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Distribution of the monarch butterfly, *Danaus plexippus* (L.) (Lepidoptera: Nymphalidae), in western North America

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The standard model for the migration of the monarch butterfly in western North America has hitherto been movement in the autumn to overwintering sites in coastal California, followed by a return inland by most individuals in the spring. This model is based largely on observational and limited tagging and recovery data. In this paper we test the model by plotting many years of museum and collection records on a monthly basis on a map of the region. Our plots suggest a movement of Oregon, Washington and other north-western populations of summer butterflies to California in the autumn, but movement of more north-easterly populations (e.g. from Idaho and Montana) along two pathways through Nevada, Utah and Arizona to Mexico. The more westerly of these two pathways may follow the Colorado River south as indicated by museum records and seasonal temperature data. The eastern pathway may enter northern Utah along the western scarp of the Wasatch Mountains and run south through Utah and Arizona. Further analysis of distributions suggests that monarch butterflies in the American West occur primarily along rivers, and there are observations indicating that autumn migrants often follow riparian corridors. More data are needed to test our new model; we suggest the nature of the data required.

ADDITIONAL KEYWORDS: ecological biogeography – migration – seasonal distribution.

INTRODUCTION

Since the classic studies of F. A. Urquhart (1960), students of monarch butterfly migration have generally regarded North American monarchs as belonging to two more or less distinct migratory populations, one in the east and one in the west. The Rocky Mountains east of the Great Basin form an indistinct boundary between the two (Brower, 1985, 1995; Malcolm, 1987; Zalucki & Rochester, 1999). Butterflies from the highly migratory eastern population migrate in the autumn some thousands of kilometres to overwinter in aggregations of tens of millions in the mountains of the Transvolcanic Range of Mexico (Urquhart & Urquhart, 1976; Calvert & Brower, 1986). A small subset of the eastern population breeds throughout the year in southern Florida (Brower, 1961; Malcolm & Brower, 1986). In the early spring the Mexican overwintering aggregations break up and the butterflies move north to breed on the early milkweeds (*Asclepias* spp.) in northern Mexico and the southern United States. Subsequent generations continue north, breeding in the southern tier of Canada as far as the northern limit of milkweed distribution (Cockrell, Malcolm & Brower, 1993; Malcolm, Cockrell & Brower, 1993).

The movement patterns of the western population are far less clear. The 'classic' model holds that monarchs from throughout the American West migrate in the autumn to overwintering aggregations along the coast of California, with most individuals returning inland in the spring (Urquhart & Urquhart, 1977;

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Brower, 1995). More recent data, however, reveal that the situation is more complicated. When overwintering California aggregations begin to break up in February, many of the butterflies move only short distances and in no particular direction and oviposit on early emerging species of milkweed. Furthermore, the successive emergence and maturation of different milkweed species means that the monarchs are present and breeding in coastal and subcoastal habitats from early spring until aggregations begin forming in the autumn (Wenner & Harris, 1993; H. Dingle, unpubl. observ.). Tagging experiments showed that other monarchs from the winter aggregations moved during a brief period in the spring up to 465 km inland from the tagging sites (Nagano *et al*., 1993). The pattern of recaptures suggested that butterflies tagged in the Los Angeles Basin moved due east, those tagged in Santa Barbara County moved east or north-east, while those tagged north of Santa Barbara moved north-east, although differences between directions were not statistically significant (Wenner in Brower, 1995). The apparent divide between butterflies from Los Angeles and those from farther north was imposed by the Mojave Desert.

With respect to autumn movement, some two dozen locally emerging butterflies tagged in the late summer and early autumn near Boise, Idaho were recovered in California coastal sites, although two others were recovered in Utah some distance to the south and east of Boise (Pyle, 1999: 139; Brower & Pyle, 2004). In the northern Rocky Mountain West, especially the Snake River valley, autumn butterflies have been observed heading SSE, with substantial southward movement in Utah in the lowlands between the Great Salt Lake and the Wasatch Mountains (Pyle, 1999). Thus the pattern of movement of western monarchs is evidently more complex than a straightforward journey back and forth between coastal overwintering sites in California and interior breeding areas. Difficulties in sorting out exactly what is going on have generated some controversy about whether western monarchs are truly migratory (Nagano *et al*., 1993) or not (Wenner & Harris, 1993).

