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REPRODUCTIVE STRATEGIES AND LIFE HISTORY EVOLUTION
OF SOME CALIFORNIA *SPEYERIA* (NYMPHALIDAE)

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ABSTRACT. Egg weights and total eggs produced by nine *Speyeria* spp. (Nymphalidae) in California allowed estimates of per-egg and lifetime reproductive effort. Interpopulation reproductive effort in four species and intrapopulation reproductive effort of two species in different years were documented. Female body weight was uncorrelated with either individual egg weight or total life-time egg weight. Smallest eggs (mean dry wt/egg = 0.05 – 0.06 ug), and the greatest number of eggs, were from *S. coronis* (Skinner) and *S. zerene* (Boisduval) whose females undergo summer reproductive diapause in dry habitats. Largest eggs (mean dry wt/egg = 0.10 ug) were from *S. nokomis* (Skinner), a wet habitat species. The greatest relative reproductive effort was made by dry habitat species lacking reproductive diapause. Reproductive effort and duration of first instar exposure to summer temperatures were positively correlated. Intrayear variation in total egg weight did not vary significantly among populations of *S. callippe* (Boisduval), *S. hesperis* (Boisduval), *S. nokomis*, or *S. zerene* but mean total egg weights were significantly different in females from the Donner Pass, CA population of *S. mormonia* (Boisduval) in two years. *S. zerene* from high elevations lacked the reproductive diapause characteristic of lower elevation populations. The reproductive strategies of *Speyeria* spp. are adaptive responses to the desiccation stress that their habitats impose on diapausing first instars.

Additional key words: female size, egg numbers, first instars

Comparative analyses of reproductive strategies among closely related species have provided significant contributions to the field of evolutionary biology (Smith & Fretwell 1974, Stearns 1992). One particularly interesting area of research involves determining the possible reasons for differences among related taxa, in offspring size, number, and traits affecting total reproductive effort. Egg size is one adaptive life history response that can be selected upon because it can confer fitness effects on both maternal parent and progeny (Bernardo 1996, Fox & Czesak 2000). For example, larvae from larger eggs may have greater resistance to environmental stresses such as starvation, desiccation, and extreme temperatures (Fox & Czesak 2000, Roff 2002), but high fecundity, and relatively small eggs, may be of selective advantage within habitats, or during growth periods, that have favorable temperature, moisture, and food (Braby 1994, Torres-Vila & Rodriguez-Molina 2002, Seko & Nakasuji 2004). There is a trade-off between egg size and fecundity (Roff 1992, Cummins 1986, Braby 1994, Sinervo & Licht 1991, Heath et al. 1999) and, within species, the selective forces acting upon egg size are not always obvious. In addition, the compromise between egg size and number plays out within the intra- and interspecific variation in female body size which usually sets a limit on the total amount of energy that can be used for reproduction (Boggs 1994, Fox & Czesak 2000).

Speyeria spp. (Nymphalidae) inhabit a range of montane habitats throughout the northern and western portions of North America. All species have one generation per year (univoltine) and utilize native violets (*Viola* spp.) exclusively as larval host plants. Females usually do not lay ova directly on the host plants but often on other vegetation near ground level. First instars immediately undergo an obligate diapause; feeding and resumption of larval development is synchronized with *Viola* regrowth the following spring. Diapausing larvae of *Speyeria* spp. from xeric habitats are exposed to considerable desiccation stress, especially during the summer and fall months. In California, desiccation stress is especially severe among species occurring in summer hot and dry habitats where adults of species such as *S. callippe* (Boisduval) often emerge in May and conclude oviposition before July (Brittnacher et al. 1978). The probability of individual larvae surviving through diapause to successfully complete development the following year is almost certainly very low and life-history strategies should reflect selection for reproductive patterns and larval adaptations that maximize larval survival and overall reproductive success (Zalucki et al. 2002, Sims & Shapiro 2014). Relatively little is known about the comparative reproductive strategies of most *Speyeria* spp. over the range of habitats they occupy. To address this, we studied interspecific differences in egg size,

total numbers of eggs produced, and female body weights and related them to preferred species habitats. We asked: 1) What is the relationship between female body size, egg size, and total reproductive effort? 2) Is there a relationship between reproductive effort and species habitats? and 3) What is the nature of intraspecific variation in the reproductive strategies?

