originated in or on buildings in cities or towns, and the 13 specimens of *S. borealis* collected in the same years originated in such habitats as crevices in dead forest trees, outdoor woodpiles, and campground buildings or furniture in state forests, or on wooden fences and bridges. These observations suggest that although *S. bipunctata* is advancing (and we regard buildings in which both species are represented as sites in which displacement is in progress), *S. borealis* persists in those parts of the landscape least influenced by humans.

Investigations into ecological and behavioural relationships between *Steatoda bipunctata* and *S. borealis*

The displacement of the native spider *S. borealis* by the introduced *S. bipunctata*, as hypothesized in the previous section, was investigated as to its mode of operation. We did

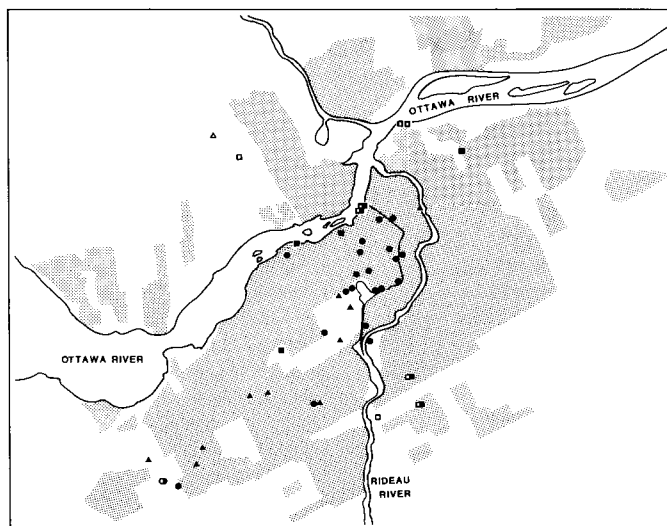


FIG. 2. Collection localities of *Steatoda bipunctata* (solid symbols) and *S. borealis* (open symbols) in Ottawa–Hull. Shaded areas indicate built-up urban communities, triangles indicate buildings, circles indicate tree trunks, and squares indicate limestone faces.

this by comparing responses of individuals of the two species to the following ecological or behavioural parameters: microhabitat, diel activity, prey utilization, seasonal life history, sexual behaviour, reproductive potential, and aggressiveness within and between species.

Microhabitat

Although individuals of both species are found in the same kinds of habitat, differences in preferred microhabitat possibly exist. To test this we recorded the precise microhabitat (in cracks or exposed on ceilings or walls, under objects on the floor) in three barns occupied by populations of both species (Table 2). Calculation of the coefficient of overlap by the Horn formula (see Methods) for the two species in the Ripping farm gave a value of 0.97, for the L. Code farm, 0.94, and for the F. Code farm, 1.00. The average overlap value was 0.97, indicating almost complete overlap in microhabitat in these barns.

Diel activity

Activity of individuals of the two species at various hours of the 24-h day was measured by hourly observations on individually caged spiders. Results (Fig. 3) indicate that spiders were feeding at every hour, though individuals of both species tended to be most active during the hours following the daily feeding, which took place between 0800 and 0900. Comparison of the two species by the Horn formula (see Methods) showed that the coefficient of overlap was 0.98. Hence there was almost total overlap in diel activity, in terms of feeding, in the two species.

Prey selection and utilization

The possibility of an advantage to representatives of one of the species through prey selection and killing rate was studied by collection and identification of prey found in webs, and by use of particular feeding regimes in the laboratory. Insufficient webs containing prey were found to permit quantitative comparison, but the observations available indicate that individuals of both species capture and feed on the same kinds of prey. In barns, houseflies were most commonly found in webs, but adult Hemiptera, larvae and adults of mealworms (*Tenebrio* sp.), and adults of various meal-infesting Lepidoptera were also found.

