JOURNAL OF
THE LEPIDOPTERISTS' SOCIETY

Volume 17 1963 Number 3

NOTES ON OVERLAPPING SUBSPECIES. II. SEGREGATION IN THE *SPEYERIA ATLANTIS* OF THE BLACK HILLS (NYMPHALIDAE)

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The authors have differing interests joined here in common cause. GREY studies distribution, morphology, and population structure of *Speyeria;* MOECK has broad acquaintance with Nearctic environments and butterfly populations; EVANS is one of the few who have mastered the tricky art of rearing *Speyeria.* EVANS's data are given separately, accreditable to him in entirety; the bulk of records and field notes are MOECK's, as are the maps; organization is by GREY, who is responsible also for suggested evaluations.

The title perhaps should have been qualified; the two described color forms apparently behave as separate "species" in the Black Hills although treated here as "subspecies" of *Speyeria atlantis* (Edwards). If they are indeed two unrelated organisms their differences in behavior and in larval and adult morphology deserve only brief description. The question of relationship will be passed over without prejudice, reserving opinion that expanded knowledge of total distributions in "species" like these will necessitate some amendments to present categorical rigidity.

GREY and MOECK (1962) stated a belief that the largest factor controlling population structure in butterflies is the residual inertia of genetic heritage, inferring that wing facies reflect earlier dispersal and isolation, relating only secondarily to present situations. Deduction of late glacial migrations from facts of present distribution has a large literature attesting that others share these apprehensions and the underlying assumption that wing facies must be relatively durable in time. However, studies often appear to indicate quite the opposite: breeding experiments show large genetic susceptability of short-term modification, and field samples reveal innumerable instances of variation correlated to particular environments, the usual interpretations of which are of "control" or "cause" by immediate factors in local environments. One or the other of these viewpoints must be seriously defective.

Following data demonstrate apparent control over population structure by factors in a present ecologic confinement, ostensibly showing that observed divergence is being encouraged or even "caused" by selective tailoring to fit the environmental cloth, the obvious correlations being analogous with those often cited as providing evolutionary mechanisms.

Exploring consequences of the latter view, of environmental pliability, which would be fatal philosophically to the conception of species developing at the slow rate allowing some present tracing of past wanderings, distributions cited in present papers are believed to represent recent contacts of intraphyletic segregates. Coercion provided by supposedly potent evolutionary factors in ecology and climate then become identical for two partially separately evolved "subspecies", which should encourage rapid blending. It appears in *Speyeria* populations, to the contrary, that present environments merely channel capacities for variations which correlate still better with inferred earlier histories and with the unknown inertial factor inasmuch as divergency remains far sharper than would seem demanded by present ecogeography. In these occurrences probably lie the best chances to arrive at some estimation of "species" and "subspecies" as they relate to time, which is the point of view suggested by examples like the following one.

MATERIAL

Photographs (see the plate) in black-and-white cannot do justice to the disparity of the color forms discussed herein. One of these (specimens A through F) is basally and marginally light above, with pale brick disk and unsilvered spots below; this form is termed "*lurana*", which is an available name for the Black Hills equivalent of the Colorado "*hesperis*" series. The other variety is darker above and has a blackish disk with silvered spots, nearly in the facies of nominotypical Appalachian *atlantis;* the tag used for this variation therefore will be "*atlantis*" (NOTE:—names herein are cited to take advantage of their descriptive values, non-categorically). Specimens G through L are illustrative of this Black Hills "*atlantis*"; speciments M, N, O are variant extremes: M approaches the "*tetonia*" of western Wyoming; N is dwarfed, has solid borders, touches of silver, reddish disk; O is silvered like "*atlantis*" but is intermediate toward "*lurana*" in discal color.

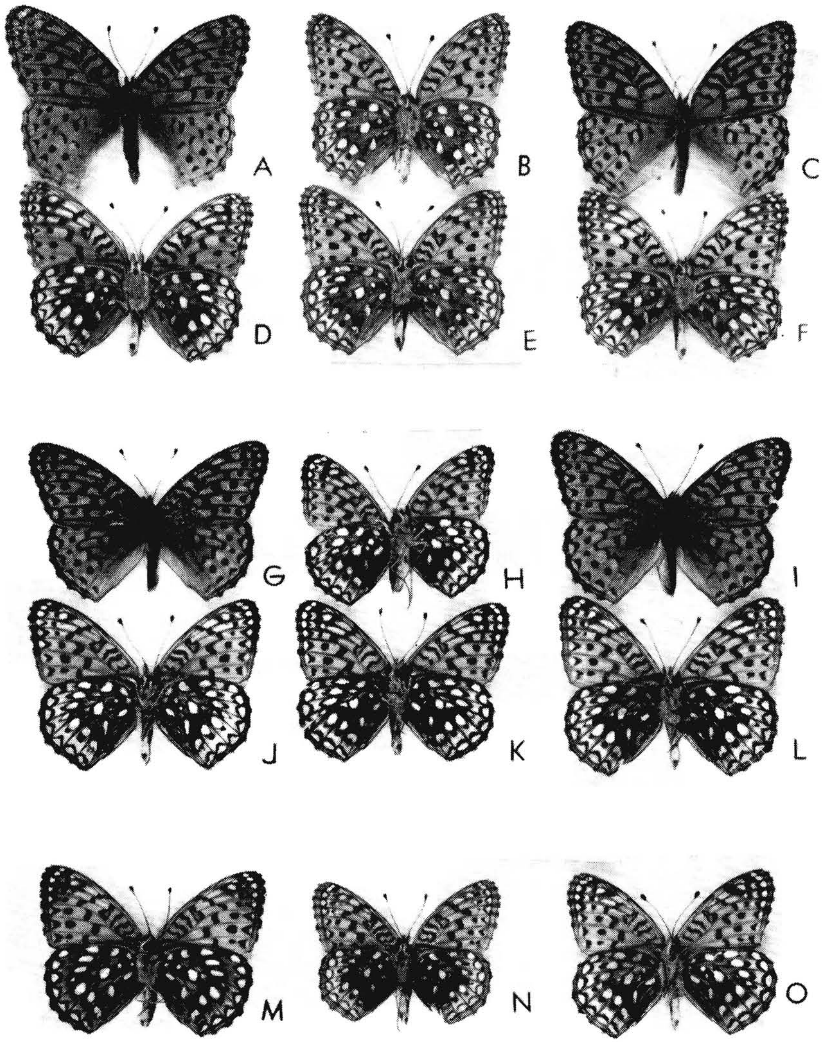


Figure 1: *Speyeria atlantis* (all males). Black Hills.