MATERIALS AND METHODS

Insects. Adult *Speyeria* spp. collection locations in California and Nevada (NV) during 1974 and 1975 were as follows: Anthony Peak, Mendocino Co., 2100 M (AP); Boggs Mountain State Forest nr. Cobb, Lake Co., 850 M (BM); Del Puerto Canyon, Stanislaus Co., 600 M (DL); Devils Gate Pass, Mono Co., 2230 M (DG); Donner Pass, Nevada Co., 2100 M (DP); Kings Canyon, Carson City Co., NV 1600 M (KC); Round Valley, Inyo Co., 1400 M (RV); Yuba Pass, Sierra Co., 2000 M (YP), Fales Hot Springs, Mono Co., 2230 M (FS)*;* Sonora Pass, Mono Co., 2900 M (SP). The species and populations studied and collection locations were:

S. callippe (Boisduval) (AP, BM, DL); *S. coronis snyderi* (Skinner) (YP); *S. cybele leto* (Behr) (KC); *S. egleis* (DP, YP); *S. hesperis irene* (Boisduval) (AP, DP); *S. hydaspe* (Boisduval) (AP); *S. mormonia* (Boisduval) (DP, SP); *S. nokomis apacheana*, (Skinner) (DG, RV); *S. zerene zerene* (Boisduval) (BM), *S. zerene conchyliatus* (Comstock) (YP), *S. zerene* malcolmi (Comstock) (FS).

Egg collection. Field-collected adult females were transported back to the laboratory in glassine envelopes under refrigeration (~4 - 8°C) in insulated coolers. Only females in freshly emerged condition, based on wing wear and scale loss, were used in the experiments. Wing wear is commonly used as a surrogate measure of age in butterflies and judged to be a reasonable index for reproductive comparisons (see Kemp 2006). Females were handled, and ova obtained, as previously described by Sims (1979, 1984). Briefly, adults were fed once daily, until replete, on a 10% honey-water solution and maintained, in 1 liter cardboard containers over leaves of *Viola papilionacea* Pursh, at a photoperiod of 15:9 (L:D) h and 24+/-1°C within an environmental

TABLE 1. Life span, temporal pattern of oviposition, egg weight, and total egg production in *Speyeria*.

Species, location	Sample size	Life span, days (SD)	Days to first ova, mean (SD)	Total # eggs, mean (SD)	Egg weight, dry, mg, mean (SD)	Total dry wt of eggs per female (mg) (SD)
S. hydaspe-AP	16	24.2 (6.7)	1.6 (1.0)	291 (92)	0.097 (0.007)	28.2 (8.9)
S. coronis-YP	8	47.5 (10.7)	36.3 (10.0)	436 (298)	0.058 (0.003)	27.1 (17.5)
S. callippe-DL	13	12.8 (3.8)	3.6 (2.2)	231 (95)	0.092 (0.005)	21.2 (11.4)
S. callippe-AP	11	23.5 (8.3)	3.2 (2.3)	278 (160)	0.097 (0.004)	27.0 (15.6)
S. callippe-BM	34	17.3 (6.0)	3.0 (2.3)	182 (98)	0.102 (0.007)	17.0 (7.5)
S. nokomis-DG, 1974	22	11.9 (2.4)	2.1 (0.6)	156 (80)	0.103 (0.001)	19.3 (6.8)
S. nokomis-RV, 1974	9	12.7 (3.7)	2.1 (0.8)	190 (59)	0.106 (0.001)	21.5 (11.1)
S. hesperis-DP	34	17.6 (9.2)	2.7 (1.9)	230 (127)	0.087 (0.004)	16.9 (10.8)
S. hesperis-AP	6	18.3 (9.2)	6.7 (3.4)	209 (151)	0.081 (0.002)	17.7 (12.5)
S. cybele leto-KC	11	12.0 (5.7)	3.9 (1.7)	246 (129)	0.069 (0.001)	14.5 (8.8)
S. zerene-YP, 1974	8	38.6 (15.2)	25.6 (11.2)	314 (118)	0.061 (0.001)	20.9 (6.4)
S. zerene-BM, 1975	29	33.2 (7.9)	20.1 (5.4)	286 (187)	0.059 (0.001)	18.3 (8.9)
S. zerene-FS, 1975	8	9.6 (3.8)	5.3 (3.3)	184 (142)	0.050 (0.001)	8.1 (9.1)
S. egleis-YP, 1974	23	19.8 (7.5)	3.4 (3.2)	162 (98)	0.089 (0.004)	14.7 (8.9)
S. egleis-DP, 1974	7	13.6 (4.4)	2.2 (1.4)	131 (43)	0.093 (0.004)	11.9 (3.8)
S. mormonia-DP, 1974	27	10.6 (6.0)	2.8 (3.1)	94 (36)	0.079 (0.001)	7.7 (2.3)
S. mormonia-DP, 1975	19	5.4 (1.6)	2.4 (1.3)	44 (13)	0.071 (0.001)	3.7 (0.9)
S. mormonia-SP, 1974	7	8.4 (6.5)	5.3 (4.2)	69 (20)	0.074 (0.002)	5.5 (1.4)

