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Teresa M. Montygierd-Loyba, Jon E. Keeley

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Notes and Comments

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DEMOGRAPHIC STRUCTURE OF ***CEANOTHUS MEGACARPUS*** *CHAPARRAL IN THE LONG ABSENCE OF FIRE*[1]

Teresa M. Montygierd-Loyba and Jon E. Keeley[2,3]

Wildfires have had a major influence on the structural and functional adaptations that have evolved in species of mediterranean-type ecosystems. In California chaparral, for example, shrubs regenerate after fires from basal sprouts or seed germination cued to the first postfire season. Certain species of *Ceanothus* and *Arctostaphylos* produce abundant seed throughout their lifespan, and the seeds lie dormant in the soil for many years until germination is stimulated by fire. These species do not resprout after fire, and thus are often referred to as obligate seeding shrubs. In the absence of fire, these species neither rejuvenate their canopy from basal sprouts as sprouting shrubs do, nor do they recruit new seedlings.

The demographic patterns for one such species, *Ceanothus megacarpus* Nutt. ssp. *megacarpus,* have been documented in studies by Schlesinger and Gill (1978, 1980). This shrub is distributed on the coastal front of the Coast Ranges from Santa Barbara County to San Diego County, often forming nearly pure, even-aged stands dating back to a previous fire. As with other obligate-seeding species, seedling populations are high in the first postfire year, but nil in later years. Mortality in the 1st yr is typically quite high. The causes of mortality probably include drought, predation, and competition from the dense herbaceous vegetation. After the 1st yr, mortality is relatively low during the first decade. However, as the shrub canopy closes in, Schlesinger and Gill (1978) found another sharp increase in mortality, and they attributed this stand-thinning to increased competition for water (Schlesinger and Gill 1980).

After stand-thinning in the second decade, mortality in *Ceanothus megacarpus* was shown to level off once again. Schlesinger and Gill's studies, however, did not extend much beyond the second decade. It is not known what happens after this time. Anecdotal observations in the literature suggest that after ≈30–40 yr another sharp increase in mortality is to be expected due to stand "senescence."

The purpose of the present study was to extend beyond the second decade Schlesinger and Gill's observations on *Ceanothus megacarpus* survivorship patterns. Due to the high frequency of (largely human-initiated) wildfires, old chaparral stands are uncommon within the range of *Ceanothus megacarpus.* We considered ourselves fortunate to find a stand of *Ceanothus megacarpus* that had not been burned for >50 yr.

Study Site and Methods

Field observations throughout its range failed to uncover any stands of pure *Ceanothus megacarpus* older than 30 yr. However, one stand largely dominated by this species and 55 yr of age (in 1984 as estimated from ring counts) was discovered along Pacific View Drive in the western section of the Santa Monica Mountains of Ventura County. It was ≈1 ha in size and on a west-facing slope of ≈25° inclination at 380 m elevation. Due to a housing development, this stand no longer exists.

To characterize the stand, area covered by *Ceanothus* was estimated from 10 10-m line transects, and density and basal area coverage were determined from 45 2 × 4 m quadrats. Transects and quadrats were placed by dividing the site into a two-dimensional grid and selecting points from a random numbers table. In each quadrat, basal diameter of all stems was recorded. Because of the convoluted shape of *C. megacarpus* stems, diameters were determined by taking the mean of two diameters measured at 90° to each other. Survivorship patterns for *C. megacarpus* were determined in a manner similar to that described by Schlesinger and Gill (1978). Over an area 40 × 40 m, all dead *Ceanothus megacarpus* were cut and a stem section at ground level was removed. As previously noted by Schlesinger and Gill (1978), we found that the wood of most standing dead shrubs was quite sound, in spite

TABLE 1. Composition of *Ceanothus megacarpus* chaparral stand.

		Canopy coverage (%)	Basal area (m²/ha)	Density (no./ha)	
				Stems	Plants
Ceanothus megacarpus	alive	79	35.8	3000	2528
	dead	2	5.0	1083	833
Adenostoma fasciculatum	alive	7	4.9	1167	4167
	dead	0	2.7	5417	333
Salvia mellifera	alive	11	2.8	2972	1055
	dead	0	4.1	4389	861
Cercocarpus betuloides	alive	26	2.6	34 306	611
	dead	1	0.7	5833	0
13 other species	alive	6	5.9	9274	3193
	dead	0	2.4	2360	306

FIG. 1. Distribution of ages of dead *Ceanothus megacarpus* shrubs, based on a random sample of 125 dead shrubs.

of having been dead for as long as 30+ yr. Stems were recut, polished, and aged by ring counts. A total of 130 dead stems were collected, but only 125 were used, as partially rotted stems were discarded.

Schlesinger and Gill (1978) estimated their ring counts to be accurate within ±1 yr on stems 10–15 yr of age, and determinations in our laboratory indicated a similar accuracy for stems 15–55 yr of age.

Results and Discussion

Ceanothus megacarpus constituted 79% of the canopy coverage and 69% of the live basal coverage, with *Adenostema fasciculatum* being the only other prominent species (Table 1).

Schlesinger and Gill (1978) noted that in stands 10–20 yr of age the variance : mean ratio for number of *C. megacarpus* plants per quadrat was greater for live plus dead plants than for live plants alone. They interpreted this to mean that during thinning, the population moved from a more clumped to a more random distribution. This pattern continues in older stands, as we found that the variance : mean ratio shifted from 2.31 for living plus dead plants to 1.76 for living plants alone (although both deviated significantly [$P < .01$ with t test] from random expectation). Schelsinger and Gill (1978, 1980) also found that mortality in young stands tended to be concentrated in the smaller plants. We found a similar pattern in this old stand: 35% of the live stems were <100 mm diameter, while in contrast 85% of the dead stems were <100 mm diameter.

