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Source: The Journal of the Lepidopterists' Society, 68(4) : 264-273

Published By: The Lepidopterists' Society

URL: <https://doi.org/10.18473/lepi.v68i4.a4>

POPULATION BIOLOGY AND BEHAVIOR OF THE IMPERILED *PHILOTIELLA LEONA*  
(LYCAENIDAE) IN SOUTH CENTRAL OREGON

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**ABSTRACT.** The sole known metapopulation of *Philotiella leona* on the Mazama Tree Farm (MTF) and adjacent areas of the Winema National Forest (WNF) in the Antelope Desert of Klamath County, Oregon was surveyed and studied during 2011–2013. The flight period extended from mid-June to mid-late July or early August (35–47 days) with higher temperatures in 2013 associated with the shortest period. Populations of *P. leona* based on Pollard walk counts were 4–5 X greater at 4 MTF sites than a WNF site. Populations appeared to be twice as large in 2011 than 2012 or 2013. Greatest numbers were seen in late June-early July with a gradual decline thereafter. Flight activity was meandering and low to the ground and mostly occurred after midday, as did mating and oviposition. Nectaring was observed on 9 plant species with *Eriogonum umbellatum* most favored. A mark, release and recapture (MRR) study was conducted at one location (~ 0.4 ha) in the MTF with 214, 95 and 105 adults marked in 2011, 2012 and 2013, respectively. Recapture rates of 5.1, 5.3 and 9.5%, respectively, indicated longevity of up to 14 days and yielded population estimates of 61–4515 individuals. Greatest populations of *E. spergulinum* and *P. leona* appear to be centered on cleared slash/burn sites (like the MRR site) which are linked by trails and tracks. Conservation of *P. leona* may depend on the periodic creation of trail-linked slash/burn sites which appear to function as sites for sub-populations of a metapopulation.

**Additional key words:** metapopulation, flight period, nectaring, population size, mark, release, recapture

Leona's little blue butterfly, *Philotiella leona* Hammond and McCorkle, is arguably the most restricted and endangered butterfly species in the United States. Discovered in 1995, *P. leona* appears to be restricted to less than 32 km<sup>2</sup> in the Antelope Desert of south central Oregon approximately 16 km east of Crater Lake (Fig. 1) (Hammond and McCorkle 1999, Pyle 2002, Warren 2005, Miller and Hammond 2007, Ross 2008, 2009, Matheson et al. 2010, James 2012). It appears to be a highly specialized species occupying a volcanic ash and pumice ecosystem, dependent upon a similarly specialized larval host plant, Spurry buckwheat, *Eriogonum spergulinum* A. Gray. (Fig. 2). *Eriogonum spergulinum* and *P. leona* occur primarily in

openings of Lodgepole pine (*Pinus contorta* Douglas) forest. *Philotiella leona* is currently being considered for listing under the Endangered Species Act (Matheson et al. 2010). Apart from brief and fragmentary notes presented by Hammond and McCorkle (1999), Ross (2008, 2009) and Matheson et al. (2010), little is known of the ecology of *P. leona*. James (2012) provided detailed observations on the life history of *P. leona*. This paper provides information on the population biology and behavior of *P. leona* obtained during three flight seasons.

MATERIALS AND METHODS

Population census and observations on behavior. Field work was conducted during May–August 2011–13 in the known habitat of *P. leona*, private land owned by the Mazama Tree Farm (MTF) and adjacent areas of the Winema National Forest (WNF) in the Antelope Desert of Klamath County, Oregon. On the first visit (May 27–28 2011, pre-flight period) 5 locations were surveyed and established as separate sites for studies on *P. leona* populations. Sites were chosen on the basis of being open and having abundant Spurry buckwheat (*Eriogonum spergulinum*) seedlings. Sites were separated by 0.5–2.5 km with 4 on MTF (sites A, B, C, E) and 1 (D) on WNF land. At each site, two ~ 0.8 km transect or walk lines were identified that followed tracks or trails (Fig. 3). During the flight period each transect was walked by one or two observers at a pace of ~ 1.6 km/hr. On all occasions walks were conducted in sunshine between 1000–1700 h in temperatures of 21–30 °C. During each walk observations on behavior



FIG. 1. Map of Oregon showing location of the known habitat of *Philotiella leona*, approximately 16 km east of Crater Lake.

