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# POPULATION BIOLOGY OF MONARCH BUTTERFLIES, *DANAUS PLEXIPPUS* (L.) (LEPIDOPTERA: NYMPHALIDAE), AT A MILKWEED-RICH SUMMER BREEDING SITE IN CENTRAL WASHINGTON

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**ABSTRACT.** The population biology of adult Monarch butterflies (*Danaus plexippus*) was studied during regular visits over three years (June–September 2013–15) at a milkweed (*Asclepias speciosa*)-rich site in central Washington. Small numbers of spring migrants colonized the site during June 5–17 each year and produced two adult generations one in early July and the other in late July–August, increasing the population at the site until mid–late August in 2013 and 2014. Greatest numbers of adults occurred in late July and August (20–24 per hour). In 2015 the population fell substantially in early August apparently as a consequence of heat wave conditions in late June–early July adversely affecting survival of second generation immature stages. Mark, release and recapture provided maximum population estimates at the site of 160–190 males, a recapture rate of 25–32% and intervals between tagging and recapture of 5–39 days. Sex ratio was imbalanced in favor of males on all dates ranging from 57–100%. Males patrolling milkweed patches was the most common behavior observed. Nectaring on *A. speciosa* and the exotic Purple Loosestrife (*Lythrum salicaria*) was frequently observed and the introduced Russian Olive (*Elaeagnus angustifolia*) was used for resting during the day. Dispersal from the site occurred in late August or early September. The use of large, dense areas of milkweed in relatively moist locations with some shade may be an important component of summer breeding of *D. plexippus* in the arid western United States. Expanding and/or creating additional such sites may be a useful conservation strategy for *D. plexippus* in the arid west.

**Additional key words:** Western North American population, *Asclepias speciosa*, population estimates, sex ratio, wing condition, generations, nectaring, heat wave, conservation

The Monarch butterfly, *Danaus plexippus* (L.) is a summer resident of the Pacific Northwest (Oregon, Washington, Idaho, British Columbia) arriving in May or June from areas further south and producing one or two generations before adults begin moving southward during September and October for overwintering (Pyle 2002, Dingle et al. 2005, James and Nunnallee 2011, Yang et al. 2015). Summer populations in the Pacific Northwest over the past two decades have declined (James and Nunnallee 2011, Pyle 2015) similar to the recent steep declines reported for the western and eastern North American populations (Stevens and Frey 2004, Brower et al. 2012, Flockhart et al. 2014, Griffiths and Villablanca 2015) but see Davis and Dyer (2015) for a dissenting view. In both the east and the west, it is believed that populations of *D. plexippus* have declined as a result of sub-optimal summer breeding caused by a reduction in milkweed incidence and abundance (e.g. Hartzler 2010, Pleasants and Oberhauser 2013) and periodic extreme weather (Brower et al. 2012). Degradation of overwintering sites in Mexico and California is also considered to be a factor in the decline (Brower et al. 2012, Griffiths and Villablanca 2015). Measures currently being adopted to reverse the decline in *D. plexippus* populations are focused on milkweed restoration replenishing and expanding the habitats needed by summer breeding Monarchs. Surprisingly, little has been published on the breeding ecology of site-specific *D. plexippus* populations in North America. Some studies on the ecology of year-round breeding populations in Florida and southern California have been reported (Brower 1961, Urquhart et al. 1970, Urquhart and Urquhart 1976, Knight and Brower 2009). Studies have also been published on regional aspects of summer breeding in more northerly areas like voltinism (Malcolm et al. 1987, Cockrell et al. 1993, Brower 1996, Flockhart et al. 2013), larval survival (Borkin 1982, Oberhauser et al. 2001, Nail et al. 2015a), larval competition (Flockhart et al. 2012) and geographic/temporal variation in egg and larval abundance (Prysby and Oberhauser 2004, Ries et al. 2015, Stenoien et al. 2015), but none have focused on the biology and ecology of site-specific summer breeding populations of *D. plexippus* in North America. Such studies are important in developing a more complete understanding of monarch population biology which will better inform development of optimal conservation strategies. In contrast, a number of such studies have been published for Monarch populations in Australia (Smithers 1972, James 1981, Zalucki and Kitching 1985, Zalucki and Suzuki 1987, Zalucki and Rochester 2004) and Bermuda (Hilburn 1989). The lack of site-specific ecological studies on North American *D. plexippus* may be a consequence of breeding in mid-high latitudes often occurring on small patches of widely separated host plants (Brower 1996, Prysby and Oberhauser 2004, Hartzler 2010, Flockhart et al. 2012). Thus, Monarchs are often not necessarily resident for more than one generation in one location, unlike the situation in Australia where milkweed (primarily *Gomphocarpus fruticosus* (L.) W. T. Alton) often occurs in large patches of up to 5000 m² (James 1981, Bull et al.

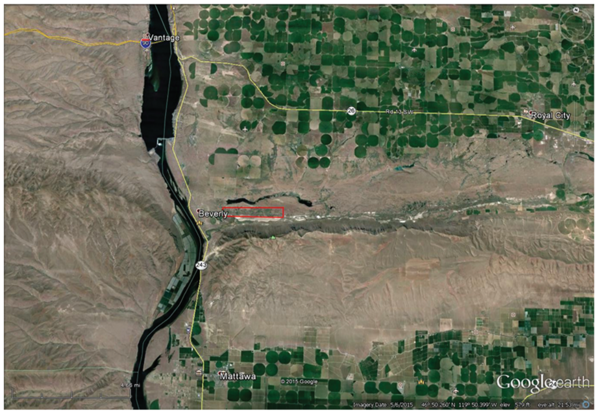


FIG. 1. Monarch butterfly (*Danaus plexippus*) summer breeding site (outlined in red) at Lower Crab Creek east of Beverly and south of Vantage in central Washington.

