Breeding Evidence for Conspecific Status of Grammia phyllira (Drury, 1773) and Grammia oithona (Strecker, 1878) (Erebidae: Arctiinae), with Notes on Natural History and Conservation Status

Author: Nelson, Michael W.

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BREEDING EVIDENCE FOR CONSPECIFIC STATUS OF *GRAMMIA PHYLLIRA* (DRURY, 1773) AND *GRAMMIA OITHONA* (STRECKER, 1878) (EREBIDAE: ARCTIINAE), WITH NOTES ON NATURAL HISTORY AND CONSERVATION STATUS

MICHAEL W. NELSON

Natural Heritage & Endangered Species Program, Massachusetts Division of Fisheries & Wildlife, Westborough, MA 01581, USA;
e-mail: mike.nelson@state.ma.us

ABSTRACT. It has long been suspected that *Grammia oithona* may be a form of *G. phyllira*, but concrete evidence has been lacking. The only obvious difference between *G. oithona* and *G. phyllira* is the presence of cream-colored scales outlining the veins of the forewing of *G. oithona*. A female *G. oithona* from Hampden County, Massachusetts, U.S.A., produced progeny consisting of 55 *phyllira* and 51 *oithona*. The following year a female *G. phyllira* from the same locality produced 33 *phyllira* and 40 *oithona*. Therefore the name *oithona* represents a wing pattern phenotype, not a species, at least in the population studied. Progeny of both wild females were bred in captivity, each cross consisting of a virgin female bred with a single male, with eight separate crosses producing offspring. The simplest, most parsimonious hypothesis consistent with the data from all eight crosses is that the wing pattern phenotype is inherited as a single autosomal gene with two alleles, a dominant *phyllira* allele and a recessive *oithona* allele; dominance may be incomplete in heterozygotes. Assuming *G. phyllira* and *G. oithona* to be conspecific across their composite range, the *phyllira* phenotype occurs with high frequency in most populations along the East Coast and in the Upper Midwest, and with low frequency in most populations to the west and south of this range. *G. phyllira* is of conservation concern in the northeastern U.S.A., where it has declined substantially during the past 50 to 100 years. The natural history of *G. phyllira* is typical of *Grammia* species, but its dependence on grassland and savanna habitat on dry, sandy soils is an important consideration in conservation and management efforts for this species.

Additional key words: allele, genetic hypothesis, incomplete dominance, phenotype, wing pattern

In 1773, Drury described and illustrated a striking tiger moth, based on a specimen collected in New York, U.S.A., giving it the name *phyllira* (Drury 1770–[1782]). Currently included in the genus *Grammia* Rambur (Lafontaine & Schmidt 2010), *phyllira* has a cream-colored head and thorax with black spots and stripes, an abdomen that is crimson with triangular black spots dorsally, matching crimson hind wings with black spots and fringes, and black forewings with, following the terminology of Ferguson (1985), transverse and postcubital bands and fringes, all cream-colored (Fig. 1). Synonyms of *phyllira* include *b-ata* (Goeze, 1781) and *dodgei* (Butler, 1881) (Smith 1938; Franclemont 1983). In 1878, Strecker described *oithona*, based on specimens collected in Texas, U.S.A. (Strecker 1872–[1877]). *Grammia oithona* is identical to *G. phyllira* in color and pattern, except for the addition of, again following the terminology of Ferguson (1985), a primary longitudinal pattern consisting of cream-colored scales outlining the veins of the forewing. The name *rectilinea* (French, 1879) is considered synonymous with *oithona* (Smith 1938; Franclemont 1983). In addition, *conspicua* (Stretch, 1906) is a named variety of *rectilinea* (= *oithona*) with only a partial primary longitudinal pattern.

Dyar (1900) was the first to note that, with the exception of the addition of the primary longitudinal pattern, *oithona* "…is absolutely the same as *phyllira*. In fact, several of my old specimens are labeled *phyllira*." He then described two specimens of the variety Stretch would name *conspicua* in 1906, "…in which only the subcostal, median, and internal veins are lined on basal portion, in fact true intergrades to *phyllira*." Dyar concluded that "…*rectilinea* [= *oithona*] is only a form of *phyllira*… …but to clinch the argument, we must do some breeding to get either form from the other. I trust the opportunity will arise to some of us." Gibson (1903) reported obtaining eggs from a female *rectilinea* (= *oithona*) and rearing the larvae, observing that they "…answered very well to the description of the larva of *phyllira* as published by Packard (1895)." Gibson's larvae failed to overwinter successfully, leaving him to lament that "Possibly some of us may again be fortunate enough to obtain eggs, and rear the species to maturity."

Barnes & McDunnough (1911, 1912) reared typical *phyllira* adults from larvae found on lupine (*Lupinus* L.) in North Carolina, and the adults were bred in captivity to produce a second generation, again all typical *phyllira*. They suggested that *phyllira* and *rectilinea* (= *oithona*) are distinct species because "…in *phyllira* larvae the spiracles are orange, whilst in *rectilinea*, according to Gibson (1903), they appear to be black." However, Gibson (1903) actually described the spiracles of final instar larvae as "black, with a dull yellowish centre."

In "A Revision of the Genus *Apantesis* Walker (Lepidoptera, Arctiidae)," Smith (1938) synonymized *oithona* with *phyllira*. She stated that "The only distinction between [*phyllira* and *oithona*] is the presence of pale lines on the veins in *oithona*. The male genitalia show no morphological differences; the larvae are indistinguishable; and the distribution of the two is essentially the same. Moreover, there are frequent intergrading specimens of the form *conspicua*.... …it seems reasonable to conclude that the two species are but varieties of the one, possibly Mendelian…. It is true that *phyllira* and *oithona* have never been bred from the same brood, but extensive breeding of typical *phyllira* has not been done." Many Lepidopterists have remained either unaware of Smith's conclusion, or unconvinced by it. Forbes (1960) treated *phyllira* and *oithona* as distinct, although he commented that *oithona* "may be a variety of *phyllira*." Franclemont (1983), Covell (1984), and Handfield (1999) all include *phyllira* and *oithona* as distinct species. In 2000, I asked the late Douglas C. Ferguson (Smithsonian Institution) about *phyllira* and *oithona*; at that time, he was not entirely convinced of their conspecific status. When I told him that Mark Mello (Lloyd Center for the Environment, Dartmouth, Massachusetts) had recently collected both *phyllira* and *oithona* at Westover Air Reserve Base in Chicopee, Massachusetts, Dr. Ferguson suggested that "maybe you can help us figure this out."

METHODS

The collection locality for this study was Westover Air Reserve Base, an active military installation on the east side of Chicopee, in Hampden County, Massachusetts, U.S.A. (elevation 73 m). Situated atop the deposits of the Chicopee delta in the eastern part of Glacial Lake Hitchcock, the Westover airfield and surrounding terrain is flat, with sand and gravel soils. The perimeter of the Westover airfield consists of sandplain grassland habitat (Fig. 2) that is maintained by mowing in the late summer or early autumn on an annual or biennial basis. The dry, sandy soils favor drought-tolerant grasses and forbs, and while native species such as little bluestem (*Schizachyrium scoparium* (Michx.) Nash) are dominant, the grassland community has a significant component of introduced species. In part due to its large size (the main landing strip is over 4 km long), the airfield provides important breeding habitat for several species of regionally rare grassland birds. The Westover airfield was visited on 6 June, 13 June, 8 August, and 16 August 2001, 4 June 2002, and 19 June 2003, in attempts to collect live females of *Grammia phyllira* and *G. oithona*. In 2001, both light traps without killing agent (15-Watt Leroy Koehn design) and a 175-Watt mercury vapor light and sheet setup were used. In 2002 and 2003, the mercury vapor light setup was used exclusively.