In this paper we take a somewhat different approach to determining seasonal population shifts in western monarchs. We mapped the label data from 2926 specimens in museums and private collections and data from the literature and from our own and others' field observations taken throughout western North America. These maps were then sorted on a month by month basis to assess the seasonal variation in distribution. The plots further allowed us to examine the relation between monarch distribution and the mountain and intermountain topography over which monarch movements take place. This western topography contrasts sharply with that of eastern North America. The eastern part of the continent has comparatively little relief from the Gulf of Mexico north into Canada, with the exception of the fairly narrow band of ridges of the Appalachian Mountains running south-west to north-east. This band divides the Atlantic coastal plain from the interior of the continent, but in only a few places does it exceed 1000 m in altitude. In contrast, most of western North America from southern Mexico to Canada west of the 100th meridian exceeds 1000 m, and relief exceeding 1000 m is also common. It would be surprising if the much greater topographic relief of the West did not exert an influence on monarch movements and seasonal distribution. The question we ask here is what that influence might be and whether it imposes specific patterns.

METHODS

Collection records for monarch butterflies in western North America were collated from museum and private databases and specimen labels. The data sources included collections from the Nevada State Museum (George Austin), Brigham Young University, the California Academy of Sciences, the Los Angeles County Museum of Natural History, the Bohart Museum (University of California, Davis), the University of Utah and Utah State University. Additional data sources were collections and observations from John Hinchliff's Oregon Butterfly Atlas (via Oregon State University), Andrew Brower, Robert Pyle, Arthur Shapiro and Larry Speers. In the source datasets, collection sites or observations were variously recorded as latitude–longitude coordinates, descriptions of collecting sites, and coordinates in US township, range and section format. Latitude–longitude coordinates were estimated from site descriptions with the Street Atlas USA software (version 7.0, DeLorme, Yarmouth, Maine, USA). Township, range and section values were converted to latitude–longitude coordinates with the TRS2LL program (Martin Wefald, San Francisco, CA 94121, USA).

Altitude data were obtained from the GTOPO30 global digital elevation model (United States Geological Survey, 1996: http://edc.usgs.gov/products/elevation/gtopo30.html). Long-term average temperature data for USA weather stations were obtained from the CLIM81 dataset (National Climatic Data Center, 1999: http://lwf.ncdc.noaa.gov/oa/climate/normals/usnormalsprods.html). River locations were obtained from the Hydrography Features of the United States GIS layer (United States Geological Survey, 1999: http://www.nationalatlas.gov/mld/hydrogm.html). To create temperature surfaces for mapping, the CLIM81 weather station data were converted to grids by inverse distance weighted interpolation. Because temperature decreases with altitude, temperatures were adjusted to sea level before interpolation and adjusted back afterwards. This was done by addition of a degreesper-metre value calculated by regression of temperature and altitude differences between nearest neighbour stations.

RESULTS

Monthly plots of the collection records of monarch butterflies in western North America clearly show shifting seasonal distribution (Fig. 1). In the winter months of December and January records are almost exclusively confined to the California coastal sites where aggregations of monarchs overwinter. In the spring (February to May) there is an increasing frequency of records eastward and northward. During the summer months of June through September there is an abundance of records throughout western North America, from southern California and southern Nevada north to southern Canada. Finally, in the

