Host specialisation and the disparate fate of *Ceropales bipunctata* (Hymenoptera: Pompilidae) in New Brunswick and Ontario, Canada

John Klymko,[1] Matthias Buck, Sarah L. Robinson

Abstract—*Ceropales bipunctata* Say (Hymenoptera: Pompilidae) is a cleptoparasitic spider wasp that has declined significantly in parts of its range. New survey work has revealed that the species is common and widespread in dune habitat along the Gulf of Saint Lawrence in New Brunswick, Canada. Its host was determined as *Anoplius cleora* (Banks) (Hymenoptera: Pompilidae), with *Arctosa littoralis* (Hentz) (Araneae: Lycosidae) as prey, the first host record for this species. The relative abundance of *C. bipunctata* in coastal New Brunswick sharply contrasts with a decline in Ontario, Canada, where it was thought to be extirpated. Based on body size, habitat, and locality overlap we postulate that the primary host of *C. bipunctata* in Ontario and western Québec, Canada, is a different species, *Anoplius aethiops* (Cresson), with *A. atrox* (Dahlbom) as a likely secondary host in southwestern Ontario. Both species are closely related to *A. cleora* and have undergone a decline in eastern Canada. Based on these new findings, we reassess the conservation status of *C. bipunctata* in Canada.

Introduction

Ceropales bipunctata Say (Hymenoptera: Pompilidae), a species of spider wasp found in the eastern United States of America and southeastern Canada, is considered to potentially be of conservation concern due to a recent decline in collected specimens. In Canada, it has been recorded from Ontario, Québec, New Brunswick, and Prince Edward Island (Townes 1957; Godsoe 2004). In southern Ontario, this relatively showy species (Fig. 1) was commonly collected from the 1880s to the 1950s (Godsoe 2004, see also Fig. 8; Table 2). No specimens were collected between 1957 and 2004, and the species was thought to be extirpated from Ontario (Godsoe 2004). After 2004, it was rediscovered at three previously unknown localities in Ontario (see Results). However, a substantial decline is evident. We are confident that this trend reflects a real decline, not a lack of collecting effort. From 1999 to 2008, M.B. and co-workers at University of Guelph (Guelph, Ontario, Canada) conducted extensive surveys for aculeate Hymenoptera in various habitats in southern Ontario, which failed to detect the species. Data for other Canadian provinces are too scanty to determine an obvious trend, yet no recent material of *C. bipunctata* was found in any of the collections we contacted. Similarly, Godsoe (2004) was unable to find specimens from the United States of America collected after the early 1960s, suggesting a decline across the entire range. Due to this precarious situation, the species was identified as a high-priority candidate for assessment by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) in 2014.

Causes for the apparent decline of *C. bipunctata* were previously unclear. Like its congeners, *C. bipunctata* is a cleptoparasite, laying its eggs in the book lung of the paralysed spider prey that another spider wasp has captured (Townes 1957). Eggs are laid either while prey is being transported by the host wasp or while prey is lying unguarded (Krombein 1979). After emergence inside the host burrow, the larva of the parasite first consumes the host egg and then the spider (Townes 1957).

Received 16 January 2017. Accepted 11 May 2017. First published online 7 September 2017.

J. Klymko,[1] S.L. Robinson, Atlantic Canada Conservation Data Centre, PO Box 6416, Sackville, New Brunswick, E4L 4G7, Canada
M. Buck, Invertebrate Zoology, Royal Alberta Museum, 9810-103a Avenue NW, Edmonton, Alberta, T5J 0G2, Canada

[1]Corresponding author (e-mail: john.klymko@accdc.ca)
Subject editor: Christopher Buddle
doi:10.4039/tce.2017.40

Fig. 1. *Ceropales bipunctata* male (Cap Lumière, New Brunswick, 20 August 2015).

Godsoe (2004) speculated on host decline as a potential cause for the decline of *C. bipunctata*. The large size of this species rules out most spider wasps as potential hosts, leaving the larger species of *Anoplius* Dufour (Hymenoptera: Pompilidae) as potential candidates (Godsoe 2004). However, no host observations were available before our study.

The initial purpose of our study was to determine the conservation status of *C. bipunctata* in New Brunswick through targeted field surveys. The inspiration for our project came from recent observations of the species at two widely separated coastal dunes (Tingley 2012, 2013), demonstrating that this COSEWIC candidate remained extant in the province. The few historic and recent data on the distribution of this species in the Maritimes are summarised in the Results.

During our survey we were able to observe the host – indeed a species of *Anoplius* as had previously been speculated (Godsoe 2004). The host was detected at most of the sites where we found *C. bipunctata*. However, when we compared Ontario records of parasite and the newfound host we noticed that they were largely incongruent. We therefore set out to determine the putative host species for Ontario and adjacent areas of Québec through a process of elimination, comparing collection data and considering relevant biological parameters. The newly gained insights allowed us to test the hypothesis whether the decline of *C. bipunctata* in Ontario is indeed host-mediated.

Methods

Survey work in New Brunswick

To determine the current distribution of *C. bipunctata* in New Brunswick, we surveyed 33 coastal sand dune and beach sites along the Gulf of Saint Lawrence and Chaleur Bay (see Table 1 and Fig. 2). Dune habitats were targeted because the few recent New Brunswick records were from dunes (Tingley 2012, 2013). Historic records from Shippagan and Tracadie (see Results) lack habitat information, but both centres are close to extensive dunes. We only became aware of the historic record from Saint John (where coastal dunes are absent) after survey sites had been selected.

Surveys were conducted between 18 August and 3 September of 2015, which falls within the flight period of *C. bipunctata* in the Maritimes and Ontario. Surveys were conducted by one or two observers walking sites between 09:00 AM and 06:00 PM Atlantic Daylight Time on days of good weather (air temperature $\geqslant 15\,^{\circ}C$, no precipitation, wind < 30 km/hour). We collected spider wasps opportunistically (including specimens of other genera), with the goal to voucher a specimen of *C. bipunctata* at every site where it was encountered. We took notes about *C. bipunctata* behaviour and captured any spider wasps plus their spider prey that were parasitised by *C. bipunctata*. All specimens are deposited at the New Brunswick Museum (Saint John, New Brunswick, Canada) and the Royal Alberta Museum (Edmonton, Alberta, Canada).

Inference of the putative *Ceropales bipunctata* host in Ontario and western Québec

To identify the host(s) of *C. bipunctata* in Ontario and western Québec we analysed the distribution, habitat, and prey preferences of putative host species. In the analysis we included species that are of similar size or larger than the newly discovered New Brunswick host species *A. cleora* (Banks). Specifically, we included species with an average female body length of at least 14 mm (see Table 2). The average female body length of *A. cleora* is 15 mm (Evans 1951).

Localities of potential host species were considered shared with *C. bipunctata* when locality names on specimen labels were the same.

https://doi.org/10.4039/tce.2017.40 Published online by Cambridge University Press

Table 1. Presence/absence of *Ceropales bipunctata* and its host *Anoplius cleora* at New Brunswick survey sites.

