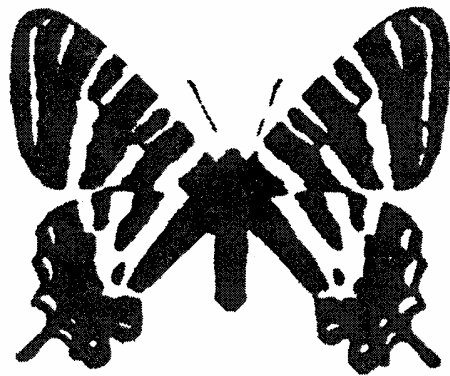


**Biology of the snout butterflies (Nymphalidae, Libytheinae)**  
**Part 2: *Libytheana* Michener**

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## Biology of the snout butterflies (Nymphalidae, Libytheinae)

### Part 2: *Libytheana* Michener

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**Abstract** The biology of the New-World snout butterfly genus *Libytheana* is reviewed. The distribution, habitat, behavior, life history, larval host plant, migration, dispersal, adult diet, predators, parasitoids, and microbiological data for each species are presented. *Libytheana carinenta* is widespread, with a distribution ranging from southern Canada to Argentina. It has multiple annual generations and can be found in various habitats, including deserts, grasslands, and forests. *Libytheana carinenta* regularly lands on the ground, frequently visits flowers, disperses in very large numbers, and has territorial males. Nothing is known about the immature stages of the three insular species.

**Key words** Adult diet, behavior, dispersal, habitat, host plant, *Libytheana*, Libytheinae, life history, microbiology, migration, parasitoid, predator.

### Introduction

*Libytheana* Michener, 1943, contains four New-World species (Kawahara, *accepted*). *Libytheana carinenta* (Cramer, 1777) has a distribution that spans from southern Canada to Argentina, while *L. fulvescens* (Lathy, 1904), *L. motya* (Hübner, 1823), and *L. terena* (Godart, 1819) are endemic to Caribbean islands. Like other Libytheinae, all *Libytheana* species have elongated labial palpi, but palpi are especially pronounced in *L. motya* and *L. terena*. At least three morphological synapomorphies support the monophyly of this genus (Kawahara, 2001).

The biology of the Old-World genus, *Libythea* Fabricius, 1807, was reviewed in the first part of this study (Kawahara, 2006). To date, a comprehensive study of the biology of *Libytheana* has not been published. d'Abrera (1988) and Motono (1993) illustrated all species, but their publications included very little or no discussion on biology. In a detailed zoogeographic study of snout butterflies, Shields (1985a) presented distributions of *Libytheana*, and briefly compared the life history and chromosome number of several species. Shields also published papers on flower visitation records, migration, ommochromes, and pterin pigments of Libytheinae (Shields 1985b, 1987a, b, c, respectively), but notable publications (*e. g.* Robertson, 1928; Gilbert, 1985) were not included in his studies. The current study includes biological information on *Libytheana* from personal communications, papers published before Shields' work, and recent studies that were reported thereafter (*e. g.* Rutowski *et al.*, 1997; Freitas, 1999). The goal of this paper is to present an updated review of the biology of *Libytheana* from all obtainable sources before 2003. Several publications dated after 2003 were added after this manuscript was submitted.

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### Species accounts

#### *Libytheana carinenta* (Cramer, 1777) (Figs 1–3)

**Distribution.** North and South America, but absent from the Caribbean islands, northwestern United States, and latitudes greater than 40°S (Fig. 10). Reported northernmost localities are from Canada (*e. g.* Champlain, Québec (Landry, 1987), Montréal, Québec (Laplante, 1985), Carleton, Ontario (Layberry, 1985), and London, Ontario (Saunders, 1868)), but in all cases, *L. carinenta* is reported infrequently in the far north and its residence there is temporary.

**Habitat.** *Libytheana carinenta* is found in forests, grasslands, deserts, canyons, tropical savannas, marshy meadows, thorn scrub woodlands (Scudder, 1889; Pyle, 1981; Shields, 1985a; Opler & Malikul, 1992; Woodbury, 1994), gardens, along roadsides (Kirby, 1896), riverbanks (Brown & Mielke, 1967), lakeshores (Heitzman & Heitzman, 1987), near swamps, ponds, and where the host plant occurs (Iftner *et al.*, 1992). In the eastern United States, *L. carinenta* often rests on gravel roads in low elevation mountains (Kawahara, 2003). In Costa Rica, adults are occasionally found between sea level and 800 m on the Pacific slope, but rarely in the Atlantic lowlands (DeVries, 1987). The highest recorded elevation is 2,133 m (Shields, 1985a).

**General behavior.** The following are notes from a study of the adult behavior of *L. carinenta* in Berea, Kentucky (summary of Kawahara (2003)). The adult is most active in the afternoon, in open areas in hills and low-elevation mountains. When searching for a place to land, it flies approximately 30 cm above the ground, in a slow, bouncy fashion, similar to the flight pattern of some satyrs (*e. g.* *Cercyonis pegala*), but with a distinct zigzag flight path. Both sexes readily land on the ground (especially in damp spots) with their wings closed. When aggregations of butterflies containing numerous species are encountered, it seemed that *Libytheana carinenta*, if present, tends to rest apart from the aggregation. DeVries (1987) noted that during the rainy season in the tropics, this species visits puddles with other nymphalids, such as *Eunica* sp., and *Marpesia* sp., but he did not mention how close *L. carinenta* lands to these butterflies.

In Berea, an adult perched on the ground will often wiggle its forewings up and down every 2–3 seconds. The butterfly also taps its proboscis on the ground, and bends its antennae up and down. It usually rests for less than two minutes in any place, and takes flight whenever sensing movement. It occasionally walks around, pausing motionless at damp spots, apparently drinking. On occasion, it lands on human clothing, in search for perspiration. The adult also angles its body toward or away from the sun, a behavior often associated with thermoregulation. When windy, it often tucks its forewings inside the hindwings, reducing the area exposed to wind.

When clouds block the sunlight, the adult flies to a nearby shrub or dead tree branch and rests for more than five minutes with its wings closed. In 12 of 17 observations, the adult landed with its head facing away from the tip of the branch or grass blade. This resting position may enhance camouflage, because it allows the antennae and labial palpi to resemble the petiole of a dead leaf. The adult was also seen resting in a similar posture at night. This resting position was previously illustrated (Shields, 1985a: 58).

