

Research Article

Abrupt Geographical Transition between Aposematic Color Forms in the Spittlebug *Prosapia ignipectus* (Fitch) (Hemiptera: Cercopidae)

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Over most of its range populations of the spittlebug *Prosapia ignipectus* (Fitch) (Hemiptera: Cercopidae) are monomorphic for black dorsal coloration. At the far northeastern margin of the species range in Maine, a cluster of populations is monomorphic for the presence of traverse orange dorsal lines against a black background. The narrow gap separating monomorphic black and monomorphic lined populations is less than 10 km wide, shows no evidence of a hybrid zone, and is without consequential physical barriers or ecological breaks. This sharp and unexpected division of color forms seems to have persisted for at least 90 years. It appears to be the sharpest divide ever recorded between geographically adjacent populations monomorphic for alternative aposematic color forms. About 45 kilometers to the southwest of this dividing line, three closely situated populations, surrounded by monomorphic black populations, are polymorphic for the two color forms. These observations are at variance with several expectations for aposematic species: (1) that local populations will be monomorphic for warning coloration, (2) that adjacent populations monomorphic for different local color forms will be linked by populations with mixed or hybrid forms, and (3) that geographic boundaries between contrasting aposematic color forms should be temporally unstable.

1. Introduction

Many organisms have conspicuous coloration that warns potential predators of strong defenses, such as toxic chemical compounds, potent venom delivery systems, or particularly effective escape mechanisms [1, 2]. This aposematic, or warning, coloration signals to potential predators that a particular species is not a desirable subject for pursuit. Individual predators learn to avoid aposematic prey through initial unpleasant or unfruitful encounters, sparing subsequently encountered individuals with similar warning coloration from predation. This results in positive frequency-dependent selection for conspicuous coloration. As a result, local populations should become monomorphic for a single color form [1–3]

and, by extension, closely adjacent populations should over time become monomorphic for the same color form through displacement of one form by another [4–6]. Here we detail the existence of local populations of the spittlebug *Prosapia ignipectus* (Fitch) that violate these expectations.

The genus *Prosapia* has 14 species distributed from the northeastern United States (and far Southern Ontario, Canada) to Colombia [7–9]. It falls within the family Cercopidae (Hemiptera: Cercopoidea), a large, predominantly tropical group with about 475 New World species [9, 10]. Only two species of Cercopidae are found in the USA (Figure 1): *Prosapia ignipectus* (Fitch) (Figures 2(a) and 2(b)), the northernmost representative of the family in the New World, and *Prosapia bicincta* (Say) (Figures 3(a) and

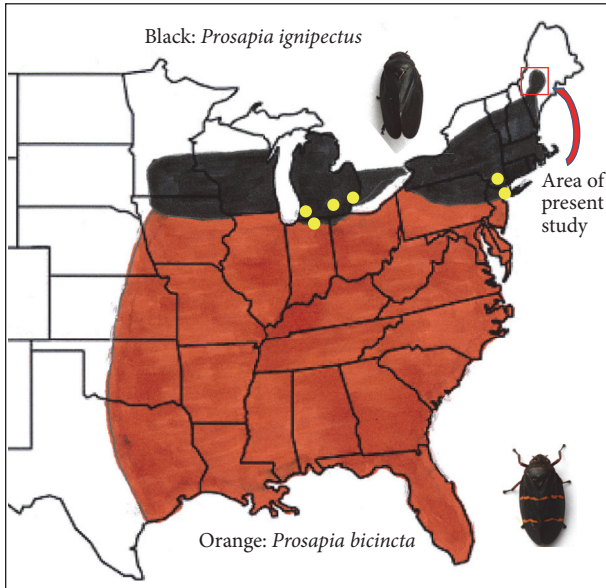


FIGURE 1: Approximate species ranges of *Prosapia ignipectus* (in black) and *Prosapia bicincta* (in orange). The populations examined in this study lie in the far northeastern portion of the *P. ignipectus* range in the area of the state of Maine outlined in red (see Figure 6). Yellow dots represent the occurrence of populations with mixed color forms, nominally all *P. ignipectus*, towards the southern part of the *P. ignipectus* range (see text for details).

