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THE LIFE HISTORY OF THE MARITIME RINGLET, *COENONYMPHA TULLIA NIPISQUIT* (SATYRIDAE)

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ABSTRACT. The immature stages of *Coenonympha tullia nipisquit* McDunnough are described and illustrated and an account of their biology and behavior under field conditions is given. The caterpillar host plant is *Spartina patens* (Ait.) Mühlenberg, a common grass in the salt marshes where this butterfly occurs. Although the immature stages are subject to inundation by salt water during the tide cycle, the life history appears to be similar to other members of the *C. tullia* complex. Comments on the taxonomic status of *C. t. nipisquit* are also given.

Additional key words: Salt marsh, host plant, endangered, *Coenonympha tullia inornata*.

The Maritime ringlet, *Coenonympha tullia nipisquit* McDunnough is the only member of the *C. tullia* (Müller) species complex in North America that is restricted to a salt marsh habitat. This subspecies has an extremely restricted distribution and is known from only a few localities, all near the Chaleur Bay in northeastern New Brunswick and Quebec on the east coast of Canada (Thomas 1980, Dion 1995, Handfield, pers. comm.). The largest colonies occur in three salt marshes within or near the city limits of Bathurst, N.B., increasing the risk that these habitats will be disturbed by urban and industrial sprawl and pollution. This could result in a reduction in the population numbers and possible extinction of this butterfly. For this reason, *C. t. nipisquit* has been recently listed as endangered in Canada by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) and by the Province of New Brunswick.

Coenonympha tullia nipisquit was described by McDunnough, in 1939, from specimens collected in salt marshes near Bathurst, N.B. Although the butterfly can be relatively numerous within the limited salt marsh habitats, little was known about the life history, biology and eco-

logical requirements of this insect. In this paper the immature stages of *C. t. nipisiquit* are described and an account of their biology and behavior under field conditions is given.

MATERIALS AND METHODS

Study sites. *Coenonympha tullia nipisiquit* was studied in salt marshes in the estuary of the Peters River in Beresford, N.B. (near the Bathurst city limit), and at the Daly Point Reserve in Bathurst, N.B. The most common plants where *C. t. nipisiquit* occurs are *Spartina patens* (Ait.) Mühlenberg (salt meadow grass), *S. alterniflora* Loiseleur-Deslongchamps (Graminaceae), *Glaux maritima* L. (Primulaceae), *Limonium nashii* Small (sea lavender) (Plumbaginaceae), *Plantago maritima* L. (Plantaginaceae) and *Solidago sempervirens* L. (seaside goldenrod) (Asteraceae). The density of each species varies throughout the two sites forming a series of distinctive plant assemblages that occur in a mosaic or in zones within the marshes. *Spartina patens* is the most abundant species of plant at these two sites and forms dense stands covering as much as 75% of the marshes. *Coenonympha tullia nipisiquit* densities are usually highest in these sections of the marsh. All the marsh habitats are periodically flooded during high tides, sometimes to a depth of 0.5 to 1.0 meters. Wetter and more frequently flooded sections of the marsh, characterized by varying densities of *S. alterniflora*, occur near tidal ponds and creeks. Drier, infrequently flooded areas occur adjacent to forests or sand dunes bordering the salt marshes. These latter sites are often invaded by plant species associated with upland habitats.

Insect rearing. The life history and description of the immature stages were determined from insects reared from ova to adults on potted *S. patens* (45 cm diam. pots) collected from the Peters River estuary and maintained outdoors under natural photoperiod and temperature conditions in Fredericton, N.B. Ova were obtained from 4 fresh female *C. t. nipisiquit* collected on August 8, 1992. Females were put into 2 liter plastic ice cream containers with a screened cover with *S. patens* as an oviposition substrate. The container was placed in a location under partial shade and the ova were removed on a daily basis and placed among the stems of the potted *S. patens*. The behavior of the immatures and measurements of each life stage were recorded periodically (day and night) throughout their development, until adult emergence. Additional data were obtained from field observations and collections of the larvae and pupae at the Peters River and Daly Point salt marshes.

All descriptions and measurements are of living larvae and pupae. Morphological observations and measurements were made with aid of a stereomicroscope equipped with an ocular micrometer.

TABLE 1. Width of the head capsule and range of body lengths (resting larva) from post-molt to pre-molt of the five instars of *Coenonympha tullia nipisiquit* McDunnough.