The male uses only its pterothoracic legs to hold onto vegetation, whereas the female typically uses all legs. When sunlight hits the perched butterfly, it opens its wings briefly, and flies several minutes later. *Libytheana carinenta* is much less responsive to movement when cryptically resting on vegetation than when visible on the ground. Furthermore, *L. carinenta*

is generally less responsive to movement than *Libythea lepita* (Kawahara, *pers. obs.*), but this hypothesis needs to be tested experimentally.

**Mating behavior.** Rutowski *et al.* (1997) studied mate-locating behavior of males. According to their study, the male erratically flies around branches of the host plant. The male tends to fly slowly up and down close to the branches. It perches on branch tips of the host plant, and approaches and chases other butterflies that fly nearby. Average perch height of the male on trees is 1.92 m above ground, and the average time that a male stays perched is 77 seconds. The male leaves the perch to inspect flying insects for an average of 12.7 seconds. When two or three males are perched within a few centimeters of each other, their bodies are oriented upwards with wings closed or partially opened. Friedlander (*vide* Scott, 1986) claimed that males seldom return to the previous resting site.

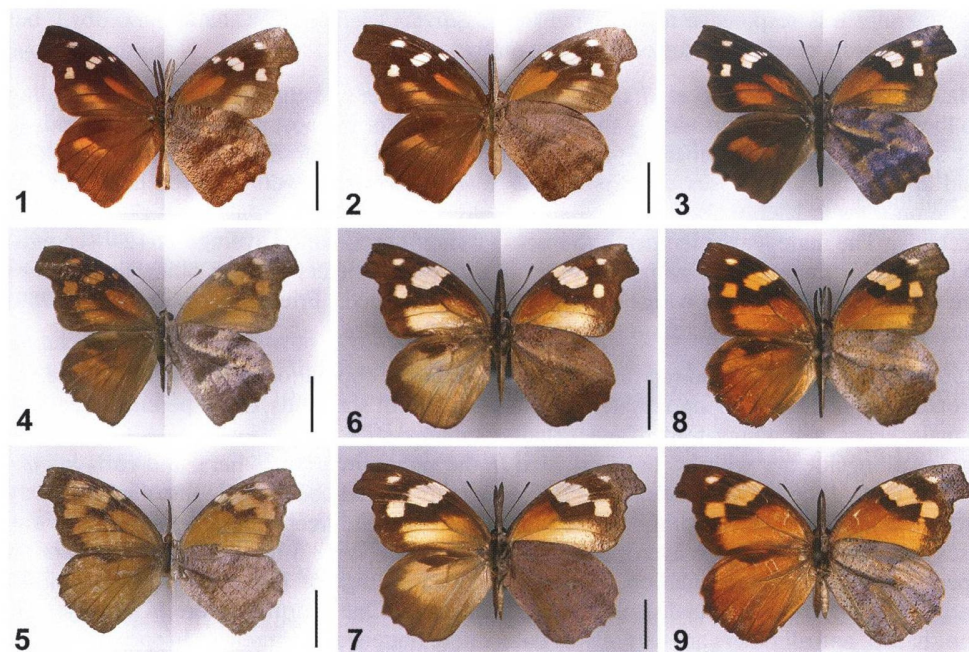
Rutowski *et al.* (1997) reported that courtship leading to copulation begins when a male approaches a perched or flying female. He chases her until she lands, and a perched receptive female keeps her wings folded and usually remains still. After landing behind her, he moves alongside her with his head oriented in the same direction as hers, and curls his abdomen toward the female, and probes until he attains genital contact. He turns to face away from the female after coupling. If the pair takes flight, he keeps his wings closed as she uses her wings to fly. The average time until separation is 88.5 minutes. He passes her a spermatophore during copulation. Females carry an average of 1.28 spermatophores, indicating that on average, females mate more than once. One spermatophore is usually tear-drop shaped, and all others are partially or completely flattened. Differences in spermatophore size led Rutowski *et al.* to believe that matings do not occur in rapid succession.

Rutowski *et al.* (1997) also observed unsuccessful courtship, which lasts an average of 44.6 seconds. During these interactions, a flying female avoids courtship by not landing, landing and fluttering her wings, or suddenly dropping toward the ground and landing. Rutowski *et al.* believed the perched female takes flight or spreads her wings and elevates her abdomen to prevent copulation.

Schappert (2000) observed a female resting on a stem of *Eupatorium compositifolium* (Asteraceae), with her abdomen elevated between partially open wings in a classic rejection posture, while “the male faced her and alternately flicked his wings shut with almost audible force, then, slowly opened them again” (Schappert, 2000: 234). Eventually, the male left without mating. Schappert suggested that the forceful wing shutting drives pheromones to the female, and concluded that she rejected him because she was in migratory diapause. A pair in copula is usually observed during the day, but a pair was found at a fluorescent light between 2235 and 2345 hrs (Heitzman, 1969). Mated pairs were also seen during migrations (Collenette, 1928).

**Generations.** Multiple, but the exact number remains uncertain. Based on observations of female oviposition periods in West Virginia, Edwards (1874) determined that there are at least two annual generations, and later stated that there are probably four (Edwards, 1881). Based on Edwards (1874), it is apparent that the time to development from egg to adult is much faster for generations that follow the first. Time to development for the second generation is faster than the first for other Libytheinae, such as *Libythea lepita* (Aonuma, 1971).