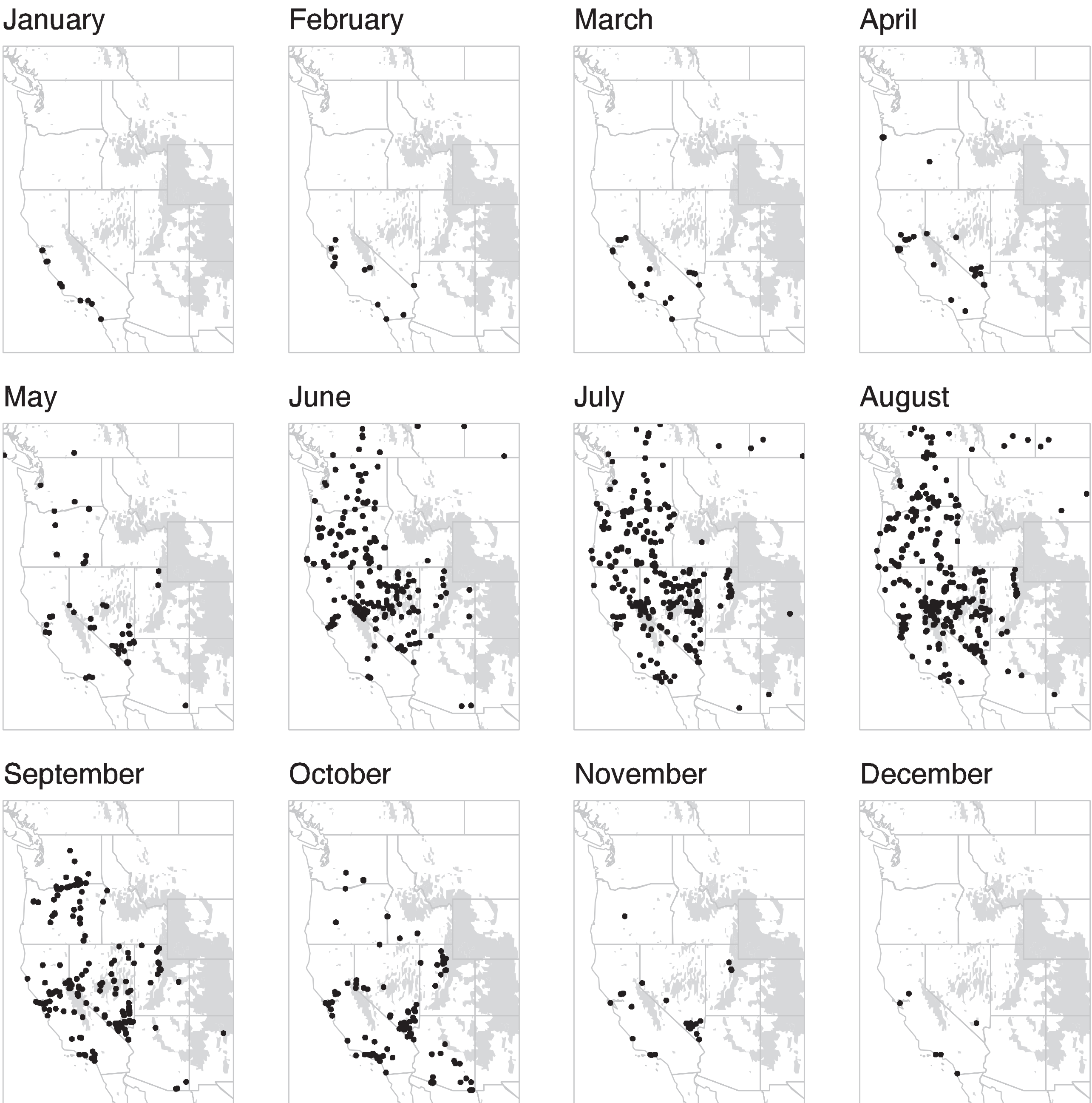

Figure 1. Collection records for monarch butterflies in western North America. Grey shaded areas are above 2000 m elevation.

autumn months of October and November the mapped distribution shrinks southward and westward. Within this overall pattern there are some interesting subsets of distributional records that may provide clues to the details of western monarch movements.

The first subsidiary pattern occurs in northern California and the regions to the east and north thereof. In February, March, and April there is a small but obvious increase in records east of San Francisco Bay. Some of these observations arise from monarchs breeding on early milkweeds such as *Asclepias cordifolia* (Benth.) in the northern foothills of the California Coast Ranges (Dingle, pers. observ.), but by April there are records for the Lake Tahoe basin (on the northern California–Nevada border), central Nevada and Oregon. These latter must be from monarchs that overwintered, because spring temperatures are not sufficient to have produced by this time a generation of butterflies arising from the early breeding in the Coast Range in either northern or southern California (see figs 3 and 4 in Wenner & Harris, 1993). Also, they are not likely to have come from Mexico (Brower & Pyle, 2004). This suggests movement of monarchs from near the coast through Sierra passes into Nevada.

