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REMARKABLE WAXING, WANING, AND WANDERING OF POPULATIONS OF *MIMULUS GUTTATUS*: AN UNEXPECTED EXAMPLE OF GLOBAL WARMING

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ABSTRACT.—The purpose of this study was to observe the dynamics of a meta-population of *Mimulus guttatus*. Changes in size and location of 16 original populations and the new populations established in their vicinities in Big Cottonwood Canyon, Salt Lake County, Utah, were observed for 25 yr. Twenty-three new populations appeared. Seven original populations and 13 new populations had become extinct by the end of the observation period in 1996. Many populations died out and were reestablished, often repeatedly, during the observation period. Altogether there were 54 population disappearances and 34 reappearances. Many populations changed size as much as 100-fold or more from year to year. There were spectacular examples of populations expanding to fill newly available, large habitats.

Frequent extinctions were due overwhelmingly to the canyon drying trend, which led to the drying up of most Mill D North drainage springs, creeks, and ponds. Precipitation and minimum temperatures increased moderately during the observation period. The growing season lengthened almost 50%, a typical consequence of global warming. The drying trend, lengthened growing season, and disappearance of *Mimulus* populations in Big Cottonwood Canyon appear to be a clear, local example of global warming.

Key words: Mimulus guttatus, *meta-population, global warming, growing season, colonization, recolonization, extinction, population fluctuations.*

Populations of *Mimulus guttatus* Fischer ex. D.C. in the upper reaches of Big Cottonwood Canyon form a *meta-population*, i.e., an interacting group of local populations (Van Der Meijden et al. 1992). This conclusion is based on my earlier study of gene exchange and selective pressures in these populations (Vickery 1978). The purpose of the present longitudinal study was to observe for a long enough period, 25 yr, the dynamics, that is, speed of turnover, of the local *M. guttatus* populations constituting the meta-population. How quickly and frequently do they increase or decrease in size, die out, colonize new habitats, or recolonize old ones? How do these changes relate to the environment—precipitation, insolation, temperature, and growing season?

STUDY SITES

For this research I studied a sample of 16 of the approximately 170 local populations of *M. guttatus* in the upper reaches (above the terminal moraine at 2150 m) of Big Cottonwood Canyon, Salt Lake County, Utah (Fig. 1). I observed the same set of populations studied in the selective pressure versus gene exchange study alluded to above (Vickery 1978). For that investigation I selected 4 side canyons of Big Cottonwood Canyon (Fig. 1, Table 1). Each side canyon or drainage is separated from the others by high ridges of up to 3000 m or more. Each contains a creek that runs from the side canyon headwaters at ca 2750 m down to its confluence with Big Cottonwood Creek at ±2250 m. I selected 4 study sites as equally spaced as possible along each of the creeks. Each study site contained 1 population of *M. guttatus*, the original study population (Table 1). Most study sites had 1 to 6 or more suitable habitats for local *M. guttatus* populations, although there was only the original study population at the beginning of the observation period.

Study sites for this moisture-loving species were in habitats by streams or springs, or along pond or lake shores. Some were in full sun but more were in partial shade of willows, small alders, or young aspen trees, while a few were in open areas or light gaps in the denser shade of the spruce forest. Habitats tended to be unstable and transitory. That is, the stream

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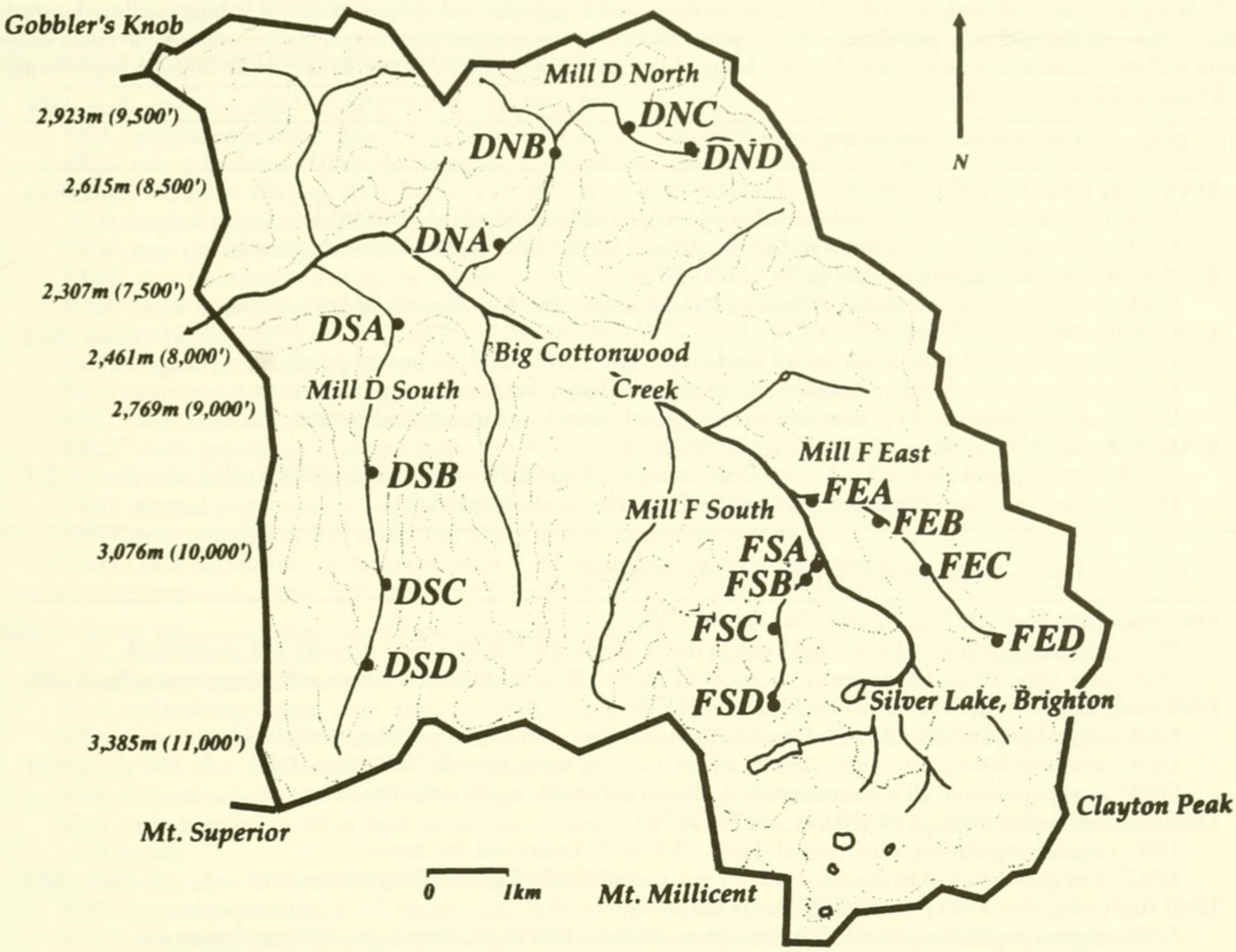

Fig. 1. Map of the upper reaches of Big Cottonwood Canyon in the Wasatch Mountains, Salt Lake County, Utah. Side canyons, drainages, and locations of study sites are indicated. (Based on maps of the area of the U.S. Geological Survey, Washington, DC 20242.)

would erode them, ponds or lakes would change level, and bushes and trees would grow, thus shading the populations; or, most importantly, streams would decrease or dry up, thereby killing the plants. Also, in some cases, deer or moose trampled the populations or pikas ate them.

