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DYNAMICS AND STRUCTURE OF A NATIVE *PIERIS* POPULATION IN THE PRESENCE OF A NON-NATIVE, TOXIC LARVAL HOST PLANT

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ABSTRACT. There have been reports of butterflies that oviposit on non-native plants that do not support the development of the larvae, and the fitness cost of this behavior has been estimated in one such case. However, the long-term consequences of this fitness cost for the population dynamics of such butterflies have not been studied. Here we report changes over 40 years in a population of *Pieris macdunnoughii* (Lepidoptera, Pieridae; formerly *Pieris napi macdunnoughii* Remington), which oviposits on a lethal, non-native plant, *Thlaspi arvense* (Brassicaceae), as well as on suitable native hosts. Mark-release-recapture (MRR) studies conducted at four intervals over 40 years showed no significant trends across years in population structure or dynamics, including estimated population density and temporal changes in the number of newly emerged individuals within a year. The estimated daily residence rate differed between the sexes. However, male estimated daily residence rate showed no significant change across years. Female residence rate was higher in the 2000s than in 1971; data were insufficient to calculate a residence rate in 1972. The average flight distance of female dispersants changed across years, but not as expected based on potential flight distance and with no clear pattern. Our detailed observations on female flights at a local scale showed that flight segments varied among different habitat types defined by aridity. Thus, although we see habitat effects on behavior, we did not detect any significant changes in *P. macdunnoughii* population dynamics and large-scale structure across four decades, a century after the plant's introduction.

Additional key words: Brassicaceae, dispersal, host mismatch, mark-release-recapture, Pieridae

Oviposition "mistakes" by butterflies on non-native plants that do not support larval development have been reported in the literature (summarized in Graves & Shapiro 2003). Because young larvae generally cannot move long distances, hatching on such a plant is usually lethal. The habitat thus consists of patches with differing butterfly fitnesses, including a fitness of zero in non-native plant patches (Nakajima et al. 2013). Given appropriate genetic variation, a population may evolve to avoid oviposition on the non-native plant, or larvae may evolve a tolerance for the non-native plant, as indicated for *Pieris oleracea* and *Alliaria petiolata* (Keeler & Chew 2008). In ecological time, the population may be reduced in size due to the fitness cost of oviposition on the non-native plant. Ecology also influences evolution: the butterfly's population structure (e.g., habitat choice, short and long range dispersal patterns as a function of habitat, age structure, daily residence rate) and population dynamics (changes in population numbers across time) influence the rate of evolution, again given appropriate genetic variation (Nakajima & Boggs in prep.).

Here we report work on the native butterfly *Pieris macdunnoughii* (Lepidoptera, Pieridae; formerly *Pieris napi macdunnoughii*; Chew & Watt 2006) in Gothic, Gunnison County, Colorado, USA (38° 57' 22.89" N, 106° 59' 18.23" W; elevation 2885 m asl). Females of this species oviposit on a lethal, Eurasian plant *Thlaspi arvense* L. (Brassicaceae) (Chew 1977, Nakajima et al. 2013). Oviposition on *T. arvense* by *P. macdunnoughii* was first reported in the 1970s (Chew 1974) and has continued since (Nakajima et al. 2013). Females in this *P. macdunnoughii* population also oviposit on four native Brassicaceae that support larval development: *Boechera* spp. (formerly *Arabis* spp.), *Cardamine cordifolia* A. Gray, *Draba aurea* Vahl ex Hornem., and *Descurainia incana* (Bernh. ex Fisch. & C.A. Mey) Dorn (formerly *D. richardsonii* Sweet) (Chew 1975, Nakajima et al. 2013). Because *P. macdunnoughii* females avoid oviposition on other unpalatable plants, including the native Brassicaceae *Erysimum asperum* (Chew 1974, 1975), oviposition on *T. arvense* most likely results from mistakes due to shared oviposition cues among *T. arvense* and the four native hosts on which larval development is successful (Chew 1974, Rodman & Chew 1980).

Thlaspi arvense most likely arrived at our site in the mid-1800s (Chew 1977). The plant readily invades early successional, disturbed sites (USDA 2013). Our study site has been subject to continuous disturbance from cattle grazing and localized human activities since the mid-19th century (Vandenbusch 1980), so it is reasonable to assume that the plant has been present in the area since its initial introduction. *Pieris macdunnoughii* has 1 generation per year at this elevation (Chew 1974). Thus, the plant has been present for more than 130 butterfly generations. The potential also exists for strong selection against oviposition on *T. arvense*, since the percentage loss of *P. macdunnoughii*'s offspring due to oviposition on *T. arvense* in the wild was estimated at 3.0 % in the late 1990s to early 2000s (Nakajima et al. 2013).

We therefore built on early studies in the 1970s on the butterfly's population structure and dynamics, comparing population size, daily adult residence rates, daily number of newly emerged individuals and dispersal probability and distance across 40 years. If the butterflies consistently lose 3.0 % of their offspring every generation, the population size at the end of our survey would be $(1 - 0.03)^{40} = 0.30$ of that in the beginning. Contrarily, if the butterflies migrated into and out of the study site, such that the local population was a sink supported by outside source populations, the population would not have declined and the selection by the non-native plant might be alleviated.

