DEMOGRAPHY OF THE UNSILVERED MORPH OF *SPEYERIA MORMONIA* IN COLORADO

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ABSTRACT. The demographies of unsilvered and silvered morphs of *Speyeria mormonia* do not differ greatly in a Colorado population with a very low frequency of unsilvered animals. The frequency of the unsilvered morph is on the order of that expected if the unsilvered morph were due to a recessive allele with fitness zero, which is maintained only by mutation. The lack of detectable difference between morphs in demographic parameters suggests, however, that other factors control the frequency of the polymorphism.

Additional key words: Nymphalidae, polymorphism.

The silver spots on the underside of the wings of *Speyeria mormonia* Edwards (Nymphalidae) consist of modified scales. These silver spots are absent in some individuals, being replaced by buff colored spots. The percentage of unsilvered morphs in a population varies substantially among populations (Remington 1956).

It is not known whether the silvered-unsilvered difference is actually heritable, although Remington (1956) speculates that it may be controlled by one autosomal locus. The frequency of the unsilvered morph in a population may therefore be determined by any of a number of factors, including mutation rate, natural selection, drift, and—if the dimorphism should prove to be due to environmental plasticity—environmental characteristics.

Even in the absence of genetic information, we can begin to understand something of the forces governing the frequency of the morphs in a population by comparing demographic parameters for the two morphs. This is particularly true for populations in which the frequency of one morph is extremely low. In such cases, an extreme discordance in demographic parameters for the two morphs would suggest that extreme selection pressures relating to the unsilvered and silvered phenotypes exist in the adult stage. In the particular population examined here, the frequency of the unsilvered morph is in the range of that expected if unsilvered is due to a recessive allele whose fitness is zero and whose frequency in the population is thus determined strictly by the mutation rate.

Here I compare demographic data obtained over four years for unsilvered and silvered morphs in a Colorado population of *S. mormonia*. Recapture rates and maximum longevities (indices of survival), dispersal, and sex ratio are compared for the two morphs. I also examine

yearly shifts in percentage of unsilvered morphs in the population. While the sample size of unsilvered animals is by necessity quite small in a population with such a low frequency of unsilvered morphs, differences in values for demographic parameters are expected to be dramatically large if mutation balanced by low adult survival yielding a fitness of zero is responsible for the unsilvered morph's low frequency. The results thus give a first indication of the type and extent of differences between the morphs.

MATERIALS AND METHODS

The study was conducted near Gothic, Gunnison Co., Colorado. The study area consists of fescue grassland (Langenheim 1962), sometimes bordered by stands of aspen or spruce. Elevation varies from 2880 to 2970 m. Most lower slopes face SW, while upper slopes face NW. The study area was divided into topographic sites for calculation of dispersal distances. Total area sampled in 1979 was 6.0 ha; in 1980, 24.7 ha; in 1981, 5.6 ha; and in 1982, 6.3 ha (see Boggs 1987 for further detail).

Standard mark-release-recapture techniques were used in this study each summer between 1979 and 1982. Date and time of capture, butterfly number, sex and site of capture were recorded. Captured individuals were immediately released at the site of capture. Recaptures of individuals on the same day in the same site were not recorded. Dispersal distances were measured between centers of sites.

RESULTS AND DISCUSSION

Frequency of unsilvered animals captured in this population varied between 0% and 0.2% (Table 1), and did not differ significantly among years (Table 2). In 1981, the one unsilvered animal caught had half of each normally silvered spot unsilvered.

If the frequency of unsilvered animals in the population were controlled by the mutation rate alone, with the fitness of homozygous recessive unsilvered animals equal to zero, then the square of the frequency of unsilvered would equal the mutation rate. Mutation rates for this population would therefore be 5.1×10^{-6} in 1980, 1.4×10^{-6} in 1981 and 4.7×10^{-6} in 1982, which are in the range reported for whole-locus mutation rates in *Drosophila* (Crow 1986).

Given a total density for this population of about 2000/ha, and an average dispersal distance of about 175 m (Boggs 1987), the lack of significant difference among years in frequency does not rule out genetic drift as a factor affecting frequencies of the morphs. For example, the time to fixation for a neutral mutant is approximately four times the effective population size (Crow 1986); the change in frequency in four generations under these circumstances would not necessarily be large enough to detect without a much larger sample size.

TABLE 1.   Number and sex ratio of silvered and unsilvered *S. mormonia* marked per year.