Site number	Locality	Habitat	Date (all 2015)	Observer(s)	Temperature (°C)	% Cloud cover	Start time (ADT)	End time (ADT)	Coordinates	*Ceropales bipunctata* observed	*Anoplius cleora* observed
1	Eel River Bar	Sand/gravel bar	02.ix	J.K., S.L.R.	19	0	09:47 AM	10:25 AM	48.0299°N, 66.3703°W	No	No
2	Hamilton Point	Sand/gravel bar	02.ix	J.K., S.L.R.	20	Not recorded	10:50 AM	11:24 AM	47.9914°N, 66.2660°W	No	No
3	Little Belledune Point	Gravel beach	02.ix	J.K., S.L.R.	25	0	12:20 PM	12:59 PM	47.9199°N, 65.8984°W	No	No
4	Petit-Rocher-Nord	Gravel beach	02.ix	J.K., S.L.R.	25	Not recorded	01:30 PM	01:50 PM	47.8010°N, 65.7270°W	No	No
5	Beresford Beach	Gravel beach	02.ix	J.K., S.L.R.	25	20	02:30 PM	03:16 PM	47.7107°N, 65.6984°W	No	No
6	Youghall Beach	Coastal sand dune	26.viii	J.K., S.L.R.	23	90	10:45 AM	11:43 AM	47.6580°N, 65.6224°W	Yes	Yes
6	Youghall Beach	Coastal sand dune	02.ix	J.K., S.L.R.	25	80	03:41 PM	05:00 PM	47.6580°N, 65.6224°W	Yes	Yes
7	Daly Point	Gravel beach	26.viii	J.K., S.L.R.	23	90	01:00 PM	01:16 PM	47.6371°N, 65.6243°W	No	No
8	East Bathurst	Sand/gravel bar	26.viii	J.K., S.L.R.	23	80	09:36 AM	09:56 AM	47.6179°N, 65.6395°W	No	No
9	Miscou Centre	Coastal sand dune	01.ix	J.K., S.L.R.	20	0	12:15 PM	02:00 PM	47.9568°N, 64.5657°W	No	Yes
10	Miscou Plains	Coastal sand dune	01.ix	J.K., S.L.R.	20	10	10:05 AM	11:40 PM	47.9996°N, 64.5497°W	No	Yes
11	Wilson Point	Coastal sand dune	01.ix	J.K., S.L.R.	18	50	02:20 PM	03:00 PM	47.9334°N, 64.4805°W	Yes	Yes
12	Chiasson	Coastal sand dune	01.ix	J.K., S.L.R.	18	0	03:53 PM	04:28 PM	47.7257°N, 64.6494°W	Yes	Yes
13	Green Point	Coastal sand dune	19.viii	J.K.	24	0	03:10 PM	05:20 PM	47.6019°N, 64.8265°W	No	No
13	Green Point	Coastal sand dune	03.ix	J.K., S.L.R.	20	0	09:34 AM	10:37 AM	47.6019°N, 64.8265°W	Yes	No
14	Val Comeau Provincial Park	Coastal sand dune	03.ix	J.K., S.L.R.	20	0	11:20 AM	11:53 AM	47.4680°N, 64.8727°W	Yes	Yes

Table 1. *Continued*

Site number	Locality	Habitat	Date (all 2015)	Observer(s)	Temperature (°C)	% Cloud cover	Start time (ADT)	End time (ADT)	Coordinates	*Ceropales bipunctata* observed	*Anoplius cleora* observed
15	Rivière-du-Portage	Coastal sand dune	19.viii	J.K.	23	0	12:30 PM	02:07 PM	47.4198°N, 64.8990°W	Yes	No
16	Hay Island Provincial Park	Coastal sand dune	19.viii	J.K.	21	0	09:20 AM	11:03 AM	47.2285°N, 65.0747°W	Yes	Yes
17	Point Escuminac	Coastal sand dune	18.viii	J.K.	26	0	03:40 PM	05:20 PM	47.0640°N, 64.8203°W	No	Yes
18	Pointe de Pruche	Coastal sand dune	18.viii	J.K.	30	0	11:30 AM	02:30 PM	46.9717°N, 64.8178°W	No	No
19	North Kouchibouguac Dune	Coastal sand dune	25.viii	J.K., S.L.R.	22	90	11:27 AM	01:32 PM	46.8434°N, 64.9122°W	Yes	Yes
20	South Kouchibouguac Dune	Coastal sand dune	25.viii	J.K., S.L.R.	27	0	03:00 PM	05:30 PM	46.8225°N, 64.9042°W	Yes	Yes
21	Cap-Lumière	Coastal sand dune	20.viii	J.K.	23	0	09:30 AM	01:00 PM	46.6772°N, 64.7143°W	Yes	Yes
22	Petit-Chockpish	Coastal sand dune	20.viii	J.K.	24	40	01:54 PM	02:56 PM	46.6026°N, 64.7224°W	Yes	Yes
23	Bouctouche Dune	Coastal sand dune	24.viii	J.K., S.L.R.	25	100	02:15 PM	03:45 PM	46.5264°N, 64.6836°W	Yes	Yes
24	Bourgeois	Coastal sand dune	28.viii	J.K., S.L.R.	17	0	09:00 AM	10:15 AM	46.3067°N, 64.5240°W	Yes	Yes
25	Bar-de-Cocagne	Coastal sand dune	24.viii	J.K., S.L.R.	24	100	04:36 PM	04:53 PM	46.4172°N, 64.6200°W	Yes	No
26	Parlee Beach	Coastal sand dune	28.viii	J.K., S.L.R.	22	0	11:08 AM	12:10 PM	46.2376°N, 64.4984°W	Yes	Yes
27	Cap Bimet	Coastal sand dune	28.viii	J.K., S.L.R.	25	0	12:46 PM	01:12 PM	46.2357°N, 64.4545°W	Yes	Yes
28	Saint-Henri-de-Barachois	Coastal sand dune	28.viii	J.K., S.L.R.	25	0	01:33 PM	02:20 PM	46.2257°N, 64.3931°W	Yes	No
29	L'Aboiteau	Coastal sand dune	31.viii	J.K., S.L.R.	26	0	04:00 PM	04:32 PM	46.2306°N, 64.3056°W	Yes	Yes

Table 1. *Continued*

Site number	Locality	Habitat	Date (all 2015)	Observer(s)	Temperature (°C)	% Cloud cover	Start time (ADT)	End time (ADT)	Coordinates	*Ceropales bipunctata* observed	*Anoplius cleora* observed
30	Johnston Point	Coastal sand dune	31.viii	J.K., S.L.R.	26	0	01:38 PM	03:00 PM	46.1738°N, 64.1020°W	Yes	Yes
31	Grants Beach	Coastal sand dune	31.viii	J.K., S.L.R.	25	0	12:53 PM	01:13 PM	46.1779°N, 64.0483°W	Yes	No
32	Bayfield	Coastal sand dune	31.viii	J.K., S.L.R.	20	0	11:21 AM	12:13 PM	46.1362°N, 63.8028°W	No	No
33	Cape Tormentine	Coastal sand dune	31.viii	J.K., S.L.R.	20	0	10:10 AM	11:00 AM	46.1328°N, 63.7849°W	Yes	Yes

Note: See Supplementary Table 1 for these data in Microsoft Excel format to facilitate use in future studies.
ADT, Atlantic Daylight Time.

Of course, this is not necessarily the case, especially for old material where locality information is often approximate. In some cases localities were considered shared when they were in immediate vicinity to each other (*e.g.*, Turkey Point Provincial Park and Turkey Point Tract). This was only done for well-known sites where we know that habitat is continuous between sites. General habitat information (as recorded in Table 3) was inferred from the literature and/or specimen data.