In addition to the long-range dispersal across the study area described above, we also report female butterfly dispersal patterns over a shorter range inside the study site, at the scale of host plant patch. We compared the butterfly's movements among different types of habitats preferred by different host plants. We examined whether dispersal differed with individuals, and if so, how they differed. Individual movements in a small spatial scale, such as foraging and oviposition, affect the individual performance and fitness, dispersal in a long range and hence the dynamics of population (Hawkes 2009, Johnson et al. 1992). Indeed, in our study system, butterfly movements at the scale of host plant patch size affect encounter probability with the lethal *T. arvense*, which directly influences fitness. We use this information to further understand the variance of the long-range dispersals and the population dynamics.

MATERIALS AND METHODS

Mark-release-recapture. We examined daily population size, daily residence rate, daily number of newly emerged individuals, and long distance dispersal using standard mark-release-recapture (MRR) techniques (Watt et al. 1977) in 1971, 1972, 2000 and 2010. The study area was divided into subsites that differed among years (Fig. 1, Table 1). We analyzed the population size, residence time and daily number of newly emerged individuals using only the subsites that were in common among all years (those in the circle in Fig. 1). These subsites used for population analysis were located in the Gothic townsite and surrounding montane meadows. All five host plants, including *T. arvense*, existed in the study site both in the 1970s (Chew 1975, 1977) and in the 2000s (Nakajima et al. 2013). The other subsites were used to examine long distance dispersal. These subsites consisted of meadows along the Copper Creek drainage system, separated by spruce-fir forest and willow. *Pieris macdunnoughii* and its native host plants were observed in these meadows in the 1970s (Chew 1977) and in the 2000s (Boggs, personal observation).

The method of MRR was consistent throughout our 40-year survey. Butterflies were captured during sunny weather with hand nets, a number written on their wings with an indelible marker, and released. We recorded date, butterfly number, sex, subsite number and wing wear. Wing wear is a surrogate measure of adult age. We scored wing wear in increments of 0.5 from 1.0 to 5.0, where 1.0 is a fresh individual whose wings are still damp and 5.0 is an individual with