Instar	Sample size	Mean width of head capsule (mm)	Mean body length (mm)	
			Post-molt	Pre-molt
First	11	0.64	2.6	4.7
Second (pre-diapause)	10	0.89	4.8	5.4
Second (post-diapause)	8	0.89	5.6	7.6
Third	6	1.07	8.2	10.0
Fourth	6	1.61	10.3	15.5
Fifth	6	2.40	13.3	23.4

Oviposition behavior. The sequence of behaviors culminating in oviposition and the host plant used for oviposition were determined from following females in flight and searching for ova from regions where females had been flushed.

RESULTS

Description of the immature stages. Egg. Eggs are subconical in shape (widest at the base), 1.0 mm in diameter and 1.1 mm in height ($N = 10$) (Fig. 1). Each egg has 40 to 48 shallow vertical ribs with a few transverse ridges. The micropyle lies on a slightly mounded prominence. Eggs are pale green when first laid and after 3 to 4 days they become light tan and mottled with irregular light brown patches. The duration of the egg stage is between 10 and 15 days under natural temperature conditions ($N = 20$).

Larvae. *Coenonympha tullia nipisiquit* has 5 larval instars. The size (head capsule width and body length) of each stage is shown in Table 1. Second through the fifth instar larvae exhibit a similar color pattern and differ only in size. These are shown in Figs. 2–5. Only the first and last instar larvae will be described.

First instar larva. Newly eclosed larvae are between 2.6 and 2.7 mm in length ($N = 10$), taper slightly and end in two short conical tails. The ends of the tails are reddish brown. The head is sub-globose and broader than the second segment. After eclosion the larvae are light tan with a mid-dorsal and 3 longitudinal light brown stripes, and a cream colored longitudinal stripe just below the spiracles. The brown spiracles are contained in the most ventral brown stripe. The head capsule and underside of the body are tan. Numerous small whitish tubercles each with a short, bent, light brownish process or seta cover the body and head. As the larvae feed they gradually become green and begin to exhibit a color pattern similar to the next four larval instars.