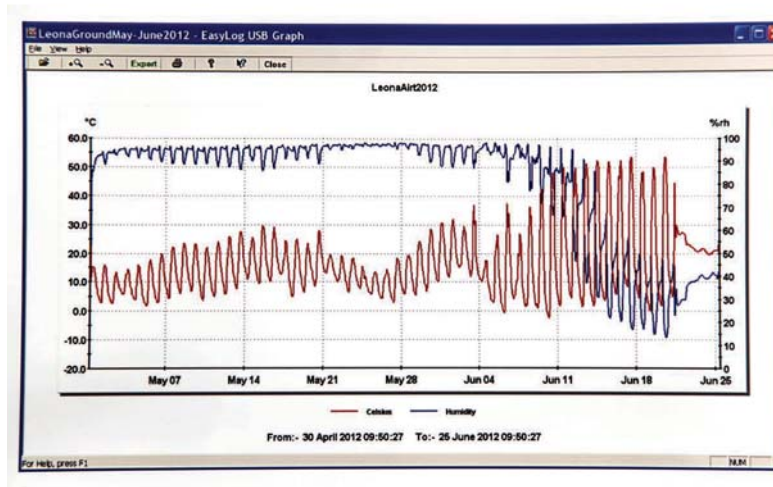


FIGS. 2–5. **2.** Spurry Buckwheat (*Eriogonum spergulinum*), host plant of *Philotiella leona*. **3.** A track used for ‘Pollard walk’ population census of *P. leona* with the Crater Lake volcano in the background. **4.** Cleared slash/burn site used for mark, release and recapture study with abundant *E. spergulinum* (pink-red ground cover). **5.** Marked *P. leona* nectaring on *P. hispidus* immediately following release.

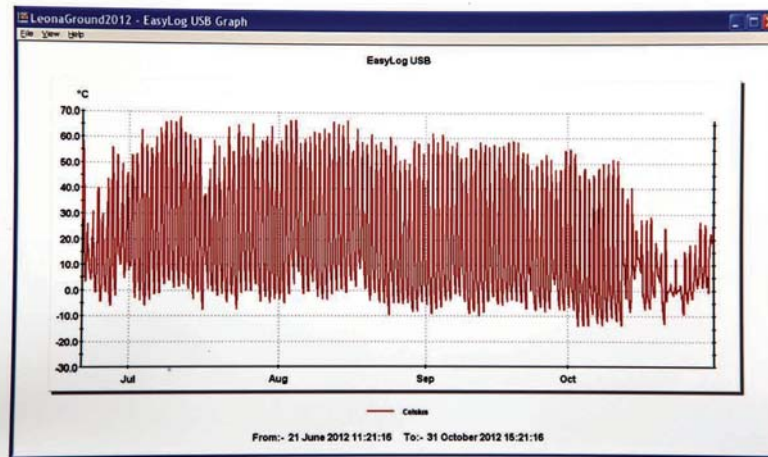
(flight, nectaring, roosting, courtship, mating, oviposition) of *P. leona* and the number of adults seen along the trail/track and ~ 5 m on each side, were recorded. This monitoring technique is based on the ‘Pollard transect walk’ for butterflies described by Pollard (1977). Occasionally, adults were netted (and released) to confirm sex and wing condition but in most instances status was assigned from observation only. Duration of walks varied from 25–35 minutes. Additional observations on behavior made between walks were also recorded.

**Mark, release and recapture study.** A mark, release and recapture (MRR) study was conducted each year in a 3888 m<sup>2</sup> (~ 0.4 ha) area near Site E. This area was a disturbed and cleared slash/burn site following tree harvest that occurred at least 5 years previously. *Eriogonum spergulinum* was abundant at the site (Fig. 4). In 2011, 7 visits at intervals of 2–14 days were made for MRR and 4 visits (6–9 day intervals) were made in 2012. The relative scarcity of recaptures in 2011 and

