

RELATIONSHIP OF HOST PLANT DENSITY TO SIZE
AND ABUNDANCE OF THE REGAL FRITILLARY
SPEYERIA IDALIA DRURY (NYMPHALIDAE)

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ABSTRACT. Populations of the Regal Fritillary, *Speyeria idalia* Drury have been declining across prairies in the USA. We hypothesized that larval food limitation may be a factor in this decline, and explored this by studying the following characteristics for *S. idalia* in Iowa, South Dakota, North Dakota, and Kansas: population size (via mark-recapture), adult weight; abdominal, thoracic, and wing lengths; adult head capsule widths. Violet densities and abundance estimates were calculated for all sites. These estimates of the insect's larval hostplant availability were correlated to the size of the butterfly populations and the weights of the insects. Iowa prairies had significantly lower violet densities. Weights of *S. idalia* were significantly lower in Iowa compared to Kansas and S. Dakota.

Additional key words: growth, geographic variation, host plants, violets, *Viola pedatifida*.

The Regal Fritillary, *Speyeria idalia* Drury (Nymphalidae, Argynniinae), is a prairie butterfly that has experienced severe population declines because of habitat destruction. *S. idalia* is one of the "most characteristic" indicators of high quality prairie in North America (Hammond & McCorkle 1983). With the disappearance of prairie habitat, widespread populations of *S. idalia* also have declined in numbers and distribution. *S. idalia* was listed as a Category II species (possible candidate for listing) under the Endangered Species Act until 1996, when this category of protection was deleted by the U.S. federal government (USFWS 1996). *S. idalia* currently has a special "status of concern" in national grasslands in North Dakota and South Dakota, and the Iowa Department of Natural Resources has listed it as a sensitive species (J. Fleckenstein, pers. comm.). Hammond and McCorkle (1983/1984), Johnson (1986) and Swengel (1997) also noted general declines in *S. idalia* populations. Hammond and McCorkle (1983/1984) specifically noted a relationship between habitat loss and population declines in *S. idalia*.

Our documentation of small population sizes of *S. idalia* in Iowa during 1995 (Table 1) suggests that the insect could go extinct locally. *Speyeria idalia* was found at only 11 of 52 prairies, and only five of these 11 prairies had populations of *S. idalia* estimated at over 50 individuals. Because we found a number of intermediate to small populations of *S.*

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TABLE 1. *Speyeria idalia* population size estimates in 1995. ¹P. C. Hammond's estimate. These data taken from Debinski & Kelly (1998).

Prairie name	Population estimate	Method
Page Private Prairie	2	individuals observed
Sheeder Prairie	50	mark-recapture
Reichelt Unit of Stephens State Forest	4	individuals observed
Polk City Prairie	1	individuals observed
Moeckley Prairie	220	mark-recapture
Ringgold Wildlife Area	7	individuals observed
Doolittle Prairie	2	individuals observed
Rolling Thunder Prairie	120	mark-recapture
Kalsow Prairie	500	visual estimate ¹
Loess Hills Wildlife Area sect. 9	160	mark-recapture
Loess Hills Wildlife Area sect. 21	2	individuals observed

idalia in Iowa in 1995, we began to focus on the causes of this species' population decline.

Other research confirms the detrimental effects of food limitation on insects. Larval food limitation in the Painted Lady Butterfly (*Vanessa cardui*) negatively affected growth, survival and body mass in a laboratory setting (Poston et al. 1977, 1978, Kelly 1996). In Diptera, reduction in adult body size and fecundity, as well as increased larval mortality, were demonstrated from larval food limitation in a laboratory setting (Collins 1980). Nymphal food limitation was implicated in reducing the fecundity of female mantids (Dictyoptera) in field populations (Eisenberg et al. 1981). A field study also demonstrated that food-limitation negatively affected bombardier beetle reproduction and suggested that such limitation may explain spatial differences in assemblage composition among age classes of these insects (Juliano 1986). Fecundity in lepidopterans is also affected by limited adult nectar sources (Boggs and Ross 1993), although there is evidence for use of stored nutrients during egg production (Boggs 1997).

Our objectives were to assess whether low host plant availability was correlated to individual body weight and overall population size of *S. idalia*. As a means of comparison, we investigated these traits in *S. idalia* from eight sites in Kansas, South Dakota, and North Dakota, where hostplant abundance is greater than in Iowa. Iowa prairies tend to be isolated plots of natural areas surrounded entirely by agricultural development, and habitat fragmentation has probably had a negative effect on this species. In contrast, *S. idalia* populations surveyed in Kansas, South Dakota, and North Dakota are bordered by habitats that still accommodate *S. idalia* to some extent, albeit in lower densities. We focused our research on the following questions: (1) does the larval host-plant, Blue Prairie Violet (*Viola pedatifida*), serve as a limiting factor for *S. idalia* populations by virtue of its limited abundance in Iowa prairies;

TABLE 2. *Viola pedatifida* population estimates in 1995. Note: Sites listed in Table 2 but not Table 1 had no *S. idalia* seen in 1995.