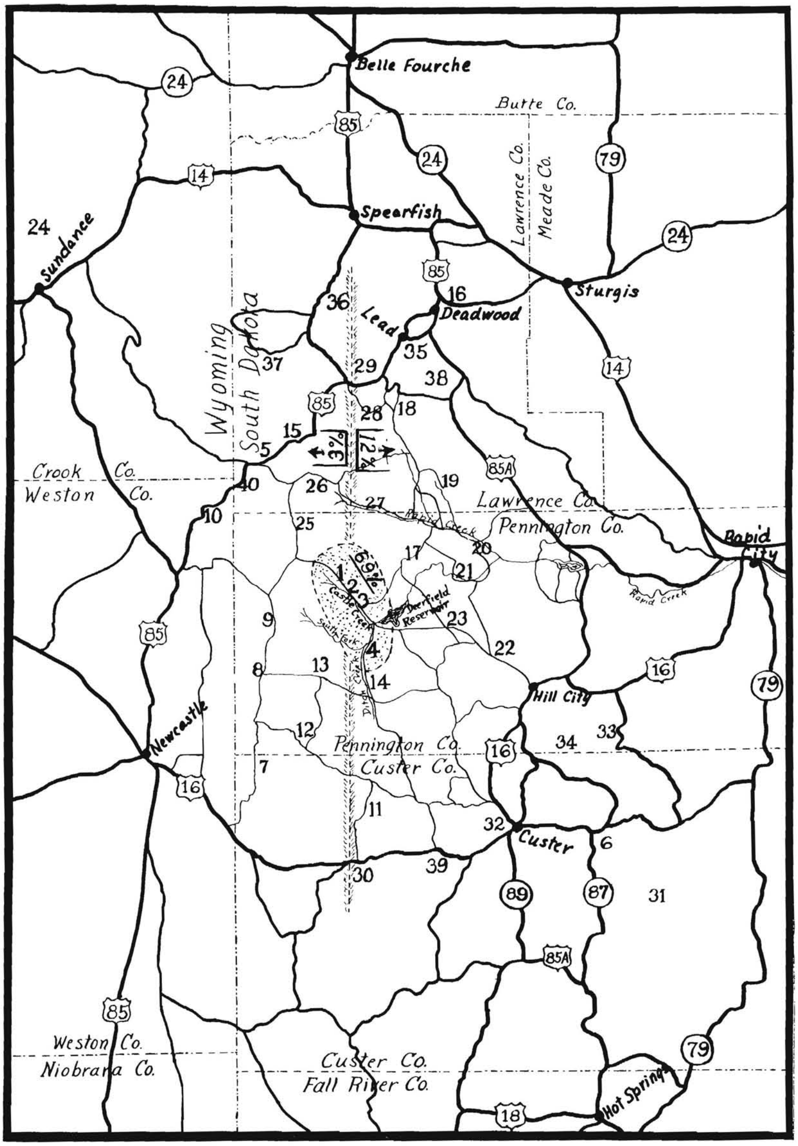
Site locations given in record table on maps 1-3:

A-F: *"lurana"* from sites 10, 40, 40, 10, 25, 17 respectively.
G-L: *"atlantis"* from sites 19, 3, 3, 1, 6, 1.
M-O: extreme variants from sites 40, 40, 4.

[Photograph by Kenneth MacArthur at the Milwaukee Museum.]

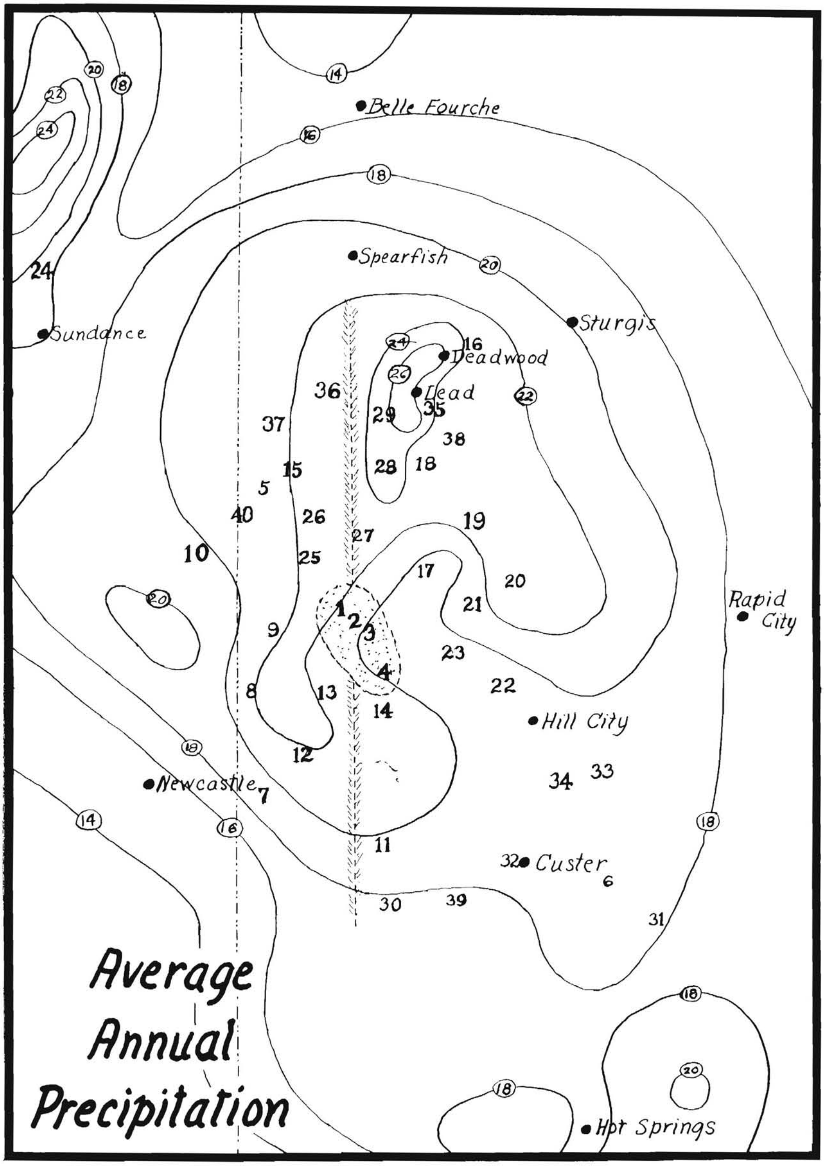
SOME BLACK HILLS RECORDS OF S. *"ATLANTIS"* AND *"LURANA"*