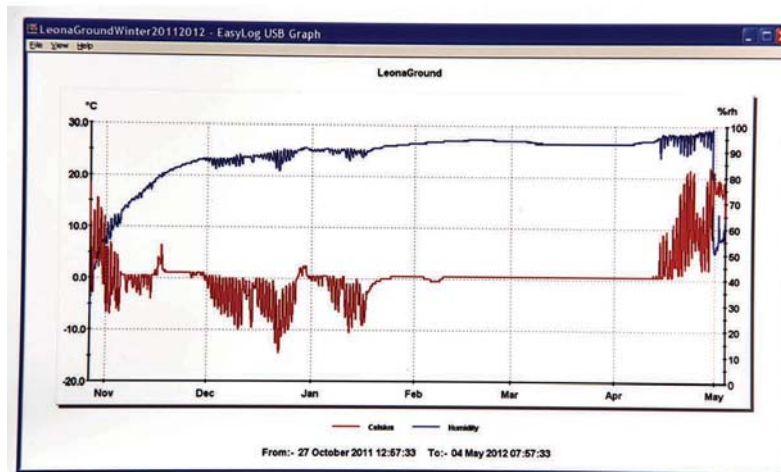
2012 prompted use of a shorter interval (24h) between MRR dates in 2013. At each visit one person spent 1–1.5 hours (1200–1400 h) collecting all the *P. leona* adults seen in the MRR area. Butterflies were placed in gauze covered plastic cylinder containers (12 cm × 13 cm) in a cooler and after the collection period were examined, marked and released at the center of the MRR area. Butterflies were allowed to disperse naturally from the opened containers. The sex and wing condition (worn, medium-worn and fresh) of each individual was recorded. Butterflies with no sign of wear or fading were classed as fresh. Faded and/or torn wings characterized worn individuals and individuals without substantial wear but lacking brightness of fresh butterflies were classed as medium-worn. Butterflies were marked by hand using fine point ‘Sharpies’® in 8 colors (red, blue, green, brown, black, yellow, pink, orange). Marks consisted of a series of 1–3 different colored dots placed on the ventral surface of the left hind wing, giving each individual a unique identity (Fig.



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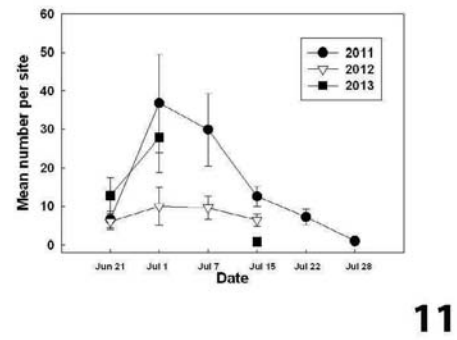
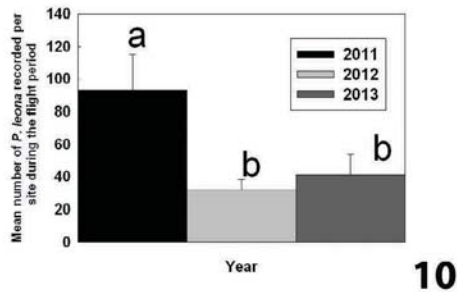
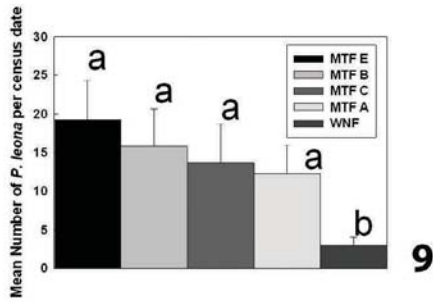


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FIGS. 6–8. **6.** Daily soil (0.5 cm below ground) temperatures and relative humidities likely experienced by *P. leona* pupae prior to commencement of the flight period at MTF (June 15) in 2012. **7.** Daily temperatures recorded by a logger exposed to direct sunlight (13 cm above ground) at the MTF from June 21 to October 31 2012. **8.** Daily soil (0.5 cm below ground) temperatures and relative humidities likely experienced by overwintering pupae of *P. leona* at MTF from October 27 2011 to May 4 2012.



FIGS. 9–11. **9.** Mean number of *P. leona* adults sighted per census date at the Mazama Tree Farm (MTF) and Winema National Forest (WNF) Pollard walk sites during June–July 2011–13. A different letter above a column indicates a significant difference ( $P < 0.011$ ). **10.** Mean number of *P. leona* adults recorded per Pollard walk site during flight periods 2011–13. A different letter above a column indicates a significant difference ( $P < 0.031$ ). **11.** Seasonal abundance of *P. leona* during 2011–13 as indicated by mean number recorded per Pollard walk site on each date. Data not obtained for July 7 in 2013 and July 22 and 28 in 2012 and 2013. Vertical bars represent standard errors.