3(b)), a pasture pest in the southeastern USA [11]. The two species are morphologically similar. *P. ignipectus* was originally described by Fitch [12] as *Monecphora ignipecta*. It was synonymized as a variety of *Monecphora bicincta* by Van Duzee [13]. Fennah designated *P. bicincta* as the type species of the newly created genus *Prosapia* [14] and later included the form *ignipecta* as a geographical subspecies of *P. bicincta* [15]. Hamilton reinstated *P. ignipectus* as a distinct species [7].

P. ignipectus is distributed across the northeastern USA from Minnesota to Maine and in the southernmost portion of Ontario, Canada. *P. bicincta* is distributed in the southeastern USA from Oklahoma to Florida (Figure 1). The two species are distinguished by geographical distribution, by subtle differences in the male genitalia [7], and by differences in host plant associations. *P. ignipectus* is monophagous on the late season C4 perennial grass *Schizachyrium scoparium* (Michx.) Nash, Little Bluestem [16, 17]. Nymphs live on Little Bluestem roots. Adults emerge in late July or early August and feed on stems of the host [18, 19]. Although the range of Little Bluestem broadly overlaps the range of *P. bicincta* (compare Figure 1 with [20]), *P. bicincta* has never been reported on Little Bluestem and appears to be absent from Little Bluestem in New Jersey (VT observations) and North Carolina (J. Urban, pers. comm.). *P. bicincta* is polyphagous on a wide variety of C4 grasses [11, 17]. Nymphs live on the roots of host grasses and adults on the upper parts of the same hosts. Adult males of *P. bicincta* feed on ornamental hollies (*Ilex* spp.) in addition to C4 grasses [21].

Adults of both species exhibit reflex bleeding ([22] and Figures 4(a) and 4(b)). When molested they release an

odiferous yellow liquid from their tarsi. This behavior deters some predators and is probably the primary basis for the colorful patterns widespread among the Cercopidae [22] (see examples of striking coloration in [9, 10]). Consistent with this behavior, both *P. bicincta* and *P. ignipectus* have dorsal coloration that is conspicuous in natural settings. *P. bicincta* individuals have a black dorsal surface traversed by a single narrow lateral orange line across the widest part of the pronotum and a pair of narrow orange lines across the elytra (Figure 3(a)). With exceptions described below, *P. ignipectus* individuals have uniformly black dorsal coloration (Figure 2(a)). Both species stand out against the grass stems on which they characteristically sit prominently exposed (Figures 5(a) and 5(b)). The abdomen of *P. ignipectus*, which is visible while flying, is predominantly red or reddish orange (Figures 2(b) and 5(b)), as are the legs, although there is variation in the intensity of the red and in its combination with darker tones on the legs and on the red and black patterned ventral surface. In contrast, red markings on the abdomen and legs of *P. bicincta* are more subdued (Figure 3(b)).

In 1920, while collecting in preparation for a report on the Orthoptera of Maine, Albert Morse stumbled across a *Prosapia* population in Norridgewock, Maine, which consisted entirely of individuals with *P. bicincta*-like dorsal coloration [18, 23]. Morse interpreted these specimens as a disjunct New England occurrence of *P. bicincta*. With the exception of one piece of contemporary work [19], Morse's observation of lined *Prosapia* in Maine went unremarked and uninvestigated for several decades. Many, including the authors, assumed that the report of lined specimens in Maine, about 500 km northeast of the known range of *P. bicincta*, was in error. However, reexamination of Maine populations has vindicated Morse's original observation, though not his interpretation, and disclosed an unusual case of polymorphic aposematism rivaling, on a smaller scale, some of the paradigmatic cases observed in the tropics [24].

2. Materials and Methods

In September 2003, VT sought Morse's original locality and found a population of lined *Prosapia* living on Little Bluestem 6 km north of Norridgewock, Maine. A second lined population was found 3.5 km north of nearby Solon Center, Maine. In 2004 VT revisited these locations and collected lined *Prosapia* in a number of nearby localities, as well as a large sample of black specimens in close proximity in New Vineyard, Maine. Examination of three historical Norridgewock specimens collected by Morse and preserved in the Museum of Comparative Zoology (MCZ) of Harvard University confirmed that lined individuals collected in 2003 and 2004 were indistinguishable from those Morse collected in the same locale more than 80 years before.

In 2006 VT made systematic investigations of the areas to the south, east, and northeast of Norridgewock. These observations confirmed that the populations in the vicinity of Norridgewock represent the northeasternmost populations of *P. ignipectus*. In 2012 VT and GC made an intensive survey



FIGURE 2: *Prosapia ignipectus*, black form: (a) dorsal view and (b) ventral view. Photographs by Tom Murray.