Acronyms of collections

We examined specimens and/or gathered distribution data from the following collections:

CNCI – Canadian National Collection of Insects, Ottawa, Ontario, Canada

DEBU – University of Guelph Insect Collection, Guelph, Ontario, Canada

LEMQ – Lyman Entomological Museum, McGill University, Ste-Anne-de-Bellevue, Québec, Canada

NBMB – New Brunswick Museum, Saint John, New Brunswick, Canada

NSPM – Nova Scotia Museum, Halifax, Nova Scotia, Canada

ROME – Royal Ontario Museum Insect Collection, Toronto, Ontario, Canada

Results

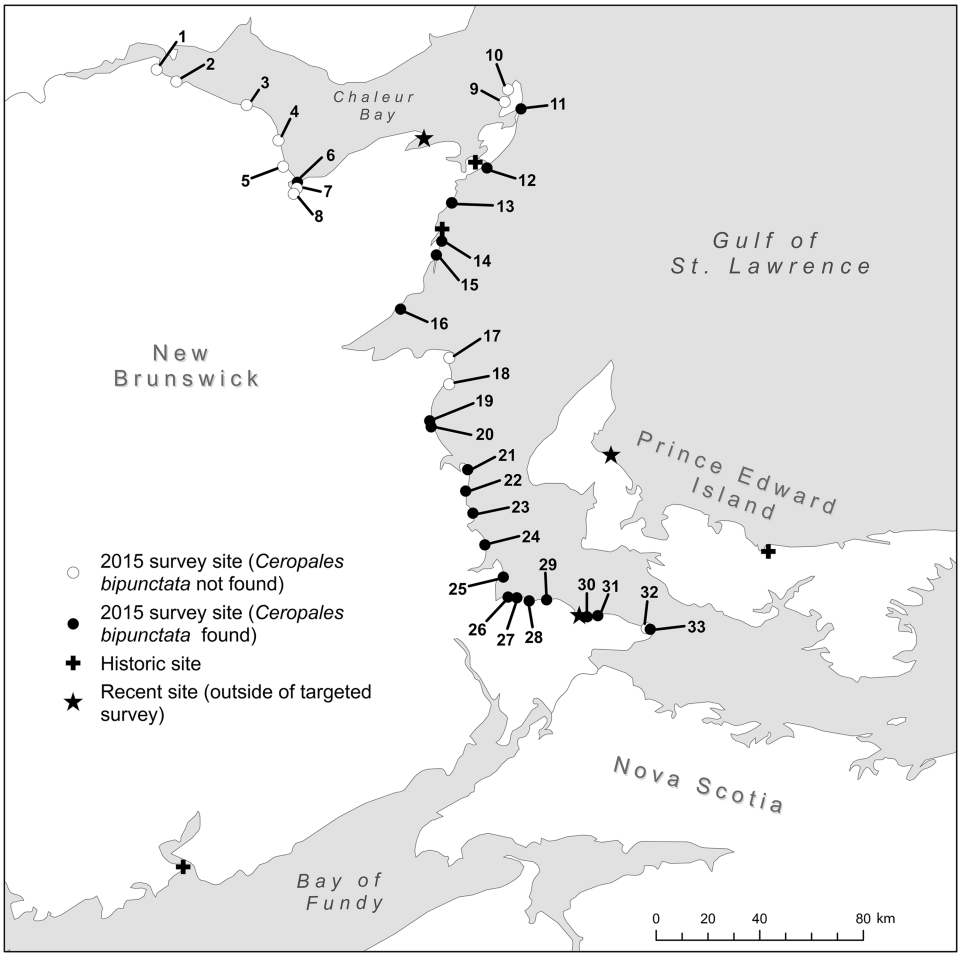
Range and habitat preference

Ceropales bipunctata was found at 21 of the 33 sites surveyed (see Fig. 2). The species occurred along the entirety of New Brunswick's Gulf of Saint Lawrence Coast, and one site on Chaleur Bay. *Ceropales bipunctata* was present at 81% of surveyed dunes sites ($n = 26$). The species was not found at any gravel beaches ($n = 4$) or sand/gravel bars ($n = 3$) studied. We suspect these habitat types are not suitable for *C. bipunctata* or its host(s) (see host discussion below).

Dunes where *C. bipunctata* was found ($n = 21$) range from very large (*e.g.*, dunes in the Tracadie area extend over 50 km) to small (*e.g.*, the dune at Bar-de-Cocagne is < 500 m long). Dune sites that lacked *C. bipunctata* ($n = 5$) showed no obvious differences from dunes where the species was present; however, no detailed assessment of dune characteristics was conducted.

https://doi.org/10.4039/tce.2017.40 Published online by Cambridge University Press

Fig. 2. 2015 survey sites with historic and recent *Ceropales bipunctata* localities in the Maritimes. Locality numbers listed in Table 1.



Hosts of *Ceropales bipunctata* and their spider prey in New Brunswick

We observed *C. bipunctata* parasitising the prey of another spider wasp on three occasions: one each at Cap Lumière, Petit-Chockpish, and Parlee Beach. Each time a group of four to six *C. bipunctata* were seen swarming a spider wasp that was dragging a subdued spider (Fig. 3). The host wasps from Petit-Chockpish and Cap Lumière were both collected and later identified as *A. cleora*; the host wasp at Parlee Beach was not collected or identified. The spider prey was collected in all three cases and identified as adult females of *Arctosa littoralis* (Hentz) (Araneae: Lycosidae). At least one swarm included a male of *C. bipunctata* (Cap Lumière). At Cap Lumière one female of the swarm landed and apparently oviposited on the spider prey during transport (Fig. 4). At Petit-Chockpish the host was observed pulling the spider into a previously dug burrow. Shortly thereafter a female *C. bipunctata* also entered the burrow, presumably to oviposit on the spider. After a minute or two *C. bipunctata* exited the burrow while the host remained inside. We then excavated the burrow and retrieved both host and prey. At Cap Lumière and Parlee Beach the pursued hosts showed aggressive behaviour towards *C. bipunctata*. They briefly left their spider prey and flew at the parasites, presumably in an attempt to drive them away.

https://doi.org/10.4039/tce.2017.40 Published online by Cambridge University Press

Table 2. Localities shared between *Ceropales bipunctata* and potential host species in Ontario and western Québec.