County and State	Map Symbol	Locality	Sample Size	% "A"
Custer Co., So. Dakota	6	intersection Hy. 16A & 87	6	33.3
	31	Custer State Park	19	31.6
	32	vic. Custer	9	22.2
	7	Boyles Canyon road	14	0.0
	11	Mud Springs road	13	0.0
	30	vic. Jewel Cave	26	0.0
	39	6 mi. E of Jewel Cave on Hy. 16	14	7.1
Pennington Co., So. Dakota	8	Moon campsite	2	0.0
	9	6 mi. N of Moon	2	0.0
	12	8 mi. S E of Moon	27	0.0
	13	5 mi. E of Moon	10	0.0
	22	9 mi. S E of Deerfield	19	5.2
	23	6 mi. E of Deerfield	13	7.6
	4	3 mi. S of Deerfield	35	42.8
	14	6 mi. S of Deerfield	40	12.5
	17	8 mi. N E of Deerfield	78	3.9
	3	2 mi. N W of Deerfield	73	90.4
	2	3 mi. N W of Deerfield	36	63.8
	1	7 mi. N W of Deerfield	72	62.7
	25	14 mi. N W of Deerfield	30	0.0
	20	1 mi. N of Mystic	38	10.5
	21	3 mi. S W of Mystic	26	3.8
	33	vic. Mt. Rushmore	5	0.0
	34	vic. Harney Peak	89	20.2
Lawrence Co., So. Dakota	35	vic. Lead	5	0.0
	36	Spearfish Canyon	19	0.0
	29	Terry Peak	5	0 0
	37	12 mi. S of Spearfish	3	0.0
	18	7 mi. S W of Lead	28	0.0
	38	6 mi. S of Deadwood	4	0.0
	16	2 mi. E of Deadwood	3	0.0
	28	vic. Hanna	18	16.6
	27	vic. Deerdale campsite	73	15.0
	26	5 mi. W of Rochford	36	5.5
	19	3 mi. N of Rochford	23	39.1
	15	3 mi. N of O'Neill Pass	7	14.2
	5	vic. O'Neill Pass	2	0.0
	40	3 mi. S of O'Neill Pass	12	0.0
Crook Co., Wyo.	24	5-6 mi. N of Sundance	30	6.6
Weston Co., Wyo.	10	Buckhorn – Four Corners road	36	5.5



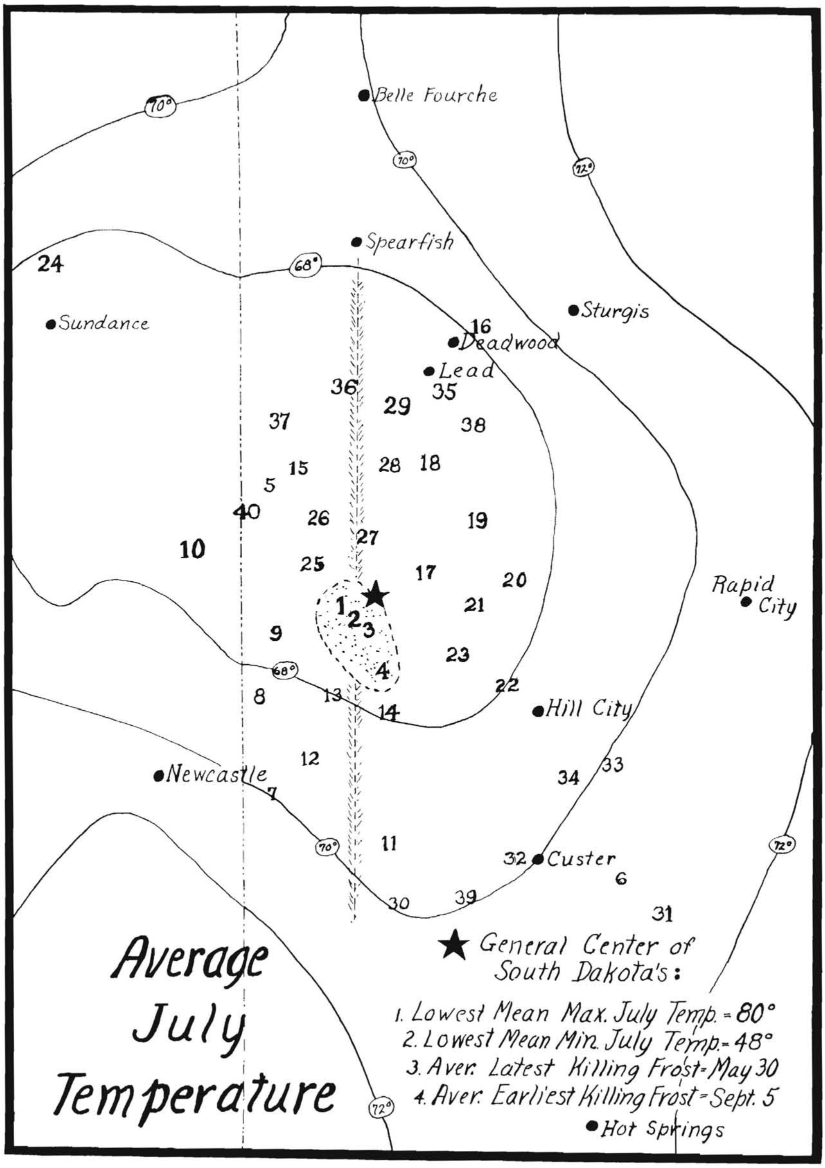
Map 1: Road network and collecting sites, Black Hills.