FIG. 2. High density, large, contiguous patches of showy milkweed (*Asclepias speciosa*), characterize the Lower Crab Creek Monarch butterfly breeding site.

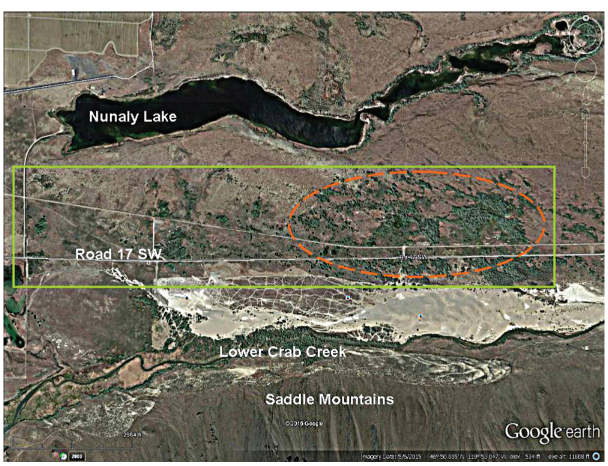


FIG. 3. Close up view of the 4.1 X 0.6 km area at Lower Crab Creek supporting large populations of *Asclepias speciosa* and *Danaus plexippus* during 2013–15. The area bounded by the dotted orange ellipse had the highest density of *A. speciosa*. The meandering walk used in this study to monitor *D. plexippus* was within this area.

1985), supporting multiple generations of *D. plexippus* continuously.

In order to develop optimal strategies for milkweed habitat restoration, more information is needed on the choice and use of milkweed habitats by *D. plexippus* as well as species, population and distribution characteristics of milkweed populations themselves. This information is particularly critical for the largely arid and mountainous western United States where milkweeds are more patchily distributed (Nelson et al. 1981, Brower, et al. 1982, Stevens and Frey 2010, Pyle 2015) than in the eastern United States and where we have very little information on the ecology of *D. plexippus* breeding in inland areas. Morris et al. (2015) reported summer breeding of two to three generations of monarchs at higher elevations (1067–1829 m) in Arizona but did not provide details of population ecology. The Pacific Northwest is occupied annually by summer breeding populations of *D. plexippus* at the greatest distance from Californian overwintering areas (Yang et al. 2015). Breeding is known to occur primarily in inland areas of Oregon, Washington, Idaho and British Columbia with limited or no incidence of milkweed in coastal areas (Pyle 2002, Stevens and Frey 2010, James and Nunnallee 2011). Much of central Washington is hot and dry during summer and milkweed occurrence is restricted to moister valleys, marshes, riversides, roadsides and irrigated areas. Most milkweed patches are small and scattered but a large concentration occurs near the Columbia River 210 km southeast of Seattle. The site was first noted as a potential Monarch breeding habitat in 1996 by R. M. Pyle during field work for his book Chasing Monarchs (Pyle 1999). Pyle observed 'acres and acres' of Showy Milkweed and tagged a Monarch on-site. The stand was visited in 2012 and found to contain area ~ 2.4 $km^2$ of almost contiguous high density milkweed. This study reports the results of a three year survey of summer breeding populations of *D. plexippus* at this site. The aim was to determine and document the existence of summer breeding of Monarchs at the site, adult population dynamics, behavior and the impact of climate and plant resources on persistence and survival.

## MATERIALS AND METHODS

Populations of adult *D. plexippus* were monitored at a single site (Lower Crab Creek LCC) 15 km south east of Vantage in central Washington from June-September 2013–15. The site is a 4.1 by 0.6 km, east-west oriented tract of largely open land (elevation 157 m) bisected by Road 17 SW (46° 49.997' N, 119° 52.915' W) (Fig. 1). A small creek (Lower Crab Creek) lies 0.5 km to the south and drains into the Columbia River, and a small natural

TABLE 1. Numbers and wing condition of male and female *Danaus plexippus* seen at the Lower Crab Creek site during each three hour survey during June-September 2013–15

| Date | Temp° C | Number of Monarchs | Male | Female | Worn | Good | Fresh |
|---|---|---|---|---|---|---|---|
| **2013** | | | | | | | |
| June 6 | 29-33 | 0 | | | | | |
| June 14 | 22-26 | 2 | 2 | 0 | 0 | 2 | 0 |
| June 27 | 20-36 | 2 | 2 | 0 | 0 | 1 | 1 |
| July 10 | 33-38 | 2 | 2 | 0 | 0 | 1 | 1 |
| July 19 | 25-31 | 3 | 2 | 1 | 1 | 2 | 0 |
| July 26 | 26-33 | 1 | 1 | 0 | 0 | 0 | 1 |
| Aug 1 | 26-28 | 23 | 13 | 10 | 1 | 1 | 21 |
| Aug 9 | 21-30 | 35 | 23 | 12 | 2 | 18 | 15 |
| Aug 16 | 21-28 | 29 | 22 | 7 | 0 | 23 | 6 |
| Aug 22 | 18-28 | 17 | 13 | 4 | 0 | 12 | 5 |
| Aug 27 | 21-27 | 21 | 13 | 8 | 0 | 12 | 9 |
| Aug 30 | 21-28 | 0 | | | | | |
| **2014** | | | | | | | |
| June 6 | 27-29 | 0 | | | | | |
| June 17 | 20-23 | 9 | 7 | 2 | 1 | 8 | 0 |
| June 25 | 23-27 | 7 | 7 | 0 | 3 | 4 | 0 |
| July 2 | 26-28 | 2 | 2 | 0 | 2 | 0 | 0 |
| July 11 | 27-31 | 21 | 18 | 3 | 2 | 1 | 18 |
| July 25 | 19-26 | 64 | 58 | 6 | 4 | 56 | 2 |
| Aug 5 | 27-32 | 51 | 43 | 8 | 4 | 44 | 1 |
| Aug 11 | 16-30 | 48 | 38 | 10 | 2 | 16 | 30 |
| Aug 18 | 21-27 | 73 | 49 | 24 | 3 | 15 | 55 |
| Aug 26 | 16-28 | 45 | 21 | 24 | 0 | 13 | 32 |
| Sep 1 | 18-25 | 23 | 13 | 10 | 1 | 5 | 17 |
| Sep 9 | 18-27 | 1 | 1 | 0 | 0 | 1 | 0 |
| **2015** | | | | | | | |
| May 29 | 28-31 | 0 | | | | | |
| June 5 | 28-30 | 1 | 1 | 0 | 0 | 1 | 0 |
| June 12 | 22-27 | 2 | 1 | 1 | 0 | 2 | 0 |
| June 23 | 26-29 | 6 | 4 | 2 | 2 | 4 | 0 |
| July 2 | 22-32 | 14 | 8 | 6 | 3 | 7 | 4 |
| July 14 | 28-32 | 38 | 28 | 10 | 4 | 13 | 21 |
| July 22 | 22-27 | 61 | 49 | 12 | 4 | 52 | 5 |
| July 29 | 18-27 | 58 | 46 | 12 | 12 | 38 | 8 |
| Aug 6 | 20-25 | 16 | 12 | 4 | 4 | 11 | 1 |
| Aug 12 | 28-32 | 29 | 24 | 5 | 5 | 13 | 11 |
| Aug 18 | 19-28 | 25 | 20 | 5 | 7 | 5 | 13 |
| Aug 26 | 18-22 | 6 | 4 | 2 | 1 | 2 | 3 |
| Sep 1 | 25-26 | 0 | | | | | |