Opler & Malikul (1992) stated two annual generations, one in May or June and a second in August, while Pyle (1981) reported three or more annual generations. Stokes *et al.* (1991) believed there are two generations in the northern limits of the distribution, and two to four in warmer regions. Based on field observations of the adult in the United States (Kawahara, *pers. obs.*), there are probably two annual generations, but climate and host plant availability



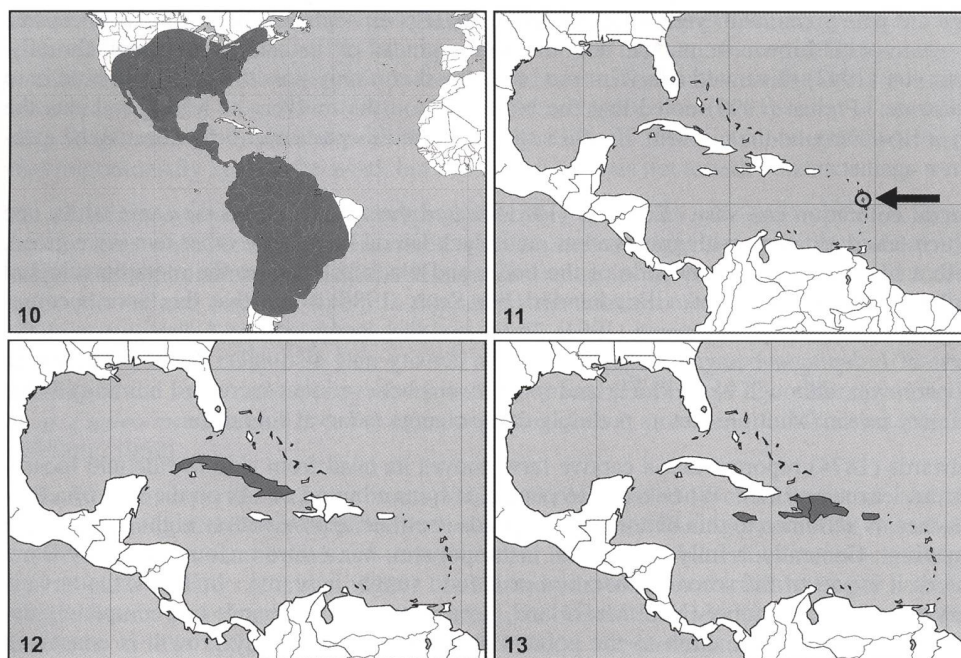
Figs 1–9. Habitus images of *Libytheana* spp. Scale bar=1 cm. Dorsal and ventral sides are shown in each figure (dorsal wing surface at left, ventral wing surface at right). 1. *Libytheana carinenta carinenta* ♂, Mexico: San Juan (CMNH). 2. *Ditto*, ♀, Panama: Canal Zone, Cocoli, 23-vi-1963, G. B. Small leg. (USNM). 3. *Libytheana c. bachmanii* ♂, United States: North Carolina, 20 mi [32.2 km] N of Raleigh, 15-vii-2000, A. Y. Kawahara leg. (AYK). 4. *Libytheana fulvescens* ♂, Dominica: 1–2 km north of Colihaut, 21-ix-1992, L. D. and J. Y. Miller leg. (MCLB). 5. *Ditto*, ♀, Dominica: Copt Hall, 11-x-1966, E. L. Todd (USNM). 6. *Libytheana motya* ♂, Cuba (CUIC). 7. *Ditto*, ♀, Cuba: Santiago, Comstock leg. (AMNH). 8. *Libytheana terena* ♂, Dominican Republic: Pedernales, La Abeja, 38 km NNW Cabo Rojo, 18°09'N 71°38'W, 11-17-xii-1987, D. Matusik & K. Johnson leg. (CMNH). 9. *Ditto*, ♀, Española (CUIC).

ty can influence generation number. In southwestern United States, generation number may be correlated with rainfall and defoliation of *Celtis pallida* (see Gilbert (1985) for further discussion on host plant availability and defoliation). *Libytheana carinenta* is not common in the northeastern United States and Canada, and is not believed to over-winter in these regions (Opler & Krizek, 1984).

Oviposition. Soon after copulation, the female searches for oviposition sites (Rutowski *et al.*, 1997). A single egg is deposited on the end of a twig, in a fork between twigs, or under a partially developed leaf of the host plant (Edwards, 1874; Freitas, 1999). In one case, a female oviposited twelve times before leaving a plant (Edwards, 1874). In New England, eggs are laid between June and September (Maynard, 1891).

Ovum. Edwards (1874, 1881) and Scudder (1889) described the egg of *L. carinenta* in detail. The ovum is pale green, 0.7 mm high, 0.45 mm wide, with 18–20 longitudinal ribs and many horizontal lines. These ribs and lines form a network of rounded cells, each with an approximate diameter of 0.017 mm. Every other longitudinal rib is more pronounced than the intervening ribs. These ribs are at most 0.065 mm apart, and are 0.05 mm high towards





Figs 10-13. Distribution maps of *Libytheana* spp. Distributions were determined from locality records provided by Shields (1985a) and museum specimens examined by Kawahara (2001). 10. *Libytheana carinenta*. 11. *Libytheana fulvescens*. 12. *Libytheana motya*. 13. *Libytheana terena*.

the top of the egg. The micropyle is 0.08 mm wide, depressed, and cells within it are rounded polygons, each with a diameter of 0.17 mm. Shields (1987b) believed that the egg may contain ommochromes because the meconium of two eggs from College Station, Texas, were light reddish orange to moderate orange with brown speckles. According to Kendall (*pers. com.*, *vide* Gilbert, 1985), the time from egg to adult can be as short as 16 days.

**Larva.** Edwards (1881) reported the following details about the larva of *L. c. bachmanii*: it chews a small hole in the eggshell slightly below the micropyle and emerges. The remaining shell is not eaten, and the larva moves to the tip of the leaf blade. The first instar is green, slightly translucent, 1 mm long, cylindrical in shape, covered with fine short hairs, and four transverse creases divide each segment. The head capsule is yellow-brown, and twice as wide as the mesothoracic segment.

The second instar is brownish-green and approximately 2 mm long. The head capsule is slightly broader than the mesothoracic segment. The third instar is approximately 3 mm long, with a dark green body, and a faint, yellow line along the dorsum. Prolegs and legs are light green, and the creases between each segment are white. The fourth instar is 7 mm long, with a green head capsule, and the body is dull green with white speckles and a yellow longitudinal line. Each of the first four instars lasts two days.

The fourth molt occurs on the eighth day after hatching, and the emerging fifth instar is dark green, approximately 20 mm long, with short hairs all over its body. The dorsal median line is pale whitish-yellow, and along each side, there is a yellow stripe. Legs and pro-

legs are pale green, with yellow "arcs" above the legs on segments 3–6. The head capsule is green with brown stemmata, and the last segment of its abdomen tapers abruptly. Schreiter (1943) illustrated a larva at rest, showing that it only uses the prolegs to hold onto substrate. Freitas (1999) noted that the larva rests on the midvein of a leaf, and eats the plant tissue around the midvein. Freitas suggested that this particular behavior may be a defense against ants.