5). Marked butterflies appeared unaffected behaviorally by the marks or process of marking and showed normal flight, courtship and nectaring behavior after release. MRR data in 2011 and 2012 were analyzed using Jolly’s stochastic method which provides estimates of population size when three or more successive samples are taken (Jolly 1965). A simple Lincoln Index (Lincoln

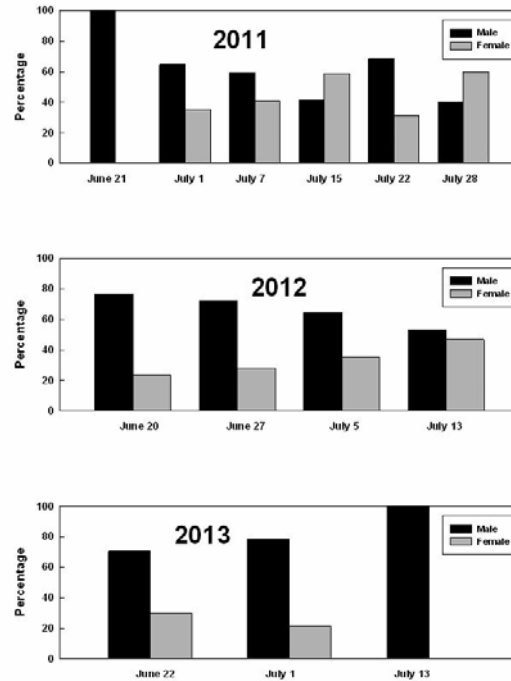


FIG. 12. Sex ratio of *P. leona* recorded on Pollard walks during each season.

1930) was used to analyze the two sets of two samples taken in 2013.

**Climate data.** A climate data logger (Lascar electronics, Erie, PA USA, model EL-USB-2) was placed 1.5 m above the ground within the shade of a MTF Lodgepole pine tree, recording hourly ambient temperature and relative humidity from May to September in 2011 and 2012. In 2013, logistics prevented on-site climate data collection, and ambient temperature data for May–September were obtained from Chemult (Station MCHUO3 Weather Underground.com), ~ 15 km NE of the MTF. Temperature in direct sunlight (13 cm above the ground) was recorded hourly by a data logger at the MRR site from June 21–October 31 2012. Temperature and relative humidity 0.5 cm below ground level (data logger buried in soil) was recorded during August–September 2011 and October 27 2011 to June 20 2012. Temperatures in direct sunlight and on the ground provide an insight to the conditions experienced by basking adults, developing eggs/larvae and diapausing pupae at or just below the soil surface.

**Data analysis.** Population census data were analyzed using one way ANOVA on ranks and Holm-Sidak multiple comparison procedures.



FIG. 13–16. 13. Typical overnight and morning roost of *P. leona* on bare twigs of low-growing plants. 14. *Philotiella leona* roosting on a warm stone on the ground. 15. *Philotiella leona* mating on bare twig close to the ground. 16. *Philotiella leona* ovipositing on flower buds of *E. spergulinum*.

## RESULTS

**Flight period.** *Philotiella leona* is univoltine with a flight period extending from mid-June to late July or early August (Table 1). The flight period in 2013 was shorter (35 d) than in 2011 (47 d) or 2012 (45 d). Mean daily maximum temperature for the first 30 days of the flight period in 2013 was 2–2.8 °C greater than in 2011 or 2012 with more days having maxima > 30 °C (Table 1). *Philotiella leona* eclose from ground level pupae (James 2012) and soil temperatures in 2012 showed a rapid warming from around 10 °C in early May to >30 °C in early June (Fig. 6). Ecdysis occurred soon after soil temperature daily maxima reached 50 °C and relative humidity fell below 90% (Fig. 6). By the end of the flight period in late July, most of the *E. spergulinum* host plants had senesced and it is likely that most larval development had been completed (James 2012) and the majority of the population was in the pupal stage. Pupae overwinter and overwinter on or perhaps just below the soil surface and are exposed to extreme

temperatures ranging from 68 °C down to -5 °C (Figs. 7–8). Snow cover during January–April 2012 maintained temperatures at 0 °C (Fig. 8).