Prairie name	Violet density estimate plants / m ²	Violet population estimate
Page Private Prairie	1.5	95
Sheeder Prairie	1.1	39,200
Reichelt Unit of Stephens State Forest	2.5	128,000
Polk City Prairie	0.9	310
Hawthorn Wildlife Area	1.9	424,000
Kish-ke-kosh Preserve	9.7	12,900
Raymond-Hilts Private Prairie	4.6	900
Howe Private Prairie	5.2	1,100
Moeckley Prairie	0.7	35,000
Ringgold Wildlife Area	0.45	22,600
Doolittle Prairie	0.62	9,200
Rolling Thunder Prairie	1.9	210,000
Kalsow Prairie	0.48	148,000
Loess Hills Wildlife Area sect. 9	2.7	183,000
Loess Hills Wildlife Area sect. 21	1.5	98,000

and (2) because body weight positively influences fecundity in lepidopterans (Boggs and Ross 1993, data on *Speyeria mormonia* Boisd.), do adult females of *S. idalia* in Iowa prairies, where hostplant density is low, weigh less than *S. idalia* females in areas where hostplant density is greater? That is, can field data demonstrate that smaller adult females emerge on prairies having lower hostplant density?

MATERIALS AND METHODS

Tall-grass prairie is deemed the primary habitat of this species (Hammond & McCorkle 1983/1984, Opler & Krizek 1984, Shull 1987, Panzer et al. 1995), and the butterfly's presence is correlated with the presence of violets (*Violaceae*). *Speyeria idalia*'s larval host plants include *Viola pedata* (Bird's-foot Violet) (Opler & Krizek 1984, Shull 1987), *V. pedatifida* (Blue Prairie Violet), *V. papilionacea* (Common Blue Violet), *V. lanceolata* (Lance-leafed Violet) (Scott 1986), and *V. nuttallii* (Nuttall's Violet) (this study). Regions in Iowa where *S. idalia* is most abundant contain largely Blue Prairie Violet.

We measured wing length (as in Boggs 1988), thoracic and abdominal length and adult head capsule width of individual *S. idalia* adults at eight field sites in Iowa. We compared these measurements with those of adult *S. idalia* adults captured on eight sites in Kansas, South Dakota, and North Dakota. Field sites in Iowa were chosen after the 1995 field season when we surveyed more than 50 prairie areas in Iowa to determine which sites had violets and, of those, which had *S. idalia* (Table 2). We chose to focus on some of the larger *S. idalia* populations in Iowa

during 1996. Then, we examined prairie sites outside Iowa known to have relatively large, consistently observed populations of *S. idalia* as comparison sites for Iowa prairies to test our food-limitation hypothesis.

We estimated hostplant abundance as the number of violet stems/m² during April–June. Violet species found in Iowa and Kansas were *V. pedatifida* and occasional small patches of *V. papilionacea*, whereas the predominant species found in the South Dakota and North Dakota prairies was *V. nuttallii*. Because the total leaf area of plants counted in sites with the Nuttall's and Blue Prairie Violets appeared quite similar, we disregarded the species of violet in the statistical analysis. Stem-per-quadrat measurements of the dominant violet species were recorded in the alternate 1 m² subplots of each of five 10 × 10 m plots (a total of 50, 1 m² subplots per 100 m²). These plots were located in the areas of highest violet density. We also estimated the percentage of total violet coverage by evenly spacing 100 1 m² plots across the surveyed area of each prairie.

From these initial data, we calculated estimated hostplant abundance by multiplying the percent hostplant coverage (average of five 10 × 10 m plots) by the number of acres of habitat present or surveyed. This type of estimate skews the results toward higher values of host plant density, but it is consistently biased across all our sample sites. In each large prairie, we surveyed *S. idalia* populations in an area of 64.8 ha (200 acres) as determined by landmarks and section lines corresponding to detailed maps. In sites of less than 64.8 ha area, we surveyed the entire habitat for *S. idalia*. There were a few cases where habitat constraints prohibited sampling larger prairies at the full 64.8 ha scale. Ultimately, we used the two violet population estimates to examine the correlation between the hostplant abundance at each site with the *S. idalia* population estimate. Table 3, "Violet Estimate (or Extrapolation) for Entire Site" reflects the number of violet plants in the entire area of contiguous undegraded prairie (areas of 6.9 to 25,911 ha), whereas "Violet Estimate for Sampled Area" reflects the violet population in the area we surveyed for insects (areas of 6.9 to 64.8 ha).

Adult *S. idalia* at each site were captured with a field net, placed in a glassine envelope and weighed using a medium resolution electronic scale with a precision of 0.01 g and repeatability to 0.005 g. The weight of the envelope was voided to determine the weight of the insect. Other body measurements of abdominal, thoracic and wing length, as well as head capsule width, were taken to the nearest 0.1 mm with dial calipers. Head capsule widths in both larval and adult Lepidoptera have been noted as measures of development and nutrition (Bastian & Hart 1990, Charlet & Gross 1990, McClellan & Logan 1994). All measurements were performed before the oviposition season (Mattoon et al. 1971).