Each of two females, a *Grammia oithona* collected on 4 June 2002, and a *G. phyllira* (form *conspicua*) collected on 19 June 2003, was set up for oviposition in a gallon-size glass jar. Each jar was covered with polyester netting, with paper towel on the bottom and a few dry little bluestem stalks for perching. Each morning the interior of each jar was misted, and a few stems of fresh clover (*Trifolium* L.), a host plant for *G. oithona* according to Robinson *et al*. (2002), added with the thought that it might help to stimulate oviposition. Caterpillars were divided into separate lots shortly after hatching, kept in plastic vials, and initially fed either clover or plantain (*Plantago* L.). Some larvae were given to D.L. Wagner (University of Connecticut), D.F. Schweitzer (Port Norris, New Jersey), and B.D. Williams (Pomfret Center, Connecticut) to help with rearing. Excess larvae were released. In later instars, larvae were fed either honeysuckle (*Lonicera* L.) or organic Romaine lettuce (*Lactuca sativa* L.). In order to reduce crowding and disease, larvae were divided into smaller lots as they grew, each lot in a plastic tray (30 cm long × 25 cm wide × 10 cm high) covered with polyester netting. Dry *Sphagnum* moss, about 5 cm deep, was added to each tray to absorb moisture from feculae, as well as to serve as a pupation medium.

Between 8 and 11 August 2002, first generation progeny of the first wild female were paired in attempts to breed them in captivity: cross 2002–01, ♀ *oithona* × ♂ *phyllira*; cross 2002–02, ♀ *oithona* × ♂ *oithona*; cross 2002–03, ♀ *phyllira* × ♂ *phyllira*; cross 2002–04, ♀ *phyllira* × ♂ *oithona*; and cross 2002–05, ♀ *oithona* × ♂ *phyllira*. Between 13 and 25 August 2003, first generation progeny of the second wild female were paired for breeding: cross 2003–01, ♀ *phyllira* × ♂ *phyllira*; cross 2003–02, ♀ *phyllira* × ♂ *oithona*; cross 2003–03, ♀ *oithona* × ♂ *oithona*; cross 2003–04, ♀ *phyllira* × ♂ *phyllira*; cross 2003–05, ♀ *phyllira* × ♂ *oithona*; cross 2003–06, ♀ *oithona* × ♂ *oithona*; cross 2003–07, ♀ *phyllira*

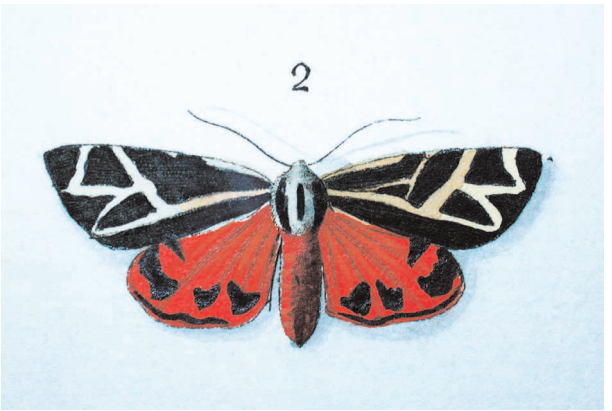


FIG. 1. Illustration accompanying the original description of *Grammia phyllira*, reproduced from Drury (1770–[1782]), Vol. 1, Pl. 7, Fig. 2 (Ernst Mayr Library, Museum of Comparative Zoology, Harvard University). Note that the illustration is asymmetrical, with no medial transverse band on the left forewing and a complete medial transverse band on the right forewing, indicating the variation in this character. The right forewing also shows a trace of the primary longitudinal pattern, as found in form *conspicua* (Stretch, 1906).

× ♂ *oithona*; and cross 2003–08, ♀ *oithona* × ♂ *oithona*. Between 12 and 18 October 2003, second generation progeny of the second wild female were paired for breeding: cross 2003–09, ♀ *phyllira* × ♂ *phyllira* (both from cross 2003–01); cross 2003–10, ♀ *oithona* × ♂ *oithona* (both from cross 2003–03); cross 2003–11, ♀ *phyllira* × ♂ *phyllira* (both from cross 2003–05); cross 2003–12, ♀ *oithona* × ♂ *phyllira* (both from cross 2003–05); cross 2003–13, ♀ *phyllira* × ♂ *phyllira* (both from cross 2003–01); cross 2003–14, ♀ *phyllira* × ♂ *phyllira* (both from cross 2003–05); and cross 2003–15, ♀ *oithona* × ♂ *phyllira* (both from cross 2003–05).

For the captive breeding attempts, each virgin female was paired with a single male in a gallon-size glass jar covered with polyester netting, with paper towel on the bottom and a few dry little bluestem stalks for perching. Each morning the interior of each jar was misted. Caterpillars were divided into separate lots shortly after hatching, kept in plastic vials, and initially fed either plantain or organic Romaine lettuce. Some larvae were given to D.L. Wagner and B.D. Williams to help with rearing, and excess larvae were either released or euthanized. In later instars, larvae were fed either honeysuckle or organic Romaine lettuce. As with the progeny of the wild-collected females, larvae were divided into smaller lots as they grew, each lot in a plastic tray covered with polyester netting. Dry *Sphagnum* moss was added to each tray to absorb moisture and to serve as a pupation medium. Captive-bred larvae were reared in an artificial indoor rearing environment in order to force continuous development. Temperature was kept between 24 and 26 °C, and containers were lit with eight 40-Watt "daylight" (5000 K) fluorescent tubes

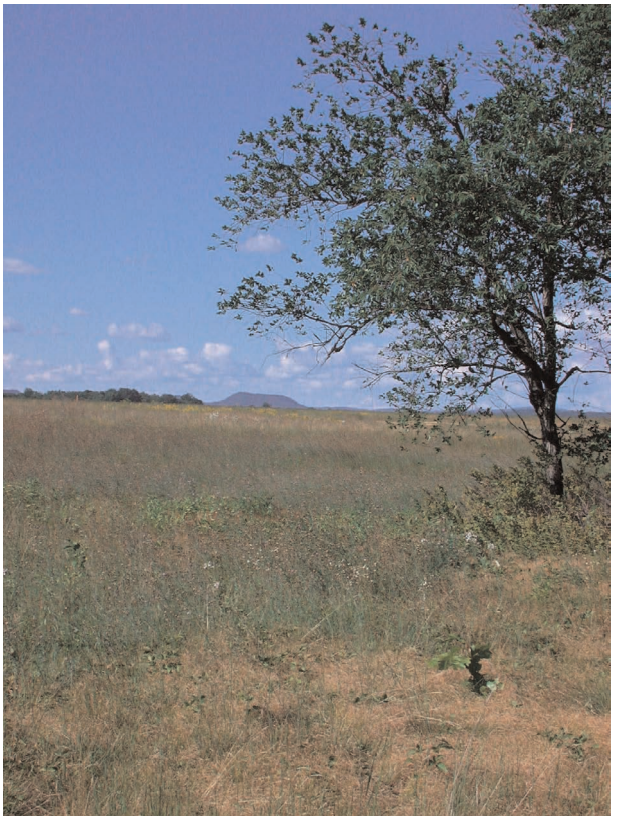


FIG. 2. Sandplain grassland habitat of *Grammia phyllira* at Westover Air Reserve Base in Chicopee, Hampden County, Massachusetts, U.S.A. The habitat consists of the perimeter of an active airfield that is maintained by mowing in the late summer or early autumn on an annual or biennial basis. The dry, sandy soils favor drought-tolerant grasses and forbs. Photographed on 8 August 2002, from the southeast side of the airfield, looking north.