M. guttatus local populations were separated one from another by spaces of several meters, often as much as 0.5 km, in which there were no *Mimulus* plants. These spaces typically were unsuitable for monkey flowers and were often filled with bushes, trees, and/or rocks.

MIMULUS GUTTATUS

Mimulus guttatus Fischer ex D.C. ranges from northern Mexico to the Aleutian Islands (type locality) and from the Pacific Coast to the Rocky Mountains; it has gone wild in Europe. A moisture-loving species that forms scattered, often isolated, local populations and only occasionally meta-populations, *M. guttatus* consists of at least 6 ecotypes (personal observation), including the Wasatch Mountains one to which the constellation of local populations of Big Cottonwood Canyon belongs. This ecotype is distinguished by its numerous rhizomes, but otherwise it is rather typical of the species. The species may be annual or rhizomatous perennial. Stems are erect, 2–60 cm high. Leaves are in opposite pairs, glabrous to pubescent, rounded-ovate, 1–10 cm long × 1–6 cm wide, with dentate margins. Lower leaves are petiolate, upper leaves sessile. Inflorescences are racemose, often few-flowered or solitary. On taller plants the flowers are mostly in pairs. Calyces are campanulate, 6–12 mm long, much inflated in maturity, the upper tooth longest. Corollas are 1–2 cm long, the throats spotted with red and the palate ridges hairy. Upper lips of the corollas are reflexed and much shorter than the

TABLE 1. Locations of study sites (by elevation, latitude, and longitude) and characteristics of habitats within the study sites of the original and new populations by location relative to the original population; area; insolation; average maximum and minimum temperatures for the 50-d heart of the season, 4 July–23 August 1973 (for the original populations); soil type; and source of moisture.

MILL D NORTH DRAINAGE—southwest facing
DNA study site, elev. 2350 m, 40°38′57″N, 111°38′9″W
DNA, original population, 0.5 m^2, partial shade, 18.0°/5.3°, sandy gravel, streamside
DNA′, new population, 8 m down and across stream, 1.0 m^2, full sun, sandy gravel, streamside
DNB study site, elev. 2520 m, 40°39′43″N, 111°37′40″W
DNB, original population, 30 m^2, full sun, 13.3°/2.6°, moss and gravelly soil, by large spring
DNC study site, elev. 2670 m, 40°39′40″N, 111°37′4″W
DNC, original population, 2 m^2, partial shade, 15.3°/4.3°, grassy soil, by beaver pond
DNC′, new population, 20 m downstream, ca 350 m^2, deep loam, moist pond bottom
DNC″, new population, 40 m downstream, ca 150 m^2, deep loam, moist pond bottom
DND study site, elev. 2760 m, 40°39′35″N, 111°36′38″W
DND, original population, 2.5 m^2, open shade of aspen, 14.3°/4.0°, sandy gravel, along a rill
DND′, new population, 30 m downstream, 6 m^2, sandy gravel, stream delta
MILL D SOUTH DRAINAGE (CARDIFF CANYON)—northeast facing
DSA study site, elev. 2277 m, 40°38′27″N, 111°39′1″W
DSA, original population, 1.5 m^2, light gap in dense shade, 19.2°/6.8°, sandy, gravelly soil, streamside
DSA′, new population, 100 m upstream, ca 24 m^2, light gap in dense shade, loamy soil, boggy spring by stream
DSB study site, elev. 2474 m, 40°37′34″N, 111°39′14″W
DSB, original population, 12 m^2, full sun, 14.3°/4.1°, moss, gravel, and pebbles, streamside
DSB′, new population, 3 m across stream, 14 m^2, full sun, moss, gravelly soil, streamside
DSB″, new population, 10 m downstream, 1 m^2, partial shade, sandy soil, streamside
DSC study site, elev. 2628 m, 40°37′1″N, 111°39′14″W
DSC, original population, 2 m^2, partial shade, 18.8°/4.2°, loamy soil, by stream
DSC′, new population, 8 m downstream, 0.1 m^2, partial shade, loamy soil, by stream
DSD study site, elev. 2763 m, 40°36′25″N, 111°39′19″W
DSD, original population, 18 m^2, full sun, shade at edges, 14.1°/4.5°, deep loam, in boggy spring
DSD′, new population, 20 m upstream, 3 m^2, partial shade, loamy soil, by small rill
DSD″, new population, 15 m downstream, 3 m^2, full sun, gravelly soil, by small rill

spreading lower ones. Capsules are oblong. Seeds are football shaped, ca 0.5 mm wide × 1.0 mm long and longitudinally striate. For fuller descriptions see Grant's monograph (Grant 1924) or the treatment in the Jepson manual (Thompson 1993).

Flowers, which are pollinated by bumble bees and occasionally by other insects, produce numerous seeds—50 to 250—per capsule. Reproduction is from seeds, but in this ecotype it is commonly from underground rhizomes as well.

M. guttatus plants of the canyon vary morphologically both within and among populations (see voucher specimens in the Garrett Herbarium [UT], University of Utah). Canyon plants range in height from 1 cm to 30 cm, in leaf length from 1 cm to 5 cm, and in number of flowers from none to a dozen or more. Differences among plants apparently are plastic responses to the varied environments of the canyon much as I showed for clone members of plants of one canyon population in the phytotron at Cal Tech (Vickery 1974). This plasticity was confirmed twice by growing sets of the 16 original study populations in uniform greenhouse environments. For the earlier set (Vickery 1978) plants were scored for over 100 traits and compared statistically. There were no significant differences. For the more recent set (Appendix A), plants were scored for a different, smaller set of traits and compared visually. There were no apparent differences.

METHODS

I counted or estimated the number of plants in each of the original study populations each year beginning in 1972 and concluding in 1996. Actual counts were made for small populations. Estimates, made for medium-sized and large populations, were based on counting 50 or 100 plants in an area and then multiplying by the number of such areas in the population

TABLE 1. Continued.

MILL F EAST DRAINAGE (GUARDSMAN PASS)—west facing
FEA study site, elev. 2524 m, 40°37′24″N, 111°35′25″W
FEA, original population, 24 m^2, deep shade, 13.5°/6.0°, moss and sand bars, in and beside stream
FEA′, new population, 100 m downstream, 1 m^2, full sun, gravelly soil, streamside
FEB study site, elev. 2615 m, 40°37′20″N, 111°35′3″W
FEB, original population, 2 m^2, open shade, 16.9°/3.1°, grassy soil, streamside
FEB′, new population, 12 m downstream, 1 m^2, open shade, sand bar, in stream
FEB″, new population, 3 m across stream, 5 m^2, open shade, loamy bank, edge of stream
FEB‴, new population, 5 m downstream, 1.5 m^2, open shade, sand bar, in stream
FEC study site, elev. 2670 m, 40°36′56″N, 111°37′33″W
FEC, original population, 6 m^2, partial shade, 14.4°/3.9°, loamy soil, by stream
FEC′, new population, 10 m upstream, 16 m^2, open shade, sand bar, in stream
FEC″, new population, 30 m upstream, 24 m^2, sunny, grassy loam, by stream
FEC‴, new population, 7 m upstream, 10 m^2, sunny, grassy loam, by stream
FED study site, elev. 2830 m, 40°36′34″N, 111°33′39″W
FED, original population, 0.5 m^2, partial shade, 16.6°/5.1°, gravelly loam, streamside
FED′, new population, 5 m upstream, 15 m^2, sunny, loamy soil, by stream
FED″, new population, 15 m downstream, 1 m^2, sunny, sandy gravel, streamside