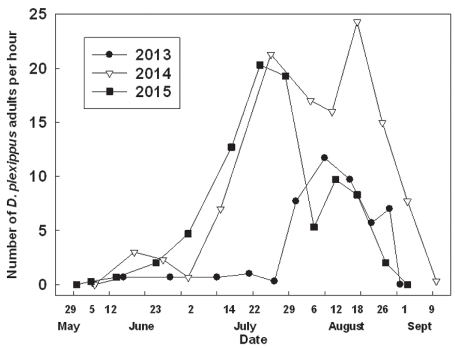


FIG. 4. Mean number per hour of *Danaus plexippus* adults seen during three hour meandering transects conducted at the Lower Crab Creek summer breeding site during June-August 2013–15.

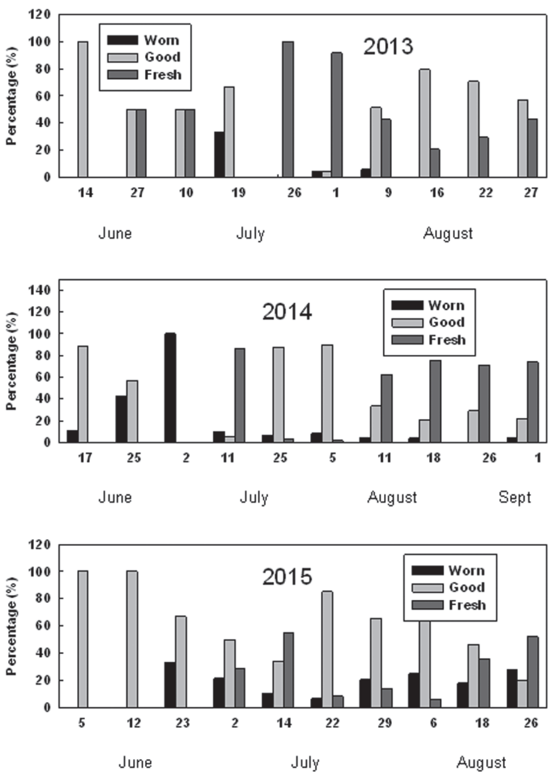


FIG. 5. Wing condition of *Danaus plexippus* adults at the Lower Crab Creek summer breeding site during June-August 2013–15.

lake (Nunaly Lake) lies 0.5 km to the north. Throughout most of the approximately 2.4 $km^2$ area, milkweed (*Asclepias speciosa* Torr.) is almost continuous and dominates the landscape occupying an estimated 70% of the land area (Fig. 2). In large areas of the site milkweed forms 100% of the ground cover with the two largest patches occupying approximately 78,000 and 144,000 $m^2$. *Asclepias speciosa* propagates effectively by underground rhizomes enabling large areas to be colonized when conditions are suitable (Borders & Mader 2014). Small trees and bushes are scattered throughout the site sometimes forming denser groups (Fig. 3). The dominant species is the introduced and declared noxious plant in Washington, Russian Olive (*Elaeagnus angustifolia* L.). Some native trees, Poplars (*Populus* spp.), bushes, Willows (*Salix* spp.) and shrubs (Buckwheats *Eriogonum* spp., Sagebrushes *Artemisia* spp., Rabbitbrushes *Ericameria nauseosa* (Pall. ex Pursh) G. L. Nesom & G. I. Baird, Purple Loosestrife *Lythrum salicaria* L., Catstails *Typha* spp.) are also present but are relatively limited within the site. The Lower Crab Creek State Wildlife area which encompasses the monitoring site is managed by the Washington Department of Fish and Wildlife. It is bounded to the south by the Saddle Mountains (700 m elevation) and to the north by irrigated agricultural land (350 m elevation). The site was first noted as a potential Monarch breeding site by Bob Pyle in his book '*Chasing Monarchs*' (Pyle 1999) who observed 'acres and acres' of Showy milkweed.