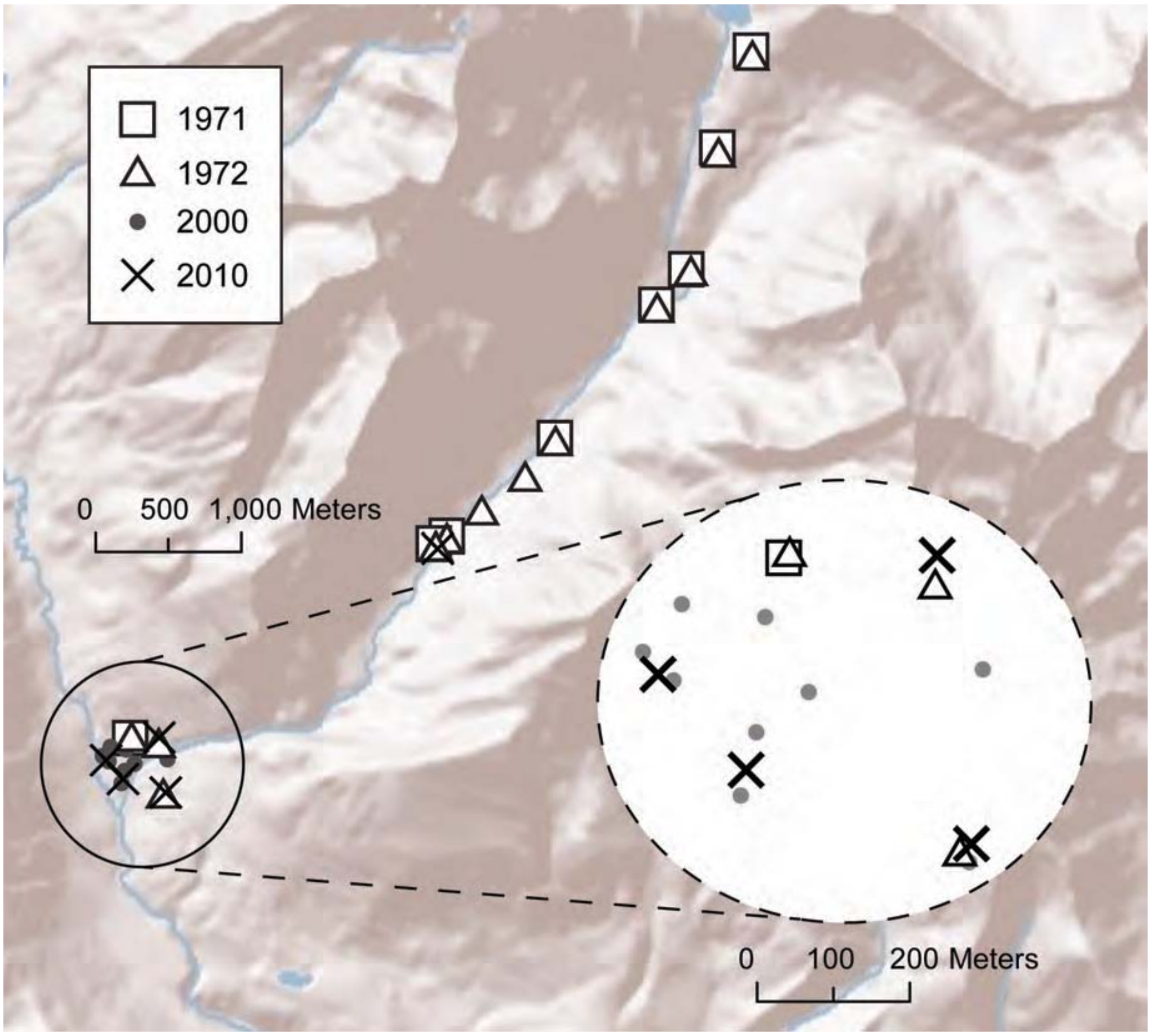

FIG. 1. Schematic map of mark-release-recapture subsites.

TABLE 1. Details of mark-release-recapture sites and the number of captured individuals

Year	# of subsites	Area covered (ha)	Min and max detectable distance (m)		# butterflies captured	
					male	female
1971	10	313.19	99	6226	488	234
1972	12	368.64	99	6226	229	93
2000	9	88.29	44	505	467	143
2010	5	16.65	160	2742	247	63

extensive scale erosion and wing damage (Watt et al. 1977, 1979).

Daily population size was estimated using POPSTRUC (Watt et al. 1977), which is based on a Jolly-Seber analysis. We analyzed males and females separately to satisfy the assumption of equal catchability among individuals. We then calculated the daily population density on each sampling day as the estimated population size divided by the sampling area. Area was calculated as the area of a polygon bounded by the subsites used in each year, calculated using ArcGIS 10.1 (Esri, Redlands, CA, USA) as shown in Table 1.

We estimated the average adult daily residence rate, Φ, for each sex and year using recapture decay plots. A recapture decay plot is the linear regression of the ln(total number of butterflies known to live at least d days) against day number d (Watt et al. 1977). The number of butterflies known to live at least d days is based on the interval between first and last capture of each individual. LnΦ is the slope of the regression line. First, we tested whether the slopes of the male and female regression lines were significantly different. We used an ANCOVA with sex as a categorical factor and "d" as a covariate. Significance of the interaction sex × d means that slopes, and therefore Φ, differ between the sexes (Zar 1999). If the slopes were different between males and females, we compared the slopes among years within each sex. If the slopes were not significantly different, we calculated the common slope (Zar 1999). We also calculated $-(\ln\Phi)^{-1}$ as the mean expectation of residence.

Daily number of newly emerged individuals was examined in order to determine whether multiple generations flew during each growing season. The number of individuals with wing wear score equal to or lower than 2.0 at any point in time was used as an