chamber (Percival Scientific, Perry, IA). Eggs, which were laid singly, were removed from containers and counted daily and this was continued until female death. Measurements were made of the time interval between initial exposure to violet leaves and the date of first oviposition because the length of this period is an indicator of reproductive diapause in females of *S. coronis* and *S. zerene* (Sims 1984). Females of *Speyeria* other than *S. coronis* and *S. zerene* are reproductively mature (i.e. with mature oocytes) when they eclose and showed little or no behavioral delay in the initiation of oviposition within the containers.

Egg and female body weight estimation. Groups of 45 to 50, 3 to 5 d old ova were weighed on a Mettler balance (Mettler-Toledo Inc., Columbus, OH) to determine mean ova weight. There were 3 to 6 replications per species representing the ova from ≥ 10 females. Following live weight determination, eggs were dried for 72 h at 75°C in a vacuum oven and then re-weighed; average dry weight and water loss were calculated. Dry female weights were obtained using field collected females in newly emerged condition from the 1974 and 1975 seasons; females were frozen, dried for 72 h at 75°C in a vacuum oven, and then weighed. These data were supplemented with weights of fresh condition dried museum specimens with the pin weight subtracted. Total mean reproductive effort was estimated by the ratio of the mean total dry egg weight to mean dry female weight.

Relationship between reproductive effort and climate variables. Monthly temperature and precipitation data were obtained for each *Speyeria* collection site or from the nearest weather station. The collection site and associated weather station (WS) were as follows: Anthony Peak (Anthony Peak WS); Boggs Mountain (Clearlake 4 SE WS); Del Puerto Canyon (Newman WS near Patterson); Devils Gate Pass (Bridgeport WS); Donner Pass (Truckee RS WS); Kings Canyon (Carson City, NV WS); Round Valley (Bishop AP WS, Bishop Creek Intake 2 WS); Yuba Pass (Loyalton WS), Fales Hot Springs (Bridgeport WS); Sonora Pass (Coalville 13 E WS). All weather stations were located <25 km from collection locations. For each species-population the mean temperature (°C) of each month during the estimated period comprising the summer first instar diapause (ending October 1 for all species) was determined. The total number of temperature degrees (sum of the mean monthly temperatures) was used as an approximation for the magnitude of desiccation stress on diapause larvae. Precipitation, or lack of it, is another stress component for larvae and therefore the sum and mean precipitation (mm) during these months was also

determined. For example, the species-population with the greatest summer diapause stress was *S. callippe*-DL with 4 months (June–September) of mean temperatures >22°C and mean precipitation of only 2.2 mm/month. In contrast, larvae from the DG and RV *S. nokomis* populations experience only two summer months (August and September) of diapause stress during which mean temperatures are 19.6 and 11.4°C and mean precipitation amounts are 18.8 and 12.7 mm, respectively.

Statistics. Because distributions deviated from normality, inter- and intra-population between-year data on female lifespan, days to first egg, total number of eggs laid, dry egg weight, total dry weight of eggs per female, and dry weight per female (Table 1) were analyzed using the Kruskal-Wallis One Way ANOVA on Ranks followed by Dunn's Test to evaluate mean differences (SAS 2001). Correlations between dry weight per female, reproductive effort, and weather parameters were determined using the Product-moment correlation coefficient. Throughout, all means are given as ±1 SD.

Results

Life span, temporal pattern of oviposition, egg weight, and total egg production of *Speyeria* spp. are summarized in Table 1. *S. coronis*-YP, *S. zerene*-YP and *S. zerene*-BM populations had females with the longest mean life spans (47.5 d, 38.6 d, 33.2 d, respectively) and the longest periods prior to production of ova (36.3 d, 25.6 d, 20.2 d, respectively). These values are consistent with female reproductive diapause previously documented in *S. coronis* and *S. zerene* (Sims, 1984; James & Nunnallee, 2011). In contrast, the high altitude *S. zerene*-FS population lacked a reproductive diapause. *S. zerene*-FS also had a significantly shorter life span than *S. zerene*-YP (q=11.711, P<0.001) and *S. zerene*-BM (q=14.688, P<0.001) and had significantly fewer days to first oviposition compared to *S. zerene*-YP (q=9.933, P<0.001) and *S. zerene*-BM (q=8.749, P<0.001). Mean egg weight, total number of eggs, and total dry egg weight per female in the *S. zerene*-FS population were also significantly less (P<0.05) than in the *S. zerene*-BM and *S. zerene*-YP populations.