	Localities					Body length (♀)		
Species	Total	Shared	Same day	Same week	List of shared localities	Minimum	Maximum	Average
Ceropales bipunctata	24	11			See below under each species	10.3	12.6	11.2
Anoplius (*Lophopompilus*) *aethiops**	37	10	3	2	Bobcaygeon, Chaffey's Lock, Chatham, De Grassi Point, Grimsby, Ottawa, Toronto, Turkey Point, Hemmingford (QC), Hull (QC) (see also Fig. 5)	13	23	18
Anoplius (*Lophopompilus*) *atrox*	9	4	3	1	Chatham, Point Pelee, Toronto, Turkey Point (see also Fig. 6)	15	24	20
Anoplius (*Arachnophroctonus*) *nigritus*	26	3		1	Point Pelee, Toronto, Turkey Point	11	21	16
Anoplius (*Arachnophroctonus*) *semicinctus*	25	3	1	2	Point Pelee, Toronto, Turkey Point	11	20	15.5
Anoplius (*Lophopompilus*) *cleora*	23	2		1	Point Pelee, Toronto (see also Fig. 7)	13†	19†	15
Anoplius (*Lophopompilus*) *bengtssoni*	9	2		1	Point Pelee, Toronto	17	26	22
Tachypompilus ferrugineus	7	2			Chaffey's Lock, Point Pelee	15	22	18
Entypus unifasciatus	12	1	1		Chatham	19	21	20
Poecilopompilus algidus	8	1			Point Pelee	17	28	22
Poecilopompilus interruptus	3	1	1		Point Pelee	10.5	18	14
Anoplius (*Anoplius*) *depressipes*	7	0				11	20	14

Total: number of localities where the species has been collected. Shared: number of localities shared between *C. bipunctata* and potential hosts. Same day: number of localities where a species was collected on the same day as *C. bipunctata*. Same week: number of localities where a species was collected within seven days from *C. bipunctata* (excluding collecting events that overlap those from previous column). Underlined are localities where *C. bipunctata* has been collected since 2000. Body length measurements according to Evans (1950, 1951), Kurczewski and Kiernan (2015) and this study (*C. bipunctata* only, $n = 9$).

* See also note below Figure 5.

† *Anoplius cleora* collected by us in New Brunswick were smaller, ranging from 10–15 mm.

Table 3. Prey and nest sites of potential host species of *Ceropales bipunctata* in Ontario and western Québec.

Species	Prey	Nest sites	Host
Anoplius (*Lophopompilus*) *aethiops*	Lycosidae	Abandoned, overgrown fields and woodland edges	Yes (ON, QC), likely (Maritimes non-dune)
Anoplius (*Lophopompilus*) *atrox*	Lycosidae, Pisauridae	Abandoned, overgrown fields and woodland edges	Very likely (ON)
Anoplius (*Lophopompilus*) *cleora*	Lycosidae	Sandy habitats near water	Yes (Maritimes dunes)
Anoplius (*Lophopompilus*) *bengtssoni*	Unknown (probably Lycosidae, perhaps Pisauridae)	Savannas, sandy fields – crepuscular/nocturnal habits	Very unlikely
Anoplius (*Arachnophroctonus*) *nigritus*	Mostly Lycosidae, also Agelenidae	Sandy habitats	Very unlikely
Anoplius (*Arachnophroctonus*) *semicinctus*	Lycosidae	Sandy habitats	Very unlikely
Tachypompilus ferrugineus	Lycosidae, Pisauridae	Rock piles, crevices in stone walls and buildings	Unlikely
Entypus unifasciatus	Lycosidae, Pisauridae	Abandoned, overgrown fields and woodland edges	Unlikely
Poecilopompilus algidus	Araneidae	Savannas, overgrown fields	Unlikely
Poecilopompilus interruptus	Araneidae	Fields with bare sandy and gravelly openings, sand/gravel pits near woodland	Unlikely
Anoplius (*Anoplius*) *depressipes*	Pisauridae	Shores of ponds, swamps, lagoons, slow-moving streams (habitat specialist)	Very unlikely

Note: Prey and nest sites based on observations in the Great Lakes region (see Kurczewski and Kiernan 2015); prey information for *P. algidus* from Kurczewski and Edwards (2012); habitat information for *A. bengtssoni* and *P. algidus* extrapolated from specimen locality data.

Fig. 3. Four *Ceropales bipunctata* (marked with white dots) swarming a female of *Anoplius cleora* (black dot) and its prey, *Arctosa littoralis* (Cap Lumière, New Brunswick, 20 August 2015).

Fig. 4. *Ceropales bipunctata* ovipositing on an *Arctosa littoralis* captured by *Anoplius cleora* (Cap Lumière, New Brunswick, 20 August 2015).

https://doi.org/10.4039/tce.2017.40 Published online by Cambridge University Press

Co-occurrence of *Ceropales bipunctata* and potential host species in Ontario and western Québec

A total of 11 species of non-parasitic Pompilidae in Ontario and western Québec are large enough to be potential hosts of *C. bipunctata* (Table 2) including five species that are new records for Canada (M.B., unpublished): *Anoplius bengtssoni* (Regan), *A. depressipes* Banks, *Entypus unifasciatus* (Say), *Poecilopompilus algidus* (Smith), and *Tachypompilus ferrugineus* (Say). *Ceropales bipunctata* is known from 24 localities in Ontario and western Québec, 11 of which are shared with one or more of the potential host species. *Anoplius aethiops* is present at 10 of the latter (Fig. 5), *Anoplius atrox* (Dahlbom) at four (Fig. 6). The remaining nine species share three or less localities each with *C. bipunctata*. Remarkably, the New Brunswick host species *A. cleora* is widely distributed in dune habitats around the Great Lakes but shares only two localities with *C. bipunctata* (Fig. 7). Unlike the New Brunswick population, *C. bipunctata* is largely absent from dune sites in this part of its range.

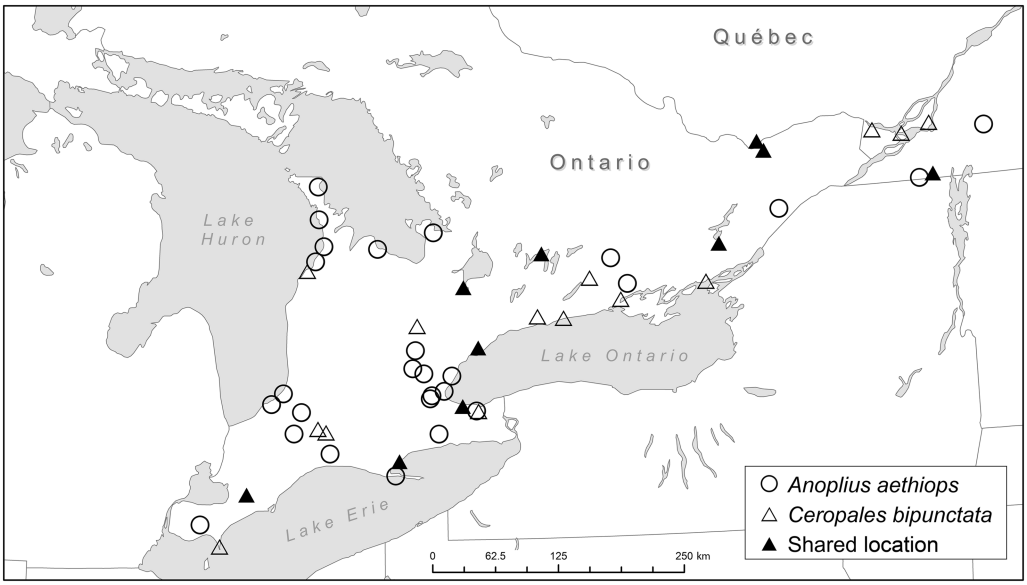
The strong correlation between *A. aethiops* and *C. bipunctata* is furthermore underlined by the fact that *A. aethiops* is the only potential host species whose range completely overlaps with that of *C. bipunctata* in Ontario and western Québec. None of the other species have ever been recorded from Québec. Two species (*Entypus unifasciatus* and *Poecilopompilus interruptus* (Say)) have a Carolinian distribution and are restricted to southwestern Ontario. The correlation between *A. aethiops* and *C. bipunctata* also has a temporal dimension (Table 2). At three localities (Bobcaygeon, Chatham, and Toronto) the two species were collected on the same day; at another two they were collected within a week from each other (De Grassi Point and Ottawa). A strong correlation was also observed between *A. atrox* and *C. bipunctata*, which were collected on the same day at three different localities (Chatham, Point Pelee, and Toronto).