TABLE 1. Status of *Steatoda bipunctata* and *S. borealis* in farm buildings southwest of Ottawa-Hull, 1983-1984

Farm	Kind of building	No. of <i>S. bipunctata</i>	No. of <i>S. borealis</i>	Total	% <i>S. bipunctata</i>	No. needed for 5% precision
Paul	Livestock barn	70	0	70	100	16
Lowry	Livestock barn	56	0	56	100	16
Schyndel	Livestock barn	55	0	55	100	16
Silver Spring	Livestock barn	52	0	52	100	16
Boutcher	Livestock barn	48	0	48	100	16
Cunningham	Livestock barn	48	0	48	100	16
Jinkinson	Livestock barn	33	0	33	100	16
Jinkinson	Storage shed	0	5	5	—	16
Blackburn	Livestock barn	45	3	48	94	78
Martin	Livestock barn	182	20	202	90	123
Manchester	Livestock barn	45	13	58	78	210
Ripping	Livestock barn	52	53	105	50	279
Hill	Livestock barn	20	50	70	29	243
Code, L.	Livestock barn	32	99	131	24	222
Code, F.	Livestock barn	35	135	170	21	204
Cunningham	Livestock barn (abandoned)	1	10	11	9	114
Miller	Livestock barn (previously abandoned, used since 1978)	1	55	56	2	30
Miller	Storage shed	0	21	21	—	16
Aitken and Drummond	Livestock barn (abandoned since 1973 or earlier)	0	29	29	—	16
Silver Lake	Livestock barn (abandoned)	0	14	14	—	16

NOTE: For explanation of final column, see Methods section of text.

TABLE 2. Microhabitat utilization by *Steatoda bipunctata* (x_i) and *S. borealis* (y_i) on three farms near Ottawa-Hull, 1983

	Ripping farm		L. Code farm		F. Code farm	
	x_i	y_i	x_i	y_i	x_i	y_i
No. of spiders collected	52	53	31	100	35	134
Ceiling, in cracks (%)	7.7	15.1	6.5	13.0	14.3	13.4
Ceiling, in webs (%)	32.7	30.2	35.5	44.0	74.3	77.6
Wall, in cracks (%)	1.9	5.7	16.1	2.0	—	—
Wall, in webs (%)	15.4	15.1	22.6	19.0	8.6	3.7
Under objects on floor (%)	42.3	34.0	19.4	22.0	2.9	5.2
Total	100	100	100	100	100	100

On rocks and tree trunks, ants, beetles, and wood lice were most often found in webs. We were unable to detect any real difference in the kinds of prey selected at any site.

Two feeding regimens were tested in the laboratory. These were conducted with individually caged adult females of the two spider species and consisted, in one regimen, of a daily feeding of one adult housefly each and, in the other, of one fly every 3 days. The fly was recorded as killed or alive 24 h after the feeding. Thirty control cages, each holding a living housefly but no spider, indicated that fly deaths in the test cages were due not to confinement but to predation.

Results of these feeding tests (Table 3) indicate that no significant difference existed in the prey-killing rates of females of the two species ($p > 0.05$ for both feeding regimes). We conclude that neither species possesses any advantage in ability to capture prey in situations involving equal prey density.

Seasonal life history

Observations in barns and in the laboratory indicate that both

S. bipunctata and *S. borealis* overwinter in various stages of development, including the adult stage for both sexes. In April and May there is a flush of maturation and mating, followed by egg laying through the summer. Many of the young resulting from spring matings reach maturity in late August or early September of the same year; these then mate and produce egg sacs and young until cold weather intervenes. These young reach various stages before winter, but probably none reach the adult stage until the following spring.

Thirteen egg sacs of *S. bipunctata*, which had been laid in the laboratory in May 1984, hatched in 15.4 days (range 13-18 days), and the spiders matured in 103.8 days (range 94-111 days). For comparison, seven egg sacs of *S. borealis* hatched in 15.9 days (range 13-21 days), and the spiders matured in 114.2 days (range 103-128 days). The number of moults for both lots was five or six. Mating may begin earlier in the spring than we observed it; Bristowe (1971) observed a pair of *S. bipunctata* copulating in March in England, and Sacher (1983) made similar observations in April in Germany. Emerton (1882)