TABLE 3. 1996 violet density estimates, violet presence over entire area, and violet density estimate. ~ No population estimate possible without recaptures.

Survey Locations	<i>Viola</i> spp.	Five Plot Density stems/sq.m	100 Point Coverage as a percent	Hectares of Habitat	Hectares surveyed	Violet est. (or extrapolation) for entire site	Violet est. for sampled area	<i>S. idalia</i> 1996 pop. est.
Iowa	<i>V. peda.</i>	1.04	0.32	101.2	20.2	33,089	67,484	143
	<i>V. peda.</i>	0.52	0.43	10.1	10.1	22,757	22,757	159
	<i>V. peda.</i>	2.38	0.07	404.9	8.1	673,430	12,472	20
	<i>V. peda.</i>	1.02	0.13	485.8	64.8	644,171	85,925	258
	<i>V. peda.</i>	0.44	0.20	64.8	64.8	57,542	57,542	296
	<i>V. peda.</i>	0.49	0.18	64.8	64.8	57,387	57,387	453
	<i>V. peda.</i>	0.55	0.38	64.8	64.8	135,924	135,924	198
	<i>V. peda.</i>	2.36	0.36	49.8	49.8	423,101	423,101	57
	<i>V. nuttallii</i>	2.78	0.13	485.8	64.8	1,755,681	234,187	408
	<i>V. nuttallii</i>	6.26	0.28	486.0	64.8	8,518,608	1,135,814	315
South Dakota	<i>V. nuttallii</i>	5.52	0.33	323.9	64.8	5,900,162	1,180,397	396
	<i>V. nuttallii</i>	5.08	0.24	161.9	64.8	1,973,885	790,042	494
	<i>V. nuttallii</i>	5.86	0.22	81.0	64.8	1,044,252	835,402	200
	<i>V. nuttallii</i>	5.56	0.65	25,910.9	64.8	936,419,926	2,341,872	444
North Dakota	<i>V. peda.</i>	1.60	0.40	6.9	6.9	44,270	44,270	98
	<i>V. peda.</i>	3.50	0.53	3,481.8	64.8	64,587,390	1,202,040	~

Thus, the abdominal length measurements reflect pre-reproductive body dimensions.

A Lincoln-Peterson estimator with continuity correction was used to estimate population size (Brower et al. 1990). On the first day of a mark-recapture exercise, each insect was marked with a Sanford® Sharpie® ultra fine permanent marker and released for potential recapture. These marks may remain on a living insect indefinitely and were not observed to induce mortality or to limit flight mobility (pers. obs., see Nagel et al. 1991). Our sequence of site surveys generally went from south to north, so that we could obtain population size estimates that included both males and females after initial emergence. Each site was surveyed for a total of six person-hours per day, usually two consecutive days during the mark-recapture effort. We limited sampling at each site to two days to allow surveying at 16 sites. *Speyeria idalia* has a long flight period, especially in Kansas (relative to other butterflies that are univoltine). Maximum adult survival time has been estimated at 57 and 69 days for males and females respectively (B. Barton, pers. comm.).

Statistical analyses were conducted using Excel for Microsoft Windows, and included *t*-tests and multiple regression analysis. For each of the comparisons, Iowa insects or violets were grouped in comparison to insects or violets from the other states. In comparing weights, males and females were analyzed separately because of their difference in size.

RESULTS

Violet density. Iowa violet densities were significantly lower than those in other states, based upon our five plot density estimates ($t = -5.17$, $df = 10$, $p < 0.001$) and our estimates for the sampled areas ($t = -3.41$, $df = 7$, $p < 0.01$). Our extrapolations of total violets on entire sites did not show significant differences between Iowa and other states; there was considerable variance among the estimates. We found a positive, but non-significant correlation between the violet estimate for sampled areas and butterfly population estimates across all states ($r^2 = 0.25$, $df = 1, 13$, $p < 0.06$), and no significant relationship between estimated *S. idalia* populations and violet density for entire sites.

***S. idalia* population sizes vs. habitat area.** We found large populations of *S. idalia* across tall and mixed prairies of larger areas (Table 4) ($r^2 = 0.52$ for *S. idalia* population estimate versus hectares surveyed, $df = 1, 13$, $p < 0.01$). The greatest correlation observed was between the size of *S. idalia* male population estimates and hectares surveyed ($r^2 = 0.75$, $df = 1, 11$, $p = 0.17$). All analyses of correlation between recapture rates and habitat area or area surveyed yielded only slightly positive values and none was statistically significant ($r^2 \leq 0.49$, $df = 1, 11$, $p = 0.22$). There was the paucity of female *S. idalia* in Iowa prairies. In two days

TABLE 4. 1996 Mark-recapture raw data and Lincoln-Petersen estimators of 16 *S. idalia* populations. ~No population estimate possible without recaptures.