Further increases in central Nevada in June are consistent with this notion, although some butterflies may be coming up from the south (see below). A corollary to this increase in Nevada is the rapid increase in observations in Oregon in May and June that suggests movement up through the Sacramento Valley of California and the Mt Shasta highlands into southern Oregon, with some movement from Nevada also a possibility. Records from the autumn months, beginning in September, suggest a reverse movement back toward the California coast from Washington, Oregon, and Nevada. The occurrence of this autumn movement is supported by many observations of monarchs moving south-westward through the Sacramento Valley in the vicinity of Davis and Sacramento, California in the autumn months (Brower, 1985; Dingle, pers. observ.; A. M. Shapiro, pers. comm.).

A second interesting subsidiary pattern occurs in southern Nevada. As early as February and as late as December there are records from this region. Inspection of the maps (Fig. 1) reveals an increasing frequency of monarch records through April and May and an apparent concentration of records in southern Nevada in October and November These records suggest movement of monarchs north through this area of Nevada in the spring, and south in the autumn. In the extreme south-east of the state, the Colorado River and Lake Powell form the border between Nevada and Arizona, with the river also dividing Arizona from California as it proceeds south. Brower & Pyle (2004) report several instances of monarchs moving south along the Colorado in the autumn. Along this southern stretch the river is mostly dammed, and the large reservoirs (and the Salton Sea just to the west) might be expected to have a climate ameliorating effect. Furthermore, irrigation in the adjacent riparian areas may produce enough flowering plants to allow migrating butterflies to forage for nectar (Brower & Pyle, 2004).

To test for climate ameliorating effects, we mapped on a monthly basis the areas of the south-western USA where minimum temperatures were 4 °C or above. This temperature was chosen because it is the minimum at which adult monarchs can still crawl, although they can survive brief periods at still lower temperatures (Masters, Malcolm & Brower, 1988; Alonso, Glendinning & Brower, 1993; Masters, 1993; Anderson & Brower, 1996). The results for December and January are shown in Figure 2. Two points are worth noting. First, the maps accurately predict the overwintering sites along the coast of California from San Francisco Bay south (Frey & Schaffner, 2004). They also reveal that an inland overwintering site in the south-western section of the Central Valley of California is an isolated pocket of temperature minima above 4 °C; this site is circled in Figure 2. An additional inland California wintering site that does not appear on our maps occurs in the Saline Valley not far from Death Valley (Brower, 1995 and references therein). At this site butterfly aggregations occur along outflows from hot springs where temperatures probably remain above our 4 °C minimum. Second, the border region along the Colorado River between California and Arizona and the adjacent agricultural and irrigated areas on both sides of the river also generally remain above 4 °C. This raises the possibility that the Colorado River valley is a thermally suitable site for at least some overwintering monarchs and a possible additional source for butterflies re-invading northern areas of the West in the spring via southern Nevada.

A third region of interest is the corridor in north-central Utah between the Great Salt Lake and the Wasatch Mountains. Although we have fewer data points from this region than from areas to the west, there are enough to suggest that movement along this corridor is a possibility. In the autumn from August through October there is an increase in butterfly observations just to the south of this region in Utah and Arizona. These observations, plus the recoveries in Utah of butterflies tagged in the autumn in Idaho (Pyle, 1999) and reports of autumn movement of monarchs south along the Green River in Utah (M. Monroe & G. Nabhan, cited in Brower & Pyle, 2004), are consistent with a movement of monarchs from Utah and Idaho south to south-eastern Arizona, where small overwintering aggregations are known from the vicinity of Tucson (Pyle, 1999). There may also be some

