

Journal of the Lepidopterists' Society
69(2), 2015, 108–113

NOTES ON THE DEMOGRAPHY, LIFE HISTORY, AND BEHAVIOR OF THE WHITE MOUNTAIN ARCTIC BUTTERFLY (*OENEIS MELISSA SEMIDEA*)

A. E. GRADISH AND G. W. OTIS

School of Environmental Sciences, University of Guelph, Guelph, ON, N1G 2W1, Canada
e-mail: agradish@uoguelph.ca and e-mail: gotis@uoguelph.ca

ABSTRACT. The White Mountain Arctic butterfly [WMA; *Oeneis melissa semidea* (Say, 1828)] is endemic to the alpine zone of the Presidential Range of the White Mountains, New Hampshire, USA. Although it has been listed as “imperiled”, many biological characteristics of the WMA important for its conservation assessment and management are unknown. We conducted field studies in 2011 and 2012 to further characterize the WMA’s demography, life history, and behavior. In both years, adults emerged in mid-June and occurred on Mts. Washington and Jefferson in association with Bigelow’s sedge (*Carex bigelowii*). On both mountains, adult numbers generally were very low, suggesting that the population has declined considerably since its first description. Adults dispersed among some of the meadows on Mt. Washington, but we were unable to confirm if they moved between Mts. Washington and Jefferson. Adults generally congregated on rocky ledges and out-croppings, where males employed both perching and patrolling mate-locating strategies. In addition to elevation (high points in the landscape), adults used other cues when choosing sites at which to congregate. Finally, although many other *Oeneis* species engage in male territoriality, our observations suggest that WMA males are not truly territorial.

Additional key words: alpine, conservation, territoriality, lek, dispersal

The White Mountain arctic [WMA; *Oeneis melissa semidea* (Say)] is endemic to the alpine zone of the Presidential Range of the White Mountains, New Hampshire, USA. Within this area, populations are confirmed only on Mts. Washington and Jefferson, where adults are localized in alpine meadows dominated by Bigelow’s sedge (*Carex bigelowii* Torr. ex Schwein), the sole larval host plant of the WMA (Scudder 1889, Anthony 1970, McFarland 2003). Because of its rarity and severely restricted range, the WMA has been listed as threatened and imperiled at state and global levels, respectively (New Hampshire Fish and Game Department 2005).

To date, most of our biological and demographic knowledge of the WMA comes from the initial descriptions of Scudder (1881, 1889, 1891, 1901). Since then, only Anthony (1970) and McFarland (2003) have attempted to systematically monitor or study the WMA, and Anthony (1970) deemed his own study to be inconclusive. Consequently, many aspects of the WMA’s biology and behavior remain unconfirmed or unknown. For instance, an estimate of present-day population size is lacking. Furthermore, although the WMA population is purportedly spatially structured into isolated fragments (Anthony 1970; McFarland 2003), adult dispersal capacity and patterns have never been determined. Finally, WMA males appear to aggregate in leks where they await the arrival of females (McFarland 2003), but the mating system has never been definitively characterized. Current, detailed knowledge of such demographic and behavioral characteristics will be critical for the continuing conservation assessment and management of the WMA.

Over two field seasons, we attempted to further quantify the WMA’s behavior and demography in the context of its conservation. However, consistent with the experiences of Anthony (1970) and McFarland (2003), making systematic and quantifiable observations of the WMA proved challenging: access to adults required long hikes, and the steep and rocky terrain made following or capturing adults very difficult. Mount Washington also routinely experiences harsh and unpredictable weather, and hence a limited number of days were suitable for adult butterfly activity. Nevertheless, we made some novel observations significant to the WMA’s conservation that we summarize here.

FIELD METHODS

We conducted field studies from 22 June–14 July, 2011, and 22 June–15 July, 2012. Each year, the area that we surveyed included the alpine meadows described by Anthony (1970) (Cow Pasture, Bigelow Lawn, and Gulf Tanks on Mt. Washington; and Monticello Lawn on Mt. Jefferson), but also encompassed most of the intervening and adjacent areas containing Bigelow’s sedge (Figure 1). Following rough transects, we surveyed each meadow at least every other day, or as weather permitted. In total, Cow Pasture, Bigelow Lawn, Gulf Tanks, and Monticello Lawn were surveyed 9, 5, 5, and 1 times, respectively, in 2011; and 9, 4, 7, and 2 times, respectively, in 2012. Because the weather conditions on Mt. Washington are variable and subject to rapid change, the number of days we were able to survey and the amount of time spent surveying in each meadow on any given day was highly variable.