Survey locations	Mark-recapture dates	Male first day m_1		Male second day m_2		Male recapture m_2		Lincoln-Petersen pop. est	Hectares surveyed	Insect density est. (insects/ha)
		Female	Male	Female	Male	Female	Male			
Iowa	Loess Hills, Section 21	4	17	4	18	4	3	143	20.2	7.1
	Sheeder Prairie	0	52	0	32	0	15	159	10.1	15.7
	Stephens State Forest	0	7	0	6	0	3	20	8.1	2.5
	Ringgold Wildlife Area	1	59	1	42	0	12	258	64.8	4.0
	Cayler State Preserve	1	36	1	60	1	8	296	64.8	4.6
	Anderson State Pres.	2	65	2	50	1	8	453	64.8	7.0
	Kalsow State Pres.	1	31	1	30	0	5	198	64.8	3.1
	Rolling Thunder	2	16	2	11	3	5	57	49.8	1.1
	Murdo	36	32	36	24	30	7	408	64.8	6.3
	Wall	34	27	34	22	27	7	315	64.8	4.9
South Dakota	Harp Dam	28	17	28	14	24	1	396	64.8	6.1
	Richland Dam	45	6	45	10	41	1	494	64.8	7.6
	Antelope Creek	29	15	29	12	26	3	200	64.8	3.1
North Dakota	Sheyenne Nat'l Grass.	22	14	22	10	34	1	444	64.8	6.9
	Dorothy Akins	13	49	13	11	7	31	98	6.9	14.3
	Konza Prairie	24	40	24	38	32	0	~	64.8	~

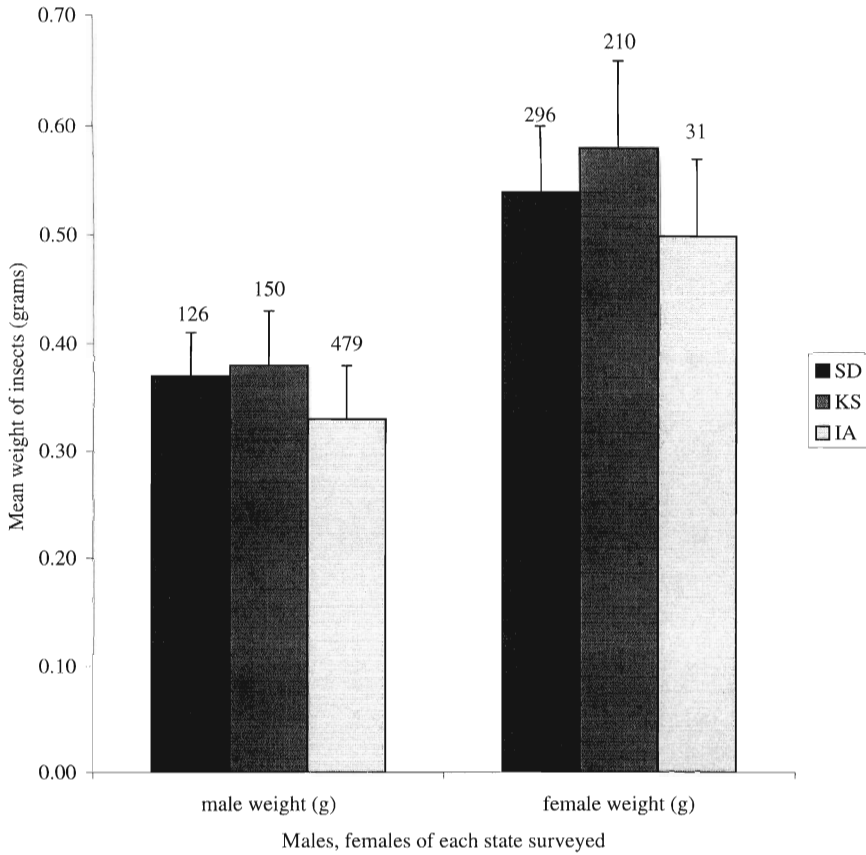


FIG. 1. Male and female mean weights (g) of Regal Fritillary (*Speyeria idalia*) adults from Iowa, South Dakota and Kansas in 1996. Bars indicate standard error and numbers indicate total insects weighed at all sites in that state.

during the peak flight period at Sheeder Prairie, we were able to catch 84 males and not a single female. Overall in Iowa, after spending nearly a month surveying areas in the state, we caught 479 males and only 31 females. Note that this number is somewhat larger than the values shown in Table 3 because there was a second site in the Loess Hills where the population was too small to conduct a mark-recapture estimate.

Insect body measurements. *S. idalia* weights were significantly lower in Iowa compared to other states (Fig. 1). Iowa male weights averaged lower than North Dakota, South Dakota, and Kansas weights for a difference significant at the $p < 0.001$ level (same results with separate t -tests: $H_A \text{ weight}_{IA} < \text{weight}_{SD \& ND}$, $df = 125$ and $H_A \text{ weight}_{IA} < \text{weight}_{KS}$,