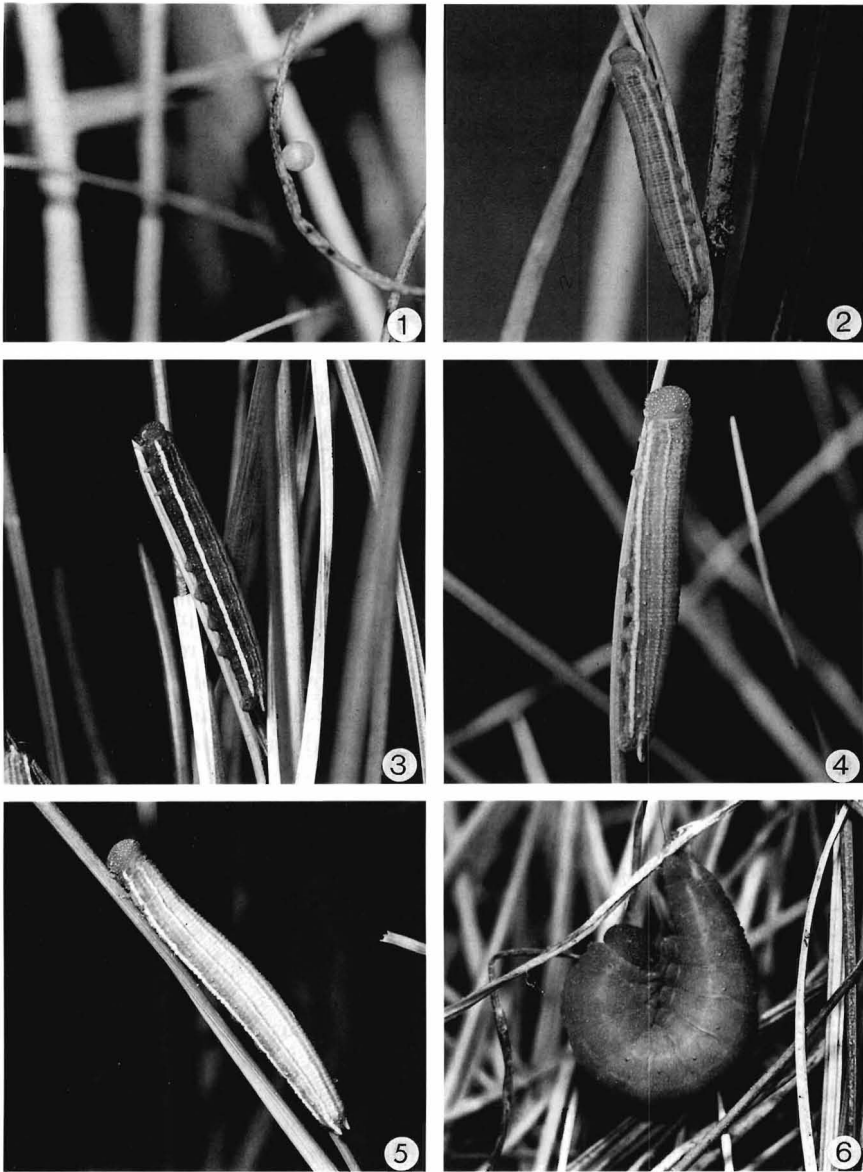


FIG. 1. Field collected egg of *C. t. nipisiquit* on dead blade of *S. patens*. FIG. 2. Post diapause second instar larva of *C. t. nipisiquit* resting on blade of *S. patens*. Length of larva was 7.0 mm. FIG. 3. Third instar larva of *C. t. nipisiquit* feeding on blade of *S. patens*. Length of larva was 9.2 mm. FIG. 4. Fourth instar larva of *C. t. nipisiquit* resting on blade of host plant. Length of larva was 12 mm. FIG. 5. Fifth (last) instar of *C. t. nipisiquit* resting on blade of host plant. Length of larva was 25 mm. FIG. 6. Prepupa of *C. t. nipisiquit* attached to stem of host plant.

Fifth instar larva. The mature last instar larvae are between 20.0 and 31.0 mm in length (mean = 23.4 mm) ($N = 6$), broadest (3.5 to 4.0 mm in width) and slightly arched dorsally between segments 3 and 7, and then taper gradually and end in two short conical tails or bifurcations (Fig. 5). The head is sub-globose, narrowing toward top and broader than first and second segments behind head. Small whitish tubercles, each with a short, bent (usually directed downward or posteriorly), light brownish semitransparent seta cover the head and body, giving the larvae a granular appearance. The overall color of the larvae is green to yellow green with a series of longitudinal stripes. Going dorsally to ventrally, there is a dark green mid-dorsal stripe edged on either side by pale yellowish green and a broad pale to yellowish green lateral stripe. These are followed by a narrow dark green lateral stripe edged on either side with pale yellow green, a broad green lateral band that gradually becomes dark green, and a yellow lateral stripe. The brown spiracles are in contact with the upper margin of this yellow band. The head is dark green and the ocelli, mandibles, and labrum are brown or light brown. The underside of the body and thoracic legs are dark green, tarsi brownish, prolegs are dark green with brown crochets. The two conical tails are yellowish green becoming reddish brown distally.

Pupa. The pupae are 11.0 mm to 13.0 mm (mean = 11.9 mm) in length and 4.0 mm to 5.0 mm (mean = 4.4 mm) in width ($N = 12$). They are cylindrical, stout, with the anterior end truncated and the abdomen swollen and conical distally. Pupae are suspended by a cremaster attached to a silk pad, usually on a grass stem. The pupae are usually bluish green with a series of black stripes. In the most common pattern (Figs. 7 & 8) there is one black stripe on the dorsal edge of each wing case from the base to inner angle. The inner margin of this stripe is whitish becoming bluish green. There is usually a curved stripe on central portion of wing case reaching the hind margin and a short stripe on hind margin of wing case. On the ventral side of the pupa there are two parallel stripes on the antennal cases and a larger stripe between the wings. There also may be a short lateral black stripe on each side of the last one or two segments of the abdomen. However, there is much variability in the extent of the pattern of stripes among individuals. The extremes of patterns among the individual pupae examined in this study (25) range from uniform bluish green with the black stripes nearly completely absent (Fig. 9) to individuals in which the black stripes have greatly expanded, obliterating all but a few green patches on the wing cases and between the abdominal segments (Fig. 10).