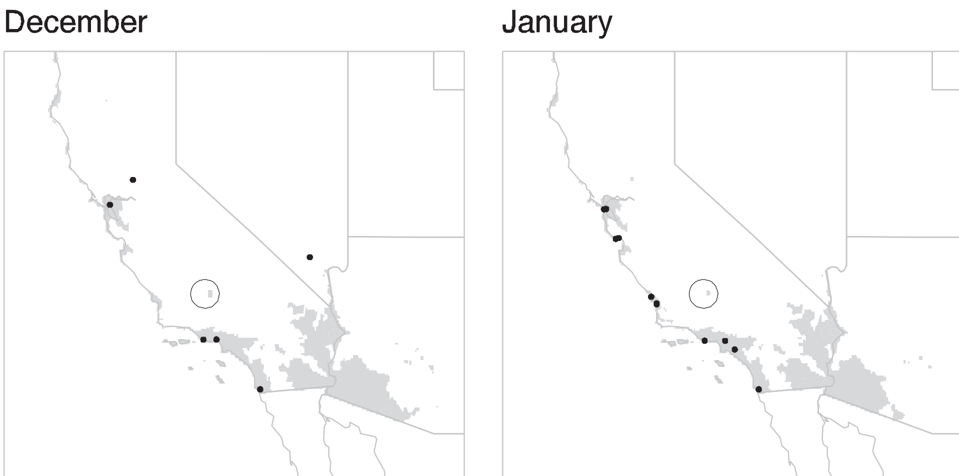

Figure 2. Monarch collection records and temperature in south-western North America. Grey shaded areas have a long-term average minimum temperature of at least 4 °C. The circled point is a monarch overwintering site reported by Frey & Schaffner (2004).

Table 1. Distance to the nearest river for collection sites and random points. The table shows the average distances (km) and one-tailed paired *t*-tests for whether distances were on average smaller for collection sites than for random points

	Collection sites		Random points		Difference			
Season	Mean	SEM	Mean	SEM	Mean	t	P	Pairs
Summer	3.8	0.2	5.1	0.2	–1.2	–6.01	0.001	737
Autumn	3.4	0.2	5.6	0.3	–2.2	–6.93	0.001	310
Winter	1.8	0.3	3.5	0.6	–1.7	–2.44	0.01	26
Spring	3.9	0.5	5.9	0.6	–2.0	–2.81	0.003	89

winter breeding in south-western Arizona (Funk, 1968), although whether these latter are residents throughout the year is not known.

A further aspect of the distribution of monarchs in western North America is revealed when maps are viewed over smaller scales. The butterflies are not randomly dispersed over the region, but rather tend to occur in distinct patterns of concentration. An example is shown in Figure 3, which displays the location of monarchs over the year on a map that also displays the river systems. From inspection of the map, it appears as if the occurrence of monarchs is correlated with the proximity of a river. To test for this relationship, distance to the nearest river was calculated for each unique collection site and a random point within 50 km of the site. Fifty-two percent of collection sites were within 2 km of a river, compared with 28% of random points (Fig. 4). In all seasons, collection sites were on average significantly ($P < 0.05$) closer to rivers than were random points (Table 1). Thus a major topographical feature influencing the distribution of monarchs in western North America is the presence of river valleys.

There is the possibility of some collection bias contributing to these results, because river valleys are generally more accessible than higher elevations. It is also worth noting that the distribution of the milkweeds upon which monarchs feed, especially *Asclepias speciosa* Torr., the commonest milkweed of the Great Basin and Rocky Mountain region (Woodson, 1954), occurs largely along riparian corridors. The tendency for monarchs to occur along rivers thus probably also reflects the distribution of the food-plant and in drier areas the presence of flowers suitable for nectaring by adults (Brower & Pyle, 2004).

DISCUSSION

Our data (Fig. 1) strongly suggest that the model of monarchs from west of the Rocky Mountains wintering exclusively along the California Coast is no longer valid. They do, however, indicate that butterflies overwintering along the northern section of the coast from approximately Santa Barbara northward are part of a