Among the *S. callippe* populations, the highest elevation population, CA-AP, had a significantly longer life span than CA-DL (q = 3.772, P < 0.05) and CA-BM (q = 3.214; P < 0.05). CA-AP and also produced significantly more eggs than CA-BM (q = 3.936; P < 0.05). The reasons for these differences are unknown.

Speyeria coronis produced the greatest total number of eggs (mean ± SD = 436 ± 298) but there was considerable interfemale variation. One *S. coronis*

female, for example, produced 1042 eggs. *Speyeria coronis* eggs were small (0.058 ± 0.003 mg) and this fell within the range of egg sizes from females of three *S. zerene* populations (0.50–0.061 mg) which were the smallest eggs of the species group (Table 1). The largest species, *S. nokomis*, produced the largest eggs (N-DG = 0.103 ± 0.001 mg and N-RV = 0.106 ± 0.001 mg but these eggs were only slightly larger than eggs from the *S. callippe*-BM population 0.102 ± 0.007) mg.

S. mormonia-DP females studied in 1974 and 1975 differed significantly in mean life span ($q = 4.244$, $P < 0.05$), mean number of eggs laid ($q = 5.904$, $P < 0.05$), and total dry weight of eggs ($q = 5.785$; $P < 0.05$) with 1974 females being greater in these categories (Table 1). Another high elevation population, M-SP, was not significantly different, in any category, from either the 1974 M-DP or the 1975 M-DP populations.

The reproductive effort of *Speyeria* spp. females in relation to body weight is shown in Table 2. The total dry weight of eggs produced as a percentage of mean female dry weight is defined as "relative reproductive effort" (RRE). Among the nine species, there was no correlation between female body size and either individual egg weight ($q = 0.127$, $P > 0.05$) or total weight of eggs produced ($q = 0.258$, $P > 0.05$).

In general, species associated with dry habitats, from low to high elevations had a greater RRE. An exception to this trend was *S. zerene* FS, a high altitude population lacking reproductive diapause. *S. cybele leto* and *S. nokomis*, species from mid to high elevation meadow habitats, had RRE values less than 50% those of dry habitat species such as *S. hydaspe* and *S. hesperis*.

For the nine species, including three samples of *S. mormonia* (two populations, one population with two sample years) and three *S. zerene* populations (two diapause, one non-diapause), the relationship between RRE and total number of temperature degrees accumulated during the months of first instar diapause was significant ($r = 0.660$, $N = 12$, $P = 0.0195$), Figure 1. However, the relationship between RRE and the mean monthly rainfall during the larval diapause period was not significant ($r = -0.301$, $N = 12$, $P = 0.342$).

DISCUSSION

Life history strategies maximizing reproductive success should be selectively favored (Roff 1992, Stearns 1992, Bernardo 1996). Models of optimal reproductive effort often assume a tradeoff between progeny size and number with progeny fitness increasing with size (Roff 1992). Reproductive success will, in theory, be maximized when females, provided with a limited amount of available resources derived
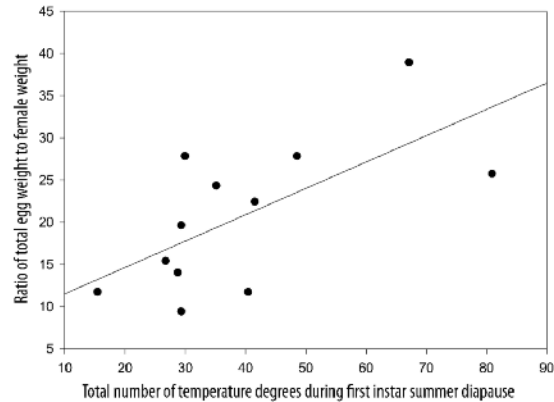

FIG. 1. Relative reproductive effort (RRE = ratio of total egg weight to female weight) of *Speyeria* species related to cumulative summer temperatures experienced by first instars ($y = 0.3121x + 8.3954$, $r^2 = 0.436$, $P = 0.0195$).

from larval feeding (e.g. fat body, proteins) and adult foraging (nectar), partition resources into progeny of optimal size and number. Timing and location of reproduction will also significantly affect reproductive success. *Speyeria* reproductive strategy components include egg size, number, and the total weight of eggs allocated in proportion to female weight (RRE). Reproductive timing appears to follow two general pathways. Females either begin to lay eggs soon after adult emergence or they delay reproduction, via reproductive diapause, until environmental conditions are more favorable for larval survival.