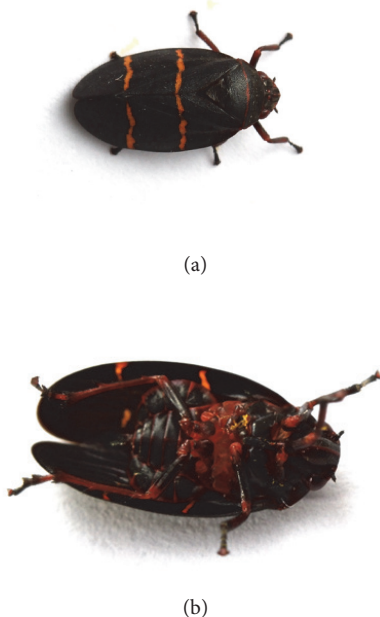


FIGURE 3: *Prosapia bicincta*: (a) dorsal view and (b) ventral view. Photographs by Brandon Woo.

of Maine roadside populations of Little Bluestem from West Bethel, near the New Hampshire border, east to Norridgewock, making a special effort to determine the northern boundary of the *Prosapia* distribution and the location of the boundary between the lined and unlined populations. Little Bluestem is a particularly tractable substrate for collections. It grows in easily accessible clumps on the verges of public roads and is readily swept for collections. Specimens were preserved in 95% ethanol or mounted dry on pins. Voucher specimens have been deposited in the American Museum of Natural History (AMNH) and the MCZ.

In 2013 and 2014 VT swept Little Bluestem in New Jersey and New York in the vicinity of the eastern *P. bicincta*-*P. ignipectus* species boundary. In addition, GC and VT

examined New York City area historical *Prosapia* specimens in the collection of the AMNH and specimens collected by James Bess in Indiana and Michigan near the local *P. bicincta*-*P. ignipectus* species boundary.

3. Results

3.1. Both the Lined and Black Maine Forms Are *P. ignipectus*, Which Is Distinct from *P. bicincta*. Morse believed that his Norridgewock specimens represented a geographically disjunct population of *P. bicincta*, a judgment apparently based solely on the presence of the lined orange pattern characteristic of *P. bicincta*. GC dissected genitalia of representative males of southern *P. bicincta* and black and lined specimens from the Maine populations in question. Male genitalia of the black and lined Maine forms are indistinguishable. Both differ from the genitalia of *P. bicincta* consistent with the subtle interspecific differences in the apices of the styles illustrated by Hamilton [7]. We conclude that both color forms belong to *P. ignipectus* and, in concurrence with Hamilton [7], that *P. ignipectus* is distinct from *P. bicincta*. The specific difference is also supported by subtle differences in shape between the species (*P. ignipectus* more slender and *P. bicincta* more robust), by the consistent difference in host plant associations noted above, and by the allopatric distribution of the taxa (Figure 1). DNA bar code analysis, based on sequences of a single mitochondrial gene, indicates that the species are closely related [25], probably reflecting recent speciation.

3.2. Populations Monomorphic for the Lined Form Are Uniquely Clustered at the Northeastern Species Margin and Separated from Populations Monomorphic for the Black Form by Less Than 10 km. Table 1 reports the color forms encountered in 32 *P. ignipectus* collections made in 2003, 2004, 2006, and 2012 between the New Hampshire border and Norridgewock. These populations represent the northeasternmost part of the species range. To the immediate south, between Norridgewock and the Atlantic coast, Little Bluestem appears to be absent. In some areas east and northeast of Norridgewock, for example, in parts of the Penobscot River Valley, Little



FIGURE 4: Reflex bleeding in *Prosapia bicincta*: (a) droplets of yellow liquid emanating from tarsi, photograph by Sam Houston; (b) bleeding in response to attack by spider (see droplet of yellow liquid on front tarsus to left in picture and another droplet caught in the spider web in the background), photograph by Andy Williams.



FIGURE 5: *Prosapia ignipectus*, lined form: (a) sitting characteristically exposed while feeding on stems of Little Bluestem and (b) mating among stems of Little Bluestem, female above and male below.