MILL F SOUTH DRAINAGE (SOLITUDE CANYON)—northeast facing
FSA study site, elev. 2528 m, 40°37′4″N, 111°35′30″W
FSA, original population, 2 m^2, sunny, 13.5°/6.0°, grassy soil, streamside
FSA′, new population, 5 m upstream, 8 m^2, full sun, loamy soil and gravel, streamside and in stream
FSB study site, elev. 2560 m, 40°37′0″ N, 111°35′40″W
FSB, original population, 15 m^2, open shade, 17.6°/5.3°, sandy soil, streamside
FSB′, new population, 20 m south along new channel, 12 m^2, full sun, pockets of sandy soil amongst cobbles, in stream
FSC study site, elev. 2708 m, 40°36′47″N, 111°35′51″W
FSC, original population, 8 m^2, sunny, 13.2°/3.6°, loamy soil, by small spring
FSC′, new population, 20 m downstream, ca 600 m^2, full sun, in new grassy, loamy meadow, near stream
FSD study site, elev. 2770 m, 40°36′29″N, 111°40′56″W
FSD, original population, 10 m^2, sunny, 13.6°/3.7°, deep loam, edge of Lake Solitude
FSD′, new population, 25 m north along lake shore, 12 m^2, sunny, deep loam, lake shore
FSD″, new population, 50 m west along lakeshore, ca 12,000 m^2, full sun, deep loam, exposed lake bottom

to obtain the estimated population size. Numbers were rounded off. A rosette was considered to be a plant. In some cases I found that 2 or 3 rosettes were connected by underground stems. Stems would decay as the season progressed so that rosettes became independent plants, although some would share the same genotype, as observed by Waser et al. (1982) for other populations of *Mimulus guttatus*. Population counts were made in late summer or early fall as populations were at their maximum toward the end of the growing season. Random duplicate counts were made to check the accuracy of counts and estimates. They varied by 10% to 20%, which is modest considering the very large differences noted among different local populations the same year or among different years of the same population. The vicinity of each population was checked to see if new populations had become established. If they had, their locations were noted and they too were scored as above.

Air temperature of each study site in 1973 (Table 1) was measured using Temp Scribe recorders (Vickery 1978). Temperature, precipitation, snowpack, and growing season data for the entire 25-yr observation period were obtained from U.S. Climatological Data for Utah (Environmental Data Services 1972–1996) for Silver Lake (40°33′48″N, 111°35′4″W), at the head of Big Cottonwood Canyon (Fig. 1).

RESULTS

Populations ranged widely in size from a single plant to 37,000 plants (Appendix B). Some populations did not vary in size from year to year while others waxed or waned with time. Still others varied dramatically over the period of a few years (Figs. 2–5).

Of the 16 original study populations, 7 had disappeared by the end of the 25-yr observation period (Appendix B). Not only were they gone, but each one had disappeared and reappeared

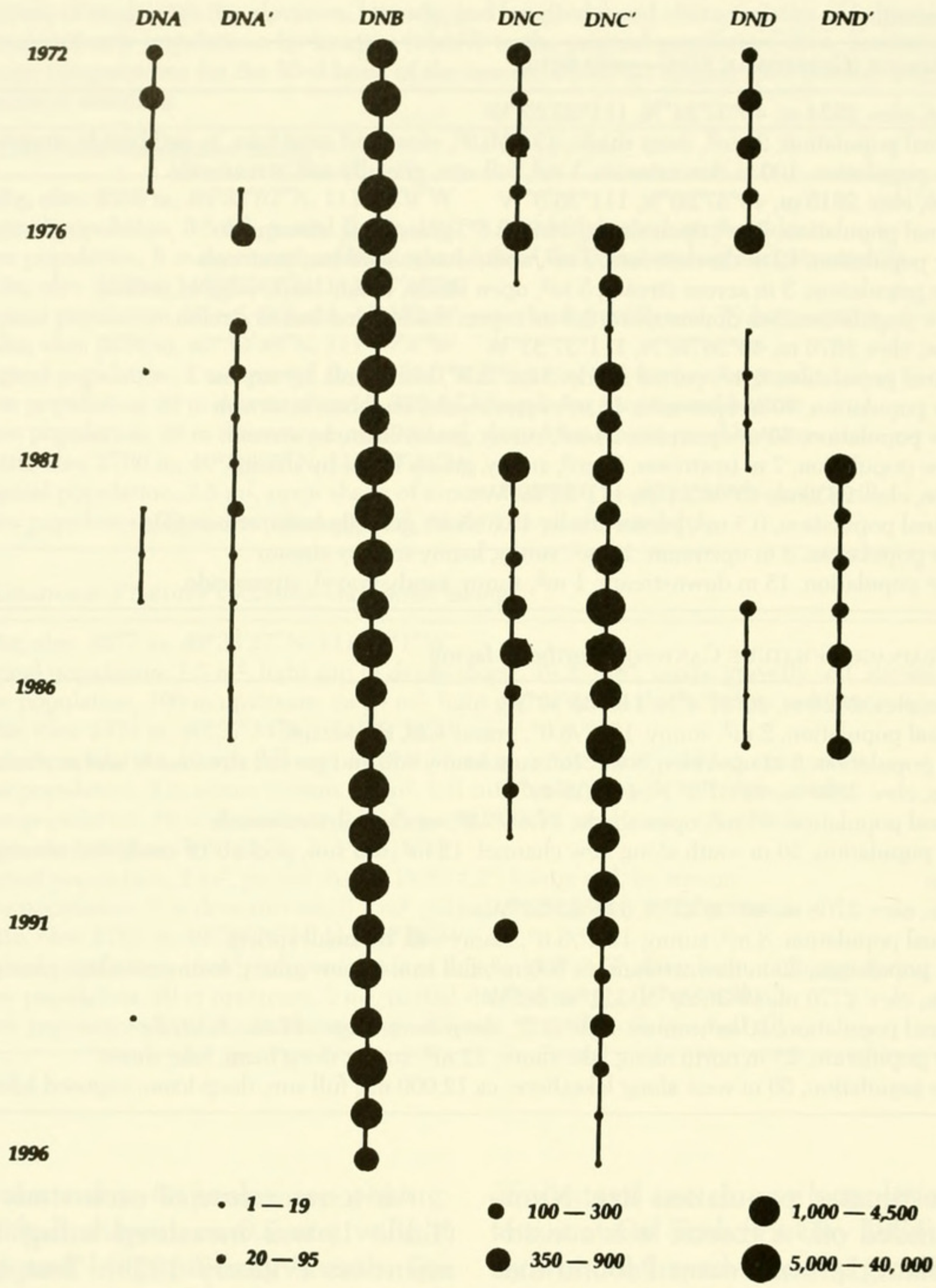

Fig. 2. Mill D North drainage. Representation of changing sizes of the original study populations and new populations over 25 yr of observation.

at least once prior to its final disappearance. Of the 9 original populations still present at the end of the observation period, 4 had disappeared and reappeared. Only 5 of the original populations had been present throughout the study (Figs. 2–5).

Twenty-three new populations—almost 1 per year—appeared in study sites in the vicinity of the original populations (Figs. 2–5, Appendix B). They disappeared and reappeared like the original populations. At the end of the observation period only 10 new populations were still present and only 4 had been consistently present since they appeared.

The number of populations climbed from the original 16 to an average of 23 (Table 2). Once the higher value was attained, there was a dynamic equilibrium of populations appearing, disappearing, and reappearing. Numbers climbed as high as 30 and declined to as low as 15 (Table 2, Fig. 6). The establishment of populations depended on availability of suitable (moist, without too much shade or plant competition) habitats within each of the 16 study sites.