FIG. 3. Final instar larva of *Grammia phyllira*, first generation progeny of the wild female taken in 2002 (Fig. 4) at Westover Air Reserve Base in Chicopee, Hampden Co., Massachusetts, U.S.A. Photographed on 25 July 2002.

on a timer. For each brood, photoperiod was started at 15 hours and gradually shortened to 13 hours at the time of pupation, in order to simulate the natural photoperiod experienced by the June to August brood in Massachusetts.

The two wild-collected females were pinned and spread, as were all reared adult moths, including those that were first mated in captivity. Larvae of each instar, as well as pupae, were preserved in ethanol. Specimens were deposited at the Massachusetts Natural Heritage & Endangered Species Program Insect Collection, the University of Connecticut Insect Collection, and the personal collections of D.F. Schweitzer and B.D. Williams.

RESULTS

Collecting, rearing, and captive breeding. The four collecting trips in 2001 yielded only males of *Grammia phyllira* and *G. oithona*. The fifth trip on 6 June 2002 yielded one female *G. oithona*, and the sixth trip on 19 June 2003 yielded a female *G. phyllira* of form *conspicua*. Both females were taken live in order to obtain eggs. Although the adult moths are not known to feed, when the jars in which the females were kept were misted, the moths were observed imbibing moisture. In 2002, the female *oithona* survived for 12 days in captivity and laid a total of 336 viable eggs. In 2003, the female *phyllira* survived for 14 days in captivity and laid a total of 215 viable eggs. Eggs were laid loose on the bottom of the jars. Freshly-laid eggs were light yellow in color, dome-shaped (spherical with a flattened base), with a smooth (not prominently sculptured) shell, approximately 0.7 mm in diameter. A few days after oviposition, eggs turned a darker, golden-yellow color, and within five or six days of oviposition they turned black, upon close inspection due to a black larval head capsule showing through the transparent shell.

Viable eggs always hatched within a week of oviposition. The hatchlings were between 1.5 and 2.0 mm long, with a shiny black head capsule about 0.4 mm wide, and a pale, grayish-yellow body covered in sparse, relatively long (2 to 3 times the diameter of the body) setae. In the second instar larvae began to develop a reddish-brown coloration, with a yellowish-white row of dorsal spots. Paired rows of black verrucae developed dorsally and laterally, each with about a half dozen black secondary setae. Average length of secondary setae was about equal to the diameter of the body. In the third instar the reddish-brown body coloration became darker, the dorsal spots more yellow and larger, merging into a dorsal stripe, flanked by gray addorsal stripes. Secondary setae from the dorsal verrucae remained about as long as the body diameter, with those from the lateral verrucae somewhat shorter. By the fourth instar the body coloration became dark gray, increasingly mottled with black in the fifth and sixth instars. The yellow dorsal stripe was well-developed by the fourth instar, and increasingly prominent in the fifth and sixth instars. Length of secondary setae remained in proportion to body size as compared to earlier instars. The larval head capsule remained black, smooth, and glossy throughout development. By 25 July 2002, most of the larvae from the wild-collected female had molted to the seventh and final instar, and one larva was photographed on this date (Fig. 3).

Description of final instar larva: Body length ~35 mm, A4 width ~5.0 mm; dark gray in color, mottled with black, especially dorsally; mid-dorsal stripe golden or orangish-yellow, narrower (occasionally broken) between segments; verruca i (dorsal verruca on A1–A8) very small, about one-eighth the size of verruca ii (subdorsal verruca), orange in color with 6–10 short setae; A1–A9 and T1–T3 with orangish-tan verrucae subdorsally, laterally, and subventrally; verruca ii often with shiny black pinaculum, especially on posterior segments; each verruca bearing a tuft of stiff, barbed secondary setae of various lengths up to ~4.0 mm, some setae on posterior segments longer; secondary setae black dorsally, less pigmented (gray or brown) towards venter; spiracles orange with black rims. Underside of thorax and abdomen dark gray, orange on and around subventral verrucae; thoracic legs black; prolegs orange. Head capsule width ~2.5 mm; solid black in color; surface smooth and shiny, unsculptured; antennae and clypeus orangish-tan; labrum and mandibles black.

Larvae pupated in loosely-constructed silk cocoons in the *Sphagnum* moss provided. Pupae bore a bluish-white, waxy coating, although to a lesser degree than some other species of *Grammia* and *Apantesis*. The shed larval integument remained attached to each pupa, held in place by the spines of a prominent cremaster.

Progeny of the wild *oithona* female obtained in 2002 emerged between 7 and 18 August, always in the early morning hours, and consisted of a total of 11 *phyllira* and 17 *oithona*. Concurrently, Wagner, Schweitzer, and Williams had reared an additional 78 moths, for a grand total of 29 female *phyllira*, 26 male *phyllira*, 27 female *oithona*, and 24 male *oithona* (Table 1). Progeny of the wild female *oithona* obtained in 2002 (Fig. 4) are shown in Figs. 5–8. Progeny of the wild *phyllira* female obtained in 2003 emerged between 9 and 17 August, and consisted of a total of 25 *phyllira* and 24 *oithona*. Concurrently, Wagner and Williams had reared an additional 24 moths, for a grand total of 19 female *phyllira*, 14 male *phyllira*, 24 female *oithona*, and 16 male *oithona* (Table 1). Progeny of the wild female *phyllira* (form *conspicua*) obtained in 2003 (Fig. 9) are shown in Figs. 10–13.

Of the five attempts to breed first generation progeny of the wild female *oithona* in 2002, one (cross 2002–01) was unsuccessful. Crosses 2002–02, 2002–03, 2002–04, and 2002–05 all produced fertile eggs. Unfortunately, the 2002 captive-bred lots suffered from slow but steady

TABLE 1. (Columns 1 to 4) Phenotype and sex of parents and progeny for each of the ten broods reared in 2002 and 2003. (Columns 5 and 6) G-test with Williams' correction (Sokal & Rohlf 1995), and associated p-value for each test, comparing the sex ratio between siblings of matching phenotype to the expected 1:1 sex ratio under the hypothesis that the phenotype is not sex-linked. (Columns 7, 8, and 9) G-test with Williams' correction, and associated p-values, comparing the actual phenotypic ratio for each brood to each of three different phenotypic ratios that commonly result from simple Mendelian inheritance. In each column, the hypothesis is that the observed phenotypic ratio for each brood represents a sample from a population with the ratio given in the top row. Values of p indicating a probable phenotypic ratio ($\alpha = 0.05$) for each brood are shown in **bold** text. The G-test could not be applied to some crosses due to a small sample size.