Bluestem is abundant but *P. ignipectus* is absent. In contrast, *P. ignipectus* is common on Little Bluestem from Norridgewock north almost to Bingham in the Kennebec River Valley and along some of its tributaries to the west as well as in a portion of the Androscoggin River Valley centering on the city of Rumford. North and west of these populations, occasional Little Bluestem patches without *P. ignipectus* extend up small river valleys into the Longfellow Mountains. The absence of *P. ignipectus* on Little Bluestem to the north and east indicates that factors other than host plant distribution limit its range.

Populations monomorphic for the lined form (Figures 5(a) and 5(b)) lie in a discrete cluster at the extreme northeastern edge of the species distribution (Figure 6). They encompass an area of about 675 km² bounded roughly by the towns of Norridgewock, Bingham, Carrabassett, and New Portland. Less than 10 km to the southwest in New Vineyard they are replaced by populations essentially monomorphic for the black form (with the exception of a single male individual taken in New Vineyard in 2004 that had

a partially obscured single orange line across the pronotum) (Figure 6 and Table 1). These populations are linked to other monomorphic black populations to the southwest by a monomorphic black population in Wilton. The area in which the collections were taken varies in elevation from about 75 to 250 m and consists of low forest cover, broken by bogs, streams, human habitations, and farmland. There are no significant barriers to *P. ignipectus* dispersal and the roadside habitats in which *P. ignipectus* occurs are similar throughout the area. All of the monomorphic lined populations lie in the Kennebec River drainage, but this drainage also includes the monomorphic black populations in New Vineyard and Wilton. Monomorphic black populations to the immediate southwest lie in the Androscoggin River drainage (Figure 6).

3.3. A Geographically Limited Area Near Rumford Has Populations with Mixed Color Forms. Most of the populations along the Androscoggin River and its tributaries are monomorphic for the black color form, but three clustered populations,