**Population census.** *Philotiella leona* populations based on Pollard walk counts were significantly larger at MTF sites than at the WNF site ( $P < 0.011$ ) (Fig. 9). There was no significant difference between numbers at the MTF sites ( $P > 0.05$ ). The overall population was significantly greater in 2011 than in 2012 or 2013 ( $P < 0.031$ ) with no significant difference between the latter years ( $P > 0.05$ ) (Fig. 10). In all years, greatest numbers were seen on the second survey date (June 21–July 1) with a gradual decline thereafter (Fig. 11).

**Sex ratio.** Combining all years and census dates we recorded 556 (66.7%) males and 277 (33.3%) females. Males were particularly dominant early in the flight period, suggesting some degree of protandry and females only outnumbered males twice during the 3 years (July 15 and 29 2011) (Fig. 12).

**Nectaring.** *Philotiella leona* was observed nectaring

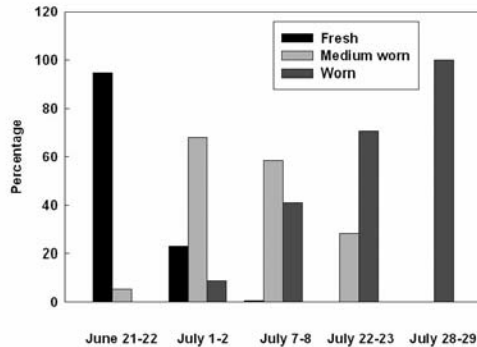


FIG. 17. Wing condition of *P. leona* during mark, release and recapture sampling at site E during 2011–2013.

on 9 flowering plants including the larval host plant *E. spergulinum* (Table 2). From 276 records, most nectaring occurred on Sulfur buckwheat (*Eriogonum umbellatum* Torr.) (32.6%) and Opposite-leaved tarweed (*Hemizonella minima* A. Gray) (23.9%). On June 26 2011 a male was observed visiting 67 *H. minima* flowers (10–20 seconds/flower) during 12 minutes.

**Roosting.** *Philotiella leona* spent much time roosting particularly before 1100 h despite sunshine and ambient temperatures of 10–20 °C. Most roosting occurred on the ground or on bare twigs of low-growing shrubs like *E. umbellatum* and *Purshia tridentata* (Pursh) (Bitterbrush) (Fig.13). Roosting *P. leona* were never found on green vegetation. Ground roosters usually chose warm stones or small rocks in direct sunlight (Fig. 14). In July 2012 the mean daily maximum temperature recorded in direct sunlight 13 cm above the ground was  $58.5 \pm 1.2$  °C (range 37–68 °C) (Fig. 7). On June 23 2011 two males were observed roosting on the ground for 2 h (1030–1230 h, ambient temp. 15–20 °C).

**Flight/courtship/mating.** The flight of *P. leona* is typically low to the ground and meandering. Flight higher than 1m above the ground was rarely seen. Most flight activity occurred from midday to 1600 h. Early in the flight period males were frequently seen flying around *E. spergulinum* patches, presumably searching for females. Male-male interactions were frequent with individuals swirling around each other for ~ 10 seconds before breaking off. Five male-female courtship events were observed on June 22 and July 7, two resulted in mating. Two of the courtship events involved the pair in an upward spiral reaching heights of up to 7 m before descending to ground level but no mating occurred. The two successful matings followed high speed chases just above ground level for 10–15 seconds before the female

alighted on a bare twig low to the ground with copulation taking place within 10 seconds. If disturbed, the female carried the male in flight. A total of 6 mating pairs were observed during the study, all on bare twigs and in the afternoon (1400–1600 h) (Fig. 15). Twenty one ovipositing females were observed, all in late June and early July. Most egg laying (86%) occurred during the afternoon (1200–1600 h). All eggs were laid on unopened flower buds of *E. spergulinum* (Fig. 16).

