INTRASPECIFIC BODY SIZE VARIATION IN MACROLEPIDOPTERA AS RELATED TO ALTITUDE OF CAPTURE SITE AND SEASONAL GENERATION

J. BOLLING SULLIVAN

200 Craven St., Beaufort, North Carolina 28516 U. S. A., sullivan14@earthlink.net

AND

WILLIAM E. MILLER

Department of Entomology, University of Minnesota 55108 U. S. A., mille014@umn.edu

Abstract. As a proxy for body size, forewing lengths of individual geometrids and noctuids were measured with respect to altitude of capture site in five species in North Carolina and one in Costa Rica. Number of specimens ranged 48–373 per species, number of capture sites 2–15 per species, and site altitudes ranged 2–2209 m. Forewing length in all six species increased significantly with increasing altitude at rates of ≈ 0.3–≈ 1.1 mm/500 m. These relations held where investigated for both first and second annual generations and for both sexes even though second-generation individuals were smaller-bodied. Thus examples of Geometridae and Noctuidae are added to a list mainly of micromoths previously known to exhibit positive size–altitude relations. Some adaptive and nonadaptive body-size hypotheses are discussed as possible explanatory factors, but thus far no explanation is fully satisfactory. In contrast to measurement results in these six macromoths, other moths known to be widely dispersive appeared to display flat size–altitude relations, and published butterfly size–altitude data varied irregularly. Degree of dispersiveness is hypothesized as a condition to the manifestation of size–altitude phenomena in lepidopterans. Many more minimally dispersive moths will likely be found to increase in body size with increasing altitude.

Additional key words: *Chytolita morbidalis*, *Eubaphe mendica*, *Glena cribrataria*, *Hypagyrtis unipunctata*, *Iridopsis pandrosus*, *Trichodezia albovittata*.

Using new and refined data, we examine here intraspecific body size relative to altitude of capture site in individuals of six species of multivoltine and univoltine Geometridae and Noctuidae, five Nearctic and one Neotropical. All six increased in body size with increasing altitude of capture site. Up to now, few moth species beyond examples of Nearctic and Neotropical Tortricidae were known to increase in body size with increasing altitude of capture site (Miller 1974, 1991a, b; 1993, Miller and Nayak 1998, and evidence in Brown 2003). Although not documented statistically, other moths known to be widely dispersive appeared to display flat relations between size and altitude of capture site. In butterflies, which also tend to be dispersive, and sometimes migratory, published body size–altitude relations are inconsistent, some decreasing, increasing, or switching erratically (Hovanitz 1942, Burns 1964, 1985; Guppy 1986, Hawkins and DeVries 1996, and others). The sum of findings in the present study leads us to hypothesize that degree of dispersiveness conditions the manifestation of lepidopteran size as related to altitude of capture site. In the six macromoths studied, we also examined where possible how different seasonal generations within the same year, gender, and to a lesser extent latitude, affected wing length. We discuss some adaptive and nonadaptive factors that might contribute to lepidopteran size–altitude phenomena.

MATERIALS AND METHODS

In Lepidoptera, forewing length serves as a surrogate for body weight, which changes approximately as the square or cube of forewing length (Miller 1977, 1997; Wasserman and Mitter 1978, Loder *et al*. 1998). The six study species here are taxonomically unambiguous, not widely dispersive, and with gender usually recognizable from secondary sexual characters. All were sufficiently common to yield ≥17 individuals per site per generation. Examination of museum holdings showed that even moderate numbers of individuals from a single site were rarely available, except at the American Museum of Natural History for *Hypagyrtis unipunctata* (Haworth), as detailed later. We trapped adults using standard 15-w ultraviolet fluorescent light traps (Hall *et al*. 1999). They were killed with potassium cyanide and promptly frozen. In the laboratory, they were spread, oven-dried, after which forewings were measured from the costal base to the outer edge of the fringe at the apex to an accuracy of 0.1 mm using a Wild binocular stereomicroscope (MS 52958) equipped with an ocular micrometer. In pristine specimens it was necessary to estimate length of the wing base beneath the tegula, and in worn specimens, to estimate fringe length. The right wing was measured unless damaged. Locations and altitudes sampled in North Carolina—the main area of study—were the coastal counties of Carteret and Craven (alt. 2–27 m), Hanging Rock State Park in