Maritimes records of *Ceropales bipunctata* and its hosts from sources other than the present survey

Ceropales bipunctata

New Brunswick: Saint John, 5 August 1901, A.G. Leavitt, NBMB (unpublished); Shippagan, 28

Fig. 5. Occurrence of *Ceropales bipunctata* and *Anoplius aethiops* in Ontario and western Québec (see also Table 2). *Anoplius aethiops* is considered to be the primary host of *C. bipunctata* in Ontario and western Québec (see Discussion). Note: the LEMQ has specimens identified as *A. aethiops* from Montréal (potentially shared with *C. bipunctata*) and Lévis, Québec. They are not included in the map because we were unable to confirm their identity.



https://doi.org/10.4039/tce.2017.40 Published online by Cambridge University Press

Fig. 6. Occurrence of *Ceropales bipunctata* and *Anoplius atrox* in Ontario and western Québec (see also Table 2). *Anoplius atrox* is considered to be a likely secondary host of *C. bipunctata* in southwestern Ontario (see Discussion).

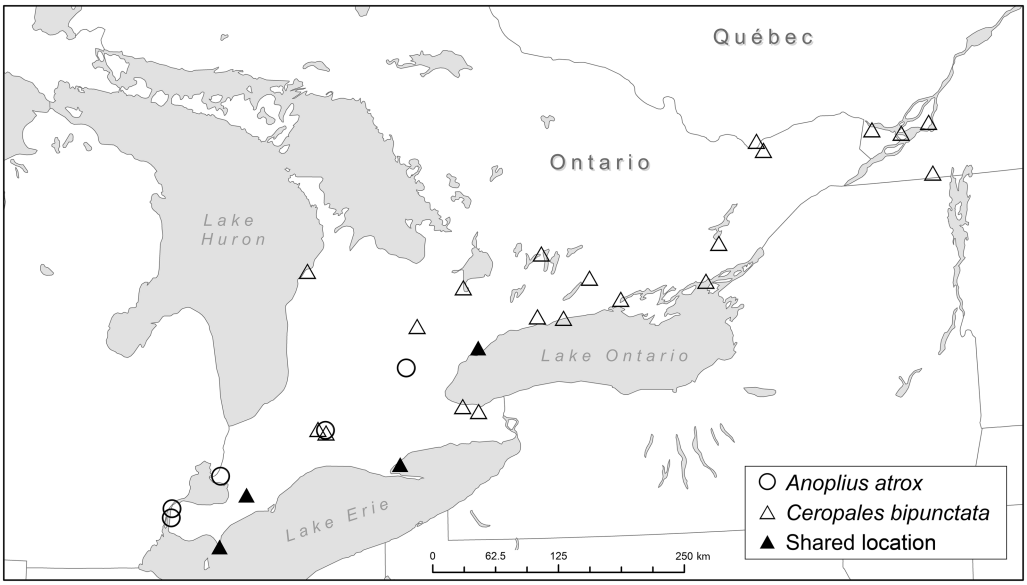
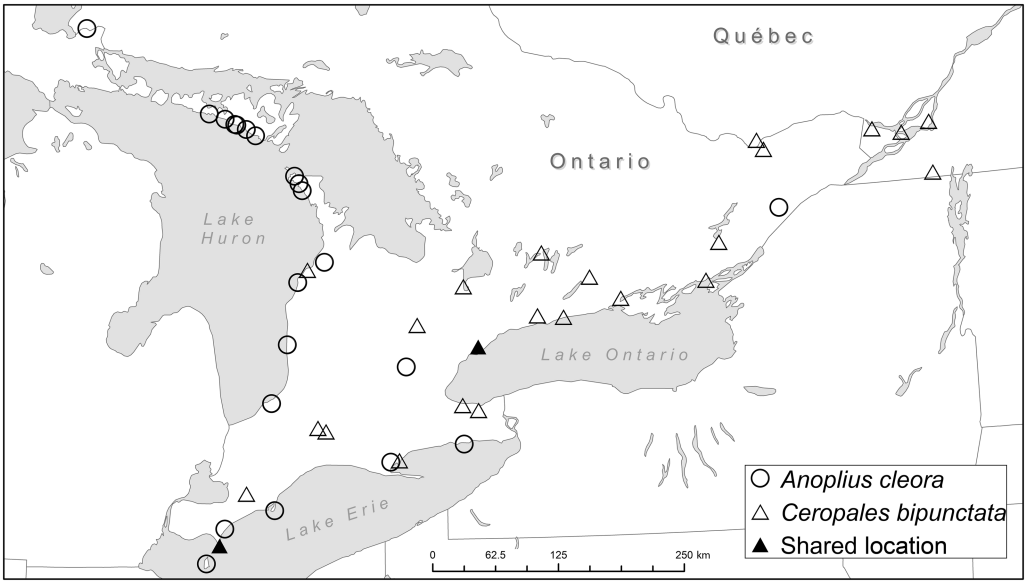


Fig. 7. Occurrence of *Ceropales bipunctata* and *Anoplius cleora* in Ontario and western Québec (see also Table 2). *Anoplius cleora* is ruled out as a host of *C. bipunctata* in this part of the range (see Discussion).



July 1939, J. McDunnough, CNCI (Townes 1957; Godsoe 2004); Tracadie, 30 July 1939, J. McDunnough, CNCI (Townes 1957; Godsoe 2004); Petit-Cap dune, 46.1801°N, 64.1407°W, 7 September 2012 and 6 August 2013, S. Tingley, photographic records (Tingley 2012, 2013);

https://doi.org/10.4039/tce.2017.40 Published online by Cambridge University Press

Maisonette dune, 47.8253°N, 64.9776°W, 30 July and 5 August 2012, S. Tingley, photographic records (Tingley 2012). **Prince Edward Island**: Brackley Beach, 14 July 1940, J. McDunnough, CNCI (Townes 1957; Godsoe 2004); Conway Sandhills, 46.7383°N, 63.9919°W, 18 September 2015, S.L. Robinson, NBMB (unpublished).

Anoplius cleora (confirmed host)
New Brunswick: Chatham, 15 August 1926, F. Johansen, CNCI (Evans 1951); Tracadie, 22 July 1939, J. McDunnough, CNCI (unpublished). **Nova Scotia**: Sable Island, West Light, 10 August 1969, F.W. Scott, NSPM (Wright 1989); two specimens, Sable Island, Meteorological Station, 23 July 1976 and 1977, B. Wright, NSPM (unpublished); Mitchells Island, 45.8941°N, 63.7971°W, 2016, J. Klymko, NBMB (unpublished). **Prince Edward Island**: two specimens, Brackley Beach, "Can. Nat. Park", 24 and 30 July 1940, J. McDunnough, CNCI (cited incompletely by Evans 1951); five specimens, Dalvay House, "Can. Nat. Park", 19 and 21 July 1940, J. McDunnough, CNCI (cited incompletely by Evans 1951).