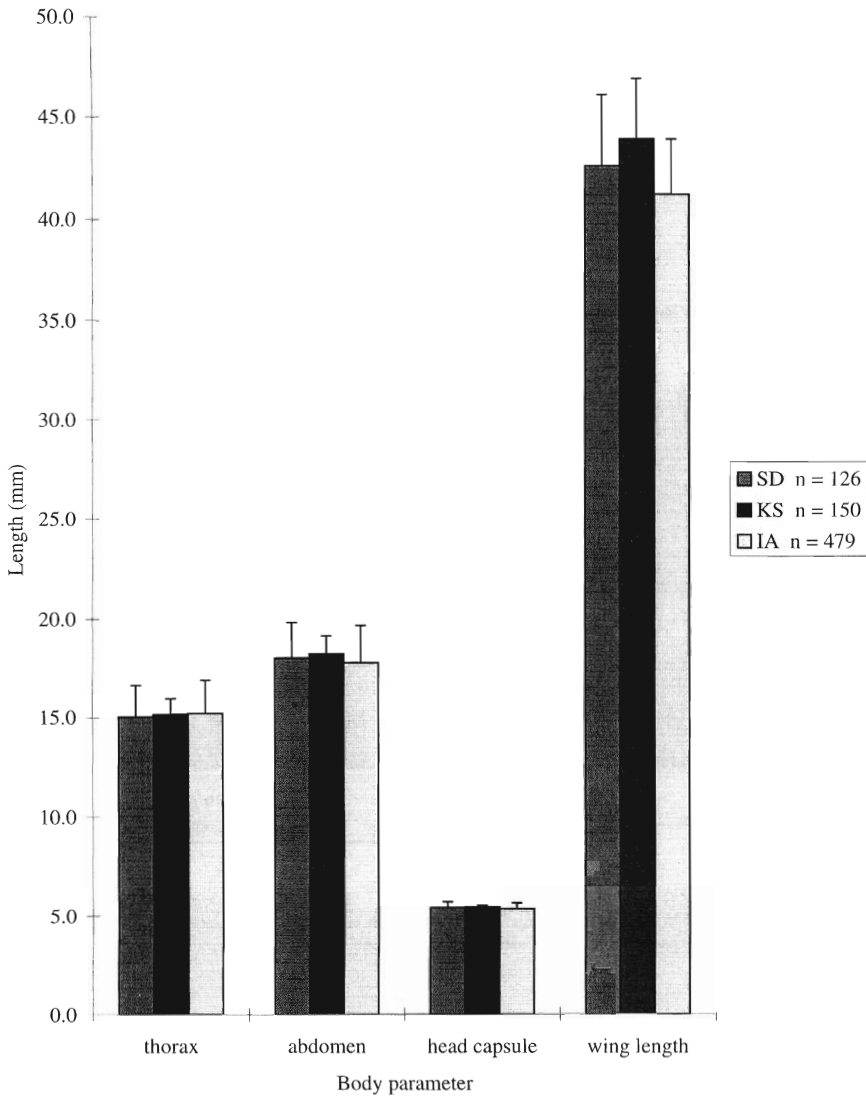


FIG. 2. Male Regal Fritillary (*Speyeria idalia*) adult body measurements from Iowa, South Dakota, and Kansas in 1996. Bars indicate standard error. Note sample size in legend.

df = 149). Iowa female weights averaged less than North Dakota and South Dakota female weights for a difference significant at the $p < 0.01$ level, df = 30 and less than Kansas weights for a difference significant at the $p < 0.001$ level, df = 30. Of the other body measurements, only male wing length seemed to vary geographically (Figs. 2, 3). Iowa male wing