Stokes Co. (alt. 274–457 m), New River and Mt. Jefferson State Parks in Alleghany and Ashe Counties (alt. 792–1402 m), Grandfather and Moore Mountains in Avery Co. (alt. 1219–1676 m) and Great Smoky Mountain National Park and nearby areas in Swain and Haywood counties (alt. 640–1478 m). Distances between these sites ranged up to ≈600 km, but most were less distant from one another. Costa Rican adults were collected at the Monteverde Biological Station in Puntarenas (alt. 1526 m) and at the Quetzal Education and Research Center in San Jose (alt. 2209 m). *Hypagyrtis unipunctata* beyond North Carolina were used only in the analyses involving latitude, which included sites in New Jersey (lat. 40º 01' N, alt. 22 m, and lat. 40º 51' N, alt. 55 m), New York (lat. 41º 13' N, alt. 93 m), Maine (lat. 45º 36' N, alt. 67 m), and Ontario (lat. 49º 07' N, alt. 344 m). Altitudes for U. S. sites were obtained at http://www.topozone.com; for Canadian sites (Ontario), they were estimated from nearby points of known altitude as given at http://GeoNames2 .NRCan.gc.ca; and for Costa Rica they were furnished by the Instituto Nacional de Biodiversidad, San Jose. Statistics were generated using SYSTAT software (SYSTAT 1992). Tests of differences between intraspecific size–altitude regressions for different seasonal generations and genders were based on the General Linear Model, with a categorical variable for generation, a continuous variable for altitude, and an interaction term between the two. The interaction term enabled testing differences in slope value; the categorical variable enabled testing differences in slope elevation.

RESULTS

***Hypagyrtis unipunctata* (Haworth)** (Geometridae: Ennominae). This species is multivoltine in North America (Wagner *et al*. 2001). We used males only, as females were rarely light-trapped. In both the first and second generations, forewing length increased with increasing altitude ≈0.4 mm/500 m (Fig. 1). Generation slope values did not differ significantly (P = 0.39), but generation slope elevations did (P < 0.001), statistically confirming the nearly uniform ≈20% smaller forewing length of the second generation. The second-generation regression is truncated (Fig. 1) because we omitted late-season (August and September) individuals due to uncertainty about the generation to which they belonged; however, casual observations suggested no further change in size after the second generation. (Incidentally, the very similar *H. piniata* Packard has been reported from North Carolina, but the records likely pertain to misidentified large, first-generation *H.*
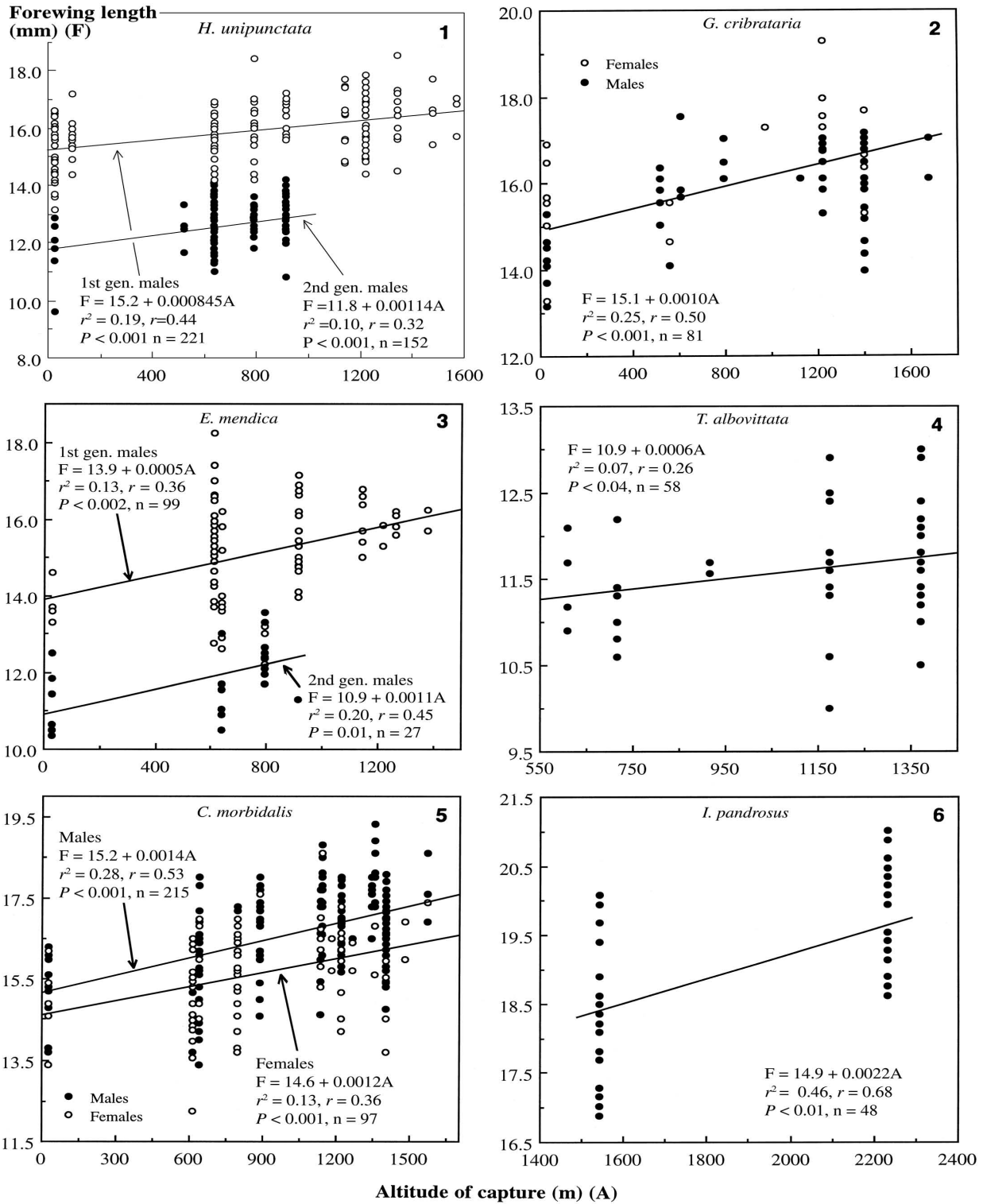
unipunctata males.)