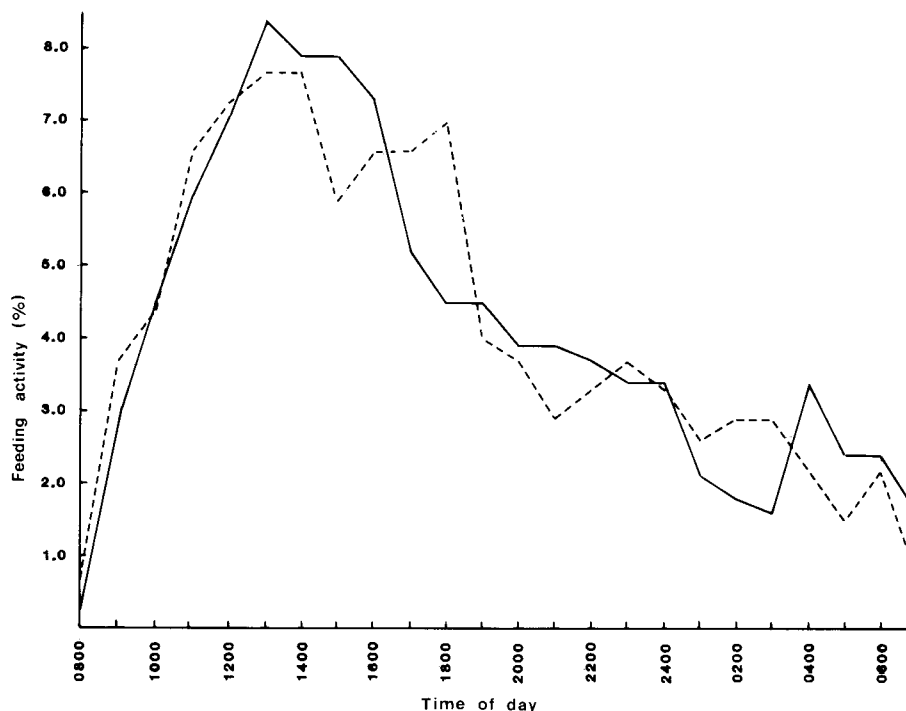


FIG. 3. Distribution of feeding activity during the 24-h day in *Steatoda bipunctata* (solid line) and *S. borealis* (broken line).

TABLE 3. Prey-killing rates of *Steatoda bipunctata* and *S. borealis* females in laboratory cages

Replicate	<i>S. bipunctata</i>			<i>S. borealis</i>		
	No. of spiders offered fly (a)	No. of spiders killing fly in 24 h (b)	Prey-killing rate (b/a)	No. of spiders offered fly (a)	No. of spiders killing fly in 24 h (b)	Prey-killing rate (b/a)
Fly offered daily						
Replicate 1	30	28	0.93	30	17	0.57
Replicate 2	30	30	1.00	30	23	0.77
Replicate 3	30	19	0.63	30	19	0.63
Replicate 4	30	25	0.83	30	27	0.90
Replicate 5	30	20	0.67	30	20	0.67
Mean ± standard error			0.81±0.07			0.71±0.06
Fly offered every 3 days						
Replicate 1	60	35	0.58	60	34	0.57
Replicate 2	60	58	0.97	60	55	0.92
Replicate 3	60	43	0.72	59	47	0.80
Replicate 4	58	22	0.38	57	25	0.44
Replicate 5	50	35	0.70	55	47	0.85
Mean ± standard error			0.67±0.10			0.72±0.09

reported mating in *S. borealis* in April and May. Only Wiehle (1937) previously reported the late-summer mating period.

Sexual behaviour

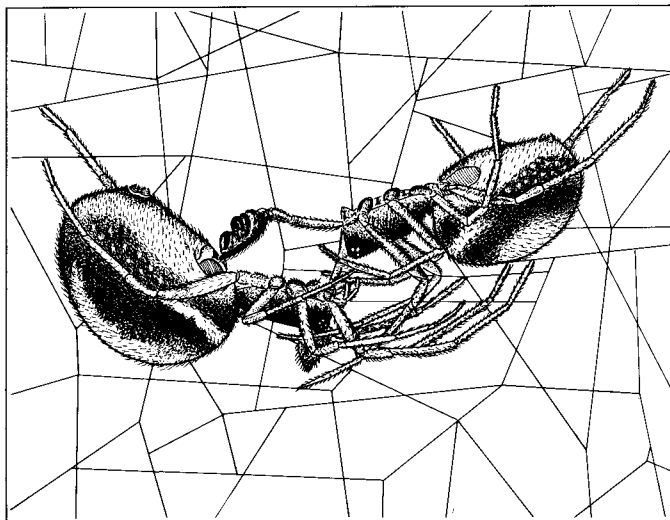
Courtship and mating were investigated comparatively in *S. bipunctata* and *S. borealis* to determine whether one species possesses a survival advantage over the other through some component of this behaviour.