Twelve-thirteen visits were made annually to the site at 7-14 day intervals during May 29–September 9 from before the first migrant arrived until the fall migration emptied the area. At each visit an observational survey of the *D. plexippus* adult population at the site was conducted during a three hour period between 0700 and 1400 h when data on numbers seen, sex ratio, wing condition and behavior were obtained. Some individuals were captured (see below) enabling close-up assessment of sex and wing condition but many were assessed by observation as they nectared, rested or flew in close proximity. Weather conditions at each visit were uniformly sunny, wind ranged from 0–25 km/h and temperatures ranged between 16–38 °C. However, on most visits temperatures were 25–30 °C and periods of temperatures above 38 °C were avoided because of consequent inhibition of *D. plexippus* activity (James unpubl obs.). The same meandering route (~ 3 km) through the site was taken at each visit. The walk traversed all major patches and areas of milkweed (*A. speciosa*) and nectar sources (primarily *L. salicaria*) in a 0.5 $km^2$ section of the site (Fig. 2). The number of adult *D. plexippus* encountered was recorded along with details of the behavior, sex and wing condition of each individual. Steady progression through the site minimized 'double-counting'. Wing condition was qualitatively assessed as 'fresh' (bright colors, immaculate), 'good' (very slight (< 5%) wing wear, good colors), or worn (> 25% wing wear, duller colors). The behavior of each individual seen was assigned to one of eight categories (1. in flight, 2. male patrolling *A. speciosa*, 3. nectaring on *A. speciosa*, 4. nectaring on *L. salicaria*, 5. resting on ground or vegetation, 6. resting on *A. speciosa*, 7. mating/courtship, 8. oviposition). Data on sex ratio and wing condition were analyzed using one way ANOVA. From early July to mid-August male *D. plexippus* were marked, released and recaptured (MRR) to provide data for estimates of male population size. No evidence was seen of post-tagging 'escape flight'. In most instances tagged butterflies were observed to resume normal behaviors shortly after release. Butterflies were marked using a white circular tag (obtained from MonarchWatch.org) with a serial number and email address affixed dorsally to a forewing. MRR data in 2014 and 2015 were analyzed using Jolly's stochastic method (Jolly 1965). Insufficient numbers of butterflies were tagged and recaptured in 2013 to justify analysis. After mid-August, when the population commenced fall migration and began to leave the site, both sexes were instead tagged ventrally on a hindwing for a migration study. During mid-July to late August in all years 10–20 females were removed from the site to produce progeny for a separate study on migration (James, in prep.). Eggs and larvae of *D. plexippus* were not searched for and not observed except for eggs laid by ovipositing females. The dense stands and large areas of *A. speciosa* made detection of eggs and larvae unlikely (Fig. 3). Climate data for June-August 2013-2015 were obtained from WSU Agweathernet (http://weather.wsu.edu) for meteorological recording stations at Desert Aire [13.8 km] south and Vantage [4.0 km] west of Lower Crab Creek. Both sites were at similar elevations (160–180 m) to the study site (157 m). The Vantage station was commissioned in September 2014, thus data from this (closer) site were only available for 2015. Weather data were used to help explain and interpret observed population fluctuations.

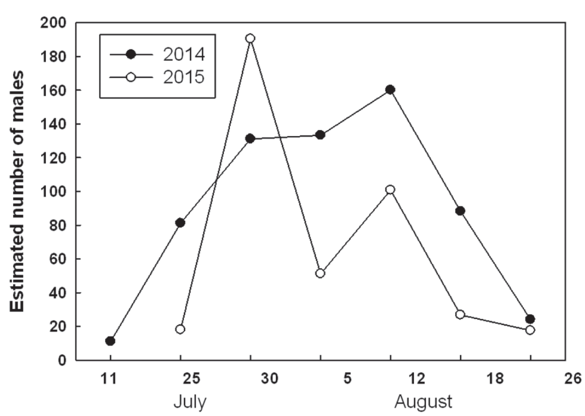


FIG. 6. Population estimates of male *Danaus plexippus* at the Lower Crab Creek site during July-August 2014 and 2015. Estimates derived from Jolly's stochastic analysis of mark, release and recapture data (Jolly 1965).

## RESULTS

No Monarchs were seen at the site on June 6 in 2013 and 2014 and May 29 2015. *Danaus plexippus* was first seen at the site on June 5 (2015), June 14 (2013) and June 17 (2014) (Table 1, Figure 4). Arrival numbers ranged from one to nine individuals seen during the three hour survey with good condition males predominating. The population remained low during June in all three years (totals of 2–9 individuals per visit, Table 1) but increased substantially during the first half of July in 2014 and 2015 (7.0–12.7/hr), suggesting emergence of a new generation. The first occurrence of fresh condition individuals at this time also indicated new generation emergence (Fig. 5). In 2013 the numbers remained low throughout July (0.3–1.0/hr)(Fig. 4), but a high proportion of fresh condition individuals at this time indicated emergence of a new generation (Fig. 5). Numbers increased further in late July in 2014 (21.3/hr) and 2015 (20.3/hr) but did not increase until August 1 (7.7/hr) in 2013. The population increased further in August 2013 (up to 11.7/hr). In 2014 the population remained high during August (15.0-24.3/hr) but in 2015 the population fell to 5.3/hr on August 6 and remained below 10.0/hr for the rest of the month (Fig. 4). Increased proportions of fresh condition individuals in late July–early August 2013 and early–late August in 2014 and 2015 provided evidence for a second generation of adults (Fig. 5). The population dispersed from the site, presumably as migrants heading south, during the last few days of August (none seen on 8/30/13 or 9/1/15) or first few days of September (none seen on 9/9/14) (Fig. 4). Population estimates of the male population derived from MRR data in 2014 and 2015 (Fig. 6) concurred with the observational data on population size showing greatest numbers in late July in both years with an earlier decline in 2015. The maximum population at the site was estimated at 160 males in 2014 and 190 in 2015 (Fig. 6). A total of 26 males was tagged in 2013 with 7 (26.9%) recaptures. In 2014 and 2015, 76 and 50 males were tagged with 19 (25%) and 16 (32%) recaptures, respectively. Intervals between tagging and recapture