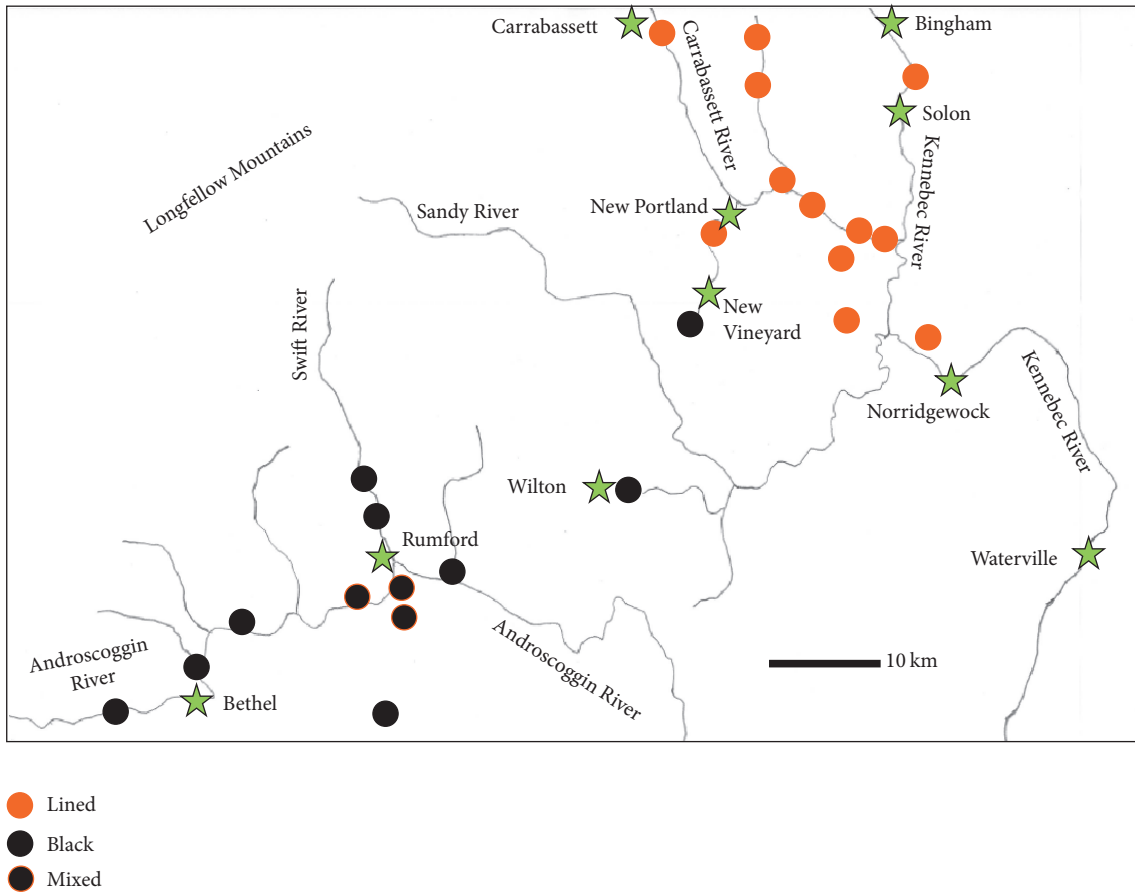


FIGURE 6: Distribution of *Prosapia ignipectus* populations with lined, black, and mixed dorsal color forms at the northeastern extremity of the species range in Maine. Some closely spaced localities sampled are represented by a single color symbol. In New Vineyard, a single partially lined specimen was observed among 114 specimens collected; the rest were black.

one in Rumford Center and two in nearby South Rumford on the opposite side of the river, exhibit a mixture of black, lined, and partially lined individuals (Figure 6 and Table 1). These populations are 45 kilometers from the nearest monomorphic lined population to the northeast. In each case the lined individuals are phenotypically variable: some fully lined and some partially lined, most of the partially lined specimens with a single line across the pronotum. All populations sampled in Maine to the south and southwest of Center Rumford as well as in adjacent parts of New Hampshire were monomorphic for the black color form (Figure 1 and VT unpublished observations), consistent with Morse's observations in Maine almost a century earlier [18].

3.4. A Few Populations near the *P. bicincta*-*P. ignipectus* Species Boundary Exhibit Mixed Color Forms. The AMNH collection includes one black specimen and one lined specimen (two elytral lines but no pronotal line) of *P. ignipectus* collected in Tuxedo Park, NY, in 1928. It also includes two lined specimens (one male and one female) collected along with two black specimens (one male and one female) on Staten Island, NY, in 1970. A sweep of Little Bluestem 20 km from Tuxedo Park by VT in August 2014 yielded 42 *P. ignipectus* specimens, all

black. The Staten Island site appears to have been obliterated by residential development. Several other AMNH historical collections from northern New Jersey and Long Island, NY, consist entirely of specimens of the black color form.

In 1993–2000 James Bess collected short series of *P. ignipectus* specimens, some lined and some black, from Little Bluestem in fens near the Michigan-Indiana border, close to what appears to be the boundary between the *P. ignipectus* and *P. bicincta* distributions in the central Midwest (see [26] for background on the habitats and insect associations). At Liberty Fen in Jackson Co., MI, Bess collected a lined male and a black male. At Sawmill Fen in LaGrange Co., IN, he collected a lined male and a black female. At Indian Bowl Fen and nearby in Berrien Co., MI, he collected a lined male and a black male. At Brant Road Fen in Oakland Co., MI, he collected a lined male.

3.5. Additional Natural History Observations. Little Bluestem, a grass of nutrient-deficient soils, is an attractive host for spittlebugs, probably because it exhibits associative nitrogen-fixation [17]. During our sampling we searched for and found *Prosapia ignipectus* nymphs living slightly below ground level in Little Bluestem clumps, confirming

TABLE 1: *Prosapia ignipictus* collections in Maine, September 2003–August 2012. All specimens were swept from patches of Little Bluestem (*Schizachyrium scoparium* (Michx.) growing on or near roadside verges.

