

2.38. Investigations on Present Climatic Refugia in North America Through Studies on the Distributions of Carabid Beetles: Concepts, Methodology and Prospectus

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For the past eight years I have studied, almost exclusively, the genus *Nebria* Latreille in North America. *Nebria* is basically an arctic/alpine (boreo-/montane) genus. Members of most species are cold- or cool-adapted and, at least in the southern half of the United States, exhibit restricted and/or fragmented distributional patterns suggesting refugial occurrence. In discussing peculiarities of the geographical and habitat ranges of various species with colleagues over the past few years, I've come to realize that, frequently, very different images form in our respective minds at mention of the word **refugium**. Most people immediately think of glacial periods and envision warm-adapted organisms shivering on some small island of frozen ground, surrounded by a sea of snow and ice! Others, myself included, see quite the opposite—cold-adapted organisms clinging to the tops of the highest mountains, sweltering in the heat rising from parched valleys and plains, perhaps praying fervently to the gods of orogeny for some miraculous uplift to deliver them to the saving coolness of the higher atmosphere! This is a vision remembered, not from dim geologic past, but from recent afternoons spent on arid peaks in the Great Basin Region of Nevada and Utah.

Clearly, both images, as well as others imaginable, reflect our appreciation for different aspects of the same phenomena. (1) Species occupy limited geographical and habitat ranges, due mainly to their innate environmental tolerance limits. (2) Through time, there are fluctuations (changes) in climate (the environment). (3) The ranges of species change with and in response to changing climate. As climate changes in a direction unfavorable for the success and/or survival of a species, it faces one of three fates. (1) Members of succeeding generations may acquire genetic innovations permitting adaptation and survival of the species *in situ*. (2) The geographical (horizontal) and/or altitudinal (vertical) ranges of the species may change, tracking, as it were, a more favorable environment. (3) In the absence of either successful adaptation to changes *in situ* or the freedom to move following favorable conditions, extinction is inevitable.

Refugia and Their Importance

The existence of past as well as present refugia is evidence for the success organisms have had in altering their ranges when they could not adapt to

life in their former ranges. Refugium, derived from the Latin **refugere** (to retreat), refers, therefore, to a place to which one retreats. Use of the term in biogeography carries both historical and contemporary connotations. We imply that species for which an area is a refugium now occupy different (usually smaller) ranges than at some previous time in their history, and further, we recognize that environmental pressures are still active in restricting their distribution at present. I limit my use of the term refugium to what might better be called **climatic refugia**—areas characterized by their peculiar abiotic, chiefly climatic, characteristics. I use the term **phyletic refugia** for areas where species or lineages have survived because of biotic peculiarities of the region (such as absence of certain predators or competitors) rather than its climate.

Because different organisms possess different environmental tolerance limits, a given change in climate of an area should result in a spectrum of effects on the regional biota. Refugia must be considered both relative and temporary: relative, because, as the ranges of one group of species contract (retreat into refugial areas), those of another group may expand out of their own refugia (see also de Lattin, 1957); temporary, because both climate and the environmental tolerances of species continue to change given sufficient time.

Why are we interested in refugia? Biogeographers have traditionally pursued interests in past refugia because of the presumed role such areas have played in the survival and evolution of biota. Of more general interest to evolutionary biologists is the fact that refugia are areas in which conditions classically considered prerequisites for rapid evolution and speciation may exist: geographical range fractionation and contraction, resulting in isolation of populations; decrease in population size; and increased environmental stress. Present refugia, therefore, may serve as natural laboratories for the study of evolutionary processes.

Carabid Beetles and Studies on Refugia

Lindroth (1963, 1965, 1968, 1969a, 1970; see also his paper on Glacial refugia in this volume) has demonstrated that carabid beetles are extremely useful organisms by which to recognize, characterize and study Glacial refugia (see also Ball, 1969, and Lindroth, 1969b, 1969c). My own interests and experience are mainly with montane regions in North America. Carabids are generally an important and conspicuous element in virtually all Nearctic high-altitude areas. That montane areas are today refugia for organisms (including carabids) more widely distributed during Glacial periods is both generally assumed and supported by abundant data from fossils (see Ashworth, 1973; Ashworth & Brophy, 1972; Coope, 1970; Coope & Brophy, 1972; and Matthews, 1968, 1974a, 1974b). Carabids should, therefore, serve as model organisms for the study of **present** as well as past refugia.

In zoogeography, as in paleoecology, geology, and other disciplines, historical reconstructions require acceptance of the principle of

uniformitarianism—here meaning that past members of given species possessed the same range of environmental tolerance limits as that exhibited by living members. If this were not true generally, and if adjustments to environmental change were achieved more rapidly, species ranges would not need to shift with climate and there would be no climatic refugia. In fact, adaptation appears to progress slowly. For carabids in general (and *Nebria* in particular), there is little evidence for such adaptive changes among montane forms, at least since Late-Wisconsinan time. [One of a few probable examples of post-Glacial adaptive shift with climate is that reported by Kavanaugh & Martinko, 1972, for a population of *Nebria purpurata* LeConte in northern New Mexico.] It seems, therefore, defensible to use data on present geographical and habitat distributions of species represented in present refugia in the formulation of hypotheses about past distributions and the histories of regional biota and climate. Paleontological, paleoecological, and paleogeographic data can then be used in independent tests of these hypotheses. In addition, analyses of vicariance patterns among related species or geographical variation patterns among isolated populations of species represented in different refugial areas can illustrate both the evolutionary importance of refugia and details of speciation processes in general.

Assessment of Present Knowledge on Nearctic Montane Carabidae

Interest in the North American carabid fauna has reached a new peak over the past two decades, due principally to the