**Mark, release and recapture study.** A total of 414 *P. leona* (65.5 % female, 34.5% male) were marked during this study and 25 (6%) were recaptured overall. However, recaptures were greater in 2013 (9.5%) when a shorter interval (1 day) between sampling dates was used compared to 2–9 days in 2011 and 2012 (5.1–5.3%). The greatest period between marking and recapture was 14 days for a male marked on July 8 2011. Seven butterflies were recaptured 7–8 days after marking in 2011 and 2012. Population estimates for *P. leona* adults in the MRR area ranged from 61–4515 individuals (Tables 3–4). The population peaked in early July in all years. Individuals caught during June 21–23 were newly eclosed and mostly in fresh condition in all years. In the first week of July the majority of butterflies were in medium-worn condition but by July 22 the majority were worn (Fig. 17).

## DISCUSSION

The data presented here constitute the first detailed study on important aspects of the population biology and behavior of *P. leona*. Previous information on the incidence and abundance of *P. leona* has been fragmentary and largely anecdotal with no direct data on population size and/or trends from year to year (Ross, 2008, 2009, Johnson, 2010, Matheson et al. 2010). The data presented here, obtained over three seasons, will serve as a reference point for future studies on population size and trends. The five monitoring sites used in this study span the center of the known distribution of *P. leona* at the MTF. The sole WNF site used is adjacent to MTF land.

The flight period of *P. leona* commenced during the second or third week of June with dates when first adults were seen ranging from June 10 to June 17. Adults eclose from pupae on the ground which experience rapid warming and drying during the month or so before eclosion. Ambient temperatures during the flight period in 2013 were greater than in the previous two years which appeared to result in a shorter flight period with the population disappearing by mid July instead of late July or early August. Senescence of the host plant of *P. leona*, *E. spergulinum* was also more rapid in 2013. Temperatures experienced by *P. leona*

(both adults and immature stages) and host plants in direct sunlight in late June and July are very high (50–70°C) and likely result in rapid development of eggs and larvae. James (2012) showed larval development takes only 10–12 days at 25–27 °C. Oviposition and larval development can only occur on buds and flowers of *E. spergulinum* (James 2012) and the period when these plant parts are available appears to be limited to the flight period of *P. leona*. Thus, it appears likely that development of larvae is completed by the end of the adult flight period. Pupae are likely formed on or close to the ground (James, 2012) and are exposed to extremely hot (68 °C) and cold (-5 °C) temperatures although snow cover in winter minimizes exposure to extreme cold. Soil moisture content is high during November–June.

Populations of *P. leona* throughout this study appeared to be 4–5 times larger on the commercial tree farm land than at the adjacent national forest site. The reasons for this are unclear although the national forest land is generally less open than the tree farm land which has experienced extensive tree-harvesting over past decades. *Eriogonum spergulinum*, the host plant of *P. leona*, requires open habitat and is an early successional species establishing rapidly in recently cleared land, appearing to thrive in areas with burnt log piles. The abundance of *E. spergulinum* and *P. leona* appears to be greatest at slash/burn sites. A Google Earth™ image of part of the *P. leona* MTF habitat clearly shows the number and extent of clearings containing slash/burn piles within the tree farm (Fig. 18). These clearings harbor population concentrations of *P. leona* which are likely population centers making up the metapopulation occupying the 32 km<sup>2</sup> range of *P. leona*.

The abundance of *P. leona* in 2011, as indicated by numbers of adults seen during Pollard walk counts and

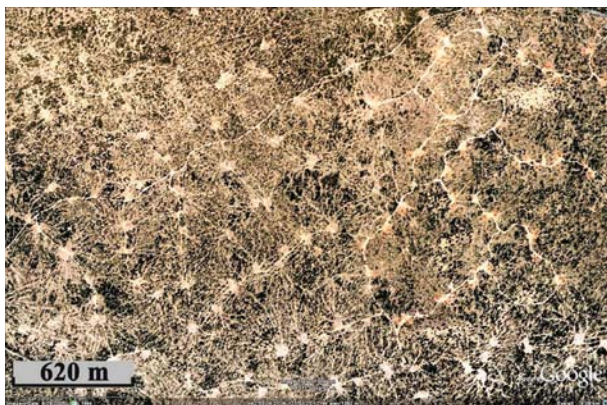


FIG. 18. A section of the Mazama Tree Farm showing multiple cleared slash and burn sites and associated trails (GoogleEarth™). The cleared sites host the densest populations of *E. spergulinum* and *P. leona*.