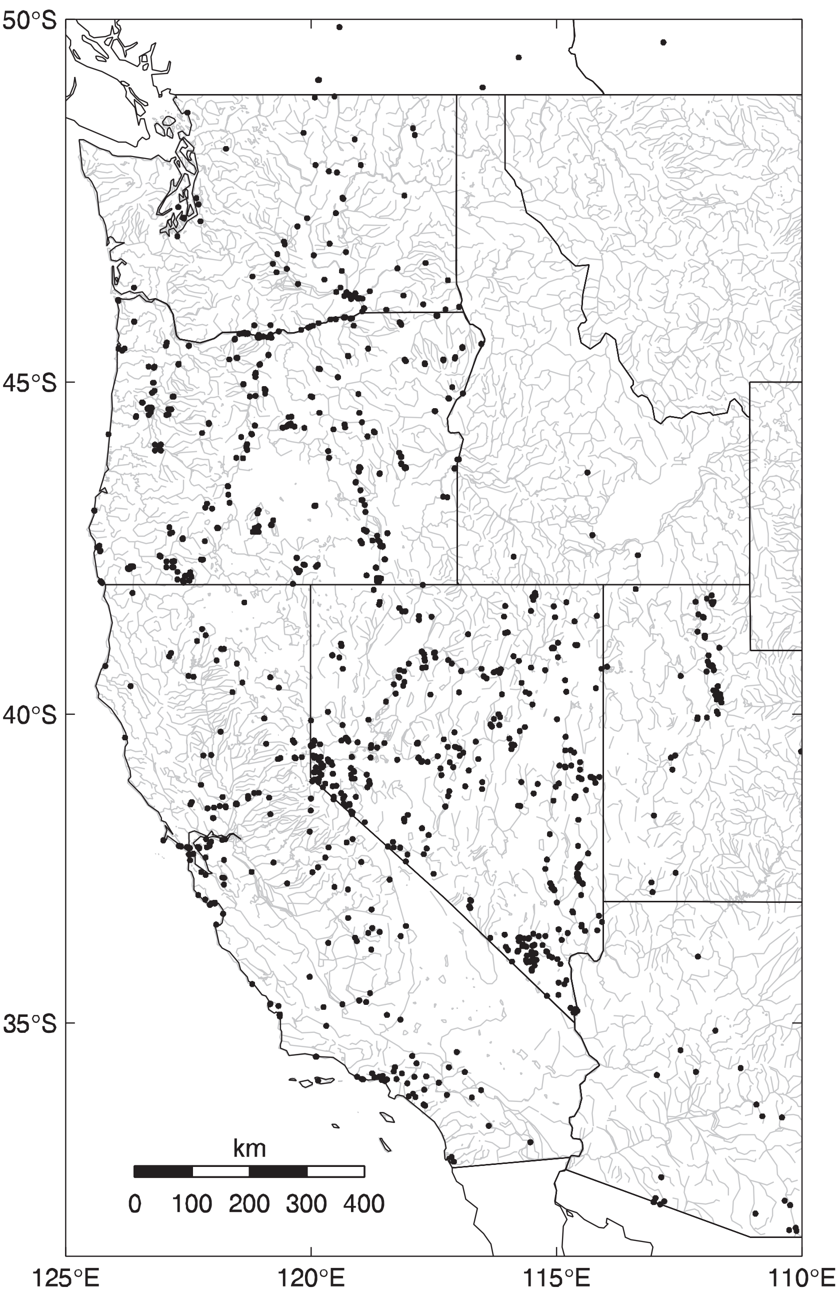

Figure 3. Monarch collection records and rivers.

population system that includes migration northward into northern California, Nevada, Oregon, Washington, western Idaho, and the southern edge of British Columbia. Interestingly, this is approximately the same area which Frey & Schaffner (2004) postulated would be the recruitment range for California overwintering aggregations based on the assumption that, like eastern monarchs, western butterflies would on average move on a flight trajectory of 195° during autumn migration (Rogg, Taylor & Gibo, 1999). Thus in the autumn many butterflies are likely to return to the same section of coast from which their parents migrated in the spring. The recapture in Santa Cruz, California of a wild-caught individual tagged in southern Washington, as well as recaptures at several places along the coast of individuals reared and tagged in western Idaho (Pyle, 1999), support this notion.

We stress that the eastern and southern boundaries of this system in all probability overlap with other subgroupings of the western monarch population (below). This is indicated by the fact that, for example, monarchs tagged in late summer in western Idaho