When regressed on latitude (L) alone in the North Carolina-to-Canada sample, forewing length (F) decreased significantly with increasing latitude, that is, wing length decreased northward, indicating a negative correlation with latitude (r = -0.13, n = 331, P < 0.02). However, in multiple regression that also included altitude (A) and the interaction [A X L], a different picture emerged, with forewing length increasing with increasing altitude (P < 0.001) as in the North Carolina-only sample (Fig. 1), reversing from decreasing to increasing with increasing latitude (P < 0.004), and decreasing with increasing interaction [A X L] (P < 0.001) (F = 0.012 A + 0.06 L - 0.0003 [L x A] + 13.2). Thus, effects of altitude and latitude modified each other, and together acted negatively on forewing length. This effect, if not spurious, is a new finding for moths. It needs confirmation and should be examined further in other moths.

***Glena cribrataria* (Guenée)** (Geometridae: Ennomiinae). This species is multivoltine in North Carolina (Wagner *et al*. 2001). Males and females of the first generation are plotted separately (Fig. 2), but their regressions did not differ significantly in slope value or slope elevation (P's ≥ 0.31). Forewing length increased with altitude ≈0.5 mm/500 m. Too few individuals of the second generation were available for analysis.

***Eubaphe mendica* (Walker)** (Geometridae: Larentiinae). Males of both the first and second generations showed positive relations between forewing length and altitude (Fig. 3). Generation slope values did not differ significantly (P = 0.37), but generation slope elevations did (P < 0.001), statistically confirming the nearly uniform ≈20% smaller forewing length of the second generation. The second-generation regression is truncated (Fig. 3) because we omitted late-season individuals, being uncertain to which generation they belonged. Forewing length increased with altitude ≈0.75 mm/500 m.

***Trichodezia albovittata* (Guenée)** (Geometridae: Larentiinae). This univoltine species is both a day- and night-flyer, and thus may be somewhat dispersive. The sample of pooled males and females increased in forewing length with increasing altitude (Fig. 4); the rate of increase, ≈0.3 mm/500 m, was the smallest of the study.