Date	Abbreviated locality designation	County	Latitude N	Longitude W	Black ♂	Black ♀	Lined ♂	Lined ♀	Partially lined ♂	Partially lined ♀
10-ix-2003	Rte. 201A 6.5 km N. of Norridgewock	Somerset	44 44 54.72	69 50 07.67				11		
09-viii-2004	Rte. 201A 6.5 km N. of Norridgewock	Somerset	44 44 54.72	69 50 07.67			29	45		
09-viii-2004	Rte. 16.1 km SE of North New Portland	Somerset	44 54 57.37	70 00 30.33			9	42		
09-viii-2004	Rte. 27.1 km SE of New Portland	Somerset	44 52 32.54	70 06 48.90			2	3		
10-ix-2003	US 202 between Solon & Bingham	Somerset	44 59 00.16	69 52 01.34				5		
09-viii-2004	US 202 between Solon & Bingham	Somerset	44 59 00.16	69 52 01.34			31	15		
16-viii-2006	US 202 between Solon & Bingham	Somerset	44 59 00.16	69 52 01.34			2	10		
28-vii-2012	US 2 & Old Jay Street, Wilton	Franklin	44 35 00.34	70 14 07.21	8	10				
09-viii-2004	Rte. 27 & Lowell Drive, New Vineyard	Franklin	44 45 05.44	70 08 05.42	45	62			1	
28-vii-2012	Rte. 27 & Lowell Drive, New Vineyard	Franklin	44 45 05.44	70 08 05.42	3	1				
28-vii-2012	Rte. 27 & Basin Road S. of New Vineyard	Franklin	44 46 23.59	70 07 42.33	1	1				
28-vii-2012	Rte. 16.1 km W. of North Anson	Somerset	44 51 42.31	69 55 43.65			2	4		
09-viii-2004	Rte. 16.2 km W. of North Anson	Somerset	44 52 01.30	69 56 24.47			1	5		
28-vii-2012	Rte. 16 & Wentworth Road	Somerset	44 52 51.67	69 58 10.10			4	17		
28-vii-2012	Long Fall Dam Road 2 km N. of Sandy Stream	Somerset	44 59 25.20	70 03 05.35			19	17		
28-vii-2012	Long Fall Dam Road & Old County Road	Somerset	45 02 05.12	70 03 55.19			4			
28-vii-2012	Rte. 16 & 27 & Carriage Road, Carrabassett	Franklin	45 04 31.88	70 12 41.95			15	19		
30-vii-2012	US 2 W. of Bethel	Oxford	44 24 03.17	70 51 59.98	7	2				
30-vii-2012	Rte. 232 between Woodstock & Hanover	Oxford	44 26 11.71	70 39 16.17	1	2				
30-vii-2012	US 2 between Bethel & Newry	Oxford	44 27 57.07	70 48 02.33	5	3				
30-vii-2012	US 2 between Newry & Hanover	Oxford	44 29 04.92	70 43 54.22	1	1				
30-vii-2012	US 2 & Dragoons Road, Rumford	Oxford	44 31 00.39	70 33 36.73	4	4	3	2	2	2
30-vii-2012	US 2 near Dixfield	Oxford	44 31 52.17	70 29 03.67	1	2				
30-vii-2012	South Rumford Road, South Rumford	Oxford	44 32 03.43	70 36 26.13	1	1	1	1		1
30-vii-2012	Rte. 17 N. of Mexico	Oxford	44 35 27.50	70 33 41.72	6	1				
30-vii-2012	US 2 W. of East Wilton	Franklin	44 36 21.79	70 12 09.12	2	2				
30-vii-2012	Rte. 148.2 km W. of Rte. 43, Industry	Somerset	44 46 09.82	69 58 04.42			10	2		
30-vii-2012	Rte. 234 near Town Farm Road	Somerset	44 51 26.96	69 55 59.06			4	8		
13-viii-2012	Milton Rd. & Waite Road	Oxford	44 27 16.92	70 35 56.56	1	4				
13-viii-2012	Near intersect Skyway & Sunday River Roads	Oxford	44 28 16.10	70 50 26.78	9	6				
13-viii-2012	South Rumford Road near No View Farm	Oxford	44 28 56.45	70 38 16.23	4	1				
13-viii-2012	Wyman Hill Road, South Rumford	Oxford	44 31 09.95	70 31 40.24	4	16	1	1	2	
<i>Total</i>					103	119	137	207	5	3

♀: female; ♂: male.

speculation by Morse [18] and Boring [19] and a statement by Hamilton [16] that the nymphs are root feeders.

Also, while surveying the Little Bluestem associated populations recorded in Table 1, we collected four other spittlebug species, all of the family Aphrophoridae: *Philaenus spumarius* and *Neophilaenus lineatus* (both introduced from Eurasia) and the native spittlebugs *Lepyronia quadrangularis* and *Philaenarcys killa*. Only *L. quadrangularis* occurred in sizable numbers at multiple sites. It is clearly associated with Little Bluestem [17] but has a much broader host range [16]. *P. killa*, in contrast, is a Little Bluestem specialist [17]. In this study it cooccurred with *P. ignipectus* only in West Bethel, the westernmost Maine site sampled. It cooccurs frequently with *P. ignipectus* on Little Bluestem in Central New Hampshire (VT observations). *P. spumarius* occurs primarily on broadleaved herbs [16] and was likely associated with herbaceous dicots mingled with Little Bluestem. *N. lineatus* lives primarily on cool season C3 grasses [17] and was likely associated with C3 grass species mingled with Little Bluestem.