The disappearance of populations reflected loss of suitable habitats, the most common cause being loss of moisture. Drying could be

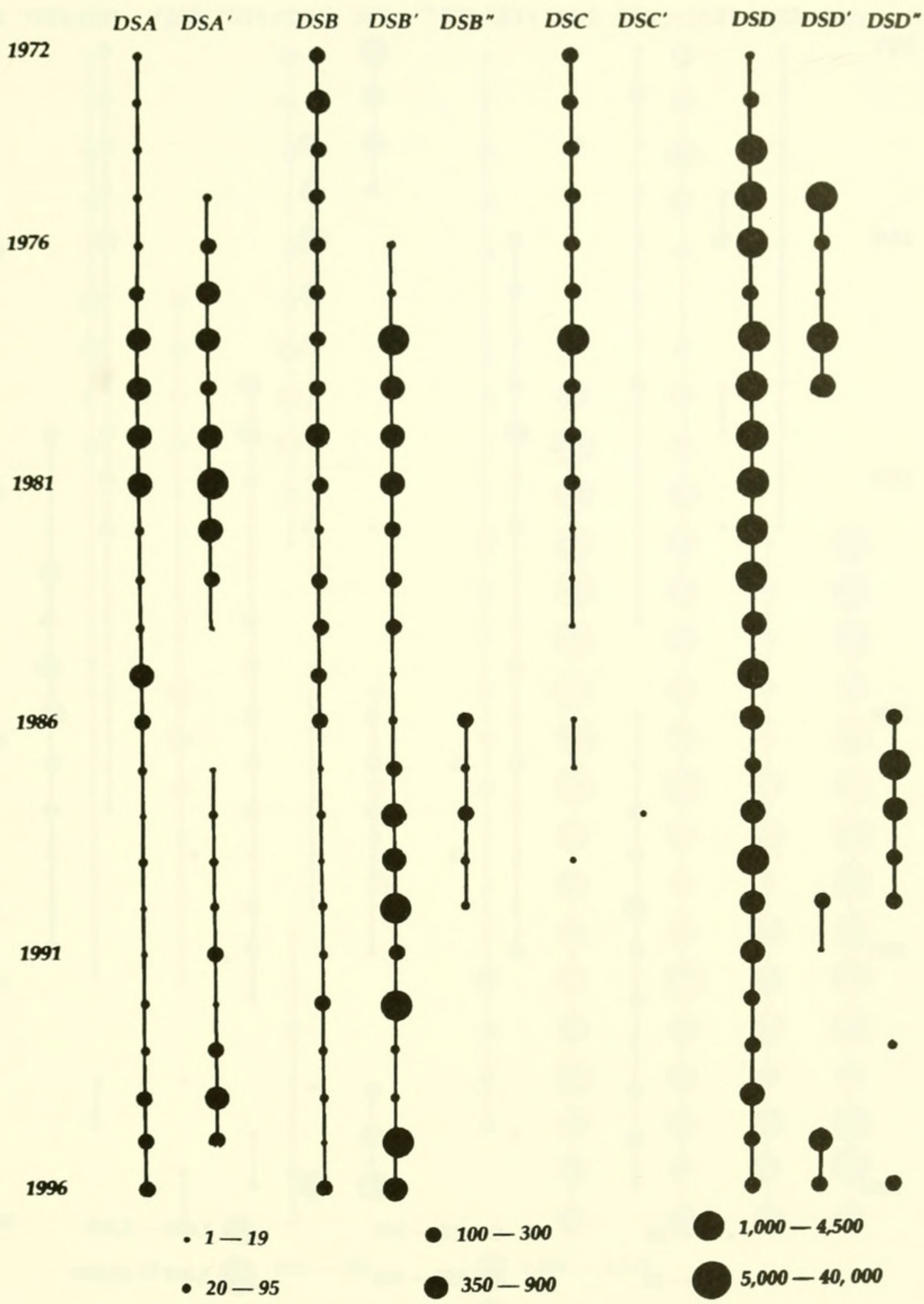

Fig. 3. Mill D South drainage (Cardiff Canyon). Representation of changing sizes of the original study populations and new populations over 25 yr of observation.

transitory (i.e., short term—1–3 yr) or prolonged (i.e., long term—more than 3 yr). Altogether there were 54 cases of populations disappearing (Table 2). Twenty-six were due to short-term drying and 12 to long-term drying. In addition to drying out, 7 populations disappeared because erosion removed their habitats, another 4 were lost apparently due to competition, and 5 more to shading from a dense overstory (Table 2).

DISCUSSION

The most striking results of my observations were fourfold: (1) the remarkably large changes in population size from one local population to the next and from one year to the next for the same population; (2) the high frequency with which populations appeared, both new ones and old ones, after an absence; (3) the high rate at which both new and old