Sexual behaviour has been observed in *S. bipunctata* in Europe (Gwinner-Hanke 1970; Bristowe 1971), and confirmed in Canadian specimens by us. When a wandering male touches the web of a female, he begins to stridulate, probably in response to a chemical deposited by the female on the threads. Stridulation is produced by the vibration of a series of

sclerotized teeth, located on the anterior part of the abdomen, against a row of parallel ridges found on the posterior declivity of the cephalothorax. Sound is produced with a frequency of about 1000 Hz. The female responds to this sound by beating on the web with her front legs. Soon the male touches the female, and then begins to run rapidly toward and away from her, spinning as he runs. The result of this "Spinnläufe" (Gwinner-Hanke 1970) is a small silken platform, or "bridge" (Bristowe 1971), about 15 mm long and 5 mm wide, within the female's web. Having completed his platform, the male resumes stridulating in front of the female. They come together and hang inverted near the platform, usually oriented front to front (Fig. 4). Copulation begins as the male extends one of his palpi to the epigynum of his partner and begins striking the epigynum.

TABLE 4. Duration of courtship and copulation in *Steatoda bipunctata* and *S. borealis* (minutes)

	Courtship			Insertion of first embolus			Insertion of alternate embolus		
	Mean \pm SE	Range	No. observed	Mean \pm SE	Range	No. observed	Mean \pm SE	Range	No. observed
<i>S. bipunctata</i> ♂ \times <i>S. bipunctata</i> ♀	297 \pm 32	131–416	11	140 \pm 24	58–228	6	120	—	1
<i>S. borealis</i> ♂ \times <i>S. borealis</i> ♀	140 \pm 12	43–383	46	94 \pm 5	15–160	42	101 \pm 8	14–153	23
<i>S. bipunctata</i> ♂ \times <i>S. borealis</i> ♀	107.9 \pm 10	52–172	29	—	—	29	—	—	29
<i>S. borealis</i> ♂ \times <i>S. bipunctata</i> ♀	117.5 \pm 5.5	65–153	36	—	—	36	—	—	36

FIG. 4. *Steatoda bipunctata* mating, with male on right (after Bristowe 1971).

Eventually the embolus engages the corresponding copulatory opening, and insemination ensues. The embolus remains inside for about 2 h, after which the spiders uncouple and the male courts again and inserts the alternate embolus into the alternate copulatory opening. The second insertion lasts a similar time.

Courtship in *S. borealis* has not been reported previously, but we observed it to be virtually identical to that of *S. bipunctata*. Touching of the female web, stridulation method and frequency, and the "Spinnläufe" of the male, and the beating on the threads by the female, proceed, according to our observations, as in *S. bipunctata*, though less time is taken (Table 4), the difference being significant at the 1% level. The mating position and copulatory procedure are the same as in *S. bipunctata*, but the insertions take less time (Table 4); this difference, however, is not statistically significant.

We also wished to know whether males of one species would court and mate with females of the other, and whether such meetings are peaceful or otherwise. Results indicate that courtship took place as for conspecific pairs, and that 17% of the males of both species struck their palpi against the epigynum for prolonged periods of time. No copulation occurred, however, presumably because of mechanical differences in the external genitalia of the two species (see Levi 1957).

Reproductive potential

The ability to produce offspring may provide an advantage to one or the other species. Laboratory counts of egg sacs and

newly hatched spiderlings were adequate for *S. borealis*, but not for *S. bipunctata*. In the former, all of a group of 30 uniformly fed females produced first sacs yielding an average of 68.1 young, 18 produced second sacs yielding 66.4 young, and 11 produced third sacs yielding 50.0 young. Females of *S. bipunctata*, for reasons unknown, fed poorly and became dull and shrunken in appearance. Eighteen of the 30 females produced first sacs yielding an average of 38.0 young, three produced second sacs yielding an average of 62.3 young, and none produced a third sac; this number of sacs appears abnormally low.