TABLE 1. Summary of *Oeneis melissa semidea* adult capture data.

Year	Captured	Males	Females	Recaptures	Recapture Distance (m)			Days to Recapture		
					mean	min	max	mean	min	max
2011	187	126	61	8	305.7	28.1	787.0	5	1	8
2012	182	110	69	8	66.3	14.8	172.0	2	1	7

As such, our surveys were unavoidably biased, and thus we were unable to accurately estimate several adult population characteristics (e.g., overall size and density, density by meadow, sex ratio).

During surveys, we employed mark-release-recapture in an attempt to assess adult distribution, movements, longevity, and population size. To uniquely mark individuals, we applied small dots to the ventral wing surface of one side of the body with water-based, colored (red, green, blue, or yellow) paint markers (Sharpie® poster-paint) using a position-based numbered coding system (Southwood 1980).

Occasionally, we searched for eggs, larvae, and pupae at the bases of sedge plants or under small, moveable rocks.

RESULTS AND DISCUSSION

Adult Life History and Demography. Adults were present for the duration of each study period. Based on the degree of wing wear of the first individuals captured, adults likely first emerged on ~22 June in 2011, and may have emerged as early as 15 June in 2012. By the end of each study period, approximately 85% of adults demonstrated some degree of wing wear, indicating that they were near the end of their flight period. We estimate the flight periods were approximately 30 and 36 days in duration in 2011 and 2012, respectively.

Adults were located in almost every sedge-containing area of the Mt. Washington alpine zone. Similarly, adults were located in association with Bigelow's sedge on Mt. Jefferson, but were concentrated southeast of the summit (Fig. 1). On both mountains, adult density generally decreased with decreasing elevation, and the beginning of the krummholz (i.e., tree line) marked the limit of adult distribution. We did not locate any eggs, larvae, or pupae, which was unsurprising as WMA life stages other than adults have rarely been observed, even with intense search effort (Scudder 1881, 1889). To our knowledge, there is only a single report of a WMA egg observed in the field (Scudder 1889). Scudder (1881, 1889, 1891) often caged WMA females on Bigelow's sedge plants, and reported that females typically deposited single eggs loosely around the bases

of the plants among the leaf litter or on loose sticks (Scudder 1881, 1891). White Mountain arctic larvae and pupae also have been located in the field but only with intense search effort. Larvae feed at night and rest during the day in between or under rocks (Scudder 1874, 1889), and pupation occurs under rocks, moss, or just below the soil surface (Scudder 1874, 1889).

In total, 187 and 182 adults were marked in 2011 and 2012, respectively (Table 1). Each year, the ratio of males to females caught was approximately 2:1 (Table 1). Very few recaptures were made (8 each year; Table 1), precluding an accurate estimate of population size. However, the WMA population certainly has declined dramatically since its earliest descriptions. At the turn of the last century, Scudder (1901) encountered a large and robust WMA population, claiming that "During the entire month of July the butterflies swarm over the rocks and sedgy plateaus of the upper summits..." and that "...hundreds, perhaps thousands, are annually captured by enthusiastic collectors...". In stark contrast, we discovered that WMA adults were low in numbers and localized. As McFarland (2003) reported, we could survey large areas and encounter only one or two adults until reaching an area of congregation. These congregations typically only contained 10–15 adults. Because of a lack of study, the specific causes of the WMA population decline remain unclear, but may include climate change (Parmesan 2006, Konvička et al. 2010), a decline in the abundance of Bigelow's sedge, population genetic factors (Gradish, unpublished data), and/or historical over-collecting of adults. However, additional research on the WMA (e.g., phenology, habitat use) in relation to historical changes to the Mt. Washington alpine zone and Bigelow's sedge is necessary to identify the specific cause(s) of the WMA population decline.