U. S. Hy. numbers in shields, State Hy. numbers in circles. Forest Service roads unnumbered (thin lines). Localities numbered 1-40 are as tabulated in the list of records. The shaded central region and shaded axis line delimit areas referred to in the text.



Map 2: Rainfall and collecting sites, Black Hills.

Isobars with average precipitations in inches, encircled. Numbers 1-40 indicate localities as listed in the record table. The shaded central region and shaded axis line delimit areas referred to in the text.



Map 3: Temperature data and collecting sites, Black Hills.

Isotherms of July temperatures in degrees F., encircled. Data as legended by the star locate the boreal center of this ecogeography. The numbers 1-40, and the shaded central region and shaded axis line refer as in maps 1-2, to tabulated collecting sites and to areas discussed in the text.

The number legend on maps 1-3 keys the location of collecting sites as numbered and listed in the table of records; map 1 orients these records to the road network, map 2 to regional precipitation, and map 3 to temperature data.

The table of records, when studied in conjunction with the maps and photographs, will show character distributions inviting closer attention.

NOTES SUPPLEMENTING THE RECORD TABLE

From field data of 1,000 specimens three points have been emphasized by tabulation, these being: 1) SITE LOCATION (charted on the maps); 2) SIZE OF SAMPLES from each site; and 3) PERCENTAGE OF "ATLANTIS" INDIVIDUALS (% "A"), *i. e.*, those with characters of blackish disk and silver spots, this % "A" being the point to note especially, in context with sample size suggesting degree of reliability and with local ecogeographic factors next described. Omitted data seem of no immediate concern but are available to interested persons, recorded for each series in GREY'S card file of *Speyeria*, viz: ALTITUDE, which does not correlate especially with population structure here, for reasons noted later; SEX PERCENTAGES — there seems to be no hint of sex-linkage except in the well-known characters of vein scaling, wing shape and pattern nuances; DATES — the flight period is well-known: one brood through July and August, surviving to mid-September, peak in late July; ECOLOGICAL NOTES — these are summarized to the extent deemed necessary by a following exposition. All of these plus NOTES ON SYMPATRY, NAMES OF COLLECTORS, DEPOSITION OF MATERIAL, would take space disproportionate to assumed value, whereas the three groups data tabulated are sufficient in demonstrating the relationship which population structure of this Black Hills "*atlantis* - *lurana*" bears to the local ecogeography.

The small samples listed are included to give available information regarding dry areas where these insects are rare; in sum, they assume considerable significance. Many records had to be omitted, for reasons of various defects in data; the majority of the specimens tabulated were taken personally by MOECK and all others are from spot localities visited and surveyed by him.

SUMMARY: The "*atlantis*" individuals are concentrated centrally in the Black Hills; the corrected proportion for locations 1-2-3-4 (shaded area on maps) is nearly 69% in the 216-specimen sample. This may be compared against a percentage of 9.44% derived from the 784 examples from *all other* Black Hills collecting sites. Another indicative correlation appears when omitting from consideration the material from central areas where "A" runs high as noted: the proportion *east* of the shaded central axis line corrects to 12.09% but drops to 3.04% *west* thereof. The western series run almost everywhere largely "pure", to *"lurana"*; the eastern set shows larger variability. There are numerous local oddities, one of the largest being the apparent rarity of *"atlantis"* in the Deadwood - Lead region, along with the scattered high percentages in a few places, for example, in the Custer State Park area, around Harney Peak, and especially the "locality 19" sample which is on the Silver Creek road north of Rochford. But this latter sample was from a boggy meadowland, reinforcing the rationale next following. The striking facts are (1) of westerly diminution of % "A" and (2) of amazing rise in a central area, both of which can be understood after taking a bird's-eye view of the Black Hills.

ECOGEOGRAPHY OF THE BLACK HILLS

The forested Black Hills upland rises out of surrounding plains and badlands, being roughly one hundred miles north-to-south and fifty miles or so across. The Belle Fourche and Bear Lodge outliers customarily are reckoned in as part of these Hills. The region is one particularly interesting to zoogeographers, by reason of its mixed Eastern and Western biota, and to geologists because of the dome formation exposed through erosion. Toward the central part of the dome there is an interior network of Forest Service roads allowing more thorough coverage of the whole bloc than ordinarily can be managed when working in mountainous uplands. The looping main highway which circumscribes this area encompasses all major ecogeographic features of the Black Hills, defining a plot which is nowhere over twenty miles in radius, a beautifully accessible natural "laboratory".