Anoplius aethiops (potential host, see Discussion)
New Brunswick: Saint John, 2 September 1900, P.R. McIntosh, NBMB (unpublished); Saint John, 15 September 1902, A.G. Leavitt, NBMB (unpublished). **Nova Scotia**: three specimens, Kentville, 7, 21, and 22 August 1915, CNCI (Evans 1951).

Ontario and Québec records of *Ceropales bipunctata* not included in Godsoe (2004)
Ontario: two specimens, Leeds and Grenville County, Chaffeys Locks, Queens University Biological Station, 1–4 August 2005, on *Solidago*, L. Best, DEBU (unpublished); Bruce County, MacGregor Point Provincial Park near Sunset Point, 7 August 2011, dead on trail, S.M. Paiero, DEBU (unpublished); Haldimand-Norfolk Region, Turkey Point Provincial Park, 42.7117°N, 80.3422°W, 3–28 August 2009, open sandy field, malaise trap, S.M. Paiero, DEBU (unpublished); Haldimand-Norfolk Region, Turkey Point Provincial Park, site 2, 42.7078°N, 80.3414°W, 17 August 2011, savannah, S.M. Paiero, DEBU (unpublished). **Québec**: Rigaud (Townes 1957); Ste-Anne-de-Bellevue, 28 August 1931, LEMQ (unpublished); two specimens, Montréal, 13 August 1922 and 22 August 1925, J.W. Buckle, LEMQ (unpublished).

Discussion

The host of *Ceropales bipunctata* in New Brunswick dune habitat

This is the first time a host of *C. bipunctata* has been documented. Little is known about the hosts of *Ceropales* Latreille species in general, with information being available on just three of the 14 Nearctic species (Krombein 1979). The most common and widespread species, the Holarctic *C. maculata* (Fabricius), appears to have a wide host spectrum that includes two records from different subfamilies (Pompilinae: *Arachnospila scelesta* (Cresson) and Pepsinae: *Priocnemis* Schiødte, species unidentified). The other two species both have hosts in the subfamily Pepsinae (*C. hatoda* Brimley: *Ageniella mintaka* Brimley and *C. robinsonii* Cresson: *Phanagenia bombycina* (Cresson)). Note that Krombein (1979) and other authors misapplied the name *Ageniella partita* Banks to *A. mintaka* before Evans (1995). The newly recorded host of *C. bipunctata*, *A. cleora*, belongs in the subfamily Pompilinae. *Ceropales bipunctata* is one of the largest species in its genus (fore wing length 10–16 mm, see Townes 1957), which rules out most of the other pompilid species from our survey sites as potential hosts. The only species of comparable size besides *A. cleora* was *Evagetes ingenuus* (Cresson), itself a cleptoparasite. There are no published host records for the latter but it seems highly likely that it also parasitises *A. cleora* in our survey area. *Episyron biguttatus* (Fabricius), a common species at our sites, is typically smaller than *A. cleora*, and therefore a less likely host. Based on these observations it appears as though *A. cleora* is the only host of *C. bipunctata* on dune sites in the survey area.

Anoplius cleora belongs in the subgenus *Lophopompilus* Radoszkowski, which includes some of the largest species in the genus. It is associated with open sand habitats, mostly near bodies of water, and ranges from southern Canada to southern Mexico (Evans 1951, 1966; Kurczewski and Kiernan 2015). The species was widespread in the dunes surveyed (present at 19 of the 26 dune sites, see Table 1). The apparent absence of this species at seven dune sites is probably due to inadequate sampling effort since *C. bipunctata* was the main focus of our study. *Anoplius cleora* was not collected at the gravel

https://doi.org/10.4039/tce.2017.40 Published online by Cambridge University Press

beaches and gravel bars on Chaleur Bay, likely because suitable open sand substrate was lacking.

The spider *A. littoralis* is one of the main prey species of *Anoplius cleora*, representing up to 97% of prey taken in the eastern Great Lakes Region (Kurczewski and Kiernan 2015). This species is also widespread in sandy habitats, ranging from southern Canada to Panama (Dondale and Redner 1990).

Distribution of *Ceropales bipunctata* in the Maritimes

Our data show that *C. bipunctata* is widespread and common in dune habitat along New Brunswick's Gulf of Saint Lawrence Coast. An additional historic record from Saint John, where dunes are absent, is discussed below. *Ceropales bipunctata* and *A. cleora* are each known from two localities on Prince Edward Island (see above). Considering how much dune habitat exists on Prince Edward Island, both species are likely widespread there. There are no published records of *C. bipunctata* from Nova Scotia, and a search for material at the New Brunswick and the Nova Scotia Museums failed to produce any new records. *Anoplius cleora* is known from Sable Island and western mainland Nova Scotia (see above). It is likely that *A. cleora* is widespread in Nova Scotia dune habitat, and that *C. bipunctata* will be discovered there in future.

Conservation status of *Ceropales bipunctata* in the Maritimes

The predominant long-term threat to *C. bipunctata* in the Maritimes is probably loss of dune habitat due to sea-level rise and coastal development. Coastal dunes grow, shrink, and shift because of natural and anthropogenic causes (Nordstrom *et al*. 1990). A study in southeastern New Brunswick detected net losses of dune and beach habitat from 8–33% at five separate study sites between 1944 and 2001 (Hanson *et al.* 2006).

Sea-level rise can result in loss of dunes when barriers prevent landward migration (Feagan *et al.* 2005; O'Carroll *et al*. 2006). Sea rise projections between 2000 and 2100 for New Brunswick's Gulf of St. Lawrence Coast range between 50 and 60 cm (Forbes *et al*. 2006). This will accelerate dune migration and will result in habitat loss where coastal development prevents this movement. Decreasing coverage of sea ice may exacerbate this trend through beach erosion during winter storms as sea ice has a dampening effect on wave formation (Parkes *et al.* 2006).

Putative hosts of *Ceropales bipunctata* in Ontario, western Québec, and non-dune sites in the Maritimes

The comparison of locality data of *C. bipunctata* and potential hosts leads to three conclusions: (1) The New Brunswick host *Anoplius cleora* can be ruled out as host in Ontario and western Québec; (2) *Anoplius aethiops* is hypothesised to be the primary host of *C. bipunctata* in Ontario and western Québec; (3) the absence of *A. aethiops* from Point Pelee points to the existence of at least one secondary host in Ontario with *A. atrox* as the most likely candidate. (1) *Ceropales bipunctata* and *A. cleora* show minimal locality overlap in southwestern Ontario (Fig. 7). Historically, both species occurred together at Point Pelee and in Toronto. However, the overlap between the two species in Toronto is tenuous, with *A. cleora* having been collected there only once (one female, 9 August 1888, ROME). At Point Pelee, *A. cleora* occurs up to the present (last record from 2003, DEBU) whereas *C. bipunctata* was last collected in 1954 (Godsoe 2004). *Anoplius cleora* occurs mostly along the shores of Lake Huron and Lake Erie, where significant dune sites are located. *Ceropales bipunctata*, on the other hand, occurs mostly at interior sites or at lakeshore sites that are not sandy. We conclude that *A. cleora* is not a suitable host for Great Lakes populations of *C. bipunctata*. Otherwise, it would be inexplicable why the latter is absent from Great Lakes dunes, the primary habitat in New Brunswick. (2) The high geographic and temporal overlap between *C. bipunctata* and *A. aethiops* leaves little doubt that the latter is the primary host of *C. bipunctata* in Ontario and western Québec. This is not surprising since *A. aethiops* is closely related to *A. cleora*, and both species prey on Lycosidae (Table 3). (3) It can be assumed that the lack of records of *A. aethiops* from Point Pelee reflects a true absence of the species. Over the course of a century, a multitude of entomologists collected a significant number of spider wasps at Point Pelee, especially during the years 1920 (material at ROME); 1954 (material at CNCI); 1978–1983,

https://doi.org/10.4039/tce.2017.40 Published online by Cambridge University Press