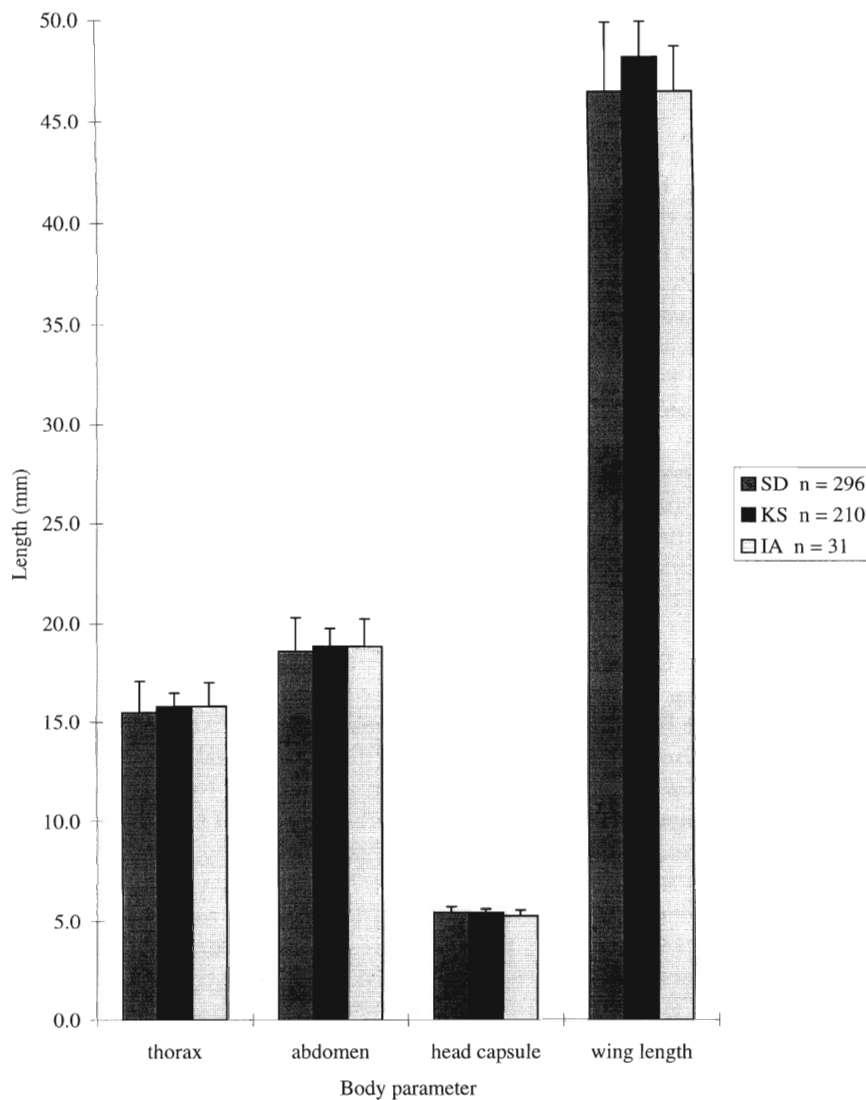


FIG. 3. Female Regal Fritillary (*Speyeria idalia*) adult body measurements from Iowa, South Dakota, and Kansas in 1996. Bars indicate standard error. Note sample size in legend.

lengths were less than North Dakota, South Dakota, and Kansas male wing lengths for a difference significant at the $p < 0.001$ level in both comparisons: H_A wing length_{IA} < wing length_{SD & ND}, $df = 125$ and H_A wing length_{IA} < wing length_{KS}, $df = 149$. None of the other insect body measurements varied significantly with geography. The correlation be-

tween insect body mass and all other parameters was between $r^2 = 0.60$ and $r^2 = 0.70$ (and not significant) at all sites surveyed for *S. idalia*.

DISCUSSION

Our data suggest that Iowa prairies produce comparable densities of *S. idalia* to the Dakotas and Kansas, but the total population size is smaller because the prairies (and thus total number of host plants available) are smaller (Table 4). These differences could have important conservation implications for the long term viability of *S. idalia* in Iowa. The correlation between *S. idalia* population sizes and violet density, however, was not as high as we had expected. Other factors obviously enter into the process of predicting an expected population size of this insect. For instance, one site in the Loess Hills Wildlife Area (section 9) in Monona County, Iowa had been burned in early 1996, and the fire may have killed most of the *S. idalia* larvae. This site was omitted from our food limitation study due to its low population size. A similar explanation may apply for the Hawthorn Wildlife Area in Mahaska County, Iowa, where a large *V. pedatifida* population consistently has been burned. Fire management may explain the low *S. idalia* populations at these sites as well, as Swengel (1996) specifically noted *S. idalia* as one of several prairie specialist butterflies that was most negatively affected by fire.

Another factor that complicates our correlations between *S. idalia* abundance and habitat parameters is the degree of isolation of some habitat areas where *S. idalia* is absent or found in small numbers. The extent of *S. idalia*'s decline and population isolation in Iowa has reached a point where distance from existing populations could be excluding the insect from otherwise suitable habitat. Sites that may have served as stepping stones (e.g., Smith & Gilpin 1997) in the past may be less effective now because of marginal hostplant and adult nectar resources. Thomas (1983) hypothesized that the butterfly *L. bellargus* may spread out in good years, but have a much more limited distribution in poor years. Similarly, Thomas and Harrison (1992) found that *Plebejus argus* populations in North Wales had high turnover of small populations and that the persistence of this spatially dynamic species depends on some suitable habitat being continuously available within relatively large areas. As each prairie site in Iowa becomes more marginal (through habitat destruction or lack of management), isolation from sites with stable *S. idalia* populations increases.

There may be a threshold value of hostplant abundance necessary to support a *S. idalia* population, and knowledge of this value would provide useful information in conservation decisions. Three other areas (not included in the 1996 mark-recapture comparisons or insect measurements) in Iowa with violets had only a few *S. idalia* individuals present.

Hostplant abundance at these sites was approximately 125,000 plants. Two other sites with an estimated violet population of around 13,000 had no *S. idalia*. We note that the violet estimates varied somewhat between 1995 and 1996, but this can probably be explained by a higher intensity of sampling during 1996.

The relationship between prairie area and male population size was not surprising given the fact that males patrol territories across the prairie. Thus, the more area we surveyed, the greater our success in marking male individuals. The females exhibited almost no territorial behavior, and to complicate our efforts at population estimates, females did not appear in sufficient numbers to provide reliable population data in Iowa prairies.