The age distribution of the dead *C. megacarpus* stems is shown in Fig. 1. We found very few dead stems <20 yr of age, undoubtedly due to deterioration of stems which died soon after fire. The highest age-specific mortality rate was observed for plants 36 yr of age. Over the past two decades, mortality rate has been quite variable from year to year but shows no pattern of increasing with age. There appears, on the contrary, to be a trend of decreasing mortality during the last decade. This may be related to the fact that this was a particularly wet decade in southern California (precipitation 1973–1983 was 25% higher than average, Climatological Data, National Oceanic and Atmospheric Administration). This idea is supported by Schlesinger and Gill's (1978) finding that drought stress is a major factor in *C. megacarpus* mortality.

An estimated survivorship curve for this population of *C. megacarpus* is shown in Fig. 2. The solid part of the curve illustrates changes over the last 30 yr, estimated from the total density of living and dead shrubs (Table 1), and the mortality observed for age classes beginning at 25 yr of age (Fig. 1). Assuming the thinning

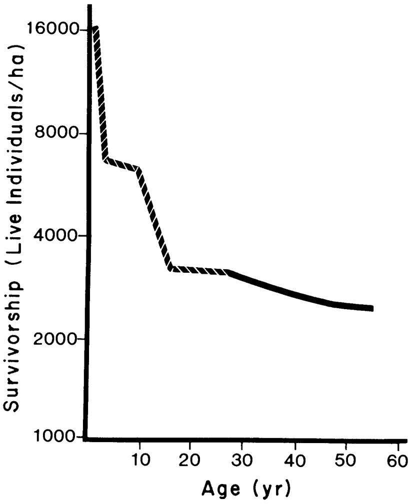

FIG. 2. Estimated survivorship curve for the *Ceanothus megacarpus* population unburned for 55 yr. The solid line was derived from the mortality observed in Fig. 1 for ages between 25 and 55 yr. The dashed line assumes survivorship rates as determined by Schlesinger et al. (1982).

curve observed by Schlesinger et al. (1982), we have extrapolated back to the time of the last fire (slashed line). In this stand of *Ceanothus* chaparral, it appears that high mortality associated with stand thinning during the second decade has been followed by a period of slow population decline. Even if we assume that the recent leveling off of the survivorship curve was transitory, projections into the future indicate that this stand of chaparral might have been well over 100 yr of age before *C. megacarpus* was completely eliminated.

Mortality rate of *Ceanothus megacarpus* shrubs in a 55 yr old chaparral stand has averaged 24 shrubs·ha^{-1}·yr^{-1} (SD = 13) over the past 30 yr. The greater numbers of dead individuals in the smaller size classes as well as the greater numbers of large living plants, suggest that mortality in *C. megacarpus* is related more to intraspecific competition than to a programmed mortality due to senescence. The notion of senescence or decadence as it relates to older stands of obligate-seeding chaparral species needs to be re-evaluated, or at least defined more clearly in light of the evidence offered by this study.

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[1] *Manuscript received 14 January 1986;*
revised and accepted 8 May 1986.
[2] *Department of Biology, Occidental College,*
Los Angeles, California 90041 USA.
[3] *Reprint requests to J. Keeley.*

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THE HUSTING DILEMMA: A METHODOLOGICAL NOTE[1]

James D. Nichols,[2] Gary R. Hepp,[2,3]
Kenneth H. Pollock,[4] and James E. Hines[2]

Recently, Gill (1985) discussed the interpretation of capture history data resulting from his own studies on the red-spotted newt, *Notophthalmus viridescens,* and work by Husting (1965) on spotted salamanders, *Ambystoma maculatum.* Both studies used drift fences and pitfall traps around breeding ponds to capture salamanders in the spring and fall. Gill (1985) noted that gaps in capture histories (years in which individuals were not captured, preceded and followed by years in which they were) could result from either of two very different possibilities: (1) failure of the animal to return to the fenced pond to breed (the alternative Husting [1965] favored), or (2) return of the animal to the breeding pond, but failure of the investigator to capture it and detect its presence. Gill (1985:346) noted that the first possibility is "demographically interesting and worthy of evolutionary interpretation" whereas the second possibility is not. He analyzed his own capture history data on newts and concluded that females and, to a lesser extent, males showed irregularities in breeding schedules that could not be explained entirely by a model incorporating "census errors" and a constant annual survival probability. Gill (1985:353) then stated that "A similar analysis of the data of Husting (1965) is not possible because independent estimates of annual mortality and census errors are not available."

We agree entirely with Gill (1985) that capture history data such as his or those of Husting (1965) should be analyzed using models that recognize the possibility of "census error," and that it is important to try to distinguish between such "error" and skipped breeding efforts. Our purpose in this note is to point out the relationship between Gill's (1985:347) null model and certain capture–recapture models, and to use capture–recapture models and tests to analyze the original data of Husting (1965). We also show a similar analysis of Gill's (1985) data.

Data

Both Husting (1965:Table 2) and Gill (1985:Table 1) published the complete capture histories on which their analyses were based. This is relatively unusual in the ecological literature, but is extremely important and permits reanalysis efforts such as those presented here. Husting (1965:354) recognized this importance and wrote that his data "are presented in the hope that readers will be tempted to apply other methods of analysis."

Methods

The methods we use are available in the open literature on capture–recapture experiments and hence