	1	2	3	4	5	6	7	8	9
	♀ parent	♂ parent	*phyllira* progeny	*oithona* progeny	1 ♀ *phyllira*: 1 ♂ *phyllira*	1 ♀ *oithona*: 1 ♂ *oithona*	1 *phyllira*: 1 *oithona*	1 *phyllira*: 3 *oithona*	3 *phyllira*: 1 *oithona*
Wild female 2002	*oithona*	?**	55 (29♀, 26♂)	51 (27♀, 24♂)	G = 0.1622 p = 0.6871	G = 0.1749 p = 0.6758	G = 0.1503 **p = 0.6983**	G = 34.8752 p < 0.0001	G = 26.1276 p < 0.0001
Cross 2002-02	*oithona*	*oithona*	0	3 (2♀, 1♂)					
Cross 2002-03	*phyllira*	*phyllira*	2 (1♀, 1♂)	0					
Cross 2002-04	*phyllira*	*oithona*	7 (5♀, 2♂)	5 (3♀, 2♂)					
Wild female 2003	*phyllira**	?**	33 (19♀, 14♂)	40 (24♀, 16♂)	G = 0.7492 p = 0.3867	G = 1.5910 p = 0.2072	G = 0.6677 **p = 0.4139**	G = 13.8876 p = 0.0002	G = 29.1636 p < 0.0001
Cross 2003-01	*phyllira*	*phyllira**	45 (25♀, 20♂)	6 (3♀, 3♂)	G = 0.5506 p = 0.4581		G = 33.4278 p < 0.0001	G = 90.3871 p < 0.0001	G = 5.5273 p = 0.0187
Cross 2003-03	*oithona*	*oithona*	0	48 (25♀, 23♂)		G = 0.0825 p = 0.7739			
Cross 2003-05	*phyllira**	*oithona*	15 (7♀, 8♂)	30 (13♀, 17♂)		G = 0.5262 p = 0.4682	G = 5.0410 p = 0.0248	G = 1.5463 **p = 0.2137**	G = 34.1425 p < 0.0001
Cross 2003-11	*phyllira**	*phyllira**	86 (42♀, 44♂)	32 (20♀, 12♂)	G = 0.0462 p = 0.8297	G = 1.9903 p = 0.1583	G = 25.5477 p < 0.0001	G = 118.4257 p < 0.0001	G = 0.2762 **p = 0.5992**
Cross 2003-12	*oithona*	*phyllira**	72 (33♀, 39♂)	59 (26♀, 33♂)	G = 0.4971 p = 0.4808	G = 0.8255 p = 0.3636	G = 1.2873 **p = 0.2565**	G = 53.0580 p < 0.0001	G = 24.6027 p < 0.0001

* form *conspicua*

**possibly more than one male parent, phenotype(s) not known

disease mortality, and few larvae survived to pupation. A small number of adults emerged between 17 October and 7 November. Cross 2002–02 produced three adults, all *oithona*; cross 2002–03 yielded 2 adults, both *phyllira*; and cross 2002–04 produced 12 adults, 7 *phyllira* and 5 *oithona* (Table 1). No individuals survived to adulthood from cross 2002–05.

Of the eight attempts to breed first generation progeny of the wild female *phyllira* in 2003, three (crosses 2003–02, 2003–07, and 2003–08) were unsuccessful. Crosses 2003–01, 2003–03, 2003–04, 2003–05, and 2003–06 all produced fertile eggs. All of the larvae from cross 2003–04 were released, as this cross was a replicate of cross 2003–01 (♀ *phyllira* × ♂ *phyllira*); likewise, all of the larvae from cross 2003–06 were released, as this cross was a replicate of cross 2003–03 (♀ *oithona* × ♂ *oithona*). Disease mortality was a relatively minor problem in the 2003 captive-bred lots, with most larvae surviving to pupation. Between 30 September and 16 October, a total of 51 adults emerged from cross 2003–01, 45 *phyllira* and 6 *oithona* (Table 1). Between 3 and 19 October, a total of 48 adults emerged from cross 2003–03, all 48 of them *oithona* (Table 1). Between 5 and 18 October, a total of 45 adults emerged from cross 2003–05, 15 *phyllira* and 30 *oithona* (Table 1).

Of the seven attempts to breed second generation progeny of the wild female *phyllira* in 2003, five (crosses 2003–09, 2003–10, 2003–13, 2003–14, and 2003–15) were unsuccessful. Crosses 2003–11 and 2003–12 produced fertile eggs. Between 28 November and 20 December, a total of 118 adults emerged from cross

2003–11, 86 *phyllira* and 32 *oithona* (Table 1). The female parent from cross 2003–11 is shown in Fig. 14, and four progeny from this cross are shown in Figs. 15–18. Between 2 and 26 December, a total of 131 adults emerged from cross 2003–12, 72 *phyllira* and 59 *oithona* (Table 1).

Analysis of phenotypic and sex ratios. In Table 1, columns 1 to 4 summarize the wing pattern phenotype and sex of parents and progeny for each of the two broods from wild-collected females, and for each of the eight broods from crosses made in captivity. Columns 5 and 6 in Table 1 show the G-test with Williams' correction (Sokal & Rohlf 1995), and associated p-value for each test, comparing the sex ratio between siblings of matching phenotype to the expected 1:1 ratio under the hypothesis that the phenotype is not sex-linked. In no case did the sex ratio among siblings of matching phenotype differ significantly from 1:1, indicating that the wing pattern phenotype is not sex-linked. Columns 7, 8, and 9 in Table 1 show the G-test with Williams' correction, and associated p-values, comparing the actual phenotypic ratio for each brood to each of three different phenotypic ratios that commonly result from simple Mendelian inheritance. The null hypothesis is that the observed phenotypic ratio for each brood represents a sample from a population with the ratio given in the top row of Table 1; values of p indicating a probable phenotypic ratio ($\alpha = 0.05$) for each brood are shown in **bold** text.

The simplest, most parsimonious hypothesis consistent with the data from all eight crosses made in captivity is that the *phyllira* and *oithona* phenotypes result from a single autosomal gene with two alleles, a dominant *phyllira* allele and a recessive *oithona* allele; dominance may be incomplete in heterozygotes, resulting in the *conspicua* phenotype. Under this hypothesis, cross 2003–12 is consistent with the 1 *phyllira* : 1 *oithona* ratio expected from a homozygote *oithona* crossed with a heterozygote *phyllira*:

Cross 2003–12 ♀ aa × ♂ Aa → 1 Aa : 1 aa

where 'A' represents the dominant *phyllira* allele, 'a' the recessive *oithona* allele, 'Aa' the heterozygous *phyllira* genotype (which may result in the *conspicua* phenotype), and 'aa' the homozygous *oithona* genotype. Furthermore, cross 2003–11 is consistent with the 3 *phyllira* : 1 *oithona* ratio expected from a heterozygote *phyllira* crossed with another heterozygote *phyllira*:

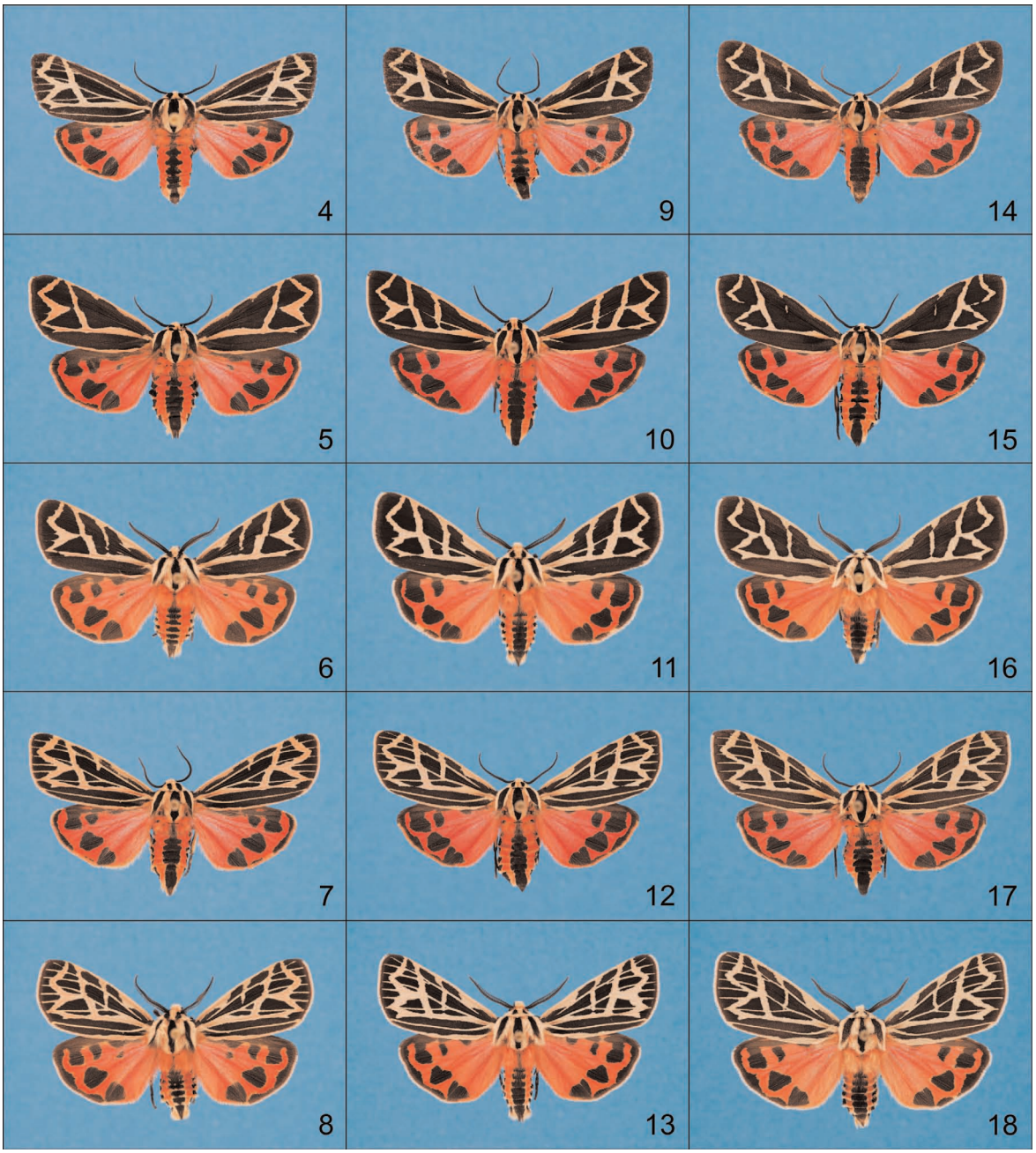
Cross 2003–11 ♀ Aa × ♂ Aa → 3 AA + Aa : 1 aa

where 'AA' represents the homozygous *phyllira* genotype.

Cross 2003–01 is problematic, in that the 45 *phyllira* : 6 *oithona* ratio would only be expected to occur 1.87% of the time in a random sample from a 3 *phyllira* : 1 *oithona* population. However, this cross clearly does not represent a 1 *phyllira* : 1 *oithona* or a 1 *phyllira* : 3 *oithona* population ($p < 0.0001$ for both hypotheses). The observed ratio for this cross may actually represent a 7 *phyllira* : 1 *oithona* population ($G = 0.0254$, $p = 0.8734$), under the alternative hypothesis that there are two unlinked genes controlling the phenotype, with one or more *phyllira* alleles at either locus resulting in the *phyllira* phenotype. However, the result of cross 2003–01 may also be due to non-random sampling, non-random survival, or both. The 51 larvae reared to adulthood (and for which phenotype was determined) only represent 13% of the individuals from cross 2003–01; the other larvae were either released or did not survive to adulthood. If only two additional larvae had been reared to adulthood, and both had been *oithona*, the result of this cross would be consistent ($G = 3.0629$, $p = 0.0801$) with a 3 *phyllira* : 1 *oithona* ratio. Therefore the result of cross 2003–01 may be explained by a slight bias of *phyllira* either in the sample of larvae retained for rearing, or among the larvae surviving to adulthood, or both. If that were indeed the case, then cross 2003–01 is consistent with the ratio expected from a heterozygote *phyllira* crossed with another heterozygote *phyllira* under the original hypothesis:

Cross 2003–01 ♀ Aa × ♂ Aa → 3 AA + Aa : 1 aa

Crosses 2003–01 and 2003–11 both support the hypothesis that the *phyllira* allele is dominant and the *oithona* allele recessive. This would appear to be contradicted by cross 2003–05, which is consistent with the 1 *phyllira* : 3 *oithona* ratio expected from a heterozygote *oithona* crossed with another heterozygote *oithona* if the *oithona* allele were dominant and the *phyllira* allele recessive. However, the result of cross 2003–05 may also be due to non-random sampling, non-random survival, or both. The 45 larvae reared to adulthood (and for which phenotype was determined) only represent 12% of the individuals from cross 2003–05; the other larvae were either released or did not survive to adulthood. If only two additional larvae had been reared to adulthood, and both had been *phyllira*, the result of this cross would be consistent ($G = 3.6047$, $p = 0.0576$) with a 1 *phyllira* : 1 *oithona* ratio. Therefore the result of cross 2003–05 may be explained by a slight bias of *oithona* either in the sample of larvae retained for rearing, or among the larvae surviving to adulthood, or both. If that were indeed the case, then cross 2003–05 is consistent with the ratio expected from a heterozygote *phyllira* crossed with a homozygote *oithona* under the original hypothesis:



FIGS. 4–18. *Grammia phyllira* adults from Westover Air Reserve Base in Chicopee, Hampden Co., Massachusetts, U.S.A., including forms *phyllira*, *oithona*, and *conspicua*. Wingspan and voucher code given for each specimen. Specimens deposited at the University of Connecticut Insect Collection (Storrs, Connecticut). **4.** Wild ♀ *oithona* collected 4 June 2002: 36 mm, SPM002384. Parent of individuals in Figs. 5, 6, 7, and 8. **5.** ♀ *phyllira*: 37 mm, SPM004028. First generation progeny of individual in Fig. 4. **6.** ♂ *phyllira* (form *conspicua*): 35 mm, SPM004023. First generation progeny of individual in Fig. 4. **7.** ♀ *oithona*: 37 mm, SPM004047. First generation progeny of individual in Fig. 4. **8.** ♂ *oithona*: 35 mm, SPM004038. First generation progeny of individual in Fig. 4. **9.** Wild ♀ *phyllira* (form *conspicua*) collected 19 June 2003: 34mm, SPM004362. Parent of individuals in Figs. 10, 11, 12, and 13. **10.** ♀ *phyllira* (form *conspicua*): 37 mm, SPM005117. First generation progeny of individual in Fig. 9. **11.** ♂ *phyllira* (form *conspicua*): 36 mm, SPM005109. First generation progeny of individual in Fig. 9. **12.** ♀ *oithona*: 36 mm, SPM005092. First generation progeny of individual in Fig. 9. **13.** ♂ *oithona*: 36 mm, SPM005108. First generation progeny of individual in Fig. 9. **14.** ♀ *phyllira* (form *conspicua*): 35 mm, SPM005379. Second generation progeny of individual in Fig. 9, captive-bred with ♂ *phyllira* (form *conspicua*) in cross 2003–11, to produce individuals in Figs. 15, 16, 17, and 18. **15.** ♀ *phyllira*: 36 mm, SPM005460. First generation progeny of individual in Fig. 14, and third generation progeny of individual in Fig. 9. **16.** ♂ *phyllira*: 36 mm, SPM005481. First generation progeny of individual in Fig. 14, and third generation progeny of individual in Fig. 9. **17.** ♀ *oithona*: 37 mm, SPM005491. First generation progeny of individual in Fig. 14, and third generation progeny of individual in Fig. 9. **18.** ♂ *oithona*: 37 mm, SPM005486. First generation progeny of individual in Fig. 14, and third generation progeny of individual in Fig. 9.

Cross 2003–05 ♀ Aa × ♂ aa → 1 Aa : 1 aa

More importantly, if the *phyllira* allele were recessive, then both cross 2003–01 and cross 2003–11 would have produced only *phyllira* offspring, which was not the case.

Cross 2003–03 is consistent with the result expected from a homozygote *oithona* crossed with another homozygote *oithona*:

Cross 2003–03 ♀ aa × ♂ aa → aa

While crosses 2002–02, 2002–03, and 2002–04 did not produce a sufficient number of progeny for statistical analysis, the results of cross 2002–02 and cross 2002–04 are nevertheless consistent with the preceding hypothesis and the results of the other crosses:

Cross 2002–02 ♀ aa × ♂ aa → aa
Cross 2002–04 ♀ Aa × ♂ aa → 1 Aa : 1 aa

Under this hypothesis cross 2002–03, which produced just two viable *phyllira* offspring, has four possibilities: ♀ AA × ♂ AA → AA; ♀ AA × ♂ Aa → 1 AA : 1 Aa; ♀ Aa × ♂ AA → 1 AA : 1 Aa; or ♀ Aa × ♂ Aa → 3 AA + Aa : 1 aa.

Each of the wild females collected in 2002 and 2003 may have mated with more than one male, and the progeny in each of these two broods may have had more than one male parent. If that were indeed the case, and if the male parents contributing to a single brood differed in their wing pattern genotypes, then a simple Mendelian genetic hypothesis cannot be made. However, the phenotypic ratio of the progeny from the wild female in 2002 (Table 1) is nevertheless consistent with the 1:1 ratio expected under the preceding hypothesis if the male parent were (or all male parents were) the heterozygous *phyllira* genotype:

Wild female 2002 ♀ aa × ♂ Aa → 1 Aa : 1 aa

Furthermore, the phenotypic ratio of the progeny from the wild female in 2003 (Table 1) is consistent with the 1:1 ratio expected under the preceding hypothesis if the male parent were (or all male parents were) the homozygous *oithona* genotype:

Wild female 2003 ♀ Aa × ♂ aa → 1 Aa : 1 aa

DISCUSSION

Wing pattern phenotype and species status. Both *Grammia phyllira* and *G. oithona* were reared from a wild *G. phyllira* female, a wild *G. oithona* female, three captive *G. phyllira* × *G. oithona* crosses, and two captive *G. phyllira* × *G. phyllira* crosses, indicating that the names *phyllira* and *oithona* represent wing pattern phenotypes, not species, at least in the population studied. Presence or absence of the primary longitudinal pattern (outlining of the veins of the forewings with light-colored scales) is typically a fixed character in species of *Grammia*. For example, as far as is known, a primary longitudinal pattern is always present in *G. virgo* (L., 1758), but always absent in *G. figurata* (Drury, 1773). However, in addition to *G. phyllira*, species in which the primary longitudinal pattern may be either present or absent include *G. ornata* (Packard, 1864) and *G. cervinoides* (Strecker, 1876) (Dyar 1900; Smith 1938; Ferguson 1985). This phenomenon is not surprising if, as suggested by the results of this study, the presence or absence of a primary longitudinal pattern is the result of alternate alleles at a single gene locus. Ferguson (1985) noted that the presence or absence of a primary longitudinal pattern is often independent of changes in other wing pattern characters, for example, melanic mutants may retain the primary longitudinal pattern. This is easily explained if the gene controlling the primary longitudinal pattern is not linked to genes controlling other wing pattern elements.

Other examples of independently inherited wing pattern elements controlled by one or a few genes are known in the Arctiinae. Probably the best-studied example is the *medionigra* gene in *Callimorpha dominula* (L., 1758). In typical specimens of *C. dominula*, the forewings are black with white (sometimes yellow) spots, and the hind wings are crimson with black spots; in specimens of the form *medionigra* (heterozygous at the *medionigra* locus), the central white spots on the forewings are absent (replaced with black), and a small black spot is added to each of the hind wings; in specimens of the form *bimacula* (homozygous at the *medionigra* locus), all but the most basal pairs of white spots on the forewings are replaced with black, and the black spots on the hind wings are enlarged and more confluent (Ford 1975). A second example is found in the work of Pease (1964), who studied five wing pattern characters among five different populations of *Utetheisa ornatrix* (L., 1758) and concluded that four of the characters are each determined by a single gene, and the fifth character by two genes, each phenotype slightly modified by genes at one or two additional loci.

In addition to presence or absence of the primary longitudinal pattern in *G. ornata* and *G. cervinoides*, several additional examples of independently inherited wing pattern elements are known in *Grammia* and *Apantesis*. Bacheler & Emmel (1974) obtained eggs from a wild *Apantesis phalerata* (Harris, 1841) from Florida, and bred the resulting progeny in captivity. *A. phalerata* has black forewings with a yellow secondary longitudinal pattern and transverse bands; the results of

Bacheler & Emmel (1974) suggest that the extent of black on the forewings may be determined by a single autosomal gene. The black is most extensive in the typical, homozygous dominant individuals; black is less extensive, and the longitudinal pattern and transverse bands wider, in heterozygous individuals. The forewings are almost completely yellow, with only traces of black, in homozygous recessive individuals. Another example is *Grammia placentia* (J.E. Smith, 1797), which was first shown to be sexually dimorphic by Barnes & McDunnough (1911). In this species the cream-colored transverse bands and secondary longitudinal pattern of the forewings, as well as the cream-colored thoracic stripes, are only found in the male. These features are all replaced with black in the female, and it is possible that the sex-linked inheritance of these traits is due to a single, maternally inherited gene. *G. figurata* appears to have a number of independently inherited wing pattern elements, including a variable extent of black on both the forewings and the hind wings, and hind wings that may be either yellow or red. An apparently very rare mutant of *G. phyllira*, with yellow hind wings instead of crimson, was collected in 1833 near Philadelphia, Pennsylvania by T.R. Peale (specimen at the Academy of Natural Sciences).