Larval coloration can vary. Edwards (1881) reared three larvae from the same adult, one which was dark green with gray, yellow, and black lateral lines. The other two were green, with a black band along the side of the body, and black patches on the metathoracic and eighth abdominal segments. Friedlander (*vide* Scott, 1986) noted that the larva becomes gray if it eats slowly. Akayama (1981) discovered that increased larval density causes the larva of *L. lepita* to become darker. Population density may also affect larval coloration in *L. carinenta*, although Noel McFarland (*pers. com.*) believed that increased humidity is the primary factor. Multiple factors probably cause change in larval coloration.

Edwards (1874) reported that a captive larva moves its head from side to side and loosely fastens leaves together. When ready to pupate, it spins a button of silk on the side of a leaf, attaches its abdomen to this button, and suspends itself for approximately eight hours before pupating. Generally, a fully-grown fifth instar pupates, but a third or fourth instar will pupate if it is part of the second generation or if food supply is scarce. In Texas, the larva is very abundant in October (Noel McFarland, *pers. com.*) and thousands can completely defoliate a *Celtis pallida* shrub to the point where most of the woody growth is consumed (Gilbert, 1985).

Pupa. 15–17 mm long, green with a yellowish-green abdomen and two white dorsal lines. The pupa has both prothoracic and abdominal humps, the latter being more pronounced (Comstock & Vazquez, 1944). The abdomen is slightly grooved and covered with pale yellow spots (Edwards, 1881). Based on Edwards (1881) and Stokes *et al.* (1991), pupation lasts 5–14 days. During outbreak years, several thousand pupae can be found on a host plant. In one case, 2027 pupae were removed from a 3 m diameter bush of *Celtis pallida* in Texas (Gilbert, 1985).

Host plants. Celtidaceae: *Celtis occidentalis* is the primary host plant, but the larva is reported to also utilize *C. boliviensis*, *C. iguanae*, *C. laevigata*, *C. pallida*, *C. reticulata*, *C. laevigata* × *reticulata*, *C. spinosa*, and *C. tenuifolia*. It may also feed on *C. douglasii* in California (Emmel & Emmel, 1973). Asteraceae: *Hymenopappus artemisiifolia*; Caprifoliaceae: *Symphoricarpos occidentalis* and *S. orbiculatus* were reported, but these reports are probably erroneous because of the specificity of Libytheinae to *Celtis* plants and because a recent phylogenetic analysis of flowering plants (APG, 1998) concluded that the Celtidaceae and Caprifoliaceae are distantly related. Host plant data are extracted from: Barber (1895), Gable & Baker (1922), Kendall & Glick (1972), Neck (1976), Scott (1986), Freitas (1999).

Dispersal. Most migrations are reported from northern Mexico and southwestern United States between late June and October after strong rainfall. *Libytheana carinenta* also migrates following strong rains in other parts of its distribution, but these migrations take place at other times of the year. Migrations were seen after rainfall at Chichen-Itza, Yucatan (Welling, 1959), in Matto Grosso, Brazil (Collenette, 1928), and in Tucumàn, Argentina (Hayward, 1969). (Migration in this paper refers to a dispersal event involving swarms of butterflies.)

Migrations are typically observed between 1000 and 1800 hrs, up to a height of 4.57 m

above the ground (Shields, 1987a). Based on numerous sources (Smyth, 1920; Parman, 1926; Gilbert, 1985; Shields, 1987a), the speed at which the butterflies travel ranges from 8 to 27.8 km per hour. Most migrations are directed toward the southwest, but other directions have been reported (*e. g.* East, Neck (1984)). Occasionally, there is a reversal of directionality from morning to afternoon (Breland, 1948; Gilbert, 1985). Gilbert (1985) believed that migrations fly against the wind, but his hypothesis was not tested.

An adult in a swarm maintains its original direction, even if its path is disrupted. A swarm can fly over walls, buildings, cars, trees, and can deviate right and left, but maintains its original direction (Shields, 1987a). If a net is swung in the path of a swarm, butterflies avoid the net and continue flying in the same direction as before (Fletcher, 1926). If an adult is caught and whirled about in a net 20–50 times, it resumes the same direction of flight after release (Gable & Baker, 1922). Adults with damaged wings were observed walking in the same direction as the main flight stream (Helfert, 1972). Other nymphalids (*e. g.* *Eunica monima* and *E. taila*) were migrating with *L. c. mexicana* in Yucatan, Mexico (Welling, 1959).

Gilbert (1985) reported localized migrations that only traveled several kilometers, and also large scale migrations over thousands of square kilometers. During swarm-like migrations, up to 1,000 adults can be seen at a time (Nininger, 1930), and butterflies can block sunlight and clog car radiators (Parman, 1926). Estimated number of butterflies seen per hour in a migration can be as much as 75 million (Rau, 1941), and the width of the migratory path can be as wide as 160 km (Knight, 1895). In 1966, *L. carinenta* was so numerous in Texas that street lamps had to be turned on during the day (Howe, 1975). Gilbert (1985) estimated that 84,000 butterflies emerged from 8.4 m<sup>2</sup> containing *C. pallida* prior to a migration.

The adult also aggregates in large numbers without any migratory movement. Aggregations are reported from an island (*e. g.* Trinidad; Barcant, 1970), and the continental mainland (*e. g.* Williams, 1938; Dawson & Blevins, 1944; Rawson, 1949; Fager, 1952; Reinthal, 1966). Shields (1987a) suggested that non-migrating butterflies aggregate in preparation for a migration, which may explain such assemblies.

Neck (1983) discovered a positive correlation between rainfall and migration, and believed that the number of adults in a migration is enhanced by the amount of rainfall preceding the migration. His hypothesis is based on two observations: that migrations at the beginning of the summer are smaller than at the end of the summer when rains are strongest, and that migrations during droughts are smaller than years with high rainfall. In the Southwest, rainfall stimulates host plant leaf growth, allowing a gravid female to oviposit on a developing leaf (Noel McFarland, *pers. com.*).