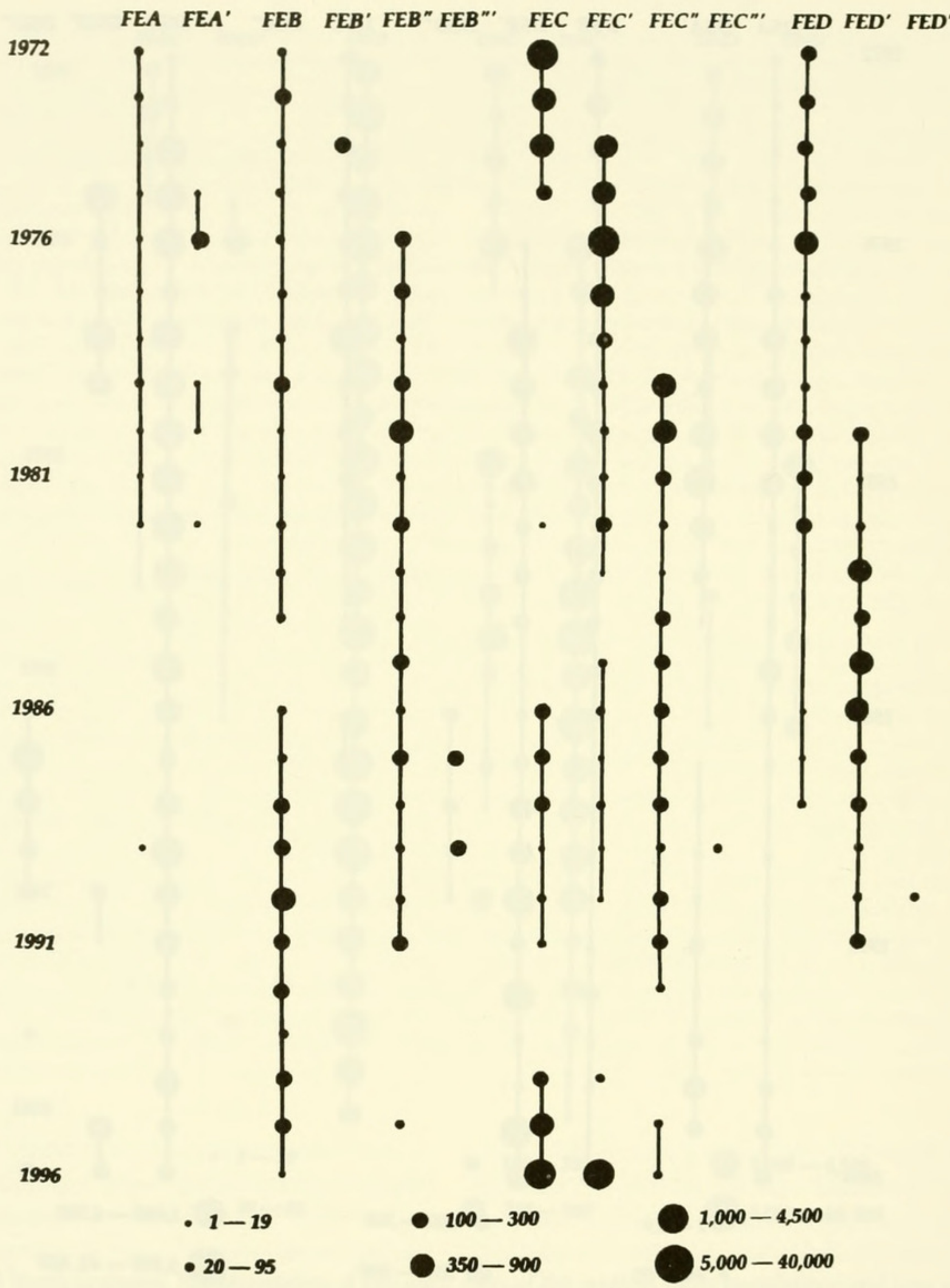

Fig. 4. Mill F East drainage. Representation of changing sizes of the original study populations and new populations over 25 yr of observation.

populations disappeared; and (4) probably the most important, the implications of population disappearance for global warming.

Population Sizes

The size of a population reflects available habitat area, which in turn reflects soil type, plant competition, and climatic parameters of insolation, precipitation, and temperature. Soil type did not appear to be limiting inasmuch as *M. guttatus* grew on all substrate types, from sand bars to loamy bogs. Competition could be limiting (e.g., dense meadow grasses), but usually it was not a determining factor. Insolation, the amount of sunlight, rarely was limiting except in the case of deep shade. Precipitation, rain and snow, at the actual habitat was irrelevant because this moisture-loving species required habitats to begin with that were steadily moist, e.g., stream banks. However, precipitation for the canyon as a whole was relevant for recharging the aquifers that supplied the springs and streams. Very wet years appeared to enhance competition at the expense

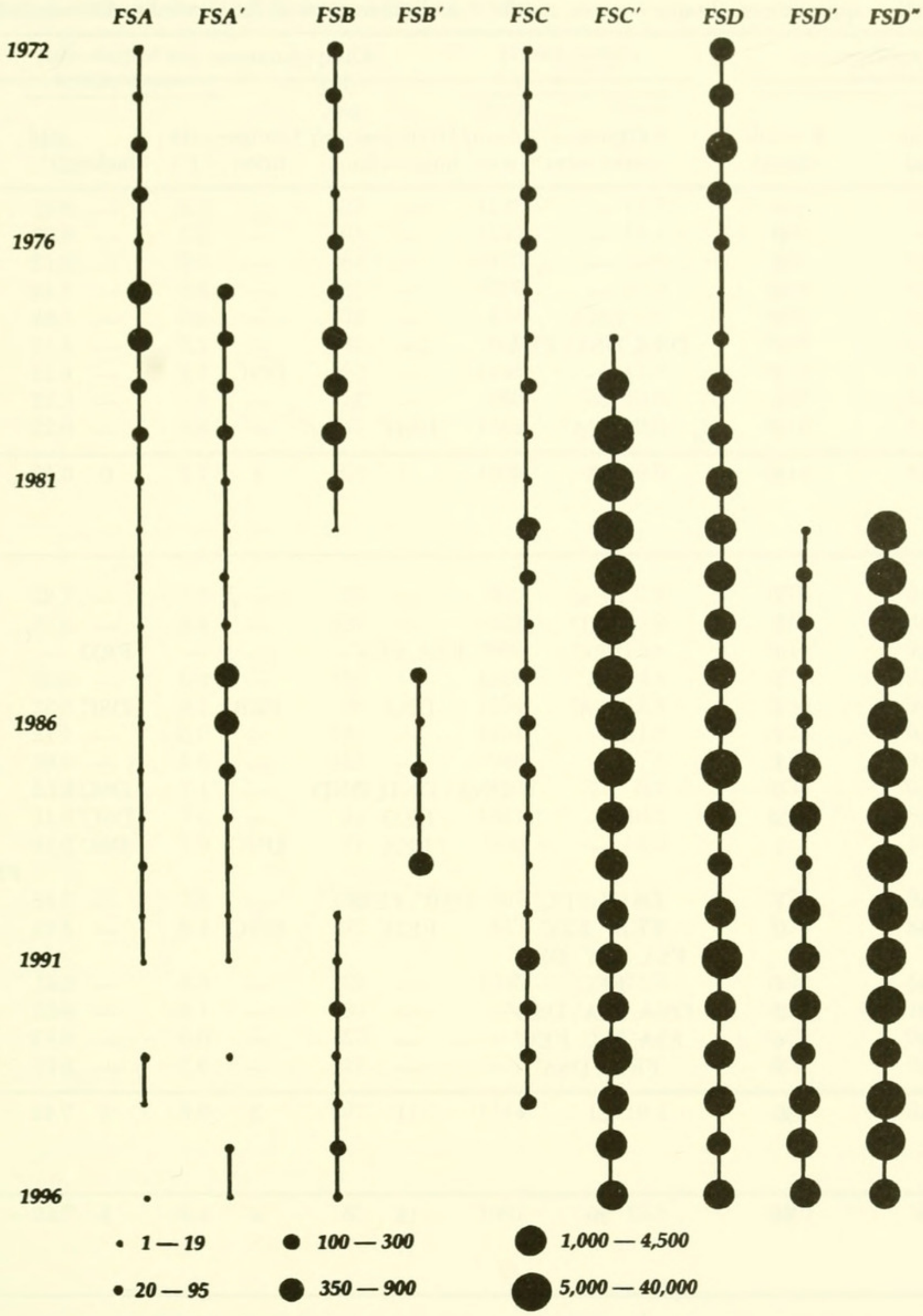

Fig. 5. Mill F south drainage (Solitude Canyon). Representation of changing sizes of the original study populations and new populations over 25 yr of observation.

of *M. guttatus* population size. Temperature of the actual habitat was relatively unimportant, as *Mimulus guttatus* has a wide norm of reaction for temperature (Vickery 1974). However, for the area as a whole, temperature was important, particularly because it shortened or lengthened the growing season (Myneni et al. 1997). Warmer temperatures did appear to lead to larger *Mimulus* populations, as seen, for example, in comparing population sizes in 1994 (the hottest year of the study) with those in 1993 (the coldest year of the study; see Appendix B).

Population sizes could be roughly grouped into 3 categories. Small populations (1 to 20) were usually part of a sequence in the process of population decline toward extinction. In many cases these populations would grow smaller and smaller, disappear, reappear, and finally disappear for the remaining observation period.