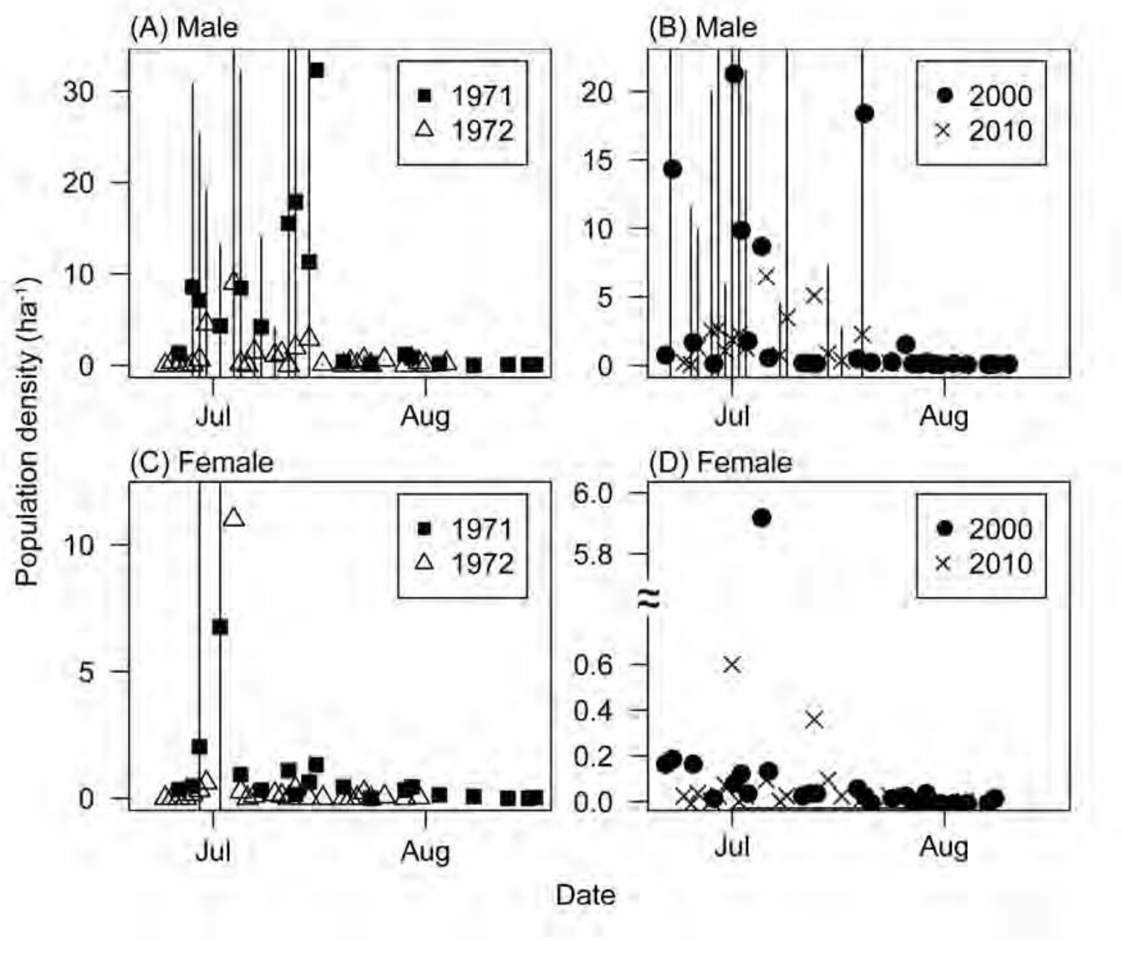

FIG. 2. Estimated daily population densities of males (A, B) and females (C, D). Error bars indicate the square roots of estimated variances of the population size standardized by the MRR sampling area. The symbol frequently hides the small error bars.

estimate of the newly emerged adults in the population. If a second generation eclosed, we would see 2 peaks in the time series of the number of newly emerged adults in one year.

To analyze dispersal probability, we used all subsites in each year. We examined the proportion of individuals that had moved to a new subsite on recapture (dispersants) out of the total individuals recaptured. We compared the proportion dispersing between males and females by χ^2 test.

Again using all subsites in each year, we approximated dispersal distance using the distance between the centers of the subsites where an individual was recaptured and where it was immediately previously captured. Therefore, the dispersal distance is 0 when an individual was recaptured in the same subsite. We calculated the dispersal distance as the sum of distances between recaptures for each butterfly; if one individual was recaptured at subsites A, B and C in this order, its dispersal distance would be the distance between A and B plus the distance between B and C. The flight distances of dispersants were compared between males and females and among years by examining the significance of the independent variables in a generalized linear model (GLM) [distance = year + sex + (year × sex)] assuming errors distributed as Poisson. We used the function "glm" in R (version 3.0.1, R Development Core Team 2013) for the analysis. We should note, however, that the minimum- and maximum-detectable flight distance differed among years (Table 1) and might have caused us to identify erroneous differences in dispersal distance. In such a case, the fractions of dispersants would be higher and the mean flight distances would be shorter in 2000 and 2010, which had shorter detectable distances than other years. Our analysis also assumes equal capture effort among years. Although the people who collected the data changed over our 40-year survey, they all used a standardized method (described in Watt et al. 1977).

Butterfly short range movement patterns. *Thlaspi arvense* preferred dry and intermediate habitats and was distributed sparsely in our study area, similar to *Boechera* spp., *De. incana* and *Dr. aurea*, whereas *C. cordifolia* preferred wet habitats and occupied larger patches with higher plant density (Nakajima et al. 2013; the details of habitat aridity classification is also described therein). To compare short range dispersal within each habitat type, we observed female butterfly movement in three 20 × 20 m quadrats in 1997 in each of three habitats: dry, intermediate and wet. Dry and intermediate plots were both grasslands with *Boechera* spp. sparsely distributed throughout the plots. We assumed that the results in the dry and intermediate plots would be equivalent to those in habitats with *T. arvense* because *Boechera* spp. and *T. arvense* often coexist, and *P. macdunnoughii* did not intentionally avoid *T. arvense* for oviposition (Chew 1974). Indeed, a previous study showed that the density of *P. macdunnoughii*'s eggs per plant was not significantly different among the host plants including *T. arvense* (Nakajima et al. 2013). The wet plot was dominated by 1.5–1.8 m tall willow (Salix sp.). The open areas within the wet plots were dominated by *C. cordifolia*.

The perimeter of each quadrat was marked with red flags at every meter on all sides. A string grid was laid across every other meter on both sides. We observed individual females that either flew into the quadrat or were released outside the quadrat and flew into it. Observers sitting on a ladder recorded female movement within the quadrat on a grid map. Alighting coordinates were marked with an "x" and time spent sitting was recorded. We then approximated the female's movement as a sequence of straight lines. We calculated flight distances (lengths of straight lines) and turning angles (angles between two consecutive flights) from each butterfly's map.