Although the WMA emerges annually, it likely is biennial (i.e., requires 2 years for development) (McFarland 2003), as is the case for all other *Oeneis* species (Scott 1986, Layberry et al. 2001). Most biennial insects emerge every year over parts of their range (Heliövaara and Väisänen 1984, Scott 1986, Heliövaara et al. 1994, Kankare et al. 2002), and these seemingly annual emergences are assumed to represent

two sympatric, allochronic cohorts (i.e., one emerging in odd-numbered years and the other emerging in even-numbered years) (Scott 1986, Heliövaara et al. 1994, Kankare et al. 2002). The WMA also is presumably structured into two allochronic cohorts (Scudder 1889). Where sympatric, allochronic cohorts of biennial insects exist, one cohort usually is consistently less common (Masters 1974, Mikkola 1976, Heliövaara and Väisänen 1984, Scott 1986, Heliövaara et al. 1988, Sperling 1993, Kankare et al. 2002). Despite our almost identical capture rates each year, the total number of adults we observed (i.e., adults that we caught and adults that we observed but failed to catch) during our surveys in 2012 seemed comparatively lower, but despite this, our capture rates were almost identical both years. Because of our initial field experience in 2011, we were more proficient at capturing adults (i.e., we knew where to locate them and how to most effectively net them) during our second field season. As such, we believe that the adult population in 2012 was smaller, but we caught a comparatively larger proportion of it, resulting in a similar capture rate each year. Therefore, the WMA even-year cohort may be smaller; however, additional monitoring will be required to confirm this.

The average time between capture and recapture of an adult was 5 and 2 days in 2011 and 2012, respectively, with a maximum of 8 days (Table 1). The average distance between capture and recapture of an adult was 306 and 66 m in 2011 and 2012, respectively (Table 1). In 2011, a male originally captured at Gulf Tanks was recaptured 787 m away at Bigelow Lawn. The distance that this male covered indicates that adults are capable of dispersing among all meadows on Mt. Washington. Although we did not directly observe dispersal between Cow Pasture and the other two meadows, we routinely encountered adults in areas among all three meadows. Thus the populations in the meadows of Mt. Washington are likely not isolated from each other as suggested by Anthony (1970). However, it remains unclear if adults actively disperse between Mt. Washington and Mt. Jefferson. These mountains are separated by the Great Gulf ravine (approximately 2.5 km wide when measured between Cow Pasture and Monticello Lawn), which adults may be unwilling or unable to cross. Yet, adults may occasionally be carried between these two areas by the wind (Anthony 1970). We did not observe adult movement between these mountains, but this could reflect in part the low numbers of adults that we marked on Mt. Jefferson (8 and 12 in 2011 and 2012, respectively).

Until recently, the WMA has been reported only from Mt. Washington and Mt. Jefferson. However,