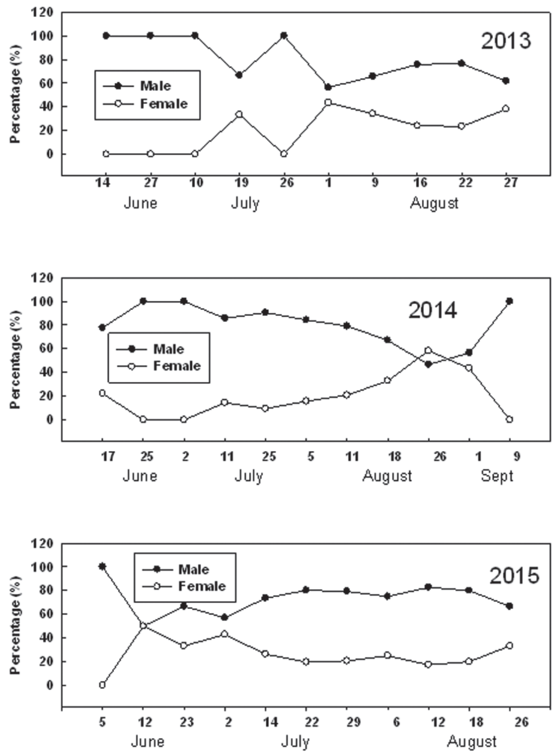


FIG. 7. Sex ratio of *Danaus plexippus* adults seen at the Lower Crab Creek summer breeding site during June-August 2013–15.

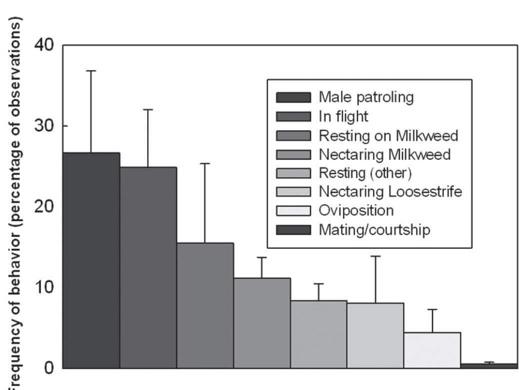


FIG. 8. Percentage frequency of adult *Danaus plexippus* behaviors at the Lower Crab Creek summer breeding site during 2013–15.

ranged from 5–27 (mean 12.1) days in 2013, 6–39 (mean 13.2) days in 2014 and 1-27 (mean 14.6) days in 2015.

Sex ratio was imbalanced in favor of males on all dates in all years ranging from 57.1–100% (Fig. 7). Overall, males accounted for 68.9% of butterflies seen in 2013, 74.7% in 2014 and 76.9% in 2015 and the observed sex ratios did not vary significantly between years ($F = 0.605$; df = 2, 29; $P > 0.553$) (Table 2). The wing condition of butterflies in 2013 and 2014 was largely good or fresh with significantly fewer worn individuals (2013: $F = 9.022$; df = 2, 27; $P < 0.001$, 2014: $F = 10.823$; df = 2, 30; $P < 0.001$) (Table 2). Butterflies in good condition were significantly more numerous in 2015 than either worn or fresh individuals ($F = 11.765$; df = 2, 30; $P < 0.001$) (Table 2). Fresh individuals accounted for 28–85.7% of the population in early to mid-July of each year (Fig. 5). A second increase in fresh individuals (indicating new generation emergence) occurred in late July and August in 2013 and 2014. This did not occur in 2015 until mid-late August (Fig. 5).

The relative frequency of different behaviors of *D. plexippus* adults during 2013-15 is shown in Fig. 8. Males patrolling milkweed patches guarding territory or seeking females was the most common behavior closely followed by non-patrolling flight (both sexes). Resting on milkweed and nectaring on milkweed were the next most frequently observed behaviors (Fig. 8). Nectaring on purple loosestrife accounted for just over 8% of behavior observed but reached 19.7% in 2014. Oviposition and mating/courtship activities were rarely observed (0.5–4.4%).

Temperature data for the nearby weather station (Desert Aire) during June to August 2013–15 are shown in Table 3. Temperature values (daily mean, daily mean minimum, daily mean maximum) varied by only 0.1–0.2 °C between 2013 and 2014 and were 0.8-1.0 °C higher than the averages for the previous eight years. However, the corresponding values for 2015 were 1.3–1.5 °C higher than the other two years and 2.3–2.4 °C higher than the eight year averages (Table 3). 2015 had a maximum high temperature of 43 °C compared to 41.2 and 42.2 °C in 2013 and 2014, respectively (Table 3). The longest period of consecutive days with maxima greater than 38 °C occurred in 2015 (15 days) compared to only 3 and 5 days in 2013 and 2014, respectively (Table 3). Daily maximum temperatures during the 2015 'heatwave' are shown for the Vantage weather station, 4 km west of the breeding site (Fig. 9). Total rainfall during June-August was sparse in 2013 (26.0 mm) and very low in 2014 (13.7 mm) and 2015 (8.8 mm).

TABLE 2. Overall sex ratio and wing condition categories (%) recorded for adult *Danaus plexippus* at the Lower Crab Creek breeding site during June-August 2013-2015. * Significantly greater than worn in 2013 and 2014. ** Significantly greater than worn and fresh in 2015 (ANOVA, P < 0.001)

| Year | Male % (n) | Female % (n) | Worn % (n) | Good % (n) | Fresh % (n) |
|---|---|---|---|---|---|
| 2013 | 68.9 (93) | 31.1 (42) | 3.0 (4) | 53.3 (72) * | 43.7 (59)* |
| 2014 | 74.7 (257) | 25.3 (87) | 6.5 (22) | 47.9 (163)* | 45.6 (155)* |
| 2015 | 76.9 (197) | 23.1 (59) | 16.4 (42) | 57.8 (148)** | 25.8 (66) |