Oviposition behavior. The adults fly during a four to five week period from mid to late July to the third week in August. Females mate shortly after emergence near the pupation site and begin to oviposit

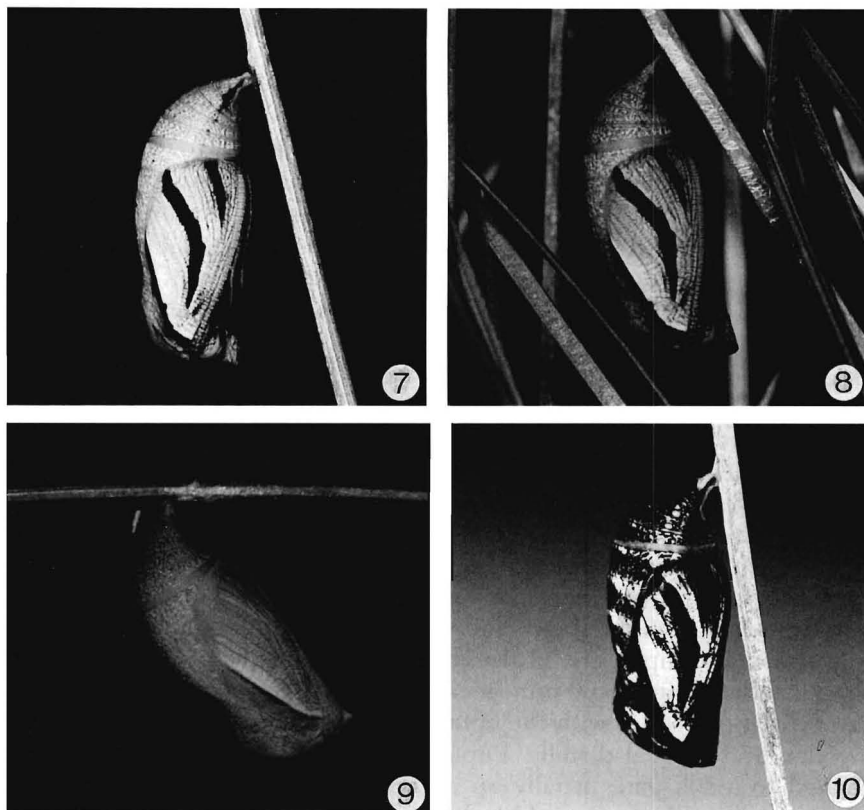


FIG. 7. Pupa of *C. t. nipisiquit* exhibiting typical pattern of dark lines. Pupal length was 12.5 mm. FIG. 8. Pupa of *C. t. nipisiquit* in typical pupation site near the base of *S. patens* canopy. Note how the color pattern confers crypsis to the pupa within the grass stems. FIG. 9. Pupa of *C. t. nipisiquit* in which dark lines are greatly reduced. Pupal length was 12.0 mm. FIG. 10. Pupa of *C. t. nipisiquit* with a greatly expanded pattern of dark stripes. Pupal length was 12.1 mm.

shortly after uncoupling. The primary larval host plant of *C. t. nipisiquit* is salt meadow grass, *S. patens*. Females were observed ovipositing on this grass and all larvae ($N = 35$) located in the marshes were either feeding or resting on this grass which is often the most abundant species of plant in the areas where *C. t. nipisiquit* is common. Larvae will complete development under laboratory conditions on *Festuca rubra* L. (Graminaceae), which also occurs in the salt marshes. However, this species of grass was generally not common where *C. t. nipisiquit* is most abundant, larvae have not been found on it, and females have not been

observed ovipositing on this plant. It therefore, remains to be determined if *F. rubra* is used by *C. t. nipisiquit* in nature.

The description of oviposition behavior was based on observations of 10 females at the Daly Point and Peters River salt marshes. Females begin to oviposit shortly after mating. Oviposition usually begins after a short flight (10 to 20 m) a short distance above the plant canopy. Most females abruptly drop into the canopy, move to the litter layer (area of dense dead grass stems) near the base of the grass, and begin to walk on the litter. Eggs are laid singly near the tips of thin (0.2 to 0.5 mm diam.) dead blades of *S. patens* near the base of the stems of the living plant between 1 and 7.5 cm (mean = 1.6 cm, N = 23) above the surface of the litter layer (Fig. 1). Each female lays 2–5 eggs (one per grass blade) before moving to another location. Eggs are scattered, but usually 3.0 to 15.0 cm from each other.

Females oviposit in a variety of microhabitats within the salt marsh, including regions dominated by *S. patens* (90 to 100% of stem density), wetter areas (more frequently flooded during high tides) where *S. alterniflora*, *G. maritima*, and *P. maritima* were dominant and *S. patens* comprised only about 10% of the stem density, and in areas with intermediate plant compositions. In all these areas eggs were laid at the base of living *S. patens* plants. Eggs are laid during the third or fourth week of July to the third week in August and hatch in 10–14 days.