Contrasts in plant associations are relatively slight; the rather sparse coniferous forest is fairly continuous except as interrupted by rock outcrops and grass or scrub patches. Altitudinal banding is hardly noticeable since elevations on the whole upland vary mostly only between 5,000 and 6,000 feet. A few extremes run into different zonal categories, down to 3,000 feet in fringe areas and up to over 7,000 feet on some of the south central monadnocks.

Erosion across the central dome has exposed surrounding sedimentary layers uptilted by the underlying laccolythic intrusion, viz, of sandstones, conglomerates and limestones which now appear as inward-facing escarpments. The outer sandstone rim and the interior "red valley" encircle a second principal rim, of limestone, which in turn surrounds an innermost core lying southerly on granites and northerly on schists.

By far the most important ecological feature of the Black Hills therefore is one which perhaps would not be appreciated at all except by a sensitive field naturalist, namely, the relative impermeability of the central granitic - schistose rocks, whereby water is retained in the soil to a much larger degree than is the case in areas with the sedimentary and conglomerate tilted layers (in fact, these aquifers are quite famous, the spectacular artesian wells which have been drilled hundreds of miles away attest to their porosity). All of the surface moisture, including the small streams, passes into the rocks and disappears in the outer regions but continues through the summer months in the interior, whereby central temperatures and humidities are kept more steadily distinctive than could be appreciated from the bare figures of annual precipitation and mean temperature (which run from about 22 inches and 43° centrally, to about 16 inches and 47° around the outer rims). Interior ground-level vegetation and dwellers thereon undoubtedly experience later-lingering fogs, reduction of nocturnal-diurnal fluctuations, more cooling through sustained evaporation and other correlated effects. It is seen in the presently described distribution that the *"atlantis"* characters dilute rapidly in samples taken when proceeding outward from the granites and schists and into the sedimentary and conglomerate rim and valley areas where temperatures average a bit higher and precipitation somewhat lower. It can be observed also that the climatic correlations, although definite, are far from precise and that it is the association with the geology, especially with the granites, which is the one most satisfying from the general viewpoint that local ecologic balances are dependent here primarily on the composition of the bedrock; all of the "large % A" samples are from granite areas. It should be emphasized again that the central area west of Deerfield Reservoir, where *"atlantis"* runs around 70% and up to over 90%, is even more boreal than climatic statistics would show: quoting Ranger WALTER RULE (personal communication) ". . . these central stream-bottom meadows once were quite boggy . . . probably the last of these wet sites left in the Hills."

[There is a recent addition to the field data: MOECK's 1962 records of 151 individuals have been worked over for last-minute notice; percentages are 92.5% "A" in 85 examples *from the shaded central area,* and 3.0% in 66 specimens from *outside the central area,* further substantiating the pronounced segregation and further suggesting that the principal ecogeographic determinants are the ones previously deduced.]

At any event, it is clear that the *"atlantis"* and *"lurana"* of the Black Hills have a distribution pattern showing a large correlation with habitat. But before assigning any particular meaning to these data in the usual terms of evolution and adaptation it might be well to pause and reflect that these two color forms pretty surely are quite recent immigrants, which then would lead to question whether the Black Hills were necessarily the spawning-ground of this segregation and might suggest a need for a somewhat larger accounting than would be possible within the confines of the Black Hills.

DISCUSSION

The material seems mostly easy to sort into one category or the other, indicating segregation of quite advanced degree. There are, nevertheless, many indications of recombinations and blendings such as would mark closely parallel genetic constitutions if not outright hybridization. For example, there are the "red-silvered" individuals of varied discal shades (like specimen O, fig. 1); these occur fairly commonly (and perhaps significantly in areas harboring highly mixed populations, although rare or absent in the purer *"lurana"* colonies). It is fair to say that students familiar with general aspects of the Western variation in this complex, as next described, but lacking knowledge of the local correlatives as hereby presented, would hardly dare to guess whether the Black Hills material represents one species or two. The rift in the variation is clear, but so is the overlap.

The present *atlantis* concept is of a continentally dispersed series of geographical replacements overlapping in various degrees according with their various stages of "subspeciation" and "speciation", as roughly outlined separately by GREY (1951) and MOECK (1957). The *"atlantis"* facies characteristic in the eastern United States also is visible in the Western complex throughout the Rocky Mountain sector, carrying southwesterly to Arizona and northwesterly to Idaho, subordinate to and often submerged by redder phases but persisting until finally lost in divergent populations of the far Southwest, far West, interior Great Basin, and northwest prairies. The common circumstances everywhere in the Rocky Mountain variations are: 1) of almost complete domination by single forms with only occasional extremes suggesting taint from contact with other "subspecies"; 2) of distinctive facies in the majority of individuals along with intergrades and sharply contrasting extremes which are too numerous and too steadily distinctive to dismiss as freaks of variation; and 3) of roughly equal balances between dissimilar forms, with few or no intergrades, suggesting presence of separate species. These situations, modified in all conceivable degrees, are part of the daily experience of collectors in Colorado, New Mexico, Wyoming, and Montana, so there is no difficulty here to make out a case for the existence of a large problem in species definition, whether or not there is any agreement with our present diagnosis relating these varied population structures to earlier confinements and migrations and to resulting clashes between intraphyletic isolates with differing capacities to blend.

On the available data there is no denying that the Black Hills situation approximates the one to be expected in the case of two reasonably discrete "species". Looking farther afield, a ready source of "*atlantis*" in this facies, with built-in tolerations of "wet" and "cold", is seen nearby in the Superior Upland population; "*lurana*" is equally easy to locate southerly, in Colorado. A good rationale would be that "*atlantis*" was the first arrival and that "*lurana*" would have had no need or inclination to go ashore here during the postglacial wetter interval when the Hills were cooler and before the Plains reached their present advanced stage of desiccation; "*lurana*" would have intruded about at the time when "*atlantis*" would have begun a retreat from peripheral drying and toward the wetter interior, as fits with the demonstrated ecological preferences.