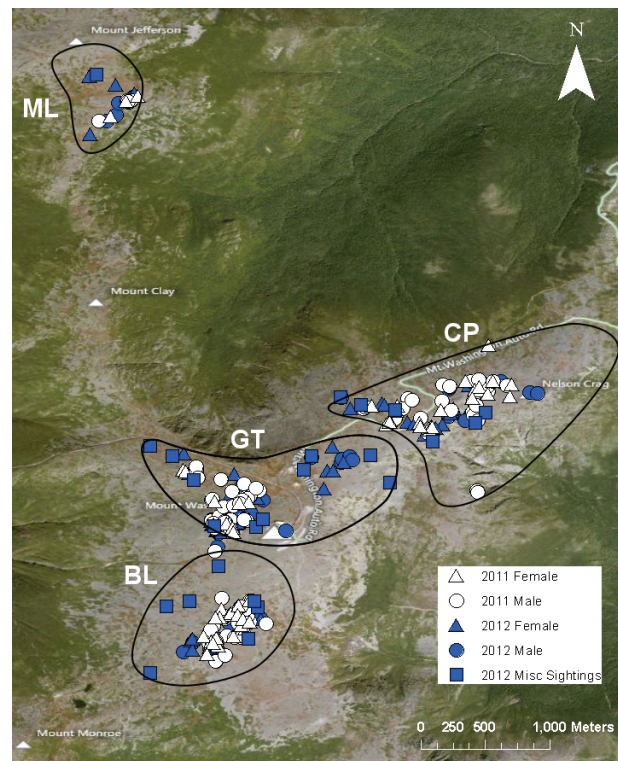


FIG. 1. Distribution of adult *Oeneis melissa semidea* on the alpine zone of Mts. Washington and Jefferson, New Hampshire, USA, determined by mark-release-recapture. Black lines indicate the areas surveyed for adults [Bigelow Lawn (BL), Gulf Tanks (GT), Cow Pasture (CP), and Monticello Lawn (ML)]. Triangles indicate locations where individual females were captured, circles where individual males were captured, and squares where an adult was sighted, but not captured. White and blue points indicate that the capture or sighting was made in 2011 and 2012, respectively.

McFarland (2003) observed one adult on Mt. Monroe in 2002 and noted the presence of suitable habitat. On 11 July 2012, a hiker familiar with the WMA encountered an adult on the southern slope of Mt. Monroe (E. Elinski, pers. comm.). We were unable to survey this area, and thus it remains unclear whether adults consistently occur on Mt. Monroe.

General Adult Behavior and Mating System.

Adults were most active on sunny days with winds below 30 km/h. However, even under cloudy skies with winds up to 60 km/h, some adults would fly if disturbed. Adults were wary and had strong and rapid flight: we occasionally observed them flying into 40–50 km/h winds to avoid capture. As reported by Scudder (1889), they frequently dove or crawled deep into rock piles if repeatedly disturbed or if we attempted to net them from directly above while they basked. Following capture and marking, we gently placed adults on a rock, where they typically basked briefly before flying away. White Mountain Arctic adults rarely nectar, but have

been observed feeding on Moss Campion (*Silene acaulis*), Mountain Sandwort (*Arenaria groenlandica*), and various *Vaccinium* spp. (Scudder 1901, McFarland 2003). In 2011, we observed one female nectaring from Mountain Cranberry (*Vaccinium vitis-idaea*).

Adults generally congregated on rocky ridges or small rocky outcroppings. These were typically characterized by a relatively flat area of sedge on the uphill side of a rocky ledge that bordered a rocky slope. The drop in elevation below the ledge was usually steep in the case of ridges, but rather slight in the case of small outcroppings. As is the case for other *Oeneis* species (Guppy 1962, Troubridge et al. 1982), this use of raised landscape features by the WMA has been interpreted as hilltopping (McFarland 2003), a mate-encounter system in which males congregate at high points in the landscape where they await the arrival of females (Shields 1967, Baughman and Murphy 1988). However, the ledges occupied by WMAs were often not the most elevated in relation to the surrounding area. For instance, the north slope of the Mt. Washington summit contains numerous ridges along a drop in elevation of approximately 120 m. Males and females routinely occurred on all of these ridges and occasionally on the rocky slopes between them. Moreover, adults frequently were found on small ridges or outcroppings at the bases of large slopes, despite the presence of seemingly identical habitat upslope. In Colorado, *Oeneis chryxus* (Doubleday) displays similar behaviour, congregating on slopes of varying elevation (Daily et al. 1991). The authors hypothesized that where males choose to congregate in a given season is dictated by female distribution and movement, and that to intercept females, males align themselves with bare areas that females were likely to move towards. Rather than simply congregating at high points in the landscape, it appears the WMA also uses additional visual cues when choosing areas in which to congregate.

Congregated WMA males appeared to use a combination of perching and patrolling as mate-locating strategies, as described by Scott (1974). They frequently perched on rocks and alternated between lateral basking and spontaneous (i.e., initiated without obvious stimulus or disturbance), presumably patrolling, flights. Males also engaged in spiral flights with passing conspecifics and other flying insects. Other butterfly species (Suzuki 1976, Lederhouse 1982, Alcock 1983), including some *Oeneis* species (Dunlop 1962, Guppy 1962, Masters et al. 1967, Daily et al. 1991, Clayton and Petr 1992), engage in a similar suite of behaviors, and these behaviors have been interpreted by some authors as male territoriality associated with a lek mating system (Dunlop 1962, Guppy 1962, Masters