We arrived at the peak of female populations in South Dakota and North Dakota in mid-August of 1996. Here, females outnumbered males in all sites we visited. None of the grasslands in either state were as isolated as most of the prairies in Iowa, with the exception of the Wall, South Dakota site. This area had many *S. idalia* in a brushy drainage, but not nearly as many were found in the surrounding grazed area that isolated the drainage. This latter site yielded the highest male recapture rate (24%) of all North Dakota and South Dakota sites. The contrast in quality of surrounding habitat seemed to influence recapture rates and thus population estimates. That is, if less acceptable habitat surrounded the patch we surveyed, we were more successful with recaptures. Perhaps this result was an effect not only of the total area of habitat used, but also of the isolation of that habitat.

One of the more interesting results of our study was that adult *S. idalia* from Iowa were significantly smaller than the *S. idalia* from other states. This difference could potentially be the product of genetic drift working on small populations. *S. idalia* is a very strong flier, and in highly fragmented habitats there could be strong selection pressure against individuals that disperse (one could view this as dispersal suicide in highly agricultural landscapes). Those that remain may be the individuals that are less likely to disperse (i.e., smaller individuals). Hence there could be an opportunity for rapid genetic evolution. This same phenomenon has been observed in *Papilio machaon* in the UK (Dempster 1995).

Nearly all body measurements were predictable from the weight of the insect, although no substantial variation existed in thoracic length, abdominal length, or adult head capsule width. With the exception of wing length and overall insect weight, we found no difference in the means of other body parameters according to location or sex. We attributed the variation in weight between sexes to the greater abdominal mass (not necessarily length of body segments) of a female developing

eggs. However, it is interesting to note that female wing length did not vary significantly between Iowa and other states even though weight did differ significantly.

Hammond and McCorkle (1983/1984) attribute the decline of a number of *Speyeria* populations to the extent of detrimental environmental disturbances caused by humans. In Iowa prairies, the almost complete elimination of tallgrass prairie, erratic distribution of the remaining remnants, as well as low abundance of violets may be responsible for the small *S. idalia* populations. We focused our research on prairies that were relatively pristine, but even some of these prairies have had disturbances that affected all or part of the landscape. Many of the sites we surveyed in Iowa have extensive areas of invasive Brome Grass (*Bromus* spp.) that contain few if any violets, but *S. idalia* adults often patrol these areas and feed at the nectar sources present in them. Such areas with no violets may be detrimental to female fecundity (i.e., sinks (Puliam 1988)) if adult females spend significant time searching there in vain for areas with hostplants where they could oviposit.

Two unanswered questions remain. First, are hostplants limiting to *S. idalia*? Second, if so, how does the limitation of larval hostplants affect this insect? Quantifying not only the total biomass required to support one insect through its life, but also an entire population, would lend helpful evidence to conservation efforts. Females probably scatter eggs in the vicinity of violets, but do not oviposit directly on the violets (D. Wagner, pers. comm., Barb Barton pers. comm.). Thus mortality is probably highest in the first larval instar. An average *S. idalia* larva consumes 3–4 *viola* plants during the course of its growth (D. Wagner, pers. comm.). Estimating the total number of individuals necessary to maintain a viable population would be another important clue in conserving the species. In addition, knowing specifically how the effects of food limitation are manifested in an individual insect (number of eggs laid, total lifespan, delayed emergence, etc.) versus a population (adverse fluctuation in population size from year to year, or perhaps unequal sex ratios) would aid in gathering more meaningful field data and interpreting results. For example, male adults emerge earlier (at least two weeks) than females. If male larvae consume host plant resources faster than females, females may lack sufficient resources to finish their larval stage.

Ideally, we would use examples of stable *S. idalia* populations in native prairies to guide decisions regarding burning, grazing, or planting restored prairies in Iowa. Laboratory data would be helpful in assessing how much violet biomass is required to support each insect. Field work suggests that hostplant density and nectar availability could be just as important to the persistence of *S. idalia* populations as the amount of habitat available. Ultimately, we are interested in a threshold value of vi-

olet biomass necessary for preserving or restoring prairie areas with *S. idalia* populations. The quality of surrounding habitat available to the insects, as well as the isolation from other *S. idalia* populations, will also undoubtedly be important factors in the long-term persistence of *S. idalia* populations.