TABLE 2. Population appearances, disappearances, numbers and parameters of the environment from U.S. Weather

Year	Appearances		Disappearances				
	# new populations	# recolonized	Drying—short term	Drying—long term	Competition	Shading	Erosion
1972	—	—	—	—	—	—	—
1973	0	0	—	—	—	—	—
1974	2	0	—	—	—	—	—
1975	4	0	—	—	—	—	FEB′
1976	3	0	DNA	—	—	—	FEC
1977	1	0	DNA, DND, FEA	—	—	—	
1978	1	2	—	—	DNC	—	—
1979	1	2	—	—	—	—	—
1980	1	0	DNA	DSD′	—	—	—
Totals (1972–1980)	13	4	5	1	1	0	2
1981	1	1	FEA′	—	—	—	—
1982	2	3	DND	—	—	—	—
1983	0	0	FEC	FEA, FEA′	—	FED	FSB
1984	0	1	FEC′	—	—	—	—
1985	1	1	DSA′	DNA	FEB	DSC	—
1986	2	4	—	—	—	—	—
1987	1	1	—	—	—	—	—
1988	1	0	—	DNA′, DND, DND′	—	DSC	FEB‴
1989	1	3	—	FED	—	DSC′	—
1990	1	2	—	FEA	DNC	DSC	FEB‴, FEC‴, FSB′
1991	0	1	DSD″, FEC′	DSB″, FED″	—	—	—
1992	0	0	FEB″, FEC, FSA, FSA′, DSD′	FED′	DNC	—	—
1993	0	4	FEC′	—	—	—	—
1994	0	2	DNA, FSA′, DSD″	—	—	—	—
1995	0	4	FSA, FSC, FEC′	—	—	—	—
1996	0	3	FEB″, DSA′	—	—	—	—
Totals (1981–1996)	10	30	21	11	3	5	5
Totals (1972–1996)	23	34	26	12	4	5	7

Medium-sized populations (20 to 900) usually reflected stable habitats. Sizes of these populations were limited by the carrying capacity of their habitats and often fluctuated around a value well below the observed maximum number of plants. Large populations (1000 or more) grew in large, favorable habitats.

The close relationship between population size and habitat area was vividly demonstrated in several cases. For example, Solitude Ski Resort bulldozed a large (30 m × 50-m) thicket of willows at the FSC study site. This not only improved the ski run but opened a large, sunny, moist meadow with little plant competition. *Mimulus* immediately invaded via seeds from FSC and upstream populations. Where there had been no *Mimulus* in 1978, in 5 yr time there were 37,000 plants in this new, large, excellent habitat (Fig. 5, Appendix B). In time the original FSC population declined as its spring source wandered off. Another example of a population explosion occurred at the DNC study site. The adjacent beaver pond dried up in 1977, exposing a large (30 m × 40-m)

Service records for Silver Lake, Big Cottonwood Canyon, Utah.

Total # populations	July–August avg. temperatures Max. (°C)	Min. (°C)	July–Aug. precip. (mm)	Winter season (< −2.2°C) Total precip. (mm)	Snowpack (m)	Growing season Start	End	Number of days
16	22.6	5.3	27	1123	11.5	—	9/12	—
16	20.8	5.5	104	1131	13.4	6/5	—	—
18	21.8	5.3	64	1073	13.6	6/9	7/13	23
21	21.1	5.3	31	1258	12.2	6/26	8/28	62
22	22.1	6.2	32	434	7.0	6/26	8/28	62
20	21.1	6.2	136	669	5.1	5/30	9/18	110
22	21.4	5.2	63	1246	11.7	6/16	8/17	61
25	21.3	5.8	72	950	10.0	6/9	9/14	96
24	22.0	6.4	47	1162	12.6	6/16	8/20	64
$\bar{x}$ = 20	21.6	5.7	64	1005	10.8	6/14	8/24	68
25	22.7	7.6	55	905	7.0	6/15	9/26	102
29	21.2	6.6	127	1422	13.9	6/9	9/12	94
24	—	—	—	1500	13.8	6/14	9/20	97
24	20.9	6.4	132	1529	14.1	6/11	9/22	102
22	22.5	6.1	66	1294	12.5	5/30	9/13	105
28	21.1	6.9	140	1401	11.8	5/23	9/16	115
30	19.9	5.6	155	968	7.5	5/26	9/17	113
26	23.2	7.4	18	794	6.7	5/31	9/11	102
28	21.8	7.6	94	1021	10.2	6/22	8/25	63
25	21.6	7.0	71	880	8.3	—	10/7	—
22	21.5	7.4	132	967	9.3	5/28	9/15	109
15	21.1	6.4	137	847	7.0	5/10	8/26	107
18	19.3	4.3	131	1345	12.7	6/24	8/30	66
17	23.8	8.1	99	—	—	6/21	10/7	138
18	21.6	6.6	57	—	—	6/22	9/22	91
19	23.2	7.6	47	—	—	5/31	9/17	108
$\bar{x}$ = 23	21.7	6.8	97	1144	10.4	6/5	9/14	101
$\bar{x}$ = 22	21.7	6.4	85	1087	10.5	6/10	9/8	90

expanse of moist pond bottom into which *Mimulus* seeds invaded from the DNC population. The new DNC′ population steadily increased for a decade from 0 to well over 8000 plants (Fig. 2, Appendix B).

Populations Appearing

Populations appeared and reappeared in suitable, moist habitats along stream banks, by ponds, along lake shores, and by or in tributary springs. Such habitats were colonized in all 16 study sites near the original study populations except in DNB with its large ($\bar{x}$ < 6500) original study population that effectively filled all suitable habitats in the vicinity of its large spring.

Populations are easily established or reestablished from seeds floating downstream from upstream plants that often overhang the stream and shed their seeds into the water (Lindsay and Vickery 1964, Waser et al. 1982). Also, populations may be established by windblown seeds (Vickery et al. 1986). Windblown seeds rarely travel more than 5 m, whereas