It seems then that these insects now are being forced into close spatial contact by the further drying and warming of the Hills and that they have been in contact temporally for some hundreds if not thousands of years. The case therefore becomes that they were different "species" to begin with or that as "subspecies" they have been remarkably exempt from the supposed leveling results of intermingling and the assumed directive mechanisms of ecology, inasmuch as they appear to be clinging stubbornly to their earlier ways of life and also to their "Colorado" and "Superior Upland" facies. In either event, the present correlations of morphology and behavior with environment are significantly reduced in meaning, to the status of secondary and incidental phenomena proceeding from genetic structure earlier acquired rather than from local evolution on a "here and now" basis. This is a minor victory for the "genetic inertia" viewpoint; a larger triumph would result if these organisms could be proved "conspecific", for then the segregation would acquire still more definite perspective as a demonstration that evolutionary changes are quite slow and that wing facies tend to provide reliable indices of population movements.

The latter proposition apparently is true to this extent: specialists are agreed that most populations are best understood as products of genetic - geographic diffusion; variation at given loci usually has observable sources in a nearby or surrounding gene pool. This being the normal thing, there has been little reason to question the validity of sympatry as a test of specificity: sharp discontinuity vis-à-vis sympatres has been accepted as final proof of discreteness. The classification of *Speyeria* by DOS PASSOS and GREY (1947) represents one of the earlier breaks with that tradition, lumping dissimilar forms known to coexist or to occur juxtaposed and without reasonable barrier between, as seemed proper for emphasizing still more basic discontinuities apparent between groups termed "species". It has appeared subsequently that other genera are plagued with similar difficulties, and it has become generally acknowledged that the species concept based on fairly uniform clinal diffusion is subject to these large exceptions introduced by collisions between partially separately evolved moieties which appear as "species" in some places, as "subspecies" in others.

Plans for future papers include further data suggestive of the extent to which local segregations may or may not be definitive of "species". For the moment, LORKOVIC's (1962) data for *Pieris* will hold the line for the view that data of sympatry, like other data, are to be sprinkled liberally with the salt of comparisons. His extensive study brings out categorical insufficiencies, in a way to suggest that taxonomy is not a proper device for indicating local degrees of racial or specific "purities". From the time of SUMNER's (1915) classical work with Deer Mice there have been many local studies of *local* problems of speciation and subspeciation which have resulted in locally defensible answers, but of many kinds, of many degrees of categorical simplicity or complexity. LORKOVIC's solution is quite straightforward: straddling the crack. Seriously, though, these many demonstrations of categorical inequalities all go to point up the need to interpret sympatry in relative terms, requiring for this purpose an expansion and cross-comparison of data sets on a scale as yet unrealized in any genus.

Far more than generally appreciated, the riddle of "species" and "subspecies", and also the even more intriguing question of evolutionary meaning in local variation and of the manner in which it may relate to time and paleogeography as well as to present local environments, all will come down to proper understanding of sympatry. In this connection *Speyeria* has virtues too often ignored, perhaps as a reaction to a bad reputation for "variability". A better standard should be availability, and richness of data afforded by numerous closely related and co-distributing "species". Who could ever hope to assemble "northern front and alpine" material to the extent needed for a comprehensive survey of Holarctic *Pieris*? The speyerians, at least, are confined to one continent and occur mostly in accessible regions, colonial and locally abundant. Even so, the needed comparative data are slow to accumulate. In "*atlantis*", for example, there are obvious gross deficiencies.

Field work is needed: in the Teton - Absoroka region of northwestern Wyoming, and also in the Laramie area in the southeastern corner of that state; on both sides of the Bear River Range in Utah and Idaho; in the foothills - prairie fringe of the east slopes of the Rocky Mountains in Montana and Alberta; in the White Mountains of Arizona; and in the Riding Mountains of Manitoba. And this names only a few of the places where need for close study is suggested by apparent segregation observed in available material. The sad feature is that most of these places have been explored, or even heavily collected; the blame for present uncertainties must fall equally on specialists and collectors.

Investigations of continental population structures are too far beyond the capacities of individuals in single lifetimes; more should be done than is being done to encourage cooperation. By and large, collectors respond well to suggestion, as can be seen in the improved standards of data-recording which have followed upon educational campaigns in recent popular manuals and journals. It has become generally appreciated that material labeled as from, *e. g.*, "Utah" is practically valueless. The time approaches when collectors must realize that even with localities and other data properly recorded, their material may well end up with the "Black Hills" and "Oregon Territory" specimens of an earlier day, in the wastebasket. Discrimination and purpose now begin to mean far more than "specimens"; museums are clogged with uncorrelated rubble.

A reorientation of effort, toward ecogeographic analysis, would require no more energies than are expended now at random. A short article by EFF (1956) comes to mind, on a Colorado *Speyeria* distribution, which as a contribution to understanding of a local "speciation" and of local sympatry is suggestive and valuable all out of proportion to the small size of material cited, simply because the collecting was done with a careful eye on the ecogeography.

Nothing could drive home this point of the sore need for improvement in field collecting more clearly than to review the present status of *"atlantis"* in Colorado. Data sets from this one state would go very far toward elucidating the subject of environmental influence vs. earlier population movements. And there is no lack of material; in fact, "specimens" are the least of the needs; the bulky records already are a cup of tea for Tantalus. This variation is abundantly well-known and has been known for many years; what need of more specimens to prove that it exists and what point in catching more unless something can be done with them? The thing needing attention of course is to relate this variation to the places where it is found. What happens, say, in Jefferson County, where samples indicate that *"hesperis"* prevails overwhelmingly in many areas – can *"atlantis"* be found there, as established populations, merely by going to nearby cooler and wetter localities, as the Black Hills data might suggest? Surely, collectors will not pass by challenges of such fascination, once they are appreciated.