***Chytolita morbidalis* (Guenée)** (Noctuidae: Herminiinae). The sexes of this univoltine species are readily distinguished by antennal characters. Males and females both showed a positive relation between forewing length and altitude (Fig. 5). Their respective slope values did not differ significantly (P = 0.44), but their respective slope elevations did (P < 0.001),

FIGS. 1–6. Relations of forewing length (F) to altitude of capture site (A) in investigated species of Geometridae and Noctuidae. 1, *Hypagyrtis unipunctata* (1st gen. males, open circles; 2nd gen. males closed circles). 2, *Glena cribrataria*. 3, *Eubaphe mendica* (1st gen males , open circles; 2nd gen. males, closed circles). 4, *Trichodezia albovittata*. 5, *Chytolita morbidalis*. 6, *Iridopsis pandrosus*. Figs. 1–5 depict North Carolina individuals, Fig. 6, Costa Rican individuals.

statistically confirming that female forewing lengths are ≈5% less than in males. Forewing length increased with altitude ≈0.75 mm/500 m.

Iridopsis pandrosus **(Schaus)** (Geometridae: Ennominae). Male forewing lengths in this Costa Rican species also increased with increasing altitude (Fig. 6). The rate of increase, ≈1.1 mm/500m, was the largest of the study. The species identity is based on similarity of maculation with the type specimen in the U. S. National Museum, the genitalia of which had not been dissected and examined at the time of this study. However, males from both altitudes had indistinguishable genitalia. Distance between the two capture sites was 130 km. Despite the limit of material to just two sites, we believe a linear (rather than curvilinear) relation is appropriate and valid here because of the large slope value and evidence of linear relations among the other geometrids (Figs. 1–4).

Other taxa and counterexamples. Many other North Carolina macromoths were seen during this study, but not in sufficient numbers for statistical analysis. Examples of Saturniidae, Notodontidae, and less dispersive Noctuidae seemed to show wing lengths positively correlated with altitude. However, wing lengths of *Paonias excaecata* (J. E. Smith) (Sphingidae), which were followed over a large altitudinal range, did not appear to increase with increasing altitude. Many sphingids, like many butterflies, are strong flyers and disperse widely so that their capture sites may not represent sites of development. The same is true of widely dispersive noctuids such as *Helicoverpa zea* (Boddie), *Pseudaletia unipuncta* (Haworth), and species of *Leucania*, *Anticarsia*, *Spodoptera*, and *Catocala*, which also seemed to show flat relations between wing length and altitude.

DISCUSSION

In all six macromoths measured, statistically significant positive relations emerged between individual forewing lengths, hence body size, and altitudes of capture sites, as previously observed mainly in the micromoth family Tortricidae (Miller 1974, 1991a, b; 1993, Miller and Nayak 1998, and evidence in Brown 2003). More examples will likely be found among other minimally dispersive moths. In North Carolina and Costa Rica, increases in size are usually apparent to the eye as one proceeds to higher altitudes provided individuals of the same generation are observed.

Also, where examined, individuals of the second generation were smaller-bodied than those of the first generation, yet still increased in size with increasing altitude. Individuals of the first generation often are larger-bodied than those of subsequent generations, as noted for geometrids by Rindge (1968, 1974, 1978, 1979, and others) and for noctuids (*Chytolita petralis* Grote) by Forbes (1954). Wagner *et al*. (2001) reported that larvae produced by first-generation *Hypagyrtis unipunctata* are smaller than last-generation larvae that become the next year's first generation, thus confirming the above adult size results in the larval stage.

In Costa Rica, it was difficult to find suitable species free of taxonomic complexities that spanned wide ranges in altitude. Because of narrow altitude distribution and greater species diversity there, fewer intraspecific individuals were collected. Moreover, on genitalic dissection, individuals from different altitudes sometimes proved to be different species despite similarities in maculation. Thus, moths that show either unusually large size increases with increasing altitude or none at all may signal taxonomic problems.

Brehm and Fiedler (2004) found geometrid wing lengths negatively correlated with altitude in the Andes, which is contrary to our findings, but their investigative approach was interspecific and thus fundamentally different from our intraspecific individual approach. Size correlations of grouped taxa with altitude can obscure inherent intraspecific responses.

No satisfactory explanation for positive size–altitude relations in moths is yet available. Some studies of single species have focused on abiotic factors, namely temperature, based on findings that lepidopterans grow to maximal size at temperatures somewhat lower than they normally experience (Atkinson 1994, Partridge and French 1996, Atkinson and Sibly 1997, Miller 2005).