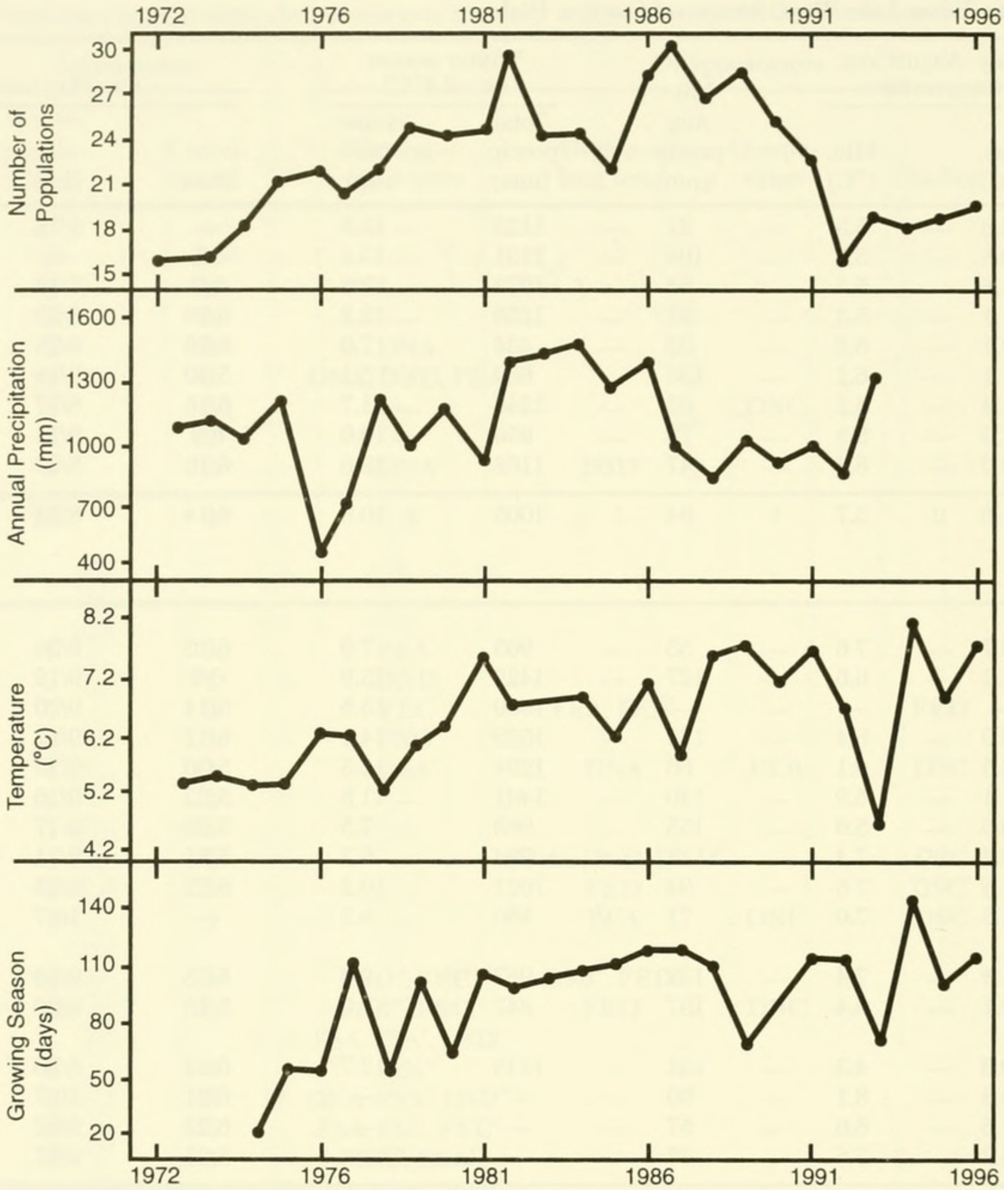

Fig. 6. Plot of population number, annual precipitation, minimum average temperatures for July–August, and length of growing season against years. The growing season is the period between the last spring minimum temperature of –2.2°C (28°F) and the first fall minimum of –2.2°C (28°F).

water-borne seeds can travel for hundreds of meters.

The actual source of the "rain" of floating seeds for population establishment or reestablishment could be identified in a few cases. For example, for the new DSD′ population the seed source must have been the original study population, DSD, because there were no other upstream populations. Windblown seeds can be inferred as the source for some populations, e.g., for the new FED′ population where seeds must have come from the only nearby, but downstream, population, FED.

Mimulus guttatus populations that reappear in 1, 2, or even 3 yr at the same site probably do so from dormant rhizomes or more likely from seeds in the seed bank at that site (Thompson 1987, Leek et al. 1989). Occasionally, I have observed dormant rhizomes under rocks. *Mimulus guttatus* seed bank seeds can readily survive for 2 or 3 yr, but not in large quantities (Vickery unpublished study).

Populations Disappearing

Disappearances of populations, both original study populations and newly established ones, were due to habitats becoming too shady or too crowded with competitors, or to their being eroded away by the stream or trampled by animals. However, the disappearance of populations was due overwhelmingly to habitat drying (Table 2).

The disappearance of several populations was caused by shading of habitats. For example, FEA was shaded out by an increasingly dense stand of spruce trees. The DSC population was first partially eaten, then trampled, and finally shaded out by the growth of willow thickets. The pattern of decline due to shading was a gradual decrease in population size accompanied by a decrease in plant size and amount of flowering, finally resulting in no monkey flower plants. Increasing competition led to much the same pattern of decline. For example, DNC declined to extinction as meadow grasses of the site increased and formed a dense turf. The stream swept away some populations, particularly ones established on sand bars, such as FEB′ and FEB‴, much as Porath et al. (1987) observed for the fugitive species *Verbascum sinaiticum* on the gravel bars of wadis in the Negev Desert.

Canyon Drying Trend

Drying of population habitats was part of a pronounced drying trend in Big Cottonwood Canyon that began in the late 1970s and early 1980s—in 1981 on average. The drying trend strongly affected Mill D North and Mill F East drainages, both of which are southwest facing, meaning they have high insolation. Also, their aquifers are shallow (D. Scheck personal communication). The whole of the initially flowing Mill D North creek dried up except for the moist beaver pond bottom at DNC and the large spring and stream immediately below it at DNB (see Fig. 1). The 4 original populations had increased to 7 in the early 1980s, but as the drying trend set in, populations declined to just 2 by the early 1990s, and those 2 were rapidly waning by the end of the observation period (Appendix B). In the Mill F East drainage, the top spring and ca 100 m of stream below it dried up as well as the bottom ca 200 m of stream. The 4 initial populations had increased to 13 in the course of the observation period. By the end of the period 5 populations had dried out and disappeared—all 3 of the top and both bottom populations. Four intermediate level populations had disappeared due to erosion. The original FEB populations appeared to be on the way to extinction. However, 3 of the FEC site populations were flourishing. Altogether over 1/3 of the population had disappeared due to the drying trend.

Global Warming

What caused the drying trend? Counterintuitively, decreased precipitation was not the cause (Fig. 6). Beginning in 1981, precipitation actually increased from an average of 1000 mm to an average of almost 1150 mm (Table 2). Insolation, presumably, remained constant. Increased temperature probably played a role. However, the July–August average maximum temperature was not higher, but the average minimum temperature was 1°C higher. These temperatures follow the same pattern noted by Karl in his global warming study of the arctic slope of Alaska, also beginning in 1981 (Waring and Running 1998). In Big Cottonwood Canyon, the growing season (Fig. 6) lengthened by almost 50%, from an average of 68 d (1971–1980) to an average of 101 d (1981–1996; see Table 2). Lengthening of the growing season is the hallmark of global warming, according to a satellite study of the northern latitudes (Myneni et al. 1997). The drying trend in Big Cottonwood Canyon appears to be a specific, local example of global warming.

How does a lengthened growing season translate into the observed drying trend? The immediate result of a longer season is increased evapotranspiration from the aspen forest and its understory of shrubs, herbs, and grasses (J. Ehleringer personal communication). The consequence of increased evapotranspiration is the drying out of surface soil, which may lead to a failure to recharge underlying aquifers, which are shallow anyway (D. Sheck personal communication). Depletion of the aquifers results in springs drying up which, in turn, leads to streams and ponds drying up. Since there is considerable normal variability in precipitation, temperature, and length of growing season and hence of spring and stream flows, *Mimulus* populations often dry out and die only to be briefly reestablished as the drying trend proceeds. The drying out and disappearance of so many local populations of the extensive meta-population of *M. guttatus* in Big Cottonwood Canyon was due to the pronounced canyon drying trend, the root cause of which appears to be global warming.

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APPENDIX A. Characteristics of the 16 original study populations when grown under standard conditions in the Biology Department greenhouse, University of Utah[a].

Population[b]	Plant height (cm)	Days to flowering	No. of flowers	Dry wt. stems (g)	Dry wt. runners (g)	Largest leaf at 1st flower (cm)		Healthy typical flower (cm)	
						Length	Width	Length	Width
DSA	24	69	9	2.4	5.9	6.1	4.3	4.1	2.5
DSB	30	86	15	1.1	3.2	7.7	3.1	3.1	2.5
DSC	26	69	24	3.1	1.4	6.8	4.8	2.9	2.6
DSD	—[c]	—	—	—	—	—	—	—	—
DNA	38	67	21	1.5	4.6	7.8	4.9	2.8	2.5
DNB	49	52	38	2.6	2.4	5.2	3.9	2.3	1.9
DNC	34	44	21	0.7	1.4	4.7	3.4	2.2	2.4
DND	33	56	20	1.2	1.5	5.6	4.4	2.4	1.9
FSA	—	65	—	—	—	5.6	3.7	2.4	2.2
FSB	30	62	20	2.3	4.6	5.6	4.4	2.7	2.3
FSC	—	—	—	—	—	—	—	—	—
FSD	—	50	—	—	—	6.6	6.3	2.6	2.3
FEA	35	59	35	2.9	3.5	9.0	5.3	2.9	2.5
FEB	40	65	63	2.4	1.8	7.2	4.1	2.6	2.1
FEC	30	74	20	1.8	6.4	5.9	3.7	2.8	2.5
FED	—	62	—	—	—	9.3	4.5	2.6	2.4
$\bar{x}$	34	63	26	2.0	33	6.6	4.3	2.7	2.3

[a]Based on the means of 5 plants
[b]See Table 1 for population site data.
[c]Virus killed plants

APPENDIX B. Sites and sizes of original and new populations. Site abbreviations are described in Table 1.