Interspecific aggression

Tests for aggression between individuals of the two species were done in vials or screen cages (see Methods). Adult females were used in all tests. First an individual of *S. bipunctata* was placed in an unoccupied web of *S. borealis*, and *vice versa*. The intruder in every case adopted the web and used it for prey capture.

In a second test, we placed in replicate an individual of *S. bipunctata* in a vial cage containing a female of *S. borealis* in her web, and *vice versa*. Results (Table 5) indicate that mortality occurred in all of the cages, but that more *bipunctata* than *borealis* females were killed, regardless of whether *bipunctata* was the web owner or the intruder.

Introductions into screen cages containing groups of up to 10 spiders of the alternate species in webs produced similar results, with *S. borealis* winning more often, regardless of which was the web owner and which the intruder (Table 5).

The foregoing tests on aggressiveness between *S. bipunctata* and *S. borealis* in cages must be qualified by an apparent loss of fitness observed in the females of *S. bipunctata*. Whereas females of *S. borealis* remained plump and shiny throughout the tests, those of *S. bipunctata* became progressively shrunken and dull. Both stocks were collected at the same time and in the same barns, and both were handled in the same way. This difference may well have contributed to the difference in kill in the tests, and needs further investigation.

Discussion

Wise (1984, p. 45) examined the criteria for interspecific competition and concluded that "Clear experimental evidence of major competitive interactions between closely related spider species is lacking." Spiller (1984) succeeded in eliciting population release in two species of orb-weavers, *Metetepeira grinnelli* and *Cyclosa turbinata*, which share space and food in a California marsh, by manipulating numbers of individuals in the field. Because of differences in seasonal life history, individuals of *C.*

TABLE 5. Aggression between individuals of *Steatoda bipunctata* and *S. borealis* in laboratory cages based on equal numbers of adult females of both species

No. of cages	Cage type	Web owner	Avg. no. of web owners per cage	Duration of test (days)	Avg. no. of spiders killed per cage and percentage of total kill	
					Intruders (%)	Web owners (%)
70	Vial	<i>bipunctata</i>	1	18	0.07(29.4)	0.18(70.6)
51	Vial	<i>borealis</i>	1	16	0.35(78.3)	0.10(21.7)
3	Screen	<i>bipunctata</i>	7.3	65	2.3 (34.5)	4.3 (65.5)
3	Screen	<i>borealis</i>	7.7	65	6.0 (66.7)	3.3 (33.3)
4	Screen	<i>bipunctata</i> alone	10	30	—	2.5
4	Screen	<i>borealis</i> alone	10	30	—	4.5

turbinata are large in the spring months, and these destroy many individuals of *M. grinnelli*, which are small at that time. The reverse takes place in summer. Removal of individuals of *C. turbinata* resulted in significantly higher prey consumption and fecundity in *M. grinnelli*, and removal of individuals of the latter resulted in significantly higher survival and broadened vertical distribution in *C. turbinata*. Spiller concluded that interspecific competition is operating, though critics would probably treat his results simply as an example of interspecific predation. His two species differ strongly in seasonal life history, which provides a seasonal advantage through size differential.

Our observations of *S. bipunctata* and *S. borealis* indicate a closer relationship between these two spiders than that seen in Spiller's orb-weavers. The two theridiids select the same microhabitat, are active at the same times of the day, utilize the same kinds of prey and at the same rate, and have the same seasonal life history and sexual behaviour. It is therefore not unexpected that displacement takes place when individuals of the European *S. bipunctata* arrive in an area previously occupied solely by the native *S. borealis*. In other words, we feel that competition is operating, with *S. bipunctata* the winner, but to date we have been unable either to identify the means by which it operates or to duplicate the phenomenon in the laboratory.

Displacement of *S. borealis* appears to be permanent, but it also appears to be restricted to those parts of the habitat range most influenced by human activity. The displaced spider persists in wooded areas, even on the east coast where, according to historical data, displacement began more than 70 years ago. Future lines of investigation ought to include studies on the nature of the protection afforded *S. borealis* in forested habitats.

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