Gilbert (1985) proposed a hypothesis based on reproductive success to explain the cause of migration. He discovered that when a migration begins, the male:female ratio is high (83.5:1), but declines two weeks later (6.91:1). Gilbert believed that a male that emerges later in the brood will face increased competition from an accumulating pool of older males. He stated, “at some point during the emergence, males will fare better if they fly off to compete for females in areas in which time of emergence is shifted later relative to their own site of origin” (Gilbert, 1985: 736). Gilbert dissected eight females from a migration, and all were gravid. The change in sex ratio and the number of gravid females suggests that males may need to disperse to increase reproductive success, but additional samples are necessary to verify this hypothesis. Most likely, rainfall and population size trigger migration events. Migrations were reported for the following years: 1895, 1912, 1916, 1921, 1925, 1929, 1937, 1940, 1948, 1956, 1958, 1960, 1963, 1966, 1971, 1975, 1976, 1977, 1978, 1979, and 1980.



Adult diet. Juice from fruit (*e. g.* Solanaceae (Preston-Mafham & Preston-Mafham, 1988)), aphids, ground water, vertebrate perspiration, urine, and flower nectar. Flower visitation records were first compiled by Shields (1972, 1985*b*) and many more have been recently discovered (Kawahara & Dirig, 2006): Amaranthaceae: *Gomphrena globosa*; Anacardiaceae: *Rhus copallina*; Apiaceae: *Cicuta maculata*, *Daucus carota*, *Pastinaca sativa*, *Sium suave*; Apocynaceae: *Asclepias incarnata*; *A. syriaca*, *Apocynum cannabinum*; Asteraceae: *Aster pilosus*, *A. vimineus*, *Baccharis glutinosa*, *B. halimifolia*, *B. sarothroides*, *Bidens alba*, *B. aristosa*, *Centaurea maculosa*, *Chrysanthemum* sp., *Chrysothamnus nauseosus*, *Cirsium arvense*, *Eupatorium fistulosum*, *E. perfoliatum*, *Euthamia tenuifolia*, *Senecio douglasii*, *Solidago* sp., *Verbesina encelioides*; Avicenniaceae: *Avicennia germinans*; Basselaceae: *Anredera cordifolia*, *Boussingaultia leptostachya*; Boraginaceae: *Cordia* sp., *Tournefortia hirsutissima*; Brassicaceae: *Berteroa incana*; Clethraceae: *Clethra alnifolia*; Cornaceae: *Cornus* sp.; Euphorbiaceae: *Croton* sp.; Fabaceae: *Eysenhardtia amorphoides*, *E. texana*, *Melilotus alba*, *Prosopis glandulosa*; Lamiaceae: *Mentha arvensis*; *Pycnanthemum flexuosum*, *Salvia guaranitica*; Lobeliaceae: *Lobelia cardinalis*; Loganiaceae: *Buddleia* × *davidii*; Malvaceae: *Tilia* sp.; Oleaceae: *Ligustrum vulgare*; Poaceae: *Heteropogon contortus*, *Sorghum* sp.; Polygonaceae: *Eriogonum* sp.; Ranunculaceae: *Clematis vitalba*, *Clematis drummondii*; Rhamnaceae: *Condalia* sp.; Rosaceae: *Potentilla fruticosa*, *Prunus caroliniana*, *P. persica*, *Rubus fruticosus*, *R. idaeus*, *Spiraea latifolia*; Rubiaceae: *Cephalanthus occidentalis*; Sapotaceae: *Bumelia lanuginosa*; Saxifragaceae: *Philadelphus coronarius*; Verbenaceae: *Aloysia* sp., *Lantana* sp., *Verbena bonariensis*.

Predators and parasitoids. Freitas (1999) hypothesized that ants are predators of the larva, but a direct observation was not made. A cliff swallow, *Hirundo pyrrhonota* (Hirundinidae), was seen capturing an adult during flight, approximately 5 m above the ground (Rutowski *et al.*, 1997). Gilbert (1985) reported that a wasp, *Brachymeria* sp. (Chalcididae) is a parasitoid of the pupa. In 1976, this wasp parasitized 8% of 658 pupae from Texas.

Chromosome number.  $N=31$ : Ciudad Victoria, Mexico (Maeki & Remington, 1960); Tuxtla, Mexico (De Lesse, 1970).

Pterin pigments. Erythropterin, leucopterin, xanthopterin, and a faint spot of isoxanthopterin (Shields, 1987*c*).

Gene sequences. *ND1* (Weller *et al.*, 1996), *Wingless* (Brower, 2000; Campbell *et al.*, 2000).

### *Libytheana fulvescens* (Lathy, 1904) (Figs 4–5)

Distribution. Restricted to the island of Dominica in the Lesser Antilles (Fig. 11).

Habitat. The adult prefers dry coastal forests and dry scrub woodlands with trees and shrubs that cover rocky slopes (Shields, 1985*a*; Smith *et al.*, 1994).

General behavior. The general behavior is similar to *L. carinenta*. Adults are active even when it is windy (Jacqueline Y. Miller and Lee D. Miller, *pers. com.*).

Generations. Unknown, but multiple generations are likely because the adult is found during different times of the year. Smith *et al.* (1994) reported specimens from July and August, and I have studied specimens collected in April and October. The adult is more common in the fall than in the spring (Jacqueline Y. Miller, *pers. com.*).

Host plant. Possibly feeds on *Celtis iguanae* (Celtidaceae) (Smith *et al.*, 1994).

Dispersal. *Libytheana fulvescens* is not gregarious, and probably not migratory (Jacqueline Y. Miller, *pers. com.*).

Adult diet. The only reported adult diet is sap exuding from wounded trees (Smith *et al.*, 1994).

Predator. The Kingbird is a predator of this species (Jacqueline Y. Miller and Lee D. Miller, *pers. com.*).

***Libytheana motya*** (Hübner, 1823) (Figs 6–7)

Distribution. According to Riley (1975), *L. motya* is widespread in Cuba (Fig. 12). The type specimen is believed to be from Georgia, but this record is questionable (Calhoun, 2004). There are also records from Guatemala (Shields, 1985a) and Texas (Heitzman & Heitzman, 1972), but these are probably strays from the main population in the Caribbean. Hering (1921) reported *L. motya* from Puerto Rico and Hispaniola, but these records are probably that of *L. terena*, because these two species were frequently confused in the nineteenth and early part of the twentieth century.

Habitat. Frequently found along the coast in tropical semi-deciduous forests and thorn scrub woodlands, but also collected inland at 1,066 m elevation (Shields, 1985a).