1999–2000, and 2003 (material at DEBU). It seems unlikely that a large and conspicuous species like *A. aethiops* would have been missed. With *A. cleora* being ruled out as a potential host in Ontario (as discussed above), the most likely alternative host is *A. atrox* (see Table 2). This species was collected at Point Pelee on the same day by the same collector as *C. bipunctata* (one female, 23 August 1920, N.K. Bigelow, ROME). Like *A. aethiops*, *A. atrox* is a close relative of *A. cleora*. Unlike the other two species it preys on Pisauridae in addition to Lycosidae (Table 3). Other pompilid species are far less likely to be hosts. *Anoplius nigritus* (Dahlbom) and *A. semicinctus* (Dahlbom) (both in the subgenus *Arachnophroctonus* Howard) are restricted to sandy habitats unlike *C. bipunctata*. *Anoplius bengtssoni*, a close relative of *A. atrox,* has mainly crepuscular/nocturnal habits (Kurczewski and Kiernan 2015), making it largely inaccessible as for parasitisation. *Tachypompilus ferrugineus* (Say) preys on similar spiders as the *Anoplius* hosts but it uses different nest sites and belongs to a different genus (Table 3). It was only recently discovered at Point Pelee (one specimen, 2003, DEBU), almost half a century after *C. bipunctata* was last collected there (Godsoe 2004). *Poecilopompilus algidus* and *P. interruptus* prey on orb-weaving spiders (Araneidae) unlike the other hosts of *C. bipunctata*. *Entypus unifasciatus*, another predator of Lycosidae, is in a different subfamily (Pepsinae). *Anoplius depressipes*, which has flattened tarsi enabling it to pursue fishing spiders (Pisauridae) on the water surface, is restricted to habitats near water.

The historic occurrence of *C. bipunctata* at Saint John, New Brunswick (see above), deserves special consideration. The area is devoid of dunes, and there are no known records of *A. cleora*, though the gravel and sand tombolo associated with "Taylors Island", just west of Saint John, may offer suitable habitat. However, three specimens of *A. aethiops* were collected at Saint John around the same time as *C. bipunctata* (one female, one male, 3 September 1900, P.R. McIntosh, and one female, 15 September 1902, A.G. Leavitt, all NBMB). This suggests that *A. aethiops* could be a host for *C. bipunctata* at non-dune sites in the Maritimes. Further study is required since it cannot be ruled out that *A. cleora* might also be present. No other records of *A. aethiops* are known from New Brunswick, but given the paucity of survey effort in the region it remains unclear how widespread *A. aethiops* was or is in the province. Elsewhere in the Maritimes, *A. aethiops* has been recorded from Kentville, Nova Scotia (three specimens from August 1915, no collector mentioned, CNCI; see also Evans 1951).

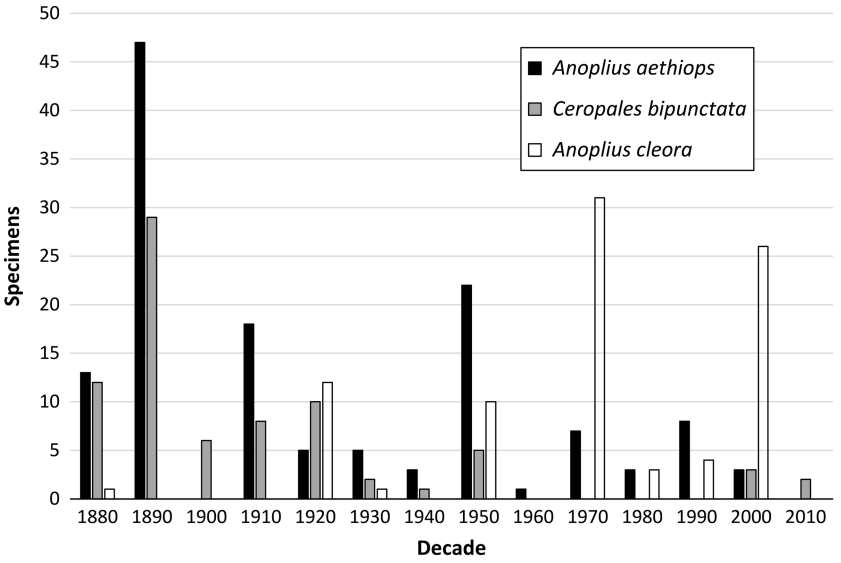
The decline of *Ceropales bipunctata* in Ontario and western Québec

Godsoe (2004) proposed that the decline of *C. bipunctata* may have been driven by a decline of its host species. The present data allows us to test this hypothesis. As discussed above, *C. bipunctata* appears to use different hosts within its Canadian range: *A. cleora* in dune habitats of the Maritimes, *A. aethiops* in Ontario, western Québec, and possibly non-dune habitat of New Brunswick, and *A. atrox*, a likely secondary host in southwestern Ontario. *Anoplius cleora* is at present widely distributed throughout shoreline dune habitats of New Brunswick and the Great Lakes. Consistent with Godsoe's hypothesis, *C. bipunctata* is doing well in New Brunswick dune habitat, where this species is being used as a host. In Ontario and western Québec, where *Anoplius aethiops* is the inferred primary host, the situation is very different. Both parasite and host formerly had robust populations there, but are currently close to extirpation (Fig. 8)[1]. Only two specimens of *A. aethiops* have been deposited in collections since 2000 (one specimen, Turkey Point Tract, 17 August 2003; one specimen, Queens University Biological Station, Chaffey's Lock, 13–18 August 2006; both DEBU). This is quite extraordinary considering that some of us (M.B. and co-workers at University of Guelph) were dedicating considerable effort on collecting aculeate wasps in Ontario. This recent rarity contrasts with significant numbers of specimens collected from 1888 to 1896 in Toronto (by W.M. Brodie; ROME, CNCI) and 1912 to 1920 in the Ottawa

[1]The same is likely true for non-dune populations of *C. bipunctata* and *A. aethiops* in the Maritimes. The only known records are from 1900 to 1915 (see above). More research is needed to ascertain the host relationships and status of non-dune populations in the Maritimes.

https://doi.org/10.4039/tce.2017.40 Published online by Cambridge University Press

Fig. 8. *Ceropales bipunctata* and potential host species: number of specimens from Ontario and western Québec deposited per decade. Explanations: data for *C. bipunctata* updated after Godsoe (2004), data for *Anoplius* species based on material at CNCI, DEBU, and ROME.



area (by F.W.L. Sladen and others, CNCI). These time periods also happen to be among the most productive for collecting *C. bipunctata*. The status of *A. atrox*, a likely secondary host in south-western Ontario, is similar to *A. aethiops*. Most of the material (24 specimens) was collected between 1890 and 1920 (at ROME, CNCI, DEBU) whereas only two specimens have been collected since 2000 (at DEBU). The different fate of *C. bipunctata* in Ontario/Québec versus the Maritimes strongly supports the hypothesis that the decline in Ontario and western Québec is indeed driven by a decline of its hosts.