Behavior of immature stages. Pre-diapause larvae. The neonate larvae initially feed on the egg shell and on the end of the dead grass blade to which the eggs were attached before moving to young shoots of *S. patens*. Most larvae feed head end up on the tips of young shoots of *S. patens* that were within or just protruding from the litter region at the base of the mature grass stems, although a few larvae also feed on the tips of mature leaves. The caterpillars consume only the distal 1/2 to 3/4 cm of the shoot before moving to another stem. When larvae are not feeding they usually rest on a grass stem with the head facing down.

The first instar larvae molt to the second instar after 15 to 17 days (early to mid Sept.). The second stage larvae continue to feed on the developing shoots within the litter zone. During mid to late October the second instar larvae stop feeding and enter diapause.

Diapause. Except for becoming slightly deeper green, the color pattern of the second instar larvae changes little after onset of diapause. Diapausing larvae range in length from 4.9 to 6.2 mm (mean = 5.4; N = 10). On potted plants most diapausing caterpillars rest along the undersides of dead grass stems between 2 and 4 cm below the surface of the previous year's litter (top layer) and 3 to 5 cm above the soil surface (N = 20). Larvae were not found near the saturated soil surface. In the salt

marsh at Daly Point one diapausing second instar larva was located a few days after the snow melt in late April. The larva was on the underside of a dead grass stem 5 cm above the soil surface within the litter zone.

Post-diapause larvae. The second instar larvae resume feeding on the developing shoots of *S. patens* from early to late May. Early in the season most of the larvae feed on the new shoots that were still within the litter layer. Later in the spring as the shoots begin to protrude above the litter zone the larvae begin feeding on shoots above this layer. During much of May and early June the larvae only feed during the day and stop feeding prior to 17:00 h and crawl into the litter, even on warm nights ($>10^{\circ}\text{C}$).

The second instar larvae molt to the third instar from mid May to early June and continue to feed on the new shoots of *S. patens*. The duration of the third instar larvae is 13 to 16 days. Most larvae molt to the fourth instar by late June.

Most fourth instar larvae feed near the top of the grass canopy and consume between 2 to 3 cm of the new growth (shoot) before moving to another stem. The larvae rest head down at the base of the grass stems at night as in the previous instars or higher up on the stems when not feeding during the day. The fourth instar lasts between 12 and 14 days.

Between mid June and early July most caterpillars molt to the last (fifth) instar. This stage lasts about 15 days and unlike the previous instars, caterpillars of this stage also feed nocturnally. The full grown caterpillars begin pupating in late June and continue to pupate until early August depending on the microclimatic conditions near the feeding site. Prior to pupation, the larvae attach themselves via a silk pad to stems of the host plant and the larval stripes become obscure or vanish entirely (Fig. 6).

Pupae. Most *C. t. nipisiquit* pupate near the base of grass stems within the grass canopy. On potted *S. patens*, pupae were attached via a silk pad to either living (86%) or dead grass stems between 2.5 cm below and 22.5 cm above the litter zone (mean = 5.2 cm; $N = 37$; canopy height was about 40 cm). In the field the cryptically colored pupae were very difficult to locate among the dense grass stems (Fig. 8). However, pupal exuvia could often be located near freshly emerged adults or mating pairs. Most pupal exuvia in the salt marsh were 2.5 cm below to 12.5 cm above the litter zone (Mean = 7.4 cm; $N = 18$) and all but two were attached to living stems of *S. patens*. Most were in areas of dense *S. patens* between 20 and 30 cm in height. However some exuvia were found in areas where *S. alterniflora*, *G. maritima*, and *P. maritima* dominated the plant community.

The pupal stage lasts 9 to 11 days. Most adult emergence occurs between 10:00 and 16:00 h ($N = 25$), however, there were insufficient ob-

servations to determine a specific emergence pattern. After eclosion, adults climb to a position near the top of the canopy, expand the wings and are ready for flight in about one hour.