Biotic factors may also be involved. Foliar nitrogen content within the same plant species, and among different plant species, also increases with increasing altitude (Körner 1989, Erelli *et al*. 1998), and lepidopterans feeding on high-nitrogen foliage grow commensurably larger (Mattson 1980, Mattson and Scriber 1987). Further, body weight in a saturniid moth was positively correlated with quantity of food consumed during the larval stage, as well as with higher altitudes and cooler temperatures (Miller and Nayak 1998). A notable positive correlation between female size and fecundity in moths insures that increased size will increase fecundity and other fitness factors (Dey *et al*. 2004, Miller 2005). The role of such factors in size–altitude relations needs investigation.

Body-size variation in butterflies. In an extensive study, Hawkins and DeVries (1996) examined butterfly size as related to altitude of capture site in Costa Rica. Their method of analyzing forewing length using the median altitude at which each species occurred is not

strictly equivalent to our intraspecific approach. Their results proved group-specific: for instance, only species of Pieridae exhibited a negative size relation with altitude among four families including Papilionidae, Nymphalidae and Riodinidae. Species of the latter three families showed some evidence of positive size relation with altitude, but these relations were irregular and not always statistically significant or linear. As stated earlier, butterflies, particularly males, tend to be dispersive so that their capture sites may not accurately represent sites of development.

Using less extensive data, Opler and Krizek (1984) reported positive and negative generational size differences within the same season for some North American butterflies. However, when dispersive tropical species and species that winter as adults were removed, the remaining butterflies increased in size after the first generation. This result is consistent with our observations of butterflies in North Carolina (unpublished). Opler and Krizek (1984) also noted that butterfly populations in Florida are often larger-bodied than those farther north, and Burns (1985) found that *Wallengrenia egeremet* (Scudder) and *W. otho* (J. E. Smith) (Hesperiidae) increased in size from north to south, revealing a negative correlation of size with latitude, except for a decrease in size of *W. egeremet* associated with its shift from uni- to bivoltinism. McQuillan and Ek (1996) also noted that body size of an Australian butterfly is larger in warmer areas. In North Carolina, many butterfly species appear larger-bodied in warmer areas (unpublished). Wagner and Hansen (1980) documented a southward size decrease in a pierid butterfly in the Great Lakes region, representing a positive correlation of size with latitude. In direct contrast, Scholtens and Wagner (1997) in the same region documented the opposite trend in a saturniid moth, representing a negative correlation. Available data suggests that butterflies and moths respond differently to the physical factors discussed in this paper.

Other factors that might influence differences between moth and butterfly size variability. A physiological and behavioral difference between moths and butterflies occurs in their preparation for flight (Bartholomew and Heinrich 1973), which can be framed in the context of altitude. All fly at temperatures above ambient (Srygley and Chai 1990, Rydell and Lancaster 2000, Utrio 1995), but butterflies usually increase body temperature by solar basking while moths do so by muscular activity. In moths encountering cool flight temperatures, increased wing length might facilitate raising body temperature by increased resistance to wing flapping. Further, larger butterfly wings can accumulate solar radiation faster than smaller

ones (Berwaerts *et al*. 2001). Individual high-altitude butterflies tend to be darkly pigmented, which speeds their accumulation of solar heat compared with low-altitude lightly pigmented conspecifics (Watt 1968, Kingsolver 1985, Guppy 1986).

Behavioral or life history modifications might artificially influence size–altitude relations, as possibly in day- and night-flyers represented in this study by *T. albovittata*. This species, which acts partly like a butterfly and may be somewhat dispersive, showed the least increase in wing length with increasing altitude. Also, where different microhabitats lead to second or third seasonal generations during the same season, or to a shift from uni- to multivoltinism, different generations may be on the wing at the same time. For instance, larvae feeding on the north slope of a mountain might be univoltine while those feeding just over the crest on the south slope might be multivoltine so that trapping nearby could include individuals of both.

In conclusion, intraspecific variability in body size has numerous ramifications, ambiguities, as well as inconsistencies in study methods. Yet it offers many possibilities for experimentation both in the field and in the laboratory to account for the evidence that body size increases with increasing altitude of development, and also to illuminate whether the underlying forces are adaptive, nonadaptive, or some combination of the two.

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