To test for the effects of plot on turning angles and flight distance using repeated measurements on butterflies, we developed generalized linear mixed models (GLMMs) with "ID", i.e., butterfly's individual ID number as a random effect, and "plot" as an independent variable. We estimated the standard deviation for the random effect to quantify the variation between individual butterflies. We then compared this GLMM to the GLMM without the independent variable "plot" (null model) by likelihood ratio test. We considered that plots affected the turning angles and the flight distances if the model with "plot" and the null model were significantly different. We predicted that the butterflies flew in shorter distances in wet sites than in drier sites because *C. cordifolia* makes relatively dense patches than other host plants in dry and intermediate habitats. We expected that the turning angles were random in all sites and therefore the frequency of turning angles would show normal distributions with the mean at 0 degrees. Models were fitted by the function "lmer" and normality of turning angles was tested by Shapiro-Wilk test using the function "shapiro.test", both in the statistical software R (R Development Core Team 2013).

Results

Population size, age, and long distance flight. The estimated population density did not show any trend across sampling years (Fig. 2). The estimated daily population densities within a year showed bell-shaped

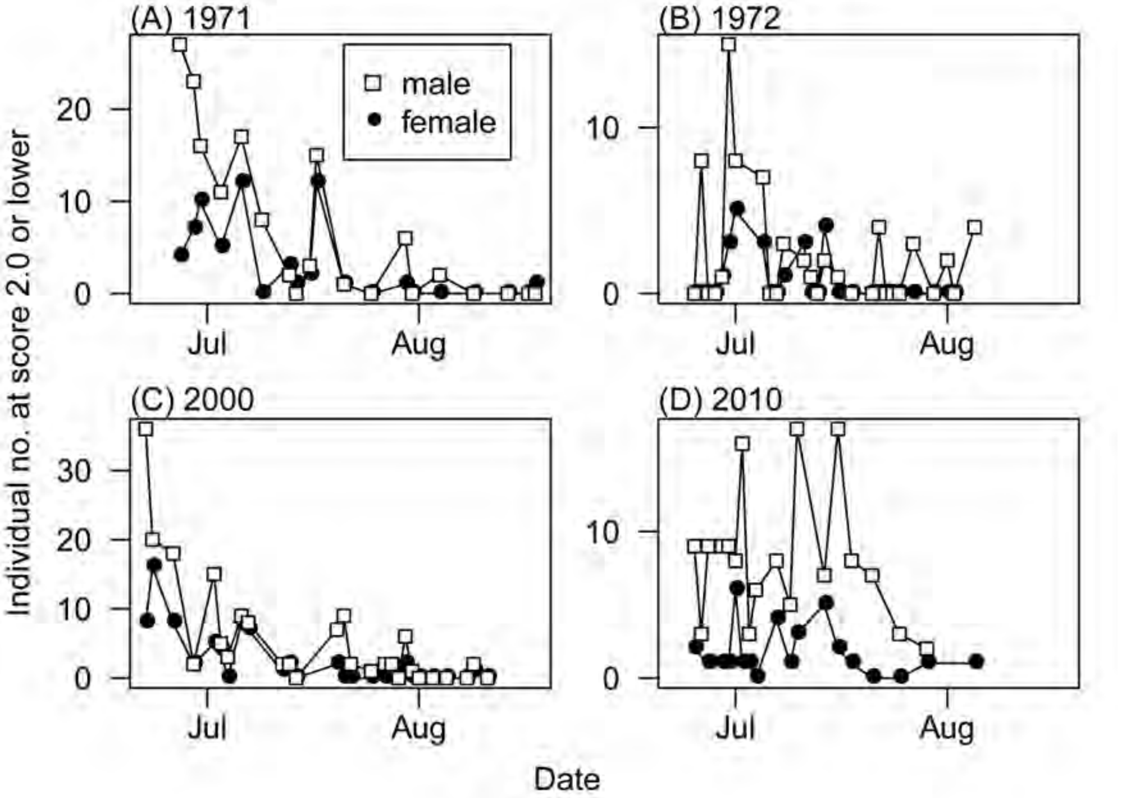

FIG. 3. Daily number of captured individuals at wing wear condition 2.0 or lower.

curves across the flight season, with large fluctuations in both sexes in all years. The estimated variances of the population size (error bars in Fig. 2) were often small, especially in females, due to small sample sizes (Jolly 1965; see Table 1 for sample sizes).

The number of individuals at condition 2.0 or lower across time within each sampling year was either monotonic or unimodal in males in 1972 and 2000, showing no signs of a second brood (Figs. 3B and 3C). In other data, a small second peak was observed in mid-July after a larger peak in mid- or late June or at the beginning of sampling (Fig. 3). These were unlikely a second brood because the time between the first and the second peaks was less than a month, which is too short for the offspring of adults emerged at the first peak to become adults. Larval development takes about 14 to 17 days for *P. macdunnoughii* (Chew 1975), and pupation lasts another 10 days (C. Boggs, pers. obs.) under laboratory conditions which promotes faster development than natural conditions. It is possible that our data did not cover the entire flight season. *Pieris macdunnoughii* emerged from pupal diapause in late May and early June, and the next generation entered pupal diapause at the end of the summer at least in the 1970s (Chew 1975). Thus, we could have missed the extreme earliest part of the flight season, although it is unlikely that an entire generation of adults preceded the sampling period.