the population estimates derived from the MRR study, was more than double that seen in 2012 and 2013. Although the 2011 flight period was cooler than in 2012 and 2013, it is unclear whether it was this that caused greater abundance. Population monitoring over a greater number of seasons is needed to determine the range of abundance levels and whether any trends are apparent. The phenology of abundance was similar in the three years with greatest numbers seen early in the flight period in late June and early July, declining during July. A male-dominated sex ratio was apparent from both Pollard walk and MRR data. This may have been caused by females avoiding male harassment by spending more time roosting, thus less easily detected or caught. James (2012) concluded that the sex ratio of *P. leona* was 'relatively balanced' but this was based on 2011 data only in which male dominance was reduced compared to the following 2 years (Fig. 12). The wing condition of individuals determined in the MRR study showed the expected clear progression from fresh to worn during the flight period.

The flight behavior of *P. leona* was characteristically low to the ground, meandering and difficult to track. Much of the flight activity was centered on and around patches of *E. spergulinum* host plants, males seeking mates and females ovipositing. Nectaring was a predominant activity with the sulfur buckwheat, *Eriogonum umbellatum*, a very important nectar source. Roosting on bare twigs or on the ground was also a characteristic behavior, often for extended periods during morning hours.

The MRR study showed that it is feasible to mark *P. leona* despite their small size (1.3–1.9 cm wingspan). Marking did not appear to interfere with post-release behavior. It is unknown whether marking caused increased mortality due to increased visibility. No



FIG. 19. *Eriogonum spergulinum* growing along a track in the Mazama Tree Farm



TABLE 1. Estimated flight periods for *P. leona* in 2011–13 and daily maximum temperature data.

Year	Estimated flight period	Mean daily maxima °C for first 30 days of flight period	Number of days in first 30 days with maxima °C > 30 °C
2011	June 17-August 3	23.7	0
2012	June 15-July 30	24.5	4
2013	June 10-July 15	26.5	8

TABLE 2. Nectaring records for *P. leona* obtained on Pollard walks during 2011–13.

Plant Species	2011	2012	2013	Total (%)
<i>Eriogonum umbellatum</i>	34	24	32	90 (32.6)
<i>Hemizonella minima</i>	64	1	1	66 (23.9)
<i>Cistanthe umbellatum</i>	17	15	0	32 (11.6)
<i>Plagiobothrys hispidus</i>	12	19	0	31 (11.2)
<i>Machaeranthera canescens</i>	15	5	11	31 (11.2)
<i>Eriogonum spergulinum</i>	7	5	8	20 (7.2)
<i>Packera cana</i>	2	0	1	3 (1.1)
<i>Gayophytum diffusum</i>	2	0	0	2 (0.8)
<i>Phacelia hastata</i>	1	0	0	1 (0.4)
All Plants	154	69	53	276 (100)

TABLE 3. Mark, release and recapture data for *P. leona* in a 3888 m<sup>2</sup> area at site E during June–July 2011 and 2012. Population estimates derived by using Jolly's stochastic method.

2011 Date	No. in 1 hr search	Caught	Marked	Recaptured (%)	Estimated population
June 23	14	21	21	-	-
July 1	59	59	50	1	301
July 6	75	105	86	1	4515
July 8	52	39	27	6	215
July 22	21	21	19	1	242
July 24	13	11	9	2	61
July 29	2	2	2	0	-
Total (all dates)		258	214	11 (5.1)	
<b>2012 Date</b>					
June 21	19	34	30	-	
June 27	16	19	15	4	90
July 6	25	51	50	1	2600
July 13	13	11	0	0	-
<b>Total (all dates)</b>		105	95	5 (5.3)	

TABLE 4. Mark, release and recapture data for *P. leona* in a 3888 m<sup>2</sup> area at site E during June–July 2013. Population estimates derived by using the Lincoln index.