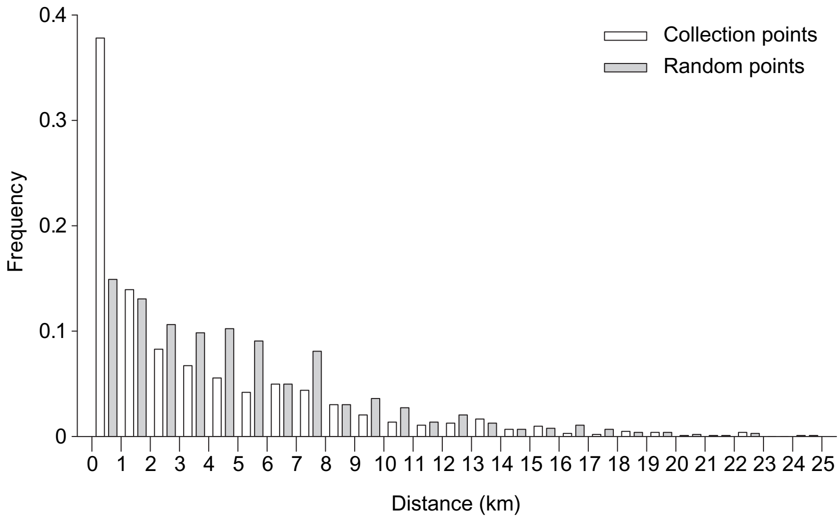

Figure 4. Frequency distribution of distance to the nearest river for collection sites and random points.

have been recovered to the south-east in Utah, while other autumn flying western monarchs have been reported moving to the south-east (Pyle, 1999). It is probable that many monarchs wintering in this northern part of the California coast either never migrate north or west in the spring or at most move only short distances, because breeding occurs throughout the spring and summer in coastal and subcoastal milkweed patches (Wenner & Harris, 1993; H. Dingle, unpubl. observ.). Alternatively, eggs may be laid on coastal milkweeds by butterflies that later move inland. We suspect that both sorts of behaviour occur, but more data are clearly needed. It is interesting to consider whether a significant number of monarchs of the overwintering generation reach Oregon and Washington in the spring or whether those entering these northern regions, where most don't usually arrive until May (Fig. 1), are mostly the offspring of butterflies that breed in the early spring farther south. A two-step spring invasion of northern regions has been documented for the migratory monarchs in eastern North America (Brower, 1995).

A second population system seems to involve migration north and south into and out of Nevada via the Colorado River valley. There may be some collection bias in southern Nevada because of gardens and plantings in and around the Las Vegas population centre, including plantings of the exotic milkweed, *Asclepias curassavica*. However, the use of southern Nevada as a corridor seems real because of the overall frequency of records from that area. In the spring, butterflies using this route enter central and eastern Nevada and probably Idaho. What happens to butterflies using this corridor in the autumn is not clear. There appear to be three possibilities: (1) a 'right turn' to overwintering sites from Santa Barbara to Baja California along the coast; (2) overwintering in the Colorado River valley and adjacent areas where winter temperatures do not fall below 4 °C (Fig. 2), and (3) continued passage to unknown wintering sites in Mexico. These possibilities are not mutually exclusive, and there are a few observations of free-flying monarchs in support of each (e.g. in Pyle, 1999). The climate ameliorating influences of the dams and agricultural areas along the Colorado River also raise the possibility that the monarch migration route is at least partly of anthropogenic origin.

A third possible population grouping may involve butterflies that move along the western scarp of the Wasatch Mountains in Utah between this range and the Great Salt Lake. The presumed migratory pathway includes southern Utah and eastern Arizona, and the small overwintering clusters near Tucson, Arizona (Pyle, 1999) may represent a portion of these butterflies. As with the presumptive Colorado River route, there are also observations of monarchs moving into Mexico in the autumn, but to what destination remains unknown.

Do our postulated three western monarch groupings represent simply arbitrary divisions of a continuous broad front of migrating butterflies or do they actually correspond to three population streams even if with indistinct borders? At least one study suggests that monarchs move in more or less distinct streams during migration. Calvert & Wagner (1999) found that eastern monarchs migrating southward through Texas tended to occur in two bands, one moving through central Texas and one along the coast. Carey (1996) has suggested, based on trapping data, that the Mediterranean fruit fly is now established in the Los

Angeles basin and will spread farther into California by streaming along mountain valleys and through passes.

A similar streaming using natural landforms, especially river valleys (Fig. 3), seems a reasonable model for monarch butterfly movements in the American West, given the topography and climatic diversity. Such a pattern should also be looked for in eastern North America where the migratory large milkweed bug (*Oncopeltus fasciatus* (Dallas)), whose annual migration cycle is very similar to that of the monarch butterfly, is more likely to occur in milkweed patches associated with riparian areas (Dingle, 1991). Direct observations of migrating monarchs indicate they do move along rivers in the American West, but they are not bound to do so if the river follows a route inappropriate to the preferred direction of migration (Pyle, 1999).