The slopes of regression lines for recapture decay plots (Fig. 4) differed significantly between males and females ($F = 62.57$, df = 1,115, $p < 10^{-11}$). The slopes did not differ among years in males ($F = 0.96$, df = 1,70, $p = 0.33$) but differed significantly in females ($F = 11.09$, df = 1,41, $p = 0.002$). Only 1971, 2000 and 2010 data were used for the females, since data were insufficient to examine the slope in 1972 females. Since the females' slopes did not differ between 2000 and 2010 ($F = 0.097$, df = 1,26, $p = 0.051$), we obtained a new, common slope for the 2000s. Thus, from the regressions, the daily residence rates, Φ, were 0.83, 0.96 and 0.73, and the expected average residence times were 5.6, 22.5 and 3.3 days for males (all years combined), females in 2000s, and females in 1971, respectively.

The proportion of recaptured animals dispersing did not differ between males and females across all years (Table 2). However, the proportion dispersing differed

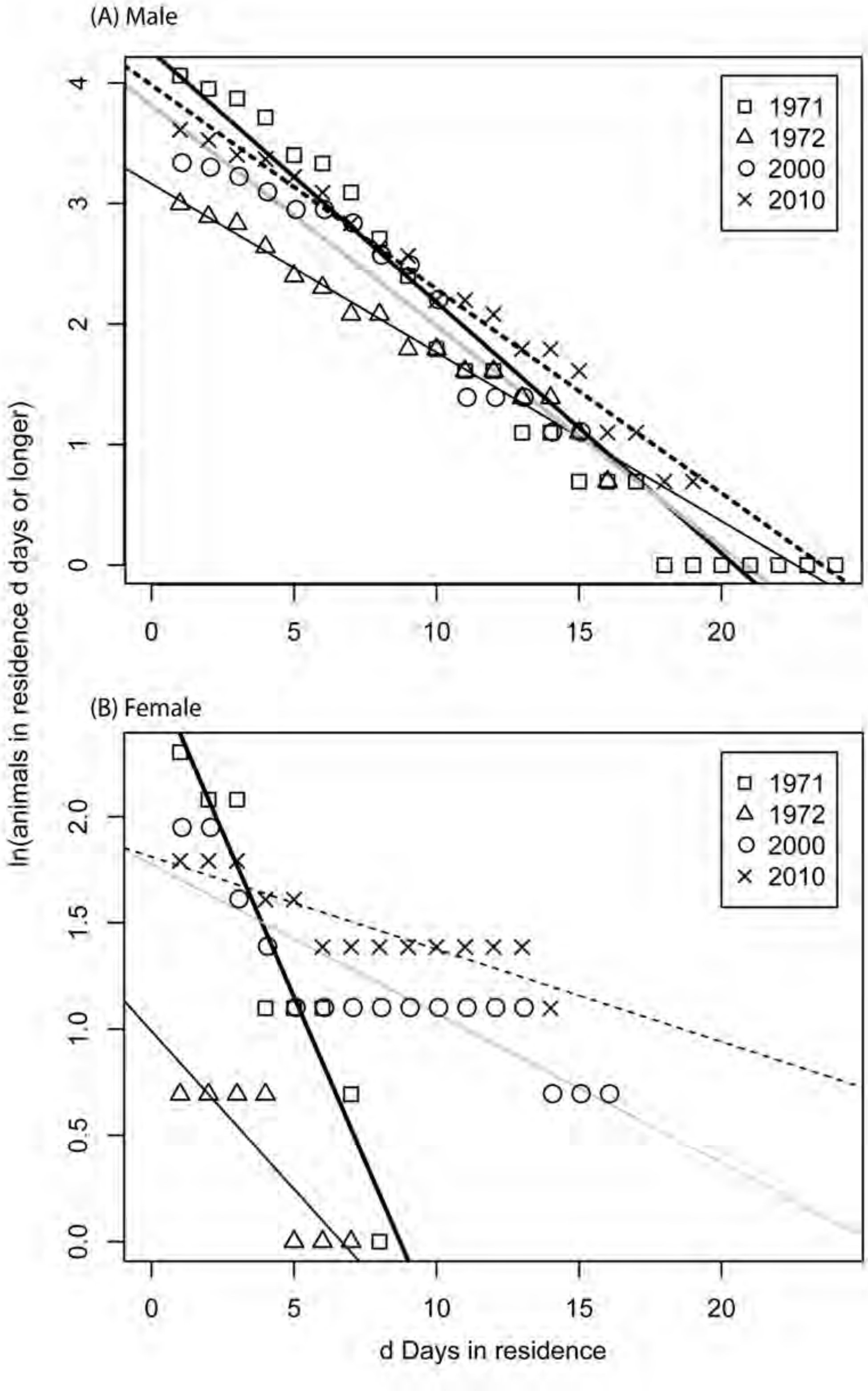

FIG. 4. Recapture decay plots for males (A) and females (B). Lines are the linear regression lines; black, thick: 1971, black, thin: 1972, gray: 2000, dashed: 2010.