Year	DNA	DNA′	DNB	DNC	DNC′	DND	DND′
MILL D NORTH DRAINAGE							
1972	100	—	2,000	500	—	200	—
1973	700	—	5,000	200	—	550	—
1974	30	—	2,500	350	—	400	—
1975	2	1	6,000	250	—	300	—
1976	0	450	20,000	1,250	2,000	1,500	—
1977	0	0	1,000	12	200	0	—
1978	0	100	10,000	0	50	1	—
1979	1	150	7,000	0	1,500	35	—
1980	0	50	3,000	0	600	60	—
1981	0	35	8,500	1,100	1,700	6	1,000
1982	4	146	27,800	50	350	0	260
1983	3	36	19,000	200	1,500	0	100
1984	7	7	3,500	350	8,500	100	150
1985	0	8	6,000	1,200	8,000	25	500
1986	0	10	2,900	200	3,000	1	5
1987	0	6	1,000	2	6,000	40	800
1988	0	0	5,000	250	4,100	0	0
1989	0	0	12,000	10	3,000	0	0
1990	0	0	5,000	0	2,000	0	0
1991	0	0	3,000	500	4,000	0	0
1992	0	0	2,400	0	300	0	0
1993	8	0	2,500	0	600	0	0
1994	0	0	9,000	0	250	0	0
1995	0	0	1,500	0	50	0	0
1996	0	0	120	0	15	0	0

Year	DSA	DSA′	DSB	DSB′	DSB″	DSC	DSC′	DSD	DSD′	DSD″
MILL D SOUTH DRAINAGE										
1972	20	—	100	—	—	100	—	30	—	—
1973	60	—	500	—	—	300	—	200	—	—
1974	55	—	176	—	—	200	—	1,100	—	—
1975	45	50	200	—	—	150	—	2,400	1,050	—
1976	50	100	200	50	—	150	—	3,000	100	—
1977	100	400	150	30	—	280	—	250	50	—
1978	850	350	300	1,000	—	2,700	—	2,200	4,400	—
1979	600	300	250	800	—	200	—	3,000	400	—
1980	700	620	600	700	—	100	—	3,000	0	—
1981	600	1,000	100	600	—	100	—	2,000	0	—
1982	81	700	95	265	—	16	—	1,015	0	—
1983	23	250	250	230	—	4	—	1,250	0	—
1984	55	12	110	200	—	5	—	475	0	—
1985	400	0	300	5	—	0	—	1,200	0	—
1986	200	0	100	25	150	6	—	900	0	300
1987	60	12	6	120	50	4	—	235	0	1,000
1988	12	40	30	400	300	0	15	750	0	600
1989	60	30	6	850	50	1	0	1,000	0	100
1990	3	80	40	1,200	40	0	0	650	200	150
1991	3	250	50	100	0	0	0	400	15	0
1992	35	5	100	1,600	0	0	0	300	0	0
1993	24	150	30	50	0	0	0	200	0	50
1994	130	350	24	75	0	0	0	575	0	0
1995	120	200	12	1,000	0	0	0	200	750	0
1996	250	0	100	500	0	0	0	100	150	100

APPENDIX B. Continued.

Year	FEA	FEA′	FEB	FEB′	FEB″	FEB‴	FEC	FEC′	FEC″	FEC‴	FED	FED′	FED″
MILL F EAST DRAINAGE													
1972	70	—	25	—	—	—	1,500	—	—	—	120	—	—
1973	24	—	150	—	—	—	500	—	—	—	200	—	—
1974	6	—	30	100	—	—	500	500	—	—	300	—	—
1975	11	5	50	0	—	—	200	600	—	—	100	—	—
1976	12	100	50	0	100	—	0	1,500	—	—	600	—	—
1977	6	0	75	0	300	—	0	500	—	—	75	—	—
1978	15	0	30	0	70	—	0	150	—	—	70	—	—
1979	25	5	150	0	220	—	0	60	450	—	50	—	—
1980	10	6	8	0	450	—	0	20	500	—	200	200	—
1981	12	0	18	0	40	—	0	20	135	—	150	10	—
1982	3	5	36	0	220	—	3	120	70	—	110	30	—
1983	0	0	50	0	50	—	0	4	6	—	0	500	—
1984	0	0	20	0	95	—	0	0	100	—	0	160	—
1985	0	0	0	0	105	—	0	35	100	—	0	450	—
1986	0	0	20	0	30	—	100	40	100	—	5	800	—
1987	0	0	30	0	150	250	200	3	200	—	10	300	—
1988	0	0	120	0	25	0	140	60	200	—	40	250	—
1989	4	0	175	0	30	120	10	10	55	25	0	24	—
1990	0	0	475	0	20	0	30	1	100	0	0	50	50
1991	0	0	150	0	150	0	50	0	150	0	0	200	0
1992	0	0	250	0	0	0	0	0	80	0	0	0	0
1993	0	0	50	0	0	0	0	0	0	0	0	0	0
1994	0	0	150	0	0	0	150	20	0	0	0	0	0
1995	0	0	200	0	50	0	600	0	40	0	0	0	0
1996	0	0	15	0	0	0	1,000	1,000	50	0	0	0	0

Year	FSA	FSA′	FSB	FSB′	FSC	FSC′	FSD	FSD′	FSD″
MILL F SOUTH DRAINAGE									
1972	50	—	100	—	30	—	500	—	—
1973	60	—	150	—	50	—	450	—	—
1974	120	—	220	—	150	—	1,000	—	—
1975	240	—	40	—	150	—	600	—	—
1976	20	—	100	—	200	—	300	—	—
1977	350	150	100	—	20	—	2	—	—
1978	500	250	600	—	30	50	150	—	—
1979	250	200	400	—	100	2,000	600	—	—
1980	250	200	600	—	60	20,000	600	—	—
1981	20	30	100	—	50	21,500	4,000	—	—
1982	2	5	1	—	500	37,000	1,500	50	7,500
1983	1	20	0	—	150	10,000	1,250	100	12,650
1984	2	30	0	—	80	10,750	1,400	100	14,500
1985	3	350	0	255	150	9,000	1,200	100	3,500
1986	12	800	0	18	250	5,650	1,100	200	9,700
1987	2	100	0	150	120	26,700	7,000	1,200	20,000
1988	1	25	0	60	20	2,900	2,500	1,500	5,000
1989	30	12	0	350	2	1,000	800	200	12,000
1990	4	12	50	0	40	1,200	3,700	1,600	14,000
1991	3	5	70	0	450	2,400	6,000	1,500	8,800
1992	0	0	220	0	100	4,200	3,000	2,000	18,000
1993	20	1	60	0	200	6,500	1,000	500	4,000
1994	8	0	30	0	100	4,300	3,000	2,000	11,000
1995	0	40	175	0	0	2,950	750	3,000	5,000
1996	1	11	60	0	0	3,850	1,500	2,300	3,500