There was no correlation between female body weight and either individual egg weight or total weight of eggs produced. The heaviest eggs produced by the largest species, *S. nokomis*, were only slightly heavier than the intermediate size *S. callippe*; the lightest eggs were produced by two species of intermediate size, *S. coronis* and *S. zerene*. The optimal reproductive strategies of *Speyeria* appear to involve other life history adaptations, less related to egg or larval size, but strongly related to larval habitat. Adaptations of diapausing first instars for surviving heat and drought are a significant component of the reproductive strategies; larvae show significant interspecific variation in desiccation resistance and diapause strength that is positively correlated to the severity of their habitat (Sims & Shapiro 2014).

The *Speyeria* fall into three general categories of reproductive strategy and life history evolution based on the duration of larval exposure to warm temperature - low precipitation conditions. Category 1 includes species such as *S. callippe* and *S. hydaspe* inhabiting xeric habitats at low to mid elevations. Female oviposition begins soon after mating and females have a

high RRE. Larvae possess a strong diapause and are very resistant to desiccation allowing survival during long exposure to warm-dry conditions. Category 2 includes two species, *S. coronis* and *S. zerene*, inhabiting xeric habitats typically at mid-elevations. Females undergo a reproductive diapause and delay oviposition until late summer. They have an intermediate RRE but partition reproductive effort into large numbers of small eggs. Larvae are small, susceptible to desiccation, with a relatively weak diapause. Because of late season oviposition, the duration of larval exposure to desiccating conditions is relatively short. Exceptions to this category are *S. zerene* populations from coastal (McCorkle & Hammond 1988) and high elevations that lack reproductive diapause (this study). Other United States *Speyeria* species, *S. aphrodite, S. diana, S. edwardsii,* and *S. idalia* occur in relatively more mesic habitats but appear to also have a reproductive diapause. Females emerge in early summer but typically delay oviposition until late August or September (Edwards 1897, Scott, 1992, Kopper et al. 2001, Adams & Finkelstein 2006). Category 3 includes species from high elevations and wet meadows. Adult emergence occurs in mid-late summer and females begin oviposition immediately; RRE is relatively low. Larvae have a weak diapause and are very susceptible to desiccation but the duration of larval exposure to desiccating conditions is brief. One species, *S. nokomis*, has larvae that actively move toward high humidity in a gradient (Sims & Shapiro 2014).

The warm, dry summer time lapse between first instar larval emergence and cool/moist fall weather represents a major period of environmental stress, and selection, on diapause first instar *Speyeria* spp. larvae. This period can extend four months or longer for populations of species such as *S. callippe.* Documentation of larval adaptations, and species-specific differences, were presented in a previous report (Sims & Shapiro 2014). Important physiological adaptations of first instars to summer habitats include desiccation resistance and diapause strength. There is a positive relationship between larval diapause strength and desiccation resistance, but neither diapause strength nor desiccation resistance was related to larval size. This suggests that desiccation resistance and larval survival has been enhanced more by physiological adaptations than by increases in size. Karlsson & Wiklund (1985) reported similar results in a group of five Satyridae that showed no correlation between either egg weight and desiccation resistance or first instar weight and starvation resistance. Reavey (1992) found no relationship between first instar size and starvation resistance in 42 species of British Lepidoptera.

Climate, especially the severity and duration of the dry season and available moisture, has been a key selective factor in the evolution of *Speyeria* spp. reproductive strategies and larval adaptations. Among species, there is significant positive relationship between RRE and the sum of summer temperatures experienced by diapause larvae. The relationship

TABLE 2. Reproductive effort of *Speyeria* females in relation to female body weight.