et al. 1967, Lederhouse 1982, Alcock 1983, Knapton 1985, Clayton and Petr 1992, McFarland 2003). Yet the behaviour of the WMA differed both from some other *Oeneis* species and the definitional criteria for lekking (Bradbury 1981, Baker 1983). First, while territories of true lekking species remain fixed for several days in succession or longer (Baker 1983), the sites occupied by individual WMA males were not temporally stable. As an example, during an extended period of favorable weather between 9 and 13 July, 2012, we were able to conduct daily surveys of a ridge in Cow Pasture where adults consistently occurred. Each day, we observed 10–15 adults, 85–95% of which we were able to capture and mark. Despite our high capture rate, we only made two recaptures on subsequent days, even on the fifth visit. Furthermore, approximately 90% of the adults captured each day showed at least some wing wear, indicating that although these adults had clearly emerged at least a few days prior to capture, we had not previously encountered them at that site. Thus, either the adults were resident on the ridge continuously but a large proportion of them were inactive on any given day, or most adults moved away from the ridge. In contrast, *Oeneis chryxus* males consistently occupy the same sites for many days in succession, which is typical for lek-forming species (Dunlop 1962, Knapton 1985).

Second, the area occupied and/or patrolled by individual males often overlapped with other males without stimulating aggression between them. Males often perched within 2 m of each other, but also occasionally perched and basked directly beside each other on the same rock. Patrolling flights usually were of short distances (< 2m from point of initiation), but some individuals would fly and resume perching at a new site up to 15 m away. In either case, the area patrolled by a given male routinely contained multiple perching males. True butterfly territories typically contain only the resident male (Dunlop 1962, Lederhouse 1982, Knapton 1985), and 'intruders' are promptly driven away by the resident male (Davies 1978, Lederhouse 1982).

Third, following any type of flight, WMA males frequently did not return to the same rock or site from which they departed. Conversely, other purportedly territorial butterfly species (Lederhouse 1982, Wickman and Wiklund 1983), including *O. chryxus* (Knapton 1985, Daily et al. 1991), consistently return to their original perch immediately following patrolling or spiral flights.

Fourth, although spiral flights may be interpreted as a form of territorial defense (Lederhouse 1982, Alcock 1983), others view such flights as investigative, being used facilitate mate recognition (Scott 1974, Suzuki

1976, Daily et al. 1991, Clayton and Petr 1992). This latter explanation appears applicable to the WMA, as spiral flights often occurred between males and females, and, in three cases, ended immediately in copulation.

Fifth, male territories at leks are by definition devoid of oviposition and feeding sites (Bradbury 1981), yet areas of WMA male congregation contained both. The rocks on which males perched were almost invariably surrounded by Bigelow's sedge, the purported ovipositional site for females and larval host plant (Scudder 1891, 1901). Many flowering plants also occurred in these areas, including Mountain Cranberry and Mountain Sandwort, on which WMA adults occasionally feed.

Thus, although at first glance the WMA appeared to display behaviors typical of hilltopping and lekking species, our more in-depth observations indicate otherwise. As has been suggested for other perching butterflies displaying similar behavior (Scott 1974, 1986, Suzuki 1976), it appears that the WMA is not truly territorial. Further study will be required to determine the specific abiotic or biotic cues for WMA adult congregation, and to further characterize its mating behavior.

In conclusion, while quantifiable study of the WMA was unsuccessful, we did gain some novel insight into its life history and behavior. First, we were able to obtain information on the WMA's adult distribution and dispersal behavior. Although the localized meadow populations likely are not isolated from each other, the population as a whole appears to be in decline. Second, we were able to better characterize its male mate-locating behavior, which involves male aggregation on rocky ledges but none of the other traits of leks. This system seems to be different from that of other species of the genus *Oeneis*. Not only does this study contribute to our knowledge of *Oeneis* butterflies in general, but this information also should aid the WMA's conservation assessment and recovery efforts.