The cause of decline of *A. aethiops* and *A. atrox* is unclear and warrants further study. Both species inhabit old fields, meadows, forest edges, and prairies (Evans 1951; Kurczewski and Kiernan 2015). The loss of unimproved farmland and prairie habitat may be a factor that contributed to their decline in Ontario or Québec. Another parameter that could be influential is the availability of large cursorial spiders (Lycosidae, and perhaps Pisauridae) that are used as prey by these species.

Outlook

The results of this study bring up a number of interesting new questions. What are the preferred hosts of *C. bipunctata* in other parts of its range? Is there a similar difference in host specialisation between coastal and interior populations in the United States of America? Do dune and non-dune populations of the Canadian Maritimes represent different host races, or are they part of a single host race that has a broader host spectrum than Ontario/Québec populations? How much are the host races of *C. bipunctata* differentiated genetically? A strong genetic differentiation would place further emphasis on conservations efforts for endangered host races.

Conservation status of *Ceropales bipunctata* in Canada

The results of this survey demonstrate that *C. bipunctata* is not at risk of extirpation from New Brunswick, or therefore Canada, in the foreseeable future. As a result, *C. bipunctata* has been moved from COSEWIC's high-priority candidate list to its low-priority candidate list. It is recommended, however, that *C. bipunctata* and its hosts be assessed at the provincial level by the Committee on the Status of Species at Risk in Ontario (COSSARO), as the strong evidence of decline in Ontario may warrant listing the species on the Ontario Endangered Species Act.

https://doi.org/10.4039/tce.2017.40 Published online by Cambridge University Press

Acknowledgements

Our field survey was funded by the New Brunswick Wildlife Trust Fund. Eric Tremblay arranged collecting permits for Kouchibouguac National Park of Canada. Stuart Tingley provided information about his observations of *C. bipunctata* in New Brunswick. Steven Paiero, Stephen Marshall (University of Guelph), Stéphanie Boucher, Terry Wheeler (Lyman Entomological Museum), Katherine Ogden (Nova Scotia Museum), and Sophie Cardinal (Canadian National Collection of Insects) kindly provided data on spider wasps from their collections. Brad Hubley and Chris Darling (Royal Ontario Museum) made *Anoplius* specimens from their collection available for verification. Andrew Hebda provided access to the Nova Scotia Museum insect collection. Donald F. McAlpine provided access to the New Brunswick Museum insect collection. Sean Blaney reviewed an earlier draft of this manuscript.

Supplementary material

To view supplementary material for this article, please visit https://doi.org/10.4039/tce.2017.40.

References

Dondale, C.D. and Redner, J.H. 1990. The insects and arachnids of Canada. The wolf spiders, nurseryweb spiders, and lynx spiders of Canada and Alaska (Araneae: Lycosidae, Pisauridae, and Oxyopidae). Agriculture Canada Publication 1856. The Insects and Arachnids of Canada, **17**: 1–383.

Evans, H.E. 1950. A taxonomic study of the Nearctic spider wasps belonging to the tribe Pompilini (Hymenoptera: Pompilidae). Part I. Transactions of the American Entomological Society, **75**: 133–270.

Evans, H.E. 1951. A taxonomic study of the Nearctic spider wasps belonging to the tribe Pompilini (Hymenoptera: Pompilidae). Part II. Genus *Anoplius* Dufour. Transactions of the American Entomological Society, **76**: 207–361.

Evans, H.E. 1966. A revision of the Mexican and Central American spider wasps of the subfamily Pompilinae (Hymenoptera: Pompilidae). Memoirs of the American Entomological Society, **20**: 1–442.

Evans, H.E. 1995. Notes and descriptions of Nearctic *Ageniella* (Hymenoptera, Pompilidae). Journal of the Kansas Entomological Society, **68**: 451–460.

Feagan, R.A., Sherman, D.J., and Grant, W.E. 2005. Coastal erosion, global sea-level rise, and the loss of sand dune plant habitats. Frontiers in Ecology and the Environment, **3**: 359–364.

Forbes, D.L., Parkes, G.S., and Ketch, L.A. 2006. Sea-level rise and regional subsidence. *In* The impacts of sea level rise and climate change on the coastal zone of southeastern New Brunswick. Environment Canada, New Brunswick, Canada. Pp. 34–94.

Godsoe, W. 2004. Evidence for the extirpation of *Ceropales bipunctata* Say (Hymenoptera: Pompilidae) in Ontario. Journal of the Entomological Society of Ontario, **134**: 135–140.

Hanson, A., Forbes, D., Bérubé, D., O'Carroll, S., Mahoney, M., Ollerhead, J., *et al*. 2006. Ecosystem impacts. *In* The impacts of sea level rise and climate change on the coastal zone of southeastern New Brunswick. Environment Canada, New Brunswick, Canada. Pp. 402–485.

Krombein, K.V. 1979. Superfamily Pompiloidea. *In* Catalog of Hymenoptera in America north of Mexico. Volume 2 Apocrita (Aculeata). *Edited by* K.V. Krombein, P.D. Hurd, D.R. Smith, and B.D. Burks. Smithsonian Institution Press, Washington, District of Columbia, United States of America. Pp. 1523–1571.

Kurczewski, F.E. and Edwards, G.B. 2012. Hosts, nesting behavior, and ecology of some North American spider wasps (Hymenoptera: Pompilidae). Southeastern Naturalist, **11**(Monograph 4): 1–71.

Kurczewski, F.E. and Kiernan, D.H. 2015. Analysis of spider wasp host selection in the eastern Great Lakes region (Hymenoptera: Pompilidae). Northeastern Naturalist, **22**(Monograph 11): 1–88.

Nordstrom, K., Psuty, N., and Carter, B. 1990. Coastal dunes: form and process. John Wiley and Sons, Toronto, Ontario, Canada.

O'Carroll, S., Bérubé, D., Forbes, D.L., Hanson, A., Jolicoeur, S., and Fréchette, A. 2006. Coastal erosion. *In* The impacts of sea level rise and climate change on the coastal zone of southeastern New Brunswick. Environment Canada, New Brunswick, Canada. Pp. 324–401.

Parkes, G.S., Manson, G.K., Chagnon, R., and Ketch, L.A. 2006. Storm-surge, wind, wave and ice climatology. *In* The impacts of sea level rise and climate change on the coastal zone of southeastern New Brunswick. Environment Canada, New Brunswick, Canada. Pp. 95–262.

Tingley, S. 2012. *Ceropales bipunctata* [online]. Available from bugguide.net/node/view/704357, bugguide.net/node/view/702208, and bugguide.net/node/view/701885 [accessed 6 January 2017].

Tingley, S. 2013. *Ceropales bipunctata* [online]. Available from bugguide.net/node/view/826211 [accessed 6 January 2017].

Townes, H. 1957. Nearctic wasps of the subfamilies Pepsinae and Ceropalinae. Bulletin of the United States National Museum, **209**: 1–286.

Wright, B. 1989. The fauna of Sable Island. Curatorial Report 68. Nova Scotia Museum, Halifax, Nova Scotia, Canada.