Species, location(s)	n	Total dry egg weight, mg, per female, mean (SD)	Female dry body weight, mg, mean (SD)	Total dry weight of eggs as percentage of dry female weight***
S. hydaspe-AP	16	28.2 (8.9)	72.5 (14.5)	38.9
S. hesperis-DP	34	16.9 (10.6)	60.9 (8.9)	27.8
S. coronis-YP	8	27.1 (17.5)	97.5 (12.7)	27.8
S. callippe-DL, AP, BM	58	19.9 (10.8)	77.3 (16.8)	25.7
S. egleis-YP, DP	30	14.1 (8.0)	58.1 (8.5)	24.3
S. zerene-YP, BM	37	18.9 (8.1)	84.4 (18.2)	22.4
S. zerene-FS	8	12.4 (9.1)*	80.3 (20.6)	15.4
S. mormonia-DP, 1974	27	7.7 (2.3)	39.3 (8.1)	19.6
S. mormonia-DP, 1975	19	3.7 (0.9)**	39.3 (8.1)	9.4
S. mormonia-SP, 1974	7	5.5 (1.4)	38.1 (13.1)	13.3
S. cybele leto-KC	11	14.5 (8.8)	123.7 (8.3)	11.7
S. nokomis-DG, RV	31	20.0 (8.1)	171.1 (22.0)	11.7

*Significantly different (p<0.05) from *S. zerene*-YP, BM

**Significantly different (p<0.05) from *S. mormonia*-DP, 1974

***Relative reproductive effort (RRE)

between RRE and mean monthly precipitation during the summer periods was not significant, but summer precipitation in many habitats may not have predictable impacts on diapause larvae. Larvae can imbibe water (Sims & Shapiro 2014) but episodes of brief or light precipitation might not reach the diapause larval habitat and thus would not be available for drinking. Species inhabiting dry habitats, from low to middle elevations, had higher RRE than wet meadow and alpine species. Intraspecific differences in reproductive strategies can be significant within *Speyeria* spp. For example, *S. zerene* populations from cool coastal habitats in California and Oregon emerge late in the summer season and probably lack a reproductive diapause (McCorkle & Hammond 1988). Similarly, high altitude *S. zerene* populations (*S. zerene* malcolmi) lack a female reproductive diapause. In contrast, mid-elevation *S. zerene* populations all show a pronounced reproductive diapause. In mid-elevation populations, reproduction is delayed until late in the season when environmental stress on diapause larvae is reduced. This is especially important with *S. zerene* which, along with *S. coronis*, has the smallest eggs and larvae of the species studied.

Boggs (1987) evaluated the population dynamics of Colorado *S. mormonia* over a 4-year period and found between-year variation in several demographic factors. Between-year variation in *S. mormonia* reproduction is documented for the first time in this report. In California *S. mormonia*, between-year variation in life span, total numbers and weight of eggs, and RRE can be significant as demonstrated by the differences between 1974 and 1975 values for the Donner Pass population. Interpopulation differences in fecundity and resource allocation have been documented in Lepidoptera and other insects (Parry et al. 2001, Franzén et al. 2013), but the reasons for between-year *S. mormonia* differences are unclear. They may be related to a severe drought in California that started in 1975 and its effects on the quality and quantity of larval host plants. Alternatively, body size and/or reproductive capacity in insects can vary over the course of a growth season with late season emergers sometimes being smaller and less fecund (Palmer 1984, Corkum et al. 1997). *S. mormonia* female samples from Donner Pass in 1974 were made on Aug. 12 (19), Aug. 20 (5), and Sept. 13 (3) while the 1975 collection was made on Aug. 24 (19). The 1974 samples predominantly represent early emergers whose size/fecundity may have been enhanced by cooler temperatures experienced during larval and pupal development (Atkinson 1994). This level of between-year variation in *S. mormonia* indicates that future studies on *Speyeria* reproductive strategies should include two or more years of data with samples taken throughout the entire emergence period.

Female weight and individual egg weight were uncorrelated and there was no relationship between female weight and either total number or total weight of eggs produced. However, the weights of eggs produced over the lifespan of individual females can vary and generally decline with female age. As females of *S. mormonia*, *S. nokomis* and *S. zerene* age, the weights of eggs they produce declines and the resulting larvae have significantly reduced diapause intensity and probably reduced resistance to desiccation (Sims & Shapiro 2014). The eggs produced at the end of female reproduction and end of the flight season produce larvae that will experience reduced exposure to desiccation stress. Smaller late season larvae might therefore be somewhat buffered from stress-related mortality. A reduction in egg weight with female age has been documented in Colorado *S. mormonia* and in other Lepidoptera (Boggs 1986, Karlsson 1987).

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