TABLE 2. Analysis of dispersal. Degrees of freedom were 1 in all χ^2 tests.

Year	Sex	Dispersants				Dispersant/ recapture fraction	Comparison of dispersant fraction between:		
		Mean dispersal (m)	n	Mean dispersal (m)	n		M and F	years	decades
1971	M	713.05	19	148.88	91	0.21	χ^2=1.31		
	F	0	0	0	12	0	p=0.25	χ^2=2.55	
1972	M	537.72	32	746.42	97	0.33	χ^2=0.05	p=0.11	
	F	308.17	6	80.40	23	0.26	p=0.82		χ^2=90.6
2000	M	326.33	18	806.6	28	0.64	χ^2=0.17		$p< 10^{15}$
	F	277.57	7	277.57	7	1	p=0.68	χ^2=0.91	
2010	M	265	17	122	37	0.46	χ^2=0	p=0.34	
	F	403	3	204	6	0.50	p=1		

between the 1970s and 2000s with sexes combined (1970s: 0.26; 2000s: 0.58; see Table 2 for statistics). Mean flight distances of dispersing animals differed among years ($z = 3.4$, $p = 0.0007$) and between the sexes ($z = 25.4$, $p < 10^{-15}$). The interaction between year and sex was also significant ($z = -25.2$, $p < 10^{-15}$), indicating that flight distance did not change in concert in the two sexes across years.

Butterfly short range movement patterns. We obtained 44, 51 and 41 flight segments from 12, 22 and 7 females at dry, intermediate and wet plots, respectively.

The standard deviations for the random effect in turning angles and flight distances were both 0.000. For turning angles, the null model was not significantly different from the full model ($\chi^2 = 0.250$, df = 1, $p = 0.62$). For flight distances, the null model was significantly different from the full model ($\chi^2 = 13.97$, df = 1, $p = 0.0009$). The full model was also significantly different from the null model when we used the data from dry and wet plots ($\chi^2 = 10.55$, df = 1, $p = 0.001$) and dry and intermediate plots ($\chi^2 = 8.00$, df = 1, $p = 0.005$), but not when we used data from wet and intermediate plots ($\chi^2 = 1.25$, df = 1, $p = 0.26$). This result indicates that flight distance differed between dry plots and intermediate/wet, with females flying shorter distances between landings in the intermediate/wet plots.

Flight distance was distributed exponentially in all plots (Figs. 5A, 5C, 5E). The distributions of turning angles (Figs. 5B, 5D, 5F) did not differ significantly from a normal distribution except for the wet plot (dry: $W = 0.97$, $p = 0.40$; intermediate: $W = 0.97$, $p = 0.31$; wet: $W = 0.94$, $p = 0.04$). The turning angles in the wet plot were distributed bimodally (Fig. 5F). The mean turning angles were −2.4, 17.0, and 5.3 degrees in dry, intermediate and wet plots, respectively.

DISCUSSION

Our results indicated that the dynamics and structure of this *P. macdunnoughii* population have not changed significantly over four decades. The estimated population density did not decrease detectably from 1971 to 2010, in spite of the continued presence of the lethal invasive plant *T. arvense*. In addition, the adult daily male residence rate did not change over time. The daily residence rate of females differed significantly between 1971 and the 2000s, although we emphasize that that could be due to small sample sizes (10 individuals recaptured in 1971 and fewer in the 2000s). Finally, the temporal changes of the number of newly emerged butterflies did not differ among years.

The dispersal of males did not differ from what we expected from the detectable flight distances. We did not find any difference between males and females in the proportion of individuals dispersing. On the other hand, the cumulative flight distance of dispersants depended on both sex and year. In males, the mean flight distance was longer in the 1970s than in the 2000s, as predicted from the detectable flight distance. However, we did not find any pattern in females. We need further study to specify the factors that influence dispersal.

Our observations of butterfly movements at small scales may provide a hint for factors governing dispersal observed at larger scales. As we predicted from the host plant distribution, the distance per flight segment was longer in dry habitat than that in wetter habitat. In