The largest fact in butterfly taxonomy today is the foundering of the species concept on the reef of segregation. The best hope for further understanding can only lie with local analyses and the ultimate integration of continentally representative data sets. The time seems ripe for a large expansion and popularization of the needed field research, assuming that students will be easily weaned from their bemusement with "storybook taxonomy" once they realize that even the specialists are largely ignorant of "species and subspecies" and that nobody can be any wiser until more is definitely known of local population structure and of the manner in which it relates both to local ecology and to specific continental distribution patterns.

REARING AND BREEDING NOTES

More from curiosity as to the ease of getting ova that from any intention of starting experiments, MOECK confined a few of the dark, brightly silvered *"atlantis"* females in paper bags and did likewise with unsilvered red *"lurana"* females; all were taken Aug. 1-2, 1962, in the Black Hills, about 1 mile above Castle Creek in a locality where % "A" runs about 44. Finding eggs in the sacks, which had been deposited during the drive home, MOECK stopped in Minnesota and airmailed them to EVANS. Aside from the initial separations, by color, which were maintained, particular ova were not associated with particular females. EVANS's foundation stock therefore consisted of 7 *"atlantis"* and 50 *"lurana"* ova, received Aug. 6, from which 3 *"atlantis"* and 27 *"lurana"* were reared through to eclosion, proving true in facies to their respective known maternal phenotypes and showing early stage differences as described later.

After hatching, each larva ate about half its eggshell, then crawled at random for about 15 minutes, finally settling on a stem or leaf (foodplant offered: a lavender-flowered cultivated *Viola*, also a transplanted purple-flowered species from lowlands of the Patuxent River, Maryland).

The well-known snag in rearing *Speyeria* is that the overwintering tiny larvae have a habit of dying, regardless of treatment. EVANS's technique, first of all, is to break the diapause. After having settled down, each larva is transferred by camel's hair brush to small bits of paper towel which have been soaked with distilled water. When the larvae crawl away they are transferred immediately to a violet leaf where they promptly go to sleep again. This disturbing has be be done repeatedly, each day and for many days, to be successful. With this material no nibbling took place until the eleventh day, after which the larvae one by one began to eat and no subsequent prodding was required.

One larva ate first on Aug. 24, another on Aug. 30; the last two did not begin to feed until Sept. 11 and 12. From the time the diapause is broken until pupation the six larval stages are passed through in a period varying between about 24 to 34 days; 2 to 7 or 8 days are spent between molts. The first molt occurs a few days after eating begins and after a rest of about 12 hours. From the second molt on, the larvae always crawl off the fresh leaf after eating and rest nearby between meals (as they do in nature, usually hiding during the day).

Rearing cages used were tiny and then progressively larger plastic boxes, ending with screen-topped cottage cheese cups with violets kept fresh by running the stems through holes in the boxes to a jar of water below. Temperatures were maintained at room levels, between 64°-74°; humidity of course was very high within the boxes, particularly in early instars when bits of leaf were kept fresh by damp sand.

Before pupation these larvae spun a heavy mat of silk over at least one square inch of screen wire and made a sheltering curtain from bits of leaves, stems and other debris tied together with many strands of tough silk. One "*lurana*" larva was observed to make a crude cocoon beneath a large dried violet leaf, spinning silk to form a roughly spherical space between the leaf and the floor of the cottage cheese cup. Lacking room to hang vertically during pupation this larva fastened its anal prolegs to a silk pad and then was able to pupate in a nearly horizontal position. None of the other larvae were furnished with leaves large enough to form such chamber.

From the time of the fourth molt the larvae of the two varieties could be told apart by color of the double dorsal stripes: light brown in "*atlantis*"; grayish white in "*lurana*". They were otherwise quite identical in black ground color and orange of spine shafts. The pupae appeared distinctive in coloration, "*atlantis*" being darker and with less of the light brown shadings which variably mottle the wingcase area in "*lurana*". These observations were limited by the stated extent of material, which also limited breeding experiments, viz:

The single "*atlantis*" male emerged on Sept. 29, too far ahead of the first female (Oct. 26) for mating. Both sexes of "*lurana*" emerged contemporaneously with the mentioned "*atlantis*" female. Mating cages used were the gauze "picnic parasols" (as sold to keep flies from food) which are about 20 inches square, 16 inches high. The butterflies were fed from pieces of wet sponge sprinkled with granulated sugar and inserted in vials with attached stiff wire handles, facilitating movement to different locations within the cages.

At the time when the first female "*lurana*" emerged, on Oct. 20, a large male of similar color was still flying vigorously in a mating cage (this male, which emerged Oct. 11, was the only one out of several males confined, to master the art of hovering without colliding with sides of the cage). This pair, identified as male #5 and female #5, were nearly identical in facies aside from the usual sexual nuances and the trifle of silver in the female submarginal lunules. When this female was introduced into the cage the male lit beside here and twitched his wings. Another male in the cage flew down to investigate and the #5 male drove him away; the extra male then was removed from the cage. Several times thereafter the male came close to the female and twisted his abdomen toward her but she ran away. For two days she kept her abdomen hidden between tightly folded wings whenever he approached. On the third day she was observed to protrude her genitalia. It is believed that a scent was emitted and further suspected that the large dorsal gland is a special organ for this purpose and that release of a scent by the female is an essential part of the courtship ritual. But when the male approached she again ran away and sometimes even dropped to the floor of the cage to evade pursuit. A second female "*lurana*" was introduced briefly; she behaved similarly when pursued by male #5.