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LITERATURE CITED

- BASTIAN, R. A. & E. R. HART. 1990. Honeylocust clonal effects on developmental biology of mimosa webworm (Lepidoptera: Plutellidae). *J. Econ. Entomol.* 83:533–538.
- BOGGS, C. L. 1988. Rates of nectar feeding in butterflies: effects of sex, size, age & nectar concentration. *Func. Ecol.* 2:289–295.
- . 1997. Reproductive allocation in butterfly species with differing adult diets. *Ecology* 78:181–191.
- BOGGS, C. L. & C. L. ROSS. 1993. The effect of adult food-limitation on life history traits in *Speyeria mormonia* Boisduval (Lepidoptera: Nymphalidae). *Ecology* 74:431–433.
- BROWER, J. E., J. H. ZAR, and C. N. VON ENDE. 1990. Field and laboratory methods for general ecology. 3rd ed. W. C. Brown Publishers, Dubuque, Iowa, 237 pp.
- CHARLET, L. D. & T. A. GROSS. 1990. Bionomics and seasonal abundance of the banded sunflower moth (Lepidoptera: Cochyliidae) on cultivated sunflower in the northern Great Plains. *J. Econ. Entomol.* 83:135–141.
- COLLINS, N. C. 1980. Developmental responses to food-limitation as indicators of environmental conditions for *Ephydra cinerea* (Diptera: Ephydriidae). *Ecology* 61:650–661.
- DEBINSKI, D. M. & L. KELLY. 1998. Decline of Iowa populations of the Regal fritillary (*Speyeria idalia* Drury). *J. Iowa Acad. Sci.* 105:16–22.
- DEMPSTER, J. P. 1995. The ecology and conservation of *Papilio machaon* in Britain, pp. 137–149. *In* Pullin, A. S. (ed.), Ecology and conservation of butterflies. Chapman and Hall, London, UK. 363 pp.
- EISENBERG, R. M., L. E. HURD & J. A. BARTLEY. 1981. Ecological consequences of food-limitation for adult mantids (*Tenodera ardifolia sinensis*, Saussure). *Am. Midl. Nat.* 106:209–218.
- HAMMOND, P. C. & D. V. MCCORKLE. 1983/1984. The decline and extinction of *Speyeria* populations resulting from human environmental disturbances (Nymphalidae: Argynninae). *J. Res. Lepid.* 22:217–224.
- KELLY, L. 1996. Exploring larval food limitation as a probable cause of decline in Iowa populations of a butterfly, *Speyeria idalia* (Lepidoptera: Nymphalidae). Unpubl. M.S. Thesis, Iowa State University, Iowa, 62 pp.
- JOHNSON, K. 1986. Prairies and plains disclimax and disappearing butterflies in the central United States. *Atala* 10–12:20–30.
- JULIANO, S. A. 1986. Food-limitation of reproduction and survival for populations of *Brachinus* (Coleoptera: Carabidae). *Ecology* 67:1036–1045.
- MATTOON, S. O., R. D. DAVIS & O. D. SPENCER. 1971. Rearing techniques for species of *Speyeria* (Nymphalidae). *J. Lepid. Soc.* 25:247–256.
- MCCLELLAN, Q. C. & J. A. LOGAN. 1994. Instar determination for the gypsy moth (Lepidoptera: Lymantriidae) based on the frequency distribution of head capsule widths. *Environ. Entomol.* 23:248–253.

- NAGEL, H. G., T. NIGHTENGALE & N. DANKERT. 1991. Regal Fritillary butterfly population estimation and natural history on Rowe Sanctuary, Nebraska. *Prairie Nat.* 23:145–152.
- OPLER, P. A. & G. O. KRIZEK. 1984. Butterflies east of the Great Plains, an illustrated natural history. John Hopkins University Press, Baltimore. 483 pp.
- PANZER, R., D. STILLWAUGH, R. GNAEDINGER & G. DERKOVITZ. 1995. Prevalence of remnant-dependence among the prairie-inhabiting insects of the Chicago region. *Nat. Areas J.* 15:101–116.
- POSTON, F. L., R. B. HAMMOND & L. P. PEDIGO. 1977. Growth and development of the Painted Lady on soybeans (Lepidoptera: Nymphalidae). *J. Kansas Entomol. Soc.* 50:31–36.
- POSTON, F. L., L. P. PEDIGO & R. B. HAMMOND. 1978. A leaf-consumption model for the Painted Lady. *J. Kansas Entomol. Soc.* 51:191–197.
- PULLIAM, R. H. 1988. Sources, sinks, and population regulation. *Am. Nat.* 132:652–661.
- SCOTT, J. A. 1986. The butterflies of North America. Stanford University Press, Stanford, California. 583 pp.
- SHULL, E. M. 1987. The butterflies of Indiana. Indiana Academy of Science, Indiana. 324 pp.
- SMITH A. T. & M. E. GILPIN. 1997. Spatially correlated dynamics in a pika metapopulation, pp. 407–428. *In* Hanski, I. A. & M. E. Gilpin (eds.), *Metapopulation biology—ecology, genetics and evolution*. Academic Press, San Diego, California. 512 pp.
- SWENGEL, A. B. 1996. Effects of fire and hay management on abundance of prairie butterflies. *Biol. Cons.* 76:73–85.
- . 1997. Habitat associations of sympatric violet-feeding fritillaries (*Euptoieta*, *Speyeria*, *Boloria*) (Lepidoptera: Nymphalidae) in tallgrass prairie. *Great Lakes Entomol.* 30:1–18.
- THOMAS, J. A. 1983. The ecology and conservation of *Lysandra bellargus* (Lepidoptera: Lycaenidae) in Britain. *J. Appl. Ecol.* 20:59–83.
- THOMAS, C. D. & S. HARRISON. 1992. Spatial dynamics of a patchily distributed butterfly species. *J. Anim. Ecol.* 61:437–446.
- USFWS, UNITED STATES DEPARTMENT OF THE INTERIOR. 1996. 50 CFR Part 17, Endangered and threatened wildlife and plants; review of plant and animal taxa that are candidates for listing as endangered or threatened. *Federal Register* 1(40):7596.

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