General behavior. Flies slowly, close to the ground, and closes its wings when resting (Smith *et al.*, 1994).

Life history. The life history remains unknown. Many authors have incorrectly attributed the original description of *L. motya* to Boisduval and Le Conte (1833). According to Calhoun (2004), Hübner (1819–1827) was the first to illustrate the species, and the illustrations of the immature stages in Boisduval and Le Conte (1833) are that of *L. carinenta bachmanii* (Kirtland). Refer to Calhoun (2004) for details on the true identity of the plates illustrated in Boisduval and Le Conte (1833).

Host plants. None reported, but the larva probably feeds on *Celtis* sp. (Celtidaceae), given the specificity of other Libytheinae to this plant genus.

Dispersal. Migrations were not directly observed (Riley, 1975; Smith *et al.*, 1994), but one specimen was collected in Guatemala (Shields, 1985a), and four in Brownsville, Texas (Heitzman & Heitzman, 1972). The report from Guatemala and Brownsville suggest that this species may be windblown across large bodies of water.

Adult diet. Fluids from the ground, and nectar from flowers of Boraginaceae: *Cordia* sp., *Tournefortia hirsutissima*; Rubiaceae: *Morinda* sp. (Hernández, 2004).

***Libytheana terena*** (Godart, 1819) (Figs 8–9)

Distribution. Hispaniola, Jamaica, and Puerto Rico (Fig. 13). There is one report from Pará, Brazil (Hering, 1921), but this report is probably erroneous, because *L. terena* and *L. carinenta* were historically often confused with each other and misidentified (Kawahara, *accepted*). *Libytheana terena* was reported as scarce on Hispaniola (Hall, 1925; Riley, 1975), but Schwartz (1989) compiled one hundred locality records and stated that this species is locally common. There are at least three records from Jamaica: a male was captured in June 1846 (Gosse, 1851), five adults were seen in 1977 and 1978 (Vyhmeister &

Donahue, 1980), and a female was collected in 1995 (Kawahara, *accepted*).

**Habitat.** In Hispaniola, *L. terena* is found along seashores, in open fields, and on mountainsides with shrubs. It is also found in *Acacia* and pine woods, xeric, transitional and mesic forests up to 1,647 m (Schwartz, 1989).

**General behavior.** Flight pattern is usually swift and erratic, but can be determinedly straight when flying down roads. The adult rests on the ground and on bare twigs and short branches that are 0.25–1.5 m above ground (Schwartz, 1989). Schwartz (1989) reported that in his collection of one hundred *L. terena* specimens, all were found between 0900–1700 hrs and 21–38°C.

**Mating behavior.** A mated pair was observed between 1030–1145 hrs (at 37°C) on June 29 at La Romana, Dominican Republic (Schwartz, 1989), but nothing more was reported on mating behavior.

**Generations.** Schwartz (1983) believed that *L. terena* is bivoltine based on his collecting data. He claimed the first generation emerges in February, and the second from July to early August. An investigation of specimens from museums (Kawahara, *accepted*) combined with the records published in Schwartz (1989) yielded 115 specimens collected in June and July, and fewer than 18 from August, October, December, April, and May combined, suggesting that at least one generation emerges in June and July. The possibility of multiple generations cannot be excluded without direct studies on the life history and generation times.

**Adult diet.** Fluids from puddles and mud on riverbanks and roads (Schwartz, 1989). Schwartz (1983, 1989) reported the following nectar sources: Apiaceae: *Daucus* sp.; Boraginaceae: *Cordia exarata*, *C. globosa*, *Tournefortia hirsutissima*; Euphorbiaceae: *Croton linearis*; Rubiaceae: *Morinda citrifolia*.

**Host plants.** Unknown, but like other Libytheinae, the larva probably feeds on *Celtis* sp. (Celtidaceae).

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## References

- Akayama, A., 1981. Phase variation in a butterfly, *Libythea celtis* Fruhstorfer (Lepidoptera, Libytheidae). *Kontyû* **49**: 334–343.
- Aonuma, S., 1971. On the second generation of the nymphalid butterfly, *Libythea celtis celtoides* Fruhstorfer from Suwa, Nagano-prefecture. *New Ent. Ueda* **20**: 27–32.
- APG, 1998. An ordinal classification for the families of flowering plants. *Ann. Mo. Bot. Gdn.* **85**: 531–553.
- Barber, H. G., 1895. A new food plant for *Hypatus (Libythea) bachmani*. *Ent. News* **6**: 190–191.
- Barcant, M., 1970. *Butterflies of Trinidad and Tobago*. 314 pp., 28 pls. Collins, London.
- Boisduval, J. A. & M. J. Le Conte, 1833. *Histoire générale et Iconographie des Lépidoptères et des Chenilles de l'Amérique septentrionale*. 228 pp., 78 pls. Librairie Encyclopédique de Roret, Paris.
- Breland, O. P., 1948. Two migrations of the snout butterfly, *Libytheana bachmanii larvata* (Strecker). *Ent. News* **59**: 128–131.
- Brower, A. V. Z., 2000. Phylogenetic relationships among the Nymphalidae (Lepidoptera) inferred from partial sequences of the wingless gene. *Proc. R. ent. Soc. Lond. (B)* **267**: 1201–1211.
- Brown, K. S. Jr. & O. H. H. Mielke, 1967. Lepidoptera of the Central Brazil Plateau. 1. Preliminary list of Rhopalocera: Introduction, Nymphalidae, Libytheidae. *J. Lepid. Soc.* **21**: 77–106.
- Campbell, D. A., Brower, A. V. Z. & N. E. Pierce, 2000. Molecular evolution of the wingless gene and its implications for the phylogenetic placement of the butterfly family Riodinidae. *Molec. Biol. Evol.* **17**: 684–696.
- Calhoun, J. V., 2004. Histoire générale et iconographie des Lépidoptères et des chenilles de l'Amérique septentrionale by Boisduval & Le Conte (1829– [1837]): Original drawings used for the engraved plates and the true identities of four figured taxa. *J. Lepid. Soc.* **58**: 143–168.
- Collenette, C. L., 1928. A migration of *Libythea carinenta carinenta* Cr. *Entomologist's mon. Mag.* **64**: 124–126.
- Comstock, J. H. & L. G. Vazquez, 1944. Ciclos biológicos en lepidópteros. *An. Inst. Biol. Univ. nac. Aut. Méx. (Zool.)* **31**: 416–418.
- d'Abrera, B., 1988. *Butterflies of the Neotropical Region*, Part 5, Nymphalidae (Conc.) & Satyridae. 198 pp. Hill House, Victoria.
- Dawson, E. Y. & T. B. Blevins, 1944. Some butterflies of the mountains of eastern Arizona. *Ent. News* **55**: 253–257.
- De Lesse, H., 1970. Les nombres de chromosomes chez les lépidoptères Rhopalocères in Amérique Centrale et Colombie. *Ann. Soc. ent. Fr.* **6**: 347–358.
- DeVries, P. J., 1987. Papilionidae, Pieridae, Nymphalidae. *Butterflies of Costa Rica and their natural History* **1**. 327 pp. Princeton University Press, Princeton.
- Edwards, W. H., 1874. *Butterflies of North America* **2**. 58 pp., 51 pls. Houghton Mifflin, Boston.
- , 1881. Description of the preparatory stages of *Libythea bachmanii* Kirtland. *Can. Ent.* **13**: 226–229.
- Emmel, T. C. & J. F. Emmel, 1973. *The Butterflies of southern California*. xi, 148 pp. Anderson, Ritchie and Simon, Los Angeles.
- Fager, E. W., 1952. Migration notes from Mexico. *Lepid. News* **6**: 44.
- Fletcher, R. K., 1926. Notes on a migration of a snout butterfly (Lepid., Libytheidae). *Ent. News* **37**: 106–107.
- Freitas, A. V. L., 1999. An anti-predator behavior in larvae of *Libytheana carinenta* (Nymphalidae, Libytheinae). *J. Lepid. Soc.* **53**: 130–131.
- Gable, C. H. & W. A. Baker, 1922. Notes on a migration of *Libytheana bachmanii* Kirtl. *Can. Ent.* **54**: 265–266.
- Gilbert, L. E., 1985. Ecological factors which influence migratory behavior in two butterflies of the semi-arid shrublands of south Texas. *Cont. Mar. Sci. Suppl.* **27**: 724–747.
- Gosse, P., 1851. *A Naturalist's Sojourn in Jamaica*. xxiv, 508 pp. Longman, Brown, Green & Longmans, London.