While this study provides concrete evidence that *phyllira* and *oithona* are phenotypes, not species, in the population from Hampden County, Massachusetts, this conclusion may or may not hold across the composite range of *Grammia phyllira* and *G. oithona*. This range extends from New England west through southern Canada to Alberta, south to Florida, and west to Texas and Colorado (Opler *et al*. 2006; Troubridge & Lafontaine 2008). If *phyllira* and *oithona* are indeed conspecific across this entire range, then the *oithona* phenotype is either rare or absent in most populations along the East Coast (with the exception of southern New England), and in many of the populations in Wisconsin and Michigan (Fig. 19). Conversely, the *phyllira* phenotype is either rare or absent in populations both west of the East Coast states and south of Wisconsin and Michigan, apparently only occurring in scattered localities in Illinois, Indiana, Kentucky, Mississippi, South Dakota, Nebraska, and Colorado (Fig. 19). An alternate hypothesis is that *G. oithona*, described from Texas, is actually a distinct species occurring to the west and south of the East Coast and Upper Midwest range of *G. phyllira* (which was described from New York). If that is the case, and the ranges of *G. phyllira* and *G. oithona* do not largely overlap, then in addition to *G. phyllira* having an *oithona*-like wing pattern phenotype, *G. oithona* must have a *phyllira*-like wing pattern phenotype. This alternate hypothesis is less than parsimonious. Additionally, Smith (1938) examined type specimens of both *phyllira* and *oithona*, and studied numerous morphological characters of both adults and immatures from across the U.S.A., and concluded that *phyllira* and *oithona* are conspecific. Furthermore, in part due to the results presented here, the taxonomic checklist of Ferguson & Opler (2006) lists *oithona* as a synonym of *phyllira*, as does the updated checklist by Schmidt & Opler (2008). The taxonomic revision of *Grammia* by Schmidt (2009) also concurs with this synonymy.

The distribution of *G. phyllira* populations with a high frequency of the *phyllira* phenotype (Fig. 19) is concordant with the combined present-day and historic ranges of wild lupine (*Lupinus perennis* L.), and three butterfly species that utilize wild lupine as a larval host: Karner blue, *Plebejus melissa samuelis* (Nabokov, 1944) (Lycaenidae); frosted elfin, *Callophrys irus* (Godart, 1824) (Lycaenidae); and Persius duskywing, *Erynnis persius persius* (Scudder, 1863) (Hesperiidae). Wild lupine, these three butterflies, the antennal-waving wasp (*Tachysphex pechumani* Krombein, 1938) (Sphecidae), and presumably an entire flora and fauna characteristic of xeric, sandy-soil habitats is thought to have survived the Wisconsinan glaciation in a refugium in the southeastern U.S.A.; as the climate warmed, these species dispersed north along the Atlantic Coast, then west through New York state and southern Ontario into Michigan and Wisconsin (Kurczewski 1998). If eastern populations of *G. phyllira* were likewise isolated in a southeastern glacial refugium, it seems likely that those populations had a high frequency of the *phyllira* phenotype, and were the source for post-glacial dispersal north along the coast to New England and west to Wisconsin. The post-glacial populations began with the same high frequency of the *phyllira* phenotype as their source, and most populations of this origin have maintained a high frequency of the *phyllira* phenotype to the present day.

Suggestions for further research. *Grammia phyllira* females should be obtained, and their progeny reared, from other parts of the species' range where both phenotypes occur (e.g., Colorado, Florida) in order to confirm (or refute) rangewide conspecific status with *Grammia oithona*. Molecular phylogenetic analysis of specimens of both phenotypes from across the entire geographic range would provide important corroborating evidence, and elucidate the biogeographic history of this species. Such investigations would be of greatest interest in the context of a larger study of the molecular genetics and biogeography of other *Grammia* species with similar variation in wing pattern phenotype (e.g., *G. ornata* and *G. cervinoides*).