2013 Date	No. in 1 hr	Caught	Marked	Recaptured (%)	Estimated population
June 21	38	19	19	-	-
June 22	36	27	18	7	73
July 1	51	35	35	0	-
July 2	53	40	33	3	467
<b>Total (all dates)</b>		121	105	10 (9.5)	

instances of avian predation were observed during the 3 years of study suggesting perhaps that this source of mortality is generally low for this tiny butterfly. Recapture rates were low even with a short (24 h) interval between marking and re sampling (~10%). However, a 24 h interval did improve the recapture rate over that obtained with 2–8 day intervals (~5%). Low recapture rates may indicate death or emigration of individuals or their dilution within an increasing population. Fifty three per cent of recaptures in 2011 and 2012 were made 7–14 days after marking. This suggests longevity of adult *P. leona* can extend to 2 weeks but clearly more information is needed on the average length of life. If emigration is occurring then it may take place along the trails and tracks that connect cleared slash/burn population sites as shown in Fig. 18. No attempt was made in this study to sample butterflies along the trails and tracks emanating from the MRR site. These corridors are also heavily colonized by *E. spergulinum* (Fig. 19). Such sampling should be conducted in future MRR studies and may shed light on dispersal behavior of *P. leona* and therefore provide an insight on the maintenance of isolated populations within the metapopulation of *P. leona*. The population estimates derived in this study indicate *P. leona* populations in a small (~0.4 ha) but highly favorable habitat (open, abundance of host plants, nectar sources) may be large containing a few thousand individuals. The relatively low number of recaptures combined with uncertainty as to how well *P. leona* individuals redistribute within the MRR area after release, suggest caution in interpreting these population estimates. The population estimates of 4515 and 2600 on July 6 2011 and 2012, respectively, seem high but the estimates obtained on most other dates (61–467), appear reasonable and consistent. If we assume all cleared slash/burn sites on the MTF (~100) contain similar-sized populations of *P. leona*, then using a conservative estimate of 200 butterflies/site, the entire metapopulation of *P. leona* may consist of ~20,000 individuals. Although all of the slash/burn sites we visited during 2011–13 (~20) supported *P. leona* populations, a comprehensive survey needs to be conducted to determine actual occupancy of all the sites. Long term survival of the discrete populations that form a metapopulation requires at least some mixing of individuals between populations. Effective dispersal of butterflies from sites with declining populations is necessary to ensure local extinctions do not significantly affect the size and viability of the metapopulation. As favored open sites develop (from logging), dispersal of individuals from nearby centers should exploit the new habitats and establish new populations.

Although the greatest population densities were seen at the cleared slash/burn sites, *P. leona* is not confined to them. The Pollard walks conducted in this study along tracks and trails revealed significant populations in these areas as well. The numerous tracks and trails that cover the MTF may be extremely important conduits for *P. leona* moving between cleared site population centers. Continued maintenance of good-sized populations of *P. leona* at the MTF may be dependent on the continued existence of a large number of cleared sites and track/trail linkage between them. Continuance of a commercial logging operation on this land, at the levels conducted over the past few decades, may be crucial for conservation of *P. leona*. The current population levels of *P. leona* may actually be a consequence of commercial logging and creation of suitable habitat for *E. spergulinum*. There are some open areas within the MTF that appear never to have supported trees. *Philotiella leona* is present in these areas but at comparatively low population densities. It is possible that these areas represent the ancestral condition of limited suitable habitat and consequent low population densities of *E. spergulinum* and *P. leona*. Although the population density of *P. leona* on the adjacent National Forest land appears to be substantially lower than on the MTF, this perhaps could be rectified using tree management and harvesting protocols similar to those used on the MTF. Opening up more cleared areas with slash/burn piles on all areas of the National Forest land where it meets MTF land, may allow dispersal and shifting of high density MTF populations into National Forest land.

This study provides a good platform for future population research on *P. leona*. Such studies incorporating Pollard walks and MRR should be conducted annually to provide a better understanding of the evolving status of *P. leona* at the MTF. Data on population dynamics and underlying factors can ultimately be used to develop land and forest management strategies that are compatible with the long term survival of this imperiled species.

#### ACKNOWLEDGMENTS

We thank the Oregon Zoo Future for Wildlife Grants Program for providing funds for this study in 2011. We also thank the Mazama Tree Farm for access and Dana Ross, Dave McCorkle and Debbie Johnson for their valuable insights on *Leona's* Little Blue and its habitat. Additional help with fieldwork was provided by Terri Knoke, Tim Yager, Jasmine James and Rhiannon James, for which we are most indebted.

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*Submitted for publication 14 November 2013; revised and accepted 13 February 2014.*