## DISCUSSION

The summer breeding ecology of *D. plexippus* in central Washington State is reported for the first time. Surprisingly, this study also appears to be the first multi-year analysis of an annually occurring resident summer breeding population of *D. plexippus* in the northern tier of North America. Brower (1961) and Urquhart et al. (1976) presented some information on resident continuously breeding populations of *D. plexippus* in Florida but focused on immature stages. Borkin (1982) studied distribution and survival of immature *D. plexippus* at a site in southeastern Wisconsin but did not report on adult dynamics and ecology. More recently, there have been a number of regional-based studies on the distribution, incidence and abundance of spring and summer breeding populations in the eastern United States (Riley 1993, Prysby and Oberhauser 1999, 2004, Flockhart et al. 2013, Ries et al. 2015, Stenoien et al. 2015) but none of these have focused on the dynamics and ecology of site-specific resident summer populations within and across seasons. In contrast, several Australian studies have provided information on adult population dynamics and ecology of *D. plexippus* breeding populations. Observations on a summer resident breeding population of *D. plexippus* were made over 4 years by Smithers (1965) south of Sydney. A similar study north of Sydney focused on winter breeding of *D. plexippus* (James 1981). A number of studies on adult population dynamics and ecology of *D. plexippus* in sub-tropical Queensland have been reported (Bull et al. 1985, Zalucki 1983, Zalucki and Kitching 1982, 1984, Zalucki and Suzuki 1987, Suzuki and Zalucki 1986).

This study indicates that a large population of *A. speciosa* (~ 70% coverage of a 2.4 km² area containing an estimated tens of thousands of plants) in the hot, dry summer climate of central Washington can annually attract and sustain a large resident breeding population of *D. plexippus* during June–August. Although it is possible that a small part of the population development observed at Lower Crab Creek during July-August was derived from itinerant *D. plexippus* colonizing the site, it is likely that most of the population increase was a result of breeding at the site. Few significant patches of Showy Milkweed are known to occur within a 50 km radius of Lower Crab Creek and it is unlikely that there is a large itinerant population of *D. plexippus* in this region during summer. Few Monarchs are reported or seen in this area during the summer (James, unpubl. obs.). Little is known about the incidence and characteristics of summer breeding sites of *D. plexippus* in the Pacific Northwest (Jepsen and Hoffman Black 2015, Pyle 2015), but anecdotal evidence suggests that breeding often occurs on small, scattered, localized patches of milkweed along roadsides, watercourses and in other moister areas. A survey of approximately 100 patches of milkweed (mostly *A. speciosa*, few *Asclepias fascicularis* Decne.) in central and eastern Oregon conducted in 2015, showed that 70% were comprised of less than 100 plants. The maximum number of plants in a patch was ~ 300 (Matt Horning USFS, pers. comm.). It is likely that the majority of milkweed patches in eastern Washington are similarly sized, except at sites like Lower Crab Creek where presumably a combination of good climate, soil moisture, companion vegetation and suitable soil types allow patches to occupy much larger areas. It is possible that the Lower Crab Creek site is unusual in supporting such a large population of *A. speciosa* but further studies on milkweed distribution and abundance in Washington and Oregon are needed to determine this.

During the three years of this study, small numbers of *D. plexippus* adults arrived at the breeding site between June 5 and 17. These were in worn to good condition and likely were migrants from further south. Records kept since 2002 show that *D. plexippus* is invariably first recorded in Washington in early-mid June (James, unpubl.). In 2014 and 2015 these early colonizers

TABLE 3. Temperature (° C) data from an Agweathernet station at Desert Aire 13.8 km south of Lower Crab Creek during June–August 2013-15. Values in parentheses represent the eight year (2005–12) mean for the site. Above average temperatures featured in all survey years especially 2015 when an extended period of > 38 °C temperatures occurred.

| | **2013** | | | | | **2014** | | | | | **2015** | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Month** | **Min (° C)** | **Mean (° C)** | **Max (° C)** | **Extreme (° C)** | **Consec. Days > 38.0** | **Min (° C)** | **Mean (° C)** | **Max (° C)** | **Extreme (° C)** | **Consec Days > 38.0** | **Min (° C)** | **Mean (° C)** | **Max (° C)** | **Extreme (° C)** | **Consec Days > 38.0** |
| **June** | 14.4 (14.0) | 20.9 (20.9) | 27.6 (28.0) | 36.2 | 0 | 14.2 (14.0) | 21.2 (20.9) | 28.2 (28.0) | 34.3 | 0 | 18.1 (14.0) | 26.0 (20.9) | 33.5 (28.0) | 43.0 | 5 |
| **July** | 19.1 (17.7) | 27.1 (25.7) | 35.3 (33.6) | 41.2 | 3 | 19.4 (17.7) | 27.4 (25.7) | 35.6 (33.6) | 42.2 | 5 | 19.9 (17.7) | 27.3 (25.7) | 34.9 (33.6) | 41.4 | 10 |
| **August** | 18.2 (17.2) | 25.4 (24.6) | 33.1 (32.4) | 37.1 | 0 | 18.5 (24.6) | 25.5 (24.6) | 33.0 (32.4) | 39.3 | 2 | 17.7 (17.2) | 24.9 (24.6) | 32.4 (32.4) | 39.5 | 0 |
| **June-August** | 17.3 (16.3) | 24.5 (23.7) | 32.1 (31.3) | 41.2 | 3 | 17.4 (16.3) | 24.7 (23.7) | 32.3 (31.3) | 42.2 | 5 | 18.6 (16.3) | 26.1 (23.7) | 33.6 (31.3) | 43.0 | 15 |