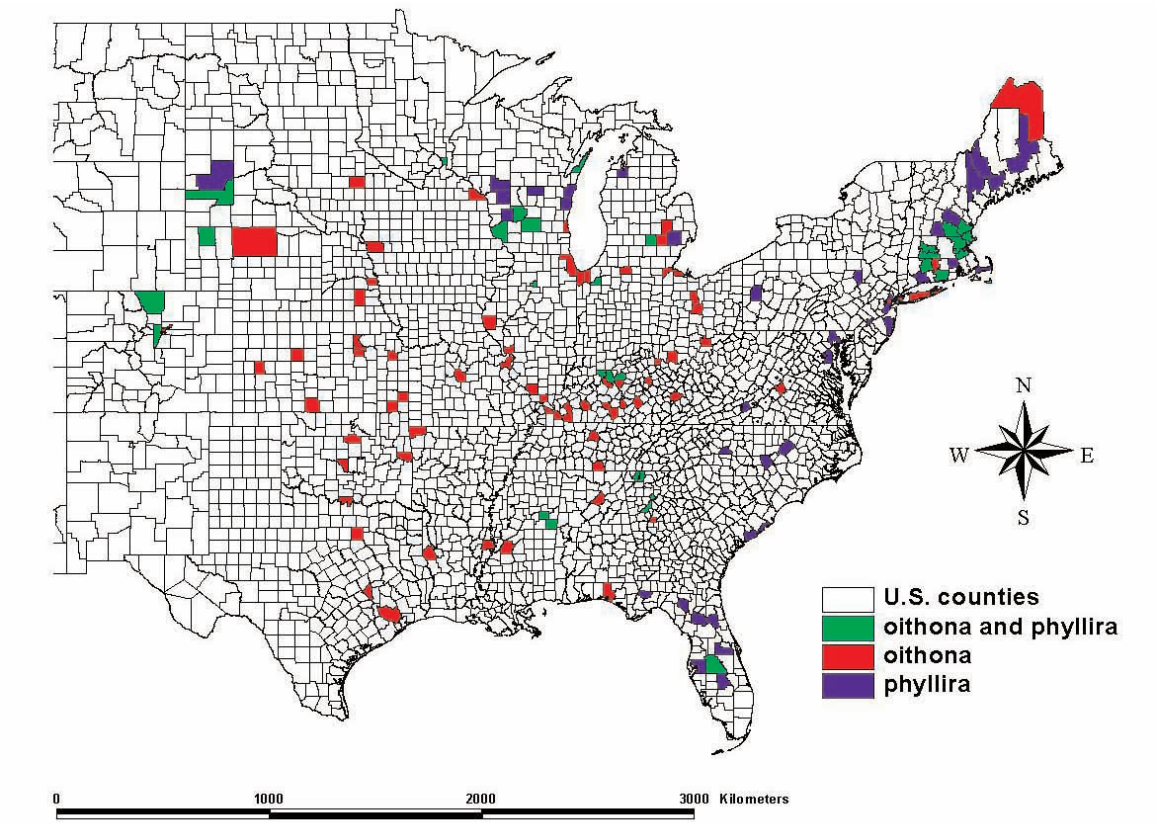


FIG. 19. Distribution of *oithona* and *phyllira* forms of *Grammia phyllira* in the U.S.A. Counties in green indicate one or more records of *oithona* plus one or more records of *phyllira*; counties in red indicate one or more records of *oithona*; and counties in blue indicate one or more records of *phyllira*. Records compiled from the literature (Strecker 1872–[1877], Farquhar 1934, Smith 1936, Smith 1938, Jones & Kimball 1943, Metzler & Lucas 1990), online databases (Opler *et al*. 2006, IN DNR 2008, WI DNR 2008), and specimens at the Harvard University Museum of Comparative Zoology (Cambridge, Massachusetts), Peabody Museum of Natural History at Yale University (New Haven, Connecticut), Carnegie Museum of Natural History (Pittsburgh, Pennsylvania), the Peale collection at the Academy of Natural Sciences (Philadelphia, Pennsylvania), the University of Connecticut Insect Collection (Storrs, Connecticut), the Lloyd Center for the Environment (Dartmouth, Massachusetts), and the personal collection of James K. Adams (Calhoun, Georgia).

FIG. 20. Adult ♀ *Grammia phyllira*, molested to elicit a "flash" display of the hind wings and subsequent release of a presumably repellant, transparent yellow fluid from the cervical glands on the prothorax. First generation progeny of the wild female taken in 2002 (Fig. 4) at Westover Air Reserve Base in Chicopee, Hampden Co., Massachusetts, U.S.A. Photographed on 17 August 2002.

The genetic hypothesis that the *phyllira* and *oithona* phenotypes result from a single autosomal gene with two alleles, a *phyllira* allele with incomplete dominance and a recessive *oithona* allele, is the simplest, most parsimonious hypothesis consistent with the data presented in this paper. However, there are many alternative, more complex hypotheses that may result in the results presented here, including the possibility of more than two alleles, or epistatic interactions between multiple genes. Although additional complex, long-term breeding experiments could be performed, the genetic mechanisms underlying wing pattern phenotype in *G. phyllira* could be more directly elucidated using modern molecular techniques.

Natural history notes. *Grammia phyllira* inhabits grasslands, savanna, and grassy openings in scrub or forest habitat, typically on dry, sandy soils (NatureServe 2008). Grasslands maintained by anthropogenic disturbance, such as pastures, old fields, powerline cuts,

and airfields are also inhabited. *Grammia phyllira* has two generations each year throughout much of its range (Wagner 2005), with three annual broods in Missouri (Heitzman & Heitzman 1996), and presumably three broods throughout the southern part of its range in general. As is the case with all *Grammia* (Ferguson 1985), winter diapause occurs as a partially grown larva. *Grammia* larvae emerge from winter diapause during the first warm spring days.

In Massachusetts, *G. phyllira* larvae complete development and pupate in May, and adults of the first brood emerge in June. Emergence occurs in the early morning hours, with the newly-emerged moth ascending a nearby plant stem to hang and expand its wings. After its wings have dried, the moth drops back to ground level and hides under foliage or detritus. The adult moths are nocturnal, and presumably most days are spent hiding and resting in this manner. If molested by a potential predator, a moth will raise its forewings to expose the aposematic coloration of its hind wings and abdomen in a "flash" display. This may be accompanied by release of a transparent yellow fluid from the cervical glands on the prothorax (Fig. 20), which is presumably repellant to predators (Adams 1990). Adult moths live for up to two weeks, some as long as three weeks. They are not known to feed, but will imbibe moisture with their short proboscis. Both mating and oviposition occur nocturnally. Mated females lay eggs loose, presumably scattering them on the ground in the vicinity of suitable host plants. Females will lay over 200 eggs, sometimes as many as 400.

The eggs of *G. phyllira* hatch within a week of oviposition, and hatchlings commence feeding immediately upon locating a suitable host plant. Larvae wander frequently and are polyphagous, feeding on a wide variety of low-growing forbs (Ferguson 1985; Robinson *et al*. 2002). Legumes (Fabaceae) such as lupines, clovers, and peas (*Lathyrus* L.) have been reported as larval hosts more often than plants in other families. It is unclear whether this is due to a preference of the larvae, an abundance of legumes in the open habitats on sandy, nutrient-poor soils inhabited by this species, or both. The habits of the larvae are typical of many ground-dwelling Arctiina, with much of the day spent hiding and resting beneath foliage or detritus, and most wandering and feeding occurring at night. They are reluctant to ascend plant stems, preferring to feed on foliage less than 10 cm above the ground. A larva in an exposed location, particularly during the day, will run and hide under the nearest object if molested. Under such circumstances, larvae run with astonishing speed (up to 0.25 m/s). This is presumably an adaptation that facilitates escape from predators. Larvae molt six times, reaching a length of about 35 mm in the seventh and final instar. Under ideal conditions of consistently warm temperatures and abundant, high-quality food, the larval period from hatching to pupation is about four weeks (25 to 31 days) for the continuously developing summer brood. Larvae stressed by a shortage of quality food or other adverse environmental conditions may take an additional one to two weeks to develop. Highly stressed larvae may live for up to eight weeks, but mortality is high under such conditions. Following a bout of wandering lasting from an hour or two to a day or more, larvae pupate in a sheltered location on the ground, in a cocoon composed of detritus loosely tied together with silk. The pupal period is normally 10 to 13 days. In Massachusetts, adults of the second brood emerge in August. Larvae from the second brood develop more slowly, with most individuals reaching the third, fourth, or fifth instar by October, at which time they seek a sheltered location and enter winter diapause.

Conservation status. Although *Grammia phyllira* has a relatively large geographic range, populations are rare and localized. Furthermore, *G. phyllira* has undergone a substantial decline in the northeastern portion of its range during the past 50 to 100 years (NatureServe 2008). In New Jersey it is much rarer than prior to 1950, and has not been recorded in Pennsylvania or New York in more than 50 years. In southern New England in the late 1800s and early 1900s, *G. phyllira* was recorded from four localities in four counties in southern New Hampshire, 16 localities in seven counties in Massachusetts, two localities in two counties in Rhode Island, and five localities in three counties in Connecticut (specimens at Harvard Museum of Comparative Zoology and Peabody Museum of Natural History at Yale, plus records from Farquhar (1934), Smith (1936, 1938), and Jones & Kimball (1943)). Despite widespread and relatively intensive collecting of Lepidoptera across southern New England in recent decades, *G. phyllira* is currently known to persist at only three localities in this region: Concord, Merrimack County, New Hampshire (last recorded in 2000, specimens at Lloyd Center for the Environment, Dartmouth, Massachusetts); Chicopee, Hampden County, Massachusetts (the population studied for this paper, last recorded in 2003, specimens at the Massachusetts Natural Heritage & Endangered Species Program Insect Collection, the University of Connecticut Insect Collection, and the personal collections of D.F. Schweitzer and B.D. Williams); and Windsor Locks, Hartford County, Connecticut (last recorded in 2003, specimens at the University of Connecticut Insect Collection). *G. phyllira* is listed as

Endangered in Massachusetts (MA DFW 2008), and as a Species of Special Concern in Connecticut (CT DEP 2004).

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