- Hall, A., 1925. List of the butterflies of Hispaniola. *Entomologist* **58**: 161–165, 186–190.
- Hayward, K. J., 1969. Notes on butterflies migration in Argentina between April 1966 and May 1968. *Entomologist* **102**: 10–11.
- Heitzman, J. E., 1969. Nocturnal copulation of Rhopalocera. *J. Lepid. Soc.* **23**: 105–106.
- Heitzman, J. R. & J. E. Heitzman, 1987. *Butterflies and Moths of Missouri*. 385 pp. Missouri Department of Conservation, Jefferson City.
- Heitzman, J. R. & R. L. Heitzman, 1972. New butterfly records for the United States (Hesperiidae & Libytheidae). *J. Res. Lepid.* **10**: 284–286.
- Helfert, M. R., 1972. Migratory behavior of the snout butterfly, *Libytheana bachmanii larvata* (Strecker). *Ent. News* **83**: 49–52.
- Hering, M., 1921. Die geographische Verbreitung der Libytheiden. *Archiv fuer naturgeschichte* **87**: 248–296.
- Hernández, L. R. 2004. *Field Guide of Cuban-West Indies Butterflies*. 269 pp., 31 pls. Ediluz, Maracaibo.
- Howe, W. H., 1975. *The Butterflies of North America*. xiii, 633 pp., 97 pls. Doubleday, Garden City, New York.
- Hübner, J., 1819–1827. *Sammlung exotischer Schmetterling* **2**. [4] pp., [225] pls. Augsburg, Germany.
- Iftner, D. C., Shuey, J. A. & J. V. Calhoun, 1992. Butterflies and Skippers of Ohio. *Ohio Lepid. Res. Rep.* **3**. 170 pp. Ohio State University College of Biological Sciences, Columbus.
- Kawahara, A. Y., 2001. *Systematics of the Snout Butterflies (Lepidoptera: Nymphalidae: Libytheinae), with and Emphasis on the Morphology and Phylogeny*. xiii, 162 pp. Honors Thesis. Cornell University, Ithaca, New York.
- , 2003. Behavioral observations of adult *Libytheana carinenta* Cramer. *News Lepid. Soc.* **47**: 107–108 + front cover.
- , 2006. Biology of the snout butterflies (Nymphalidae: Libytheinae) Part 1: *Libythea* Fabricius. *Trans. lepid. Soc. Japan* **57**: 13–33.
- , (accepted). Systematic revision of the extant and fossil snout butterflies (Lepidoptera: Nymphalidae: Libytheinae). *Thomas Say Publications in Entomology, Monographs*. Entomological Society of America, Lanham, Maryland.
- Kawahara, A. Y. & R. Dirig, 2006. Review of nectar source records for *Libytheana carinenta* (Cramer) (Nymphalidae: Libytheinae). *J. Lepid. Soc.*
- Kendall, R. O. & P. A. Glick, 1972. Rhopalocera collected at night in Texas. *J. Res. Lepid.* **10**: 273–283.
- Kirby, W. F., 1896. *A Hand-Book to the Order Lepidoptera* **2**. xx, 332 pp., 30 pls. Edward Lloyd, London.
- Knight, G. W., 1895. A remarkable migration of butterflies. *Insect Life* **7**: 357–358.
- Landry, L.-P., 1987. Capture du *Libytheana bachmanii* (Kirtland) (Lepidoptera; Libytheidae) dans la division de recensement de Champlain, Québec. *Fabriques* **13**: 57–58.
- Laplante, J. P., 1985. *Papillons et chenilles du Québec et de l'est du Canada*. 280 pp. Éditions France-Amérique, Montréal.
- Layberry, R. A., 1985. *Libytheana bachmanii* Kirtland. *Toronto Entomol. Assoc. Occ. Publ.* **16**: 19.
- Maeki, K. & C. L. Remington, 1960. Studies of the chromosomes of North American Rhopalocera. 4. Nymphalinae, Charaxidiniinae, Libytheinae. *J. Lepid. Soc.* **14**: 179–201.
- Maynard, C. J., 1891. *The Butterflies of New England*. iv, 74 pp., 10 pls. Published by the author, Netwonville.
- Motono, S., 1993. *Libytheidae of the World*. 52 pp. Kirihara Shoten, Tokyo.
- Neck, R. W., 1976. Lepidopteran foodplant records from Texas. *J. Res. Lepid.* **15**: 75–82.
- , 1983. Causal analysis of a migration of the snout butterfly, *Libytheana bachmanii larvata* (Strecker) (Libytheidae). *J. Lepid. Soc.* **37**: 121–128.
- , 1984. On the origin of snout butterflies (*Libytheana bachmanii larvata*, Libytheidae) in a 1978 migration in southern Texas. *J. Lepid. Soc.* **38**: 319–322.
- Nininger, H. II., 1930. Brief notes on Mexican insects. *J. Kansas Entom. Soc.* **3**: 28.
- Opler, P. A. & G. O. Krizek, 1984. *Butterflies east of the Great Plains: an illustrated natural History*. xvii, 294 pp., 54 pls. Johns Hopkins University Press, Baltimore.
- Opler, P. A. & V. Malikul, 1992. *A Field Guide to eastern Butterflies*. xvii, 396 pp. Houghton Mifflin, Boston.
- Parman, D. C., 1926. Migrations of the long-beaked butterfly, *Libythea bachmani* Kirtland (Lepid.: Libytheidae). *Ent. News* **37**: 101–106.
- Preston-Mafham, R. & K. Preston-Mafham, 1988. *Butterflies of the World*. 192 pp. Facts on File Publications, New York.
- Pyle, R. M., 1981. *Audubon Society Field Guide to North American Butterflies*. 916 pp. Alfred Knopf, New York.