persisted at low levels (0.7–2.3 adults per hour) until early July when the first locally produced adults increased the population 7–10 fold. The first locally produced generation was very small in 2013 with no detectable increase in numbers but the presence of fresh condition adults in late June–early July indicated newly eclosed individuals were present. A second generation of adults, as indicated by increase in population size and incidence of fresh individuals was produced in late July–mid-August in all years. The MRR data provided a maximum population estimate of 190 males on July 29 2015, which if a 1:1 sex ratio is assumed, corresponds to an estimated population of 380 individuals. Undoubtedly, some emigration and immigration occurred at the site but the relatively high recapture rate of tagged males (25–32%) and recaptures of males at the site up to 39 days after tagging, suggests good site fidelity. These populations of an estimated 300–400 adult *D. plexippus* at the 2.4 km² Lower Crab Creek site are remarkable and challenge our concepts of summer breeding of *D. plexippus* in the Pacific Northwest. Small, separated patches of milkweed which appear to be the 'normal' distribution of *Asclepias* spp. across the landscape in at least eastern and probably western North America (Hartzler 2010, Pleasants and Oberhauser 2013, Flockhart et al. 2012, Jepson and Hoffman Black 2015, Pyle 2015) will clearly not support large residential populations of *D. plexippus* like those documented in this study. Similar-sized largely resident populations of *D. plexippus* have been reported from large milkweed patches in Australia. James (1981) reported a winter breeding population of an estimated maximum of 348 adult *D. plexippus* during three months at a north Sydney site with milkweed in two 900 m² patches. Zalucki and Kitching (1984) in southeast Queensland estimated adult populations of 50–200 *D. plexippus* per milkweed patch site although the size of patches was not reported. However, the extent of milkweed in these Australian studies was not as great as the dominance of *A. speciosa* on the landscape at Lower Crab Creek. Isolated large areas of high density *Asclepias* spp. may be a characteristic of the arid zone of the western US and therefore an important part of the ecology of *D. plexippus* in the west. Clearly, there is an urgent need to determine the distribution and frequency of small and large, high density *Asclepias* spp. dominated sites in the western US.

In 2015 the second generation of locally produced *D. plexippus* adults at Lower Crab Creek was small and did not result in a population increase as in the previous two years. Instead the population declined by about 75%. The summer of 2015 was the hottest on record for many parts of central Washington (http://nws.weather.gov/blog/nwspendleton/wp-content/uploads/sites/13/2015/09/Season-In-Review_Summer_2015.pdf) and the climate data from the two weather stations near Lower Crab Creek reflected this. Whilst mean temperatures were 1.3–1.5 °C higher in 2015 than the

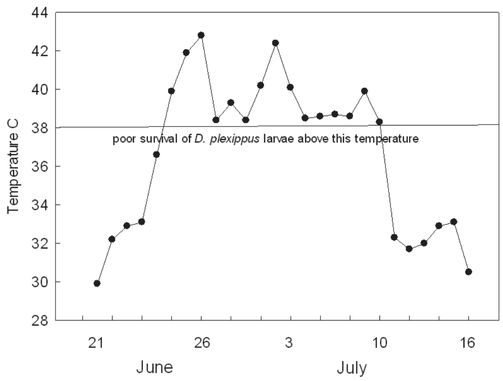


FIG. 9. Daily maximum temperatures (° C) at an Agweathernet station at Vantage 4 km west of Lower Crab Creek during June 21 to July 16 2015.

previous years and 2.3–2.4 °C higher than the eight year average, the more important statistic biologically was the number of consecutive days (15, June 26–July 10) with maxima above 38 °C. In 2013 and 2014, this number was 3 and 5, respectively. The immature stages of *D. plexippus* suffer increased mortality from temperatures of 36 °C and above depending on length of exposure and stage (Zalucki 1982). A constant temperature of 42 °C for 12 out of 24 hrs for two days resulted in 80–90% mortality of early and late instar larvae (Nail et al. 2015b). A constant temperature of 38 °C for 12 out of every 24 hrs for six days resulted in 30% mortality of third instar larvae (Nail et al. 2015b). While the 15 day period of daily maxima above 38 °C temperatures in June–July 2015 would not be as thermally severe as the examples above (night time temperatures ranged from 19.2–24.7 °C), it is possible that substantial heat-induced mortality occurred amongst immature stages of *D. plexippus* during this period. The peak of oviposition by migrant females arriving at the site likely occurred during the third week of June and larvae from these eggs would have been exposed to the 15 day heat wave. The first local generation of adults emerged in good numbers at the site from July 2–14, suggesting that pupae were not adversely affected by the heat. However, the anticipated second generation of adults did not occur until August 12 and numbers were relatively small. Egg to adult development of *D. plexippus* takes 25–28 days at temperatures of 25–35 °C (Zalucki 1982, James unpubl. obs), thus the second generation individuals would have developed after the heat wave. The expected time of second generation emergence based on 2013 and 2014 observations was late July–early August. The relatively low numbers of fresh newly eclosed individuals during this period in 2015 may have resulted from increased mortality in developing eggs and larvae during the 15 day heat wave in late June–early July. The effect of high temperatures on adult *D. plexippus* is uncertain although temperatures above 35 °C have been observed to cause individuals to rest in the shade (James, unpubl. obs., Masters et al. 1988). High temperatures may also cause dispersal. Observations (two to five monarchs per minute flying west along Crab Creek) made by Mark Genich (pers. comm.) on July 27 2015, 1.5 km southwest of the breeding site, support this.