It was deduced finally that perhaps the room lighting was inadequate to simulate natural conditions, and a 60-watt incandescent bulb was placed 10 inches from the cage. This was on Oct. 31. Male #5 then flew to female #5 within a few minutes after the light was turned on. He hovered some seconds below her as she hung from the top of the cage, brushing against her wingtips several times (perhaps releasing his own scent from the androconial scale pouches); then he settled beside her and initiated copulation, which lasted 95 minutes. From Nov. 1 through 8 this female laid 327 eggs while confined in a quart-sized cheese container with gauze cover, placed 2 inches below a 20-watt fluorescent bulb. About 200 eggs were placed on the gauze cover, the rest on enclosed dried violet stems and leaves. About half of these ova hatched; the rest changed color in a way to suggest fertility. This female was 11 days old, the male 20 days, at the time of mating. This stock, of known "*lurana*" parentage on both sides, is being maintained for study, and notes will be published if anything further of significance is found.

The female "*atlantis*" (#A-1) which had emerged on Oct. 26 then was placed in a cage with this same #5 "*lurana*" male. The following day she protruded her genitalia when he pursued her. Several times he nudged the tip and sides of her abdomen with his head; she would move forward an inch; he would nudge her several more times until she moved forward again. This alternate nudging and walking was repeated many times, until the male flew away after having followed her for a distance of some 12 inches. Over a period of 7 days this highly peculiar courtship was continued, sometimes under artificial light, sometimes with only daylight. The male did not twist his abdomen toward her at any time as he had been observed to do consistently with females of his own kind. EVANS believes that the male coaxes the female to release a scent which in this case may have been similar enough to his own kind to keep his interest, but still not quite the proper mating stimulus (a keen point, this, as to which sex has the final word in selectivity). At any event, nothing came of this attempt and a further experiment was initiated, using another male.

Three males from the "*lurana*" batch differed from their brethren in being lighter orange above and light brown below. One of these, #6, had full silver and thus was somewhat intermediate in facies. When released in a cage with the "*atlantis*" female #A-1 this silvered male #6 paid court after the same fashion as male #5, although less aggressively. Copulation was not induced. The male #6 gave no regard at all to a "*lurana*" female with which he was confined for 12 days; this male was comparatively inactive, anyhow. Finally, on Nov. 14, when both male #6 and the "*lurana*" female were getting worn, artificial pairing was undertaken. Each specimen was fastened to a separate strip of yucca pith, the wings clamped with folded cardboard and bodies held by surrounding pins; the abdomens then were brought into contact by moving together the yucca strips; they were then left undisturbed in a semi-darkened room. Copulation had begun when they were checked 15 minutes later and lasted 90 minutes after they were released from the clamps. Results: 80 ova produced, all infertile.

An attempt to pair the "*atlantis*" female #A-1 with a male "*lurana*", by this same technique, was not successful; both specimens died the next day after this attempt, so the failure may have been due more to physical condition than to incompatability.

CONCLUSIONS: Aside from the obvious indication, namely, that these comparisons and experiments suggest "specific" differences, nothing else can be urged except that more work could be given profitably to this fascinating subject of mating behaviors, as well as to genetic structures since the latter remain wholly unknown. Even the former judgment, of "specificity", seems unsafe, remembering that BROWN (1961) refuses to admit unqualified separation of *Coenonympha* populations on one island which differ to the extent of having different flight periods and apparent larval differences. BROWN's mathematical treatment of wing-character comparisions provides evidence of probable gene interchange of surprisingly high frequency even though those populations at the same time are obviously discrete to some large degree. Unequivocal determination of "species" would seem equally suspect in the present instance, although the Black Hills segregates of *atlantis* exhibit a degree of independence which is certainly large. There are reasons to believe that further studies here and in other localities would be profitable since this case history of largely segregated color forms seems intimately associated with the basic problems of species.

SUMMARY

1. This paper is the second in a series developing the viewpoint that butterfly population structures probably reflect earlier isolations and movements to an extent larger than might be supposed from the emphasis customarily given to present environments.

2. From joint study of behavior and variation of *Speyeria "atlantis"* and *"lurana"* in the Black Hills, MOECK, who took extensive population samples, discovered a large correlation with environment; the *"atlantis"* percentages increase toward the central granites and rise very high in the boggy meadows in the middle of the Hills.

3. EVANS, who conducted rearing studies, reports differences in pupal color and in color of larval dorsal stripes; behavior which may indicate courtship barriers also was noted during attempted matings.

4. GREY, who is assembling comparative data of the "cluster group species" in *Speyeria,* attributes this segregation to earlier history, to collision between Superior Upland and Rocky Mountains populations, suggesting also that comparisons in other regions almost surely will reveal that there are large differences in the local extent of blending and separation. The authors agree that there can be no prospect of correcting or finalizing present tentative classifications until regionally adequate data sets become available to permit comparisons on a much larger scale.

References

Brown, F. Martin, 1961. *Coenonympha tullia* on islands in the St. Lawrence River. *Can. ent.* 93: 107-117.

Eff, Donald, 1956. Notes on *Speyeria egleis secreta. Lepid. news* 10: 101-106.

dos Passos, C. F., & L. P. Grey, 1947. Systematic catalogue of *Speyeria* (Lepidoptera, Nymphalidae) with designations of types and fixations of type localities. *Amer. mus. novitates* 1370: 1-30.

Grey, L. P., 1951. The subspeciation of *Speyeria atlantis. Lepid. news* 5: 31-35.

Grey, L. P., & A. H. Moeck, 1962. Notes on overlapping subspecies. I. An example in *Speyeria zerene. Journ. lepid. soc.* 16: 81-97.

Lorkovič, Z., 1962. The genetics and reproductive isolating mechanisms of the *Pieris napi-bryoniae* group (continued). *Journ. lepid. soc.* 16: 105-127.

Moeck, A. H., 1957. *Geographic variability in* Speyeria. *Comments, records and description of a new subspecies.* Privately printed, sponsored by the Milwaukee Entomological Society. 48 pp., 2 pls.

Sumner, F. B., 1915. Genetic studies of several geographic races of California Deer-mice. *Amer. nat.* 49: 688-701.

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