4. Discussion

The observation that *P. ignipectus* has populations monomorphic for alternative aposematic color forms sharply separated by only a few kilometers seems to be unique among polymorphic aposematic organisms. The closest parallels that have come to our attention form part of a complex Müllerian mimicry system involving the millipede genera *Apheloria* and *Brachoria* in the Appalachian Mountains of the USA. Marek and Bond [27] present detailed data suggesting that, in three of the seven species they investigated, populations monomorphic or nearly monomorphic for contrasting light and dark color forms occur in close geographical proximity. In the taxon *Apheloria* clade B a series of apparently monomorphic “chess” color form populations is separated from an apparently monomorphic “striped” color form population by only about 20 km. Similarly, in *Brachoria mendota* a series of populations that appear to be monomorphic for the “taillight” color form is separated by only 8–10 kilometers from populations that appear to be monomorphic for the contrasting “caution/road” color forms. Neither of these cases involves separation by a major mountain ridge, but a high ridge does separate a single population of *Brachoria dentata* monomorphic for the “headlight” color form from populations apparently monomorphic for the contrasting “caution/road” color form about 10 km distant. In many of these localities the sample sizes are small, but in each case the distributions suggest a sharp boundary of less than 10–20 km separating populations monomorphic or nearly monomorphic for contrasting aposematic forms.

In other reported cases, populations monomorphic for alternative warning color forms are clearly linked by mixed populations in the intervening territory. For example, in the bumblebee *Bombus melanopygus*, California populations monomorphic for red abdominal color are separated from Washington State populations monomorphic for black

abdominal color by a 600 km cline of populations polymorphic for both [28, 29]. In Peru, populations of the poison-dart frog *Ranitomeya imitator* lying just 15 km apart are monomorphic for alternative aposematic color forms but are linked by intermediate mixed populations [30, 31]. In the well-studied Müllerian mimicry system involving the Neotropical butterflies *Heliconius erato* and *Heliconius melpomene*, populations of each species monomorphic for parallel mimetic forms are linked by hybrid clines [4, 32]. At one location in Peru, populations monomorphic for the “postman” and “ray” forms of these butterflies are separated by a zone as narrow as 10 km [3], but in this and similar cases hybrid linking populations are the rule (see Figure 1 of [33]).

Sharp contact zones imply strong natural selection; the narrower the zone the stronger the selection [3]. The continued separation for at least 90 years of Maine lined and black populations in close proximity suggests that strong natural selection is maintaining homogeneity for the alternative color forms. Though there are no direct data bearing on their dispersal ability, *P. ignipectus* adults are strong fliers, making substantial gene flow over the short distance between monomorphic black and monomorphic lined populations not only possible but likely. In addition, there are indications that contact zones between aposematic forms may be temporally unstable and subject to a sweep of one form by another [4–6]. This raises two questions concerning the Maine populations: what special selective forces, if any, maintain the lined color form and why is the division between the forms so sharp and, apparently, stable? We say apparently stable recognizing that Morse seems to have sampled only one location in the area covered in this study. He reported observing black specimens in unspecified locations between Norway, Maine, and Norridgewock [18], indicating that the separation in 1920 was, at most, shorter than the 80 km separating those locations.

Part of the answer may lie in the migratory avian predators that *P. ignipectus* encounters in its Maine habitats. Insectivorous birds migrating to and from the southeastern USA would encounter *P. bicincta* in abundance in many grassy habitats, including cattle pastures. Likewise, birds migrating to and from Mexico and Central America would encounter Neotropical pasture spittlebugs with similar lined color patterns, including the phenotypically similar species *Prosapia simulans*, *Aeneolamia contigua*, and *Aeneolamia albofasciata* [34, 35], which constitute parts of a putative Müllerian mimicry ring in pastures and sugar cane plantations from Mexico to Costa Rica (VT observations).