Another factor in the population decline of *D. plexippus* during August 2015 may have been reduced nectar availability compared to the previous two years. The principal nectar sources used by *D. plexippus* at Lower Crab Creek are milkweed and Purple Loosestrife, the latter occurs only in parts of the site that retain at least some moisture during the summer. Milkweed finishes blooming by the end of July and blooming of loosestrife was very limited in 2015 due to dry conditions throughout the site with only 8 mm of rainfall during the monitoring period. Nectaring on Purple Loosestrife accounted for 19.7% of behavior observations in 2014 but only 2.4% of observations in 2015 because of the scarcity of blooming loosestrife. Pyle (1999) reported finding 'lots of monarchs' nectaring on Purple Loosestrife during southward migration near Hells Canyon in Idaho. Purple Loosestrife is a declared noxious weed in Washington (http://www.nwcb.wa.gov/detail.asp?weed=90) because of its propensity to disrupt wetland ecosystems by displacing native plants and animals. Its occurrence at Lower Crab Creek is limited however by moisture deficits minimizing adverse impacts on the ecosystem. In contrast, its high value as a nectar resource makes it an important factor in the suitability of Lower Crab Creek as a summer breeding area for *D. plexippus*. The issue of limited nectar resources in large areas of the arid west during mid-late summer may have a region-wide impact on monarch survival and deserves study. Aside from milkweed and loosestrife, the other plant which appears to be important to the persistence and survival of *D. plexippus* at Lower Crab Creek is *E. angustifolia* (Russian Olive). This large bush or small tree is also a declared noxious weed in Washington (http://www.nwcb.wa.gov/detail.asp?weed=187). Its importance to *D. plexippus* at Lower Crab Creek accrues from being the dominant shade tree. The observations reported here as 'resting on ground or vegetation' were largely made up of adults resting in the shade on Russian Olive. Additionally, female *D.*

*plexippus* were observed ovipositing on young milkweed plants growing in the shade underneath Russian Olives. Russian Olive is a nitrogen-fixing plant (Zitzer and Dawson 1989) raising the possibility that its presence may be a factor in the high abundance of milkweed at Lower Crab Creek. Pyle (1999) mentions Monarchs using Russian Olives as a night time roosting tree in various locations (including Lower Crab Creek) during his travels in the Pacific Northwest. Given that these two invasive plants have only been in eastern Washington since the early 1900s (see links above), it is possible that the existence of large summer breeding populations of *D. plexippus* at this site is a relatively recent phenomenon. Monarch occurrence at the site before the invasive plants arrived may have been limited to the period of milkweed flowering. Lower Crab Creek is described from 1879 to the 1950s by Bentley (2010) noting that the creek ran dry by September each year before the advent of irrigated agriculture in the 1950s. It is likely that Purple Loosestrife and Russian Olive did not establish at Lower Crab Creek until the 1950s.

The sex ratio of *D. plexippus* populations at the breeding site was consistently male-biased which accords with data from breeding populations in Australia (James 1981, Zalucki and Kitching 1984, Bull et al. 1985, Zalucki and Suzuki 1987). Interestingly, Davis and Rendon-Salinas (2009) reported increasingly male-biased sex ratios in the Mexican overwintering colonies over a 30 year period. However, the well-known aggressive male courtship and mating behavior of *D. plexippus* (Pliske 1974) is the most likely reason for the apparent low numbers of females at the Lower Crab Creek site during this study. Since the study area with almost contiguous milkweed was essentially one enormous patch of *A. speciosa*, it is likely that most oviposition occurred on the perimeters of the site away from frequent male interference. During the three years (108 hrs of observation) 20 oviposition events were recorded and all of them were either on the outer edges of the site or within the shade or thickets of Russian Olives located in central or perimeter areas. Oviposition within the shade and understory of Russian Olives provided females with protection from patrolling males as well as providing young, vigorous *A. speciosa* plants. This 'clandestine' oviposition behavior curiously appeared to reduce encounters with egg-laying females beyond what might be expected in a large population of *D. plexippus*. Zalucki (1993) suggested that female *D. plexippus* treat milkweed patches with resident males as resources and 'hang around' perimeter areas venturing in when amenable to courtship and mating. The single instances of courtship flight and mating seen over three seasons occurred within central areas of the site.

The Lower Crab Creek site appears to offer a valuable and dependable resource for migrant reproductive *D. plexippus* adults in early June. Peak bloom of *A. speciosa* occurs at this time and the noticeable fragrance emanating from the extensive area of plants could perhaps help attract *D. plexippus* to the site. This study demonstrates that the reproductive potential of small numbers of migrant *D. plexippus* colonizing a large, milkweed-rich site in early summer is substantial. Although the maximum population estimate derived from MRR for males and adjusted for both sexes was close to 400, it is likely there was some permanent emigration from the site, thus this site's contribution to the region's *D. plexippus* population likely exceeded 500 at least in 2014. It is interesting to speculate on the maximum population size that could be sustained by this site. Milkweed is unlikely to be a limiting resource for immature stages of *D. plexippus* at Lower Crab Creek so population regulation would likely be mediated by natural enemies, climate, nectar resources and/or adult behavior. Extreme heat and lack of nectar resources appeared to curtail maximum population size in 2015. Given sufficient nectar resources and average summer temperatures it is reasonable to expect a maximum potential population of 1000–1500 individuals at the site.

A key finding of a long term study on immature *D. plexippus* populations across the eastern United States was a positive association between survival and the number of plants in a milkweed patch (Nail et al. 2015a). The authors of this study suggested that 'conservation actions should encourage plantings with large numbers of milkweed plants, not only because more plants will support more Monarchs but also because survival is likely to be higher'. Thus, it would seem appropriate and beneficial for *D. plexippus* conservation strategies in arid areas of the western United States to focus on the protection, expansion and creation of isolated, *Asclepias*-rich sites. High production of *D. plexippus* in isolated, large, dense patches of milkweed like Lower Crab Creek may be more characteristic of the arid west than production on widely distributed small patches of milkweed. Large, isolated patches of dense milkweed in moister areas, is also characteristic of Arizona (Gail Morris, pers. comm.). The few currently known summer breeding sites of *D. plexippus* in eastern Washington all contain substantially less *Asclepias* in terms of number of plants and area occupied, than Lower Crab Creek. They also support substantially smaller populations of *D. plexippus* (James unpubl. obs.). It is possible that simply expanding the milkweed acreage at these sites may be the most effective and economic way of enhancing the summer breeding potential of *D. plexippus* in Washington. However, more research is clearly needed on the relative production of Monarchs in large and small milkweed patches over broad areas of the inland Northwest to determine optimal strategies for increasing milkweed and Monarch populations.

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