ACKNOWLEDGMENTS

We sincerely thank Thanushi Eagalle, Amy Reinert, and Andrew Frewin for their assistance in the field; Kent McFarland for his insight and advice on studying the WMA; and Nusha Keyghobadi, Felix Sperling, and Steve Marshall for their editorial comments. Our field work also would not have been possible without the generosity of Howie Wemyss of the Mount Washington Auto Road and Chris Costello of the USDA Forest Service. Permission for our field work was granted by the USDA Forest Service and the New Hampshire Fish and Game Department, and funding was provided by a Natural Sciences and Engineering Research Council of Canada (NSERC) Industrial Postgraduate Scholarship in partnership with the Cambridge Butterfly Conservatory, Ontario, Canada awarded to Angela Gradish, and a NSERC Discovery Grant to Gard Otis.

LITERATURE CITED

- ALCOCK, J. 1983. Territoriality by hilltopping males of the great purple hairstreak, *Atlides halesus* (Lepidoptera, Lycaenidae): convergent evolution with a pompilid wasp. *Behav. Ecol. Sociobiol.* 13: 57-62.
- ANTHONY, G. S. 1970. Field work on the population structure of *Oeneis melissa semidea* (Satyridae) from the Presidential Range, New Hampshire. *J. Res. Lepid.* 7: 133-148.
- BAKER, R. R. 1983. Insect territoriality. *Annu. Rev. Entomol.* 28: 65-89.
- BAUGHMAN, J. F. & D. D. MURPHY. 1988. What constitutes a hill to a hilltopping butterfly? *Am. Midl. Nat.* 120: 441-443.
- BRADBURY, J. W. 1981. The evolution of leks, pp. 138-169. In Alexander R.D. and D. W. Tinkle (eds.), *Natural Selection and Social Behavior*. Chiron Press, New York.
- CLAYTON, D. L. & D. PETR. 1992. Sexual differences in habitat preference and behavior of *Oeneis chryxus* (Nymphalidae: Satyrinae). *J. Lepid. Soc.* 46: 110-118.
- DAILY, G. C., P. R. EHRLICH, & D. WHEYE. 1991. Determinants of spatial distribution in a population of the subalpine butterfly *Oeneis chryxus*. *Oecologia* 88: 587-596.
- DAVIES, N.B. 1978. Territorial defence in the speckled wood butterfly (*Pararge aegeria*): the resident always wins. *Anim. Behav.* 26: 138-147.
- DUNLOP, D. J. 1962. Territorial habits of the chryxus arctic butterfly. *Ontario Field Biologist*: 20-24.
- ELINSKI, E. July 23, 2012, personal communication.
- GUPPY, R. 1962. Collecting *Oeneis nevadensis* (Satyrinae) and other genera on Vancouver Island with a theory to account for hilltopping. *J. Lepid. Soc.* 16: 64-66.
- HELIÖVAARA, K., & R. VÄISÄNEN. 1984. The biogeographical mystery of the alternate-year populations of *Aradus cinnamomeus* (Heteroptera, Aradidae). *J. Biogeogr.* 11: 491-499.
- HELIÖVAARA, K., R. VÄISÄNEN, J. HANTULA, J. LOKKI, & A. SAURA. 1988. Genetic differentiation in sympatric but temporally isolated pine bark bugs. *Hereditas* 109: 29-36.
- HELIÖVAARA, K., R. VÄISÄNEN, & C. SIMON. 1994. Evolutionary ecology of periodical insects. *Trends Ecol. Evol.* 9: 475-480.
- KANKARE, M., G. VÄRKONYI, & I. SACCHERI. 2002. Genetic differentiation between alternate-year cohorts of *Xestia tecta* (Lepidoptera, Noctuidae) in Finnish Lapland. *Hereditas* 136: 169-176.
- KNAPTON, R. W. 1985. Lek structure and territoriality in the chryxus arctic butterfly, *Oeneis chryxus* (Satyridae). *Behav. Ecol. Sociobiol.* 17: 389-395.
- KONVIČKA, M., J. BENES, & T. SCHMITT. 2010. Ecological limits vis-à-vis changing climate: relic *Erebia* butterflies in insular Sedeten mountains, pp. 341-355. In Habel, J. C. and T. Assmann (eds.), *Relict Species: Phylogeography and Conservation Biology*. Springer-Verlag, Berlin.
- LAYBERRY, R. A., P. W. HALL, AND J. D. LAFONTAINE. 2001. *The butterflies of Canada*. University of Toronto Press, Toronto.
- LEDERHOUSE, R. C. 1982. Territorial defense and lek behavior of the black swallowtail butterfly, *Papilio polyxenes*. *Behav. Ecol. Sociobiol.* 10: 109-118.
- MASTERS, J. H., J. T. SORESENSEN, & J. CONWAY. 1967. Observations on *Oeneis macounii* (Satyridae) in Manitoba and Minnesota. *J. Lepid. Soc.* 21: 258-260.
- MASTERS, J. H. 1974. Biennialism in *Oeneis macounii* (Satyridae). *J. Lep. Soc.* 28: 237-242.
- McFARLAND, K. 2003. Conservation assessment of two endemic butterflies (White Mountain Arctic, *Oeneis melissa semidea*, and White Mountain Fritillary, *Boloria titania montinus*) in the Presidential Range Alpine Zone, White Mountains, New Hampshire. Prepared for the White Mountain National Forest, 42 pp. Available from: www.vtecostudies.org/PDF/wmalpinebuttrep03.pdf (3 May, 2011).
- Mikkola, K. 1976. Alternate-year flight of northern *Xestia* species (Lep., Noctuidae) and its adaptive significance. *Ann. Entomol. Fenn.* 42: 191-199.