DISCUSSION

The immature stages of *C. t. nipisiquit* are similar to those of the other members of the *C. tullia* complex in North America (Edwards 1887, 1897, Davenport 1941, Brown 1955, 1958, 1964, Brown & Heineman 1961). The ova of *C. t. nipisiquit* are slightly larger (1.1 mm high, 1.0 mm diam.) than the ova from females of *C. t. "inornata."* from Grindstone and Picton Islands in the St Lawrence River (0.9 mm high, 0.7 mm diam., May–June flight; 0.71 high, 0.75 diam., late August flight) (Brown 1958, Brown & Heineman 1961), but similar in size to ova of *C. t. inornata* from Lake Nominique, Quebec (about 1.0 mm) (Davenport 1941). Egg size was not given in the descriptions of the other North American populations. The only significant difference among the larvae of the subspecies, where descriptions are available, is that the larvae and chrysalids of some western populations, such as *C. t. californica* Westwood and *C. t. ampelos* Edwards exhibit a brownish color form (Edwards 1897, Brown 1964) not observed in *C. t. nipisiquit* or *C. t. inornata* (Davenport 1941, Webster in litt.).

Coenonympha tullia nipisiquit is unusual among the North American *Coenonympha* in that the entire life cycle of the butterfly occurs in a salt marsh habitat. During parts of the monthly tide cycle the entire marsh may be covered to a depth of 0.5 to 1.0 meters and thus all life stages of this butterfly are subject to the effects of flooding by salt water. Because of this, Brown (1955) suggested that the life history would differ from other *tullia* in North America. However, the life cycle of *C. t. nipisiquit* appears to be similar to other members of the *C. tullia* complex (Davenport 1941, Brown 1955, 1964). How the various life stages of *C. t. nipisiquit* withstand the effects of the salt water during high tides remains to be determined.

Coenonympha tullia nipisiquit is distinctive in the late summer flight season of the single generation of adults that is 3 to 5 weeks later than *C. t. inornata* in Bathurst, N.B. (Webster, in litt.). The difference in timing is probably in part, related to differences in the diapause characteristics of the two subspecies. *Coenonympha tullia inornata* diapauses as a third or fourth instar larvae in N. B. (Webster, in litt.), while *C. t. nipisiquit* diapauses in the second instar. Microclimatic differences between the preferred habitats of these two subspecies may accentuate the differences in emergence patterns created by diapausing in different instars. In the Bathurst area, *C. t. inornata* occurs in fields adjacent to the salt marshes. These upland habitats are slightly warmer because they are

less directly affected by the cooling effects of the sea breezes and they are not subject to the effects of inundation by cold water during the tide cycle. This would accelerate development of the larvae in the upland habitats compared to those in the salt marshes.

The late flight season of *C. t. nipisiquit* may also be linked to the availability of nectar which is generally unavailable prior to late July in the salt marsh habitat. Emergence of *C. t. nipisiquit* generally coincides with the flowering of a number of species of plants in the salt marshes including *L. nashii*, the principal nectar source of *C. t. nipisiquit* (Webster, in litt.).

A few comments are required regarding the taxonomic status of *C. t. nipisiquit*. *Coenonympha tullia nipisiquit* was arbitrarily classified as a subspecies of *C. inornata* (Edwards) in Brown (1955), Miller and Brown (1981), and Hodges (1983) and a subspecies of *C. tullia* in Scott (1986). However, Davenport (1941) has provided the only complete taxonomic revision of *Coenonympha* to date and showed that both *inornata* and *nipisiquit* should be classified as subspecies of *C. tullia*. This classification scheme may need to be revised in view of the recent range expansion of *C. t. inornata* in New Brunswick.

Prior to the 1970's, *C. t. nipisiquit* was the only *Coenonympha* in New Brunswick. During the 1970's *C. tullia inornata* moved into New Brunswick from the west and can now be found in almost any open grassy area throughout the province (Christie 1983, Thomas 1996) including the edges of the salt marshes occupied by *C. t. nipisiquit*. The two subspecies are now sympatric and they appear to be reproductively isolated due to differences in flight season and habitat preference and behave as separate species. Although the two subspecies appear to be reproductively isolated, little evidence is available on the genetic relatedness of the two subspecies in the area of sympatry. In a study by Wier-naz (1989), in which genetic changes associated with the recent range expansion of *C. tullia inornata* were examined, it was shown that the allele frequencies of *C. t. nipisiquit* were significantly different from all populations of *C. tullia inornata* examined. However the author did not comment on the taxonomic significance of these results and was apparently unaware that these two subspecies were sympatric in Bathurst, N.B. Studies are currently underway to re-examine the taxonomic relationship between these two subspecies.

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