It is likely that some of the avian predators that encounter *P. ignipectus* in Maine have already learned an aversion to lined color patterns at points south and are predisposed to select in favor of lined color patterns in Maine. However, this in itself does not explain why the lined form has achieved monomorphism in one small geographical area over a protracted period of time. Work with the arctiid moth *Parasemia plantaginis* in Finland suggests that the composition of local avian predator communities can influence the relative fitness of polymorphic aposematic color forms [36] and local populations of the same avian predator can

vary in their response to aposematic prey [37]. This suggests that detailed study of the foraging and migration patterns of Maine insectivorous birds might shed light on *P. ignipectus* color form selection. There are hints in the literature that some Neotropical insectivorous birds specialize in jumping Hemiptera, including Cercopidae [38, 39], though none of the species studied are migratory to Maine.

Independent of the selective factors that might maintain the two distinct aposematic color forms in close proximity, the sharp boundary, apparently without intermediate polymorphic populations, itself poses interesting evolutionary questions. How is it possible to maintain such a sharp boundary for a strong flier in a region with no significant barriers to dispersal? One possibility is that factors other than aposematic selection reinforce the separation of populations. For example, Lis et al. [40] suggest that the endosymbiont bacterium *Wolbachia* may play a role in maintaining genetic barriers at contact zones between mitochondrial lineages of the spittlebug *Philaenus spumarius* in Eastern Europe. Likewise, in the absence of definitive genetic evidence to the contrary, it is possible that the lined and unlined Maine populations represent an undetected case of cryptic speciation. If so, similar questions regarding lack of long-term selection for a single color form would still apply, but in the context of two species, not one.

The existence of three Rumford area populations polymorphic for aposematic forms violates the expectation that local populations of aposematic organisms will be monomorphic, but there is ample precedent for polymorphic warning coloration in the Cercopidae. For example, *P. simulans*, an abundant and widespread pasture grass pest in Mexico and Central America, has females polymorphic for a lined form and a dark form [34, 35]. Color polymorphism is also present in populations of the Costa Rican pasture pests *Prosapia plagiata* and *Zulia vilior* [35], the Costa Rican *Heliconia* spittlebug *Mahanarva costaricensis* [41], and the South American sugar cane pest *Mahanarva bipars* [42], among others. Consequently, whether the Rumford area local polymorphism proves to be stable or fleeting, it is consistent with the observation that the Cercopidae as a group are susceptible to color polymorphism [10].

Interestingly, local polymorphisms for aposematic color forms also occur in many other taxa, despite ample theoretical expectation that they should be rare and transient [1, 2, 6, 36, 43–46]. These “almost embarrassingly frequent” occurrences of polymorphism [6, 47] may be due to simultaneous multiple predator selection for warning coloration and rarity [48]; to spatially varying selection pressures in complex Müllerian mimicry systems [6]; to complexities of predator sampling strategy [47]; to balancing selection for warning coloration, sexual signaling, and thermal melanism [2]; or to a mélange of factors [43, 49]. Additionally, it has been suggested that relatively weak defenses [43, 50–52] or defenses that vary in effectiveness against mixed predators [53] might be especially conducive to polymorphism for aposematic forms. This hypothesis may be applicable to spittlebugs as a group, including some species in the Aphrophoridae and Clastopteridae that lack the reflex bleeding characteristic of the Cercopidae (see [54] and Figures 7 and 42–45 in [16]).

The rare cooccurrence of black and lined forms of *P. ignipectus* in populations close to the *bicincta-ignipectus* species boundary raises another set of questions, unlikely to be resolved in the absence of molecular genetic analysis. These populations might reflect introgression through hybridization, analogous to the hybrid zones between parallel color forms of *Heliconius erato* and *H. melpomene* [3]. Alternatively, they could reflect incomplete selection for homogeneity of the black form following an earlier speciation event in which *P. bicincta* gave rise to *P. ignipectus*; genetic reversion to a lined phenotype only recently lost as suggested by Boring [19]; or altered avian selection regimes due to closer proximity to *P. bicincta* populations to the south.

In his initial report of lined Maine spittlebugs, Morse [18] put the question succinctly: “Why the banded form alone should be found at the Norridgewock locality and only there . . . at the northern limit of the distribution of the species . . . is as yet an unsolved problem.” The problem is still unsolved but perhaps now within reach of solution, given recognition that the color forms in question are aposematic and the ongoing development of comprehensive tools for the analysis of selection for warning coloration [1, 6, 44, 47]. Because they involve a single species, without the complicating presence of local Müllerian mimics, Maine *P. ignipectus* populations may present an especially tractable case for analysis of the causes and context of polymorphism for warning coloration.

Competing Interests

The authors declare that there are no competing interests regarding the publication of this paper.

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