- NEW HAMPSHIRE FISH AND GAME DEPARTMENT. 2005. Species profile: White Mountain arctic, *Oeneis melissa semidea*, pp. A74-A78. In New Hampshire Wildlife Action Plan. http://www.wildlife.state.nh.us/Wildlife/wildlife_plan.htm
- PARMESAN, C. 2006. Ecological and evolutionary responses to recent climate change. *Annu. Rev. Ecol. Evol. Syst.* 37: 637-669.
- SCOTT, J. A. 1974. Mate-locating behavior of butterflies. *Am. Midl. Nat.* 91: 103-117.
- SCOTT, J. A. 1986. The butterflies of North America: a natural history and field guide, Stanford University Press, Stanford. 583 pp.
- SCUDDER, S. H. 1874. The distribution of insects in New Hampshire, a chapter from the first volume of the final report upon the geology of New Hampshire. Edward A. Jenks, State Printer, Concord, New Hampshire. 68 pp.
- SCUDDER, S. H. 1881. Butterflies: their structure, changes, and life-histories, with special reference to American forms. Henry Holt & Co., New York. 322 pp.
- SCUDDER, S. H. 1889. The butterflies of eastern United States and Canada with special reference to New England, volume I: introduction, Nymphalidae. S. H. Scudder, Cambridge, Massachusetts. 766 pp.
- SCUDDER, S. H. 1891. Experiments with alpine butterflies. *Psyche* 6: 129-130.
- SCUDDER, S. H. 1901. A courageous butterfly, *Oeneis semidea*. *Psyche* 9: 194-197.
- SHIELDS, O. 1967. Hilltopping. *J. Res. Lepid.* 6: 69-178.
- SOUTHWOOD, T. R. E. 1980. Ecological methods with particular reference to the study of insect populations. 2nd ed. Chapman and Hall, New York. 524 pp.
- SPELRLING, F. A. H. 1993. Twenty-seven years of butterfly observations at Fish Butte, Alberta. *Blue Jay* 51: 132-137.
- SUZUKI, Y. 1976. So-called territorial behaviour of the small copper, *Lycaena phlaeas daimio* Seitz (Lepidoptera, Lycaenidae). *Kontyu* 44: 193-204.
- TROUBRIDGE, J. T., K. W. PHILIP, J. A. SCOTT, & J. H. SHEPARD. 1982. A new species of *Oeneis* (Satyridae) from the North American arctic. *Can. Entomol.* 114: 881-889.
- WICKMAN, P.-O. & C. WIKLUND. 1983. Territorial defence and its seasonal decline in the speckled wood butterfly (*Pararge aegeria*). *Anim. Behav.* 31: 1206-1216.

Submitted for publication 15 August 2014; revised and accepted 28 October 2014.