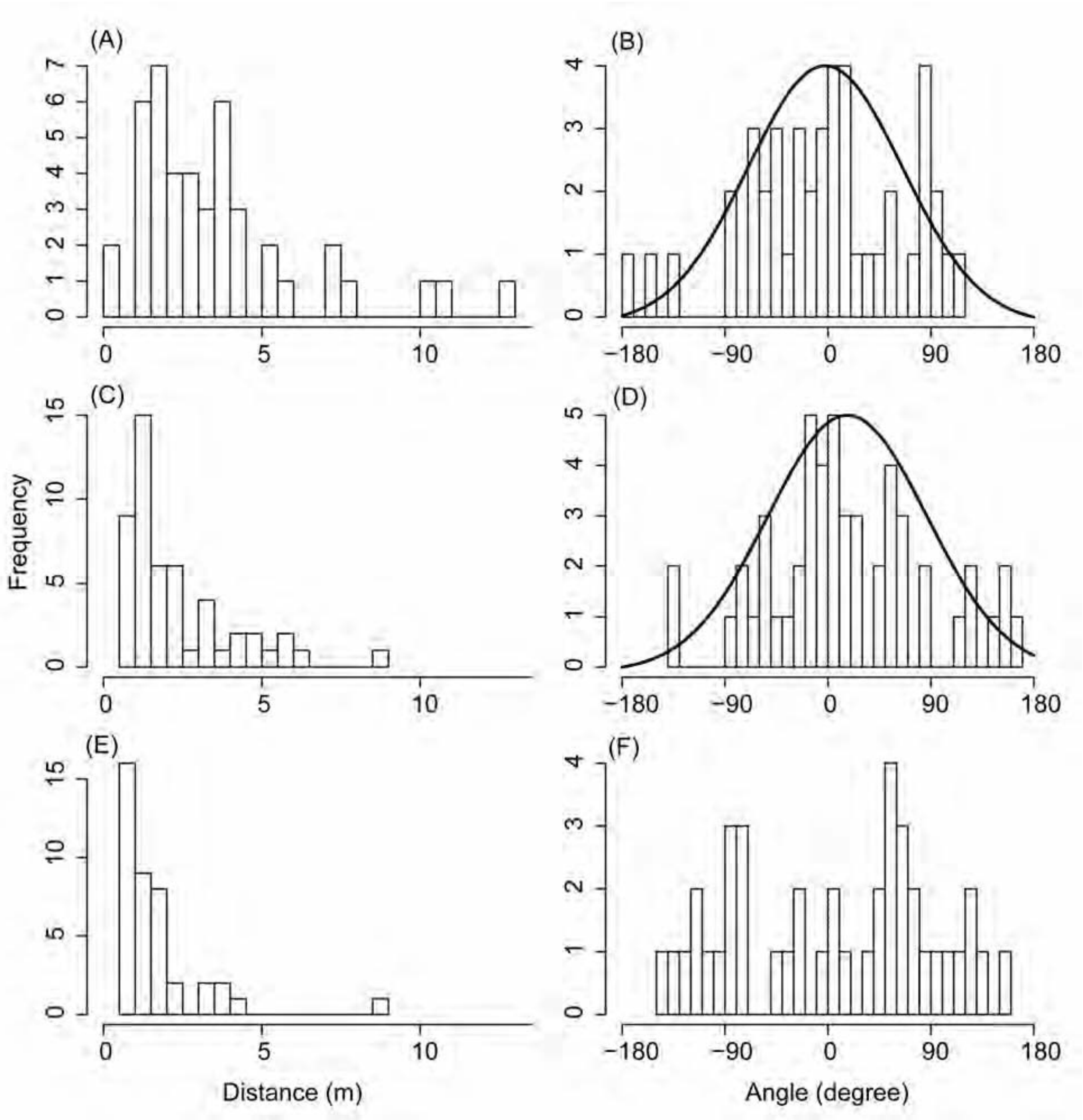

FIG. 5. Frequency distributions of flight distance (A, C, E) and turning angle (B, D, F) observed in 1997 at dry, intermediate and wet plots (A and B, C and D, E and F, respectively). The mean and SD of normal distributions fitted to panels B and D were –2.4 and 67.4, and 17.0 and 69.5, respectively.

addition, our wet plot contained tall willows. In avoiding these obstacles, butterflies may have made shorter flights with turning angles avoiding the willows rather than longer direct flights, resulting in the bimodal distribution of turning angles observed only in the wet plot. Thus, the different host plant distributions in different plot types may have caused the observed difference in dispersal. Our study also suggested that the dispersal pattern did not vary among individuals. Furthermore, female *P. macdunnoughii* were caught more frequently in wetter sites than in dryer sites in another MRR study on the same system (Nakajima et al. 2013), suggesting that females tend to stay longer in wetter sites. This habitat effect may also apply at the larger scale of our MRR study.

In conclusion, we did not detect any negative changes on *P. macdunnoughii* population dynamics. This suggested that the lethal, non-native plant had not significantly affected the butterfly's population. Several factors may have maintained variation for oviposition on this plant in the intervening time, including immigration, shifting host plant patch geography and drift (Nakajima & Boggs in prep.). Our study confirmed migration of *P. macdunnoughii* between Gothic townsite where *T. arvense* existed and Copper Creek where *T. arvense* had not been seen (Chew 1977, Boggs, personal observation). It is possible that the habitats in Copper Creek served as population source.

There is a potential for *T. arvense*, however, to affect population size and structure in the future. For example, *T. arvense* may increase in abundance because it favors disturbed areas and our study site experiences frequent human disturbance from construction and other activities (Boggs, pers. obs.). It is also possible for butterfly to evolve in response to *T. arvense*. Genetic variation does exist within the population for female oviposition choice (Boggs et al. in prep.). Contrarily, there is no indication of variation within the Colorado population in ability to complete development on the plant, although hybrid crosses with Swedish *P. napi* suggest that normal larval development on the plant is controlled by one or a few autosomal genes (Boggs & Wiklund in prep.). Further analysis combining the data reported here and prospective modeling of dynamics at our study site will provide important information for other systems involving lethal non-native "hosts".

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