Year	Total no. silvered	Total no. unsilvered	Sex ratio	
			Silvered	Unsilvered
1979	590	0	3.7:1	—
1980	2646	6	3.6:1	1:1
1981	846	1*	6.2:1	1:0
1982	2762	6	2.4:1	5:1
Total	6844	13	3.2:1	2.2:1

* Half-silvered.

The sex ratio of unsilvered animals showed no consistent pattern (Table 1). Taken over all four years, the sex ratio of unsilvered animals did not differ significantly from that of silvered animals (Table 2). This is consistent with the hypothesis of determination of silvering by an autosomal locus.

Unsilvered individuals showed no pronounced difference from the silvered in other demographic attributes. Based on recapture frequencies for silvered animals (Boggs 1987), I expected to recapture 0.1, 0, and 0.2 unsilvered females in 1980, 1981, and 1982, respectively. None were ever recaptured. I expected to recapture 0.4, 0.1, and 1.8 unsilvered males in 1980, 1981, and 1982, respectively; 1, 0, and 2 males were recaptured in 1980, 1981, and 1982, respectively. The extremely close correspondence of these data to expectations over several years, in spite of the small numbers involved, indicates that survival and catchability of unsilvered individuals paralleled that of silvered butterflies among years. Ordinary statistical tests are precluded by the small numbers intrinsic to the situation. However, it is clear that, compared to silvered morphs, the unsilvered did not suffer massively greater mortality in the adult stage.

Maximum residence time is indicated by the interval between first and last capture. Maximum residence time in 1980 was 8 days for the one unsilvered male recaptured, whereas it was 15 and 28 days for the two unsilvered males recaptured in 1982. These values are not inconsistent with values for silvered individuals. For such butterflies, daily survival rates were lower in 1980 than in 1982, and maximum residence seen was 28 and 40 days, respectively, in 1980 and 1982 (Boggs 1987).

Dispersal characteristics of unsilvered and silvered morphs did not differ greatly either. The recaptured male in 1980 was recaptured in the same site as originally caught, yielding a dispersal distance of 0 m. Distances moved by the recaptured males in 1982 were 180 m and 580 m. Average distance moved by silvered morphs was about 175 m, with 60–80% of the recaptured animals dispersing (Boggs 1987).

TABLE 2. Tests of significance of differences among years in percentage of unsilvered morphs in the population, and of differences between morphs in the four year total sex ratio. The test statistic, x*, Goldstein's (1964) exact binomial test for differences of proportions, equals the difference between the proportions divided by a pooled standard deviation, and is compared to values for t_∞. 95% confidence intervals for the difference between proportions indicate the amount of difference which could exist but not be detected as significant at P = 0.05.

Test	x*	P	95% confidence interval for difference between percentages
Percentage unsilvered between years			
1979 (0%) vs. 1980 (0.23%)	−1.158	>0.05	−0.15% to 0.61%
1979 (0%) vs. 1981 (0.12%)	−0.835	>0.05	−0.16% to 0.39%
1979 (0%) vs. 1982 (0.22%)	−1.133	>0.05	−0.16% to 0.59%
1980 (0.23%) vs. 1981 (0.12%)	0.614	>0.05	−0.24% to 0.45%
1980 (0.23%) vs. 1982 (0.22%)	0.074	>0.05	−0.24% to 0.26%
1981 (0.12%) vs. 1982 (0.22%)	−0.573	>0.05	−0.24% to 0.44%
Percentage males between morphs			
Silvered (76.3%) vs. unsilvered (69.2%)	0.595	>0.05	−16.2% to 30.2%

There was thus no evidence for an extreme survival-residence disadvantage of the unsilvered morph. This is contrary to expectations if the frequency of the unsilvered morph is maintained by mutation in combination with an extreme selective disadvantage. However, the evidence presented here does not completely rule out maintenance of the unsilvered morph by a balance between mutation and selection, as, for example, ability to successfully lay eggs or mate was not examined.

LITERATURE CITED

BOGGS, C. 1987. Within population variation in the demography of *Speyeria mormonia* (Lepidoptera: Nymphalidae). Holarctic Ecology. In press.
CROW, J. 1986. Basic concepts in population, quantitative and evolutionary genetics. W. H. Freeman, New York. 273 pp.
GOLDSTEIN, A. 1964. Biostatistics. MacMillan, New York. 272 pp.
LANGENHEIM, J. 1962. Vegetation and environmental patterns in the Crested Butte area, Gunnison County, Colorado. Ecol. Monogr. 32:249–285.
REMINGTON, C. L. 1956. Genetics of populations of Lepidoptera. Proc. 10th Int. Congress Entomol. 2:787–828.