Ours is not the only alternative model to the 'classic' one of all western monarchs wintering on the California coast and migrating to and returning from inland areas in the spring and autumn, respectively. Wenner & Harris (1993), based on the observation of breeding throughout spring and summer in California coastal areas, proposed that western butterflies do not migrate. Rather, they suggest that the coastal populations simply experience a range extension in the late spring and summer and a contraction back to the coast in the autumn with no 'directed migration' involved. This model seems too simplistic for several reasons. First, tagging experiments reveal movement over long distances from coastal to inland sites in a relatively short time (Nagano *et al*., 1993). Second, observations of inland monarchs in the autumn, especially, strongly suggest directed movement in directions that are predominantly southward (or westward in the case of the California Central Valley). Third, our maps indicate that northern areas acquire butterflies in a manner consistent with rapid invasion from the south, too rapid an invasion to be accounted for by (random?) spread but easily accounted for on the assumption of relatively long distance migration. Note the presence of monarchs in Oregon in April and British Columbia in May.

We do, however, point out that there has been no behavioural test of migration in monarchs. Such a test would require careful observations of responses to 'vegetative' stimuli (nectaring or oviposition sites) and the degree of straightened out movement. Lack of response to stimuli that ordinarily stop movement and a tendency to straighten out are characteristics of migratory behaviour (Kennedy, 1985; Dingle, 1996). So too is reproductive diapause, which is present in the autumn in both eastern and western monarchs. Note that migrants may pause during migration to refuel and that distance *per se* is not a criterion for migration. There are many field observations of, in particular, autumn flying eastern monarchs that indicate true migration, although observations of western monarchs are more ambiguous.

A second model for the movements of western monarchs is that proposed by Brower & Pyle (2004). This resembles ours in several ways, although they stress movements into Mexico and do not suggest the three broad streams characteristic of our model. They also comment extensively on the general lack of observed genetic or other sorts of differentiation between eastern and western monarchs (Brower & Boyce, 1991; Altizer, Oberhauser & Brower, 2000; Shephard, Hughes & Zalucki, 2002). From this, as well as from suggestive evidence based on synoptic wind patterns, and from the observed movements into Mexico from Arizona, Brower & Pyle postulate frequent interchange and gene flow between monarchs breeding in the two regions of North America, with possible mixing of the populations in Mexican overwintering sites. They also suggest that the West Coast population depends on seasonal replenishment from the Mexican winter population. We suggest that the population overwintering in coastal California and breeding in the north-west is large enough to withstand major swings in abundance and thus to be self-sustaining, but we agree with Brower & Pyle that there is no reason to doubt fluctuating but more or less continuous interchange of butterflies and therefore genes between breeding populations of eastern and western North America.

Several sorts of data will be needed to ascertain the accuracy of these new models of monarch butterfly population dynamics in western North America. To determine whether our postulated three streams of migrating monarchs bear a resemblance to reality, both tagging and observational data will be required. Tagging has not been extensive in the West, and with a few notable exceptions, what has been done has been poorly designed (see Brower & Pyle, 2004 for a critique); it has also been focused on California. It would be very useful if tagging and release were to take place at the site of collection of butterflies raised from larvae across the northern tier of states and from southern Canada west of the 100th meridian. In particular it will be necessary to alert potential observers in Arizona and Utah to be on the lookout for tagged migrating individuals. A second useful approach might be a series of east–west transects across the southern regions of the West similar to the transects across Texas to map butterfly migratory pathways (Calvert & Wagner, 1999). Less labour intensive would be monitoring of potential river pathways like the Colorado along the California–Arizona border, the Green and possibly the Rio Grande through New Mexico and the San Pedro in southern Arizona. Finally, following fall migrants into Mexico as suggested by Brower & Pyle (2004), along the lines of Pyle's 1996 field monitoring (Pyle, 1999), would no doubt be a worthwhile undertaking. Perhaps most importantly, data should be taken and analysed with the explicit intent of testing from among the alternative models.

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