- Rau, P., 1941. Migrating butterflies *Libytheana bachmanii* larvata Stkr. in Texas. *Ent. News* **53**: 277-278.
- Rawson, G. W., 1949. A migration of the snout butterfly (*Libytheana bachmanii*) in eastern Arizona. *Lepid. News* **3**: 28.
- Reinthal, W. J., 1966. Butterfly aggregations. *J. Res. Lepid.* **5**: 51-59.
- Riley, N. D., 1975. *A Field Guide to the Butterflies of the West Indies*. 224 pp., 12 pls. Williams Collins, London.
- Robertson, C. 1928. *Flowers and insects: lists of visitors of four hundred and fifty-three flowers*. 221 pp. Clarinville.
- Rutowski, R., Terkanian, B., Eitan, O. & A. Knebel, 1997. Male mate-locating behavior and yearly population cycles in the snout butterfly, *Libytheana bachmanii* (Libytheidae). *J. Lepid. Soc.* **51**: 197-207.
- Saunders, W., 1868. Entomological notes, paper No. 2. *Can. Ent.* **1**: 25-27.
- Schappert, P., 2000. *A World for Butterflies: their Lives, Behavior and Future*. 320 pp. Key Porter Books, Toronto.
- Schreiter, R., 1943. Notas entomo-biológicas y otras. *Acta Zool. Lilloana* **1**: 1-44.
- Schwartz, A., 1983. *Haitian Butterflies*. 69 pp. Museo Nacional de Historia de Santo Domingo, Santo Domingo.
- , 1989. *The Butterflies of Hispaniola*. xiv, 580 pp. University of Florida Press, Gainesville.
- Scott, J. A., 1986. *The Butterflies of North America: a natural History and Field Guide*. xii, 583 pp. Stanford University Press, Stanford.
- Scudder, S. H., 1889. *The Butterflies of the eastern United States and Canada with special Reference to New England*. 3 vols., 1958 pp., 89 pls. Published by the author, Cambridge.
- Shields, O., 1972. Flower visitation records for butterflies (Lepidoptera). *Pan-Pacif. Ent.* **48**: 189-203.
- , 1985a. Zoogeography of the Libytheidae (snouts or breaks [sic]). *Tokurana* **9**: 1-58.
- , 1985b. Flower visitation records for snout butterflies (Libytheidae). *J. Lepid. Soc.* **39**: 340-341.
- , 1987a. A review of migration in Libytheidae. *Tokurana* **12**: 1-14.
- , 1987b. Ommochromes in Libytheidae. *J. Res. Lepid.* **26**: 266.
- , 1987c. Presence of pterin pigments in wings of Libytheidae butterflies. *J. chem. Ecol.* **13**: 1843-1847.
- Smith, D. S., Miller, L. D. & J. Y. Miller, 1994. *The Butterflies of the West Indies and south Florida*. viii, 264 pp., 34 pls. Oxford University Press, Oxford.
- Smyth, E. G., 1920. Butterfly migrations. *J. econ. Ent.* **13**: 259-260.
- Stokes, D. W., Stokes, L. Q. & E. Williams, 1991. *The Butterfly Book: an easy Guide to Butterfly gardening, Identification, and Behavior*. 96 pp. Little, Brown, Boston.
- Vyhmeister, G. & J. P. Donahue, 1980. The rediscovery of *Libytheana terena* in Jamaica (Libytheidae). *J. Lepid. Soc.* **34**: 102.
- Weller, S. J., Pashley, D. P. & J. A. Martin, 1996. Reassessment of butterfly family relationships using independent genes and morphology. *Ann. ent. Soc. Am.* **89**: 184-192.
- Welling, E. C., 1959. Notes on butterfly migrations in the Peninsula of Yucatan. *J. Lepid. Soc.* **13**: 62-64.
- Williams, C. B., 1938. Recent progress in the study of some North American migrant butterflies. *Ann. ent. Soc. Am.* **31**: 211-239.
- Woodbury, E. N., 1994. *Butterflies of Delmarva*. xxii, 138 pp., 32 pls. Tidewater Publishers, Centreville.

## 摘 要

テングチョウ 13 種の生活態 2: リビシアナテングチョウ属 (河原 章人)

この論文にはアメリカ大陸に生息するテングチョウ属, *Libytheana* 各種の分布図, 生息地, 生態, 成虫食, 食草, 移住, 天敵, 擬態, カムフラージュ及びクロモソーム数, プテリン色素などをまとめて報告する。*Libytheana carineneta* は毎年数回発生し, 様々な環境から報告されている。成虫は地面や花によくとまり, 雄が縄張りをもつ。大発生や移住をすることも知られている。カリブ海の島々に生息する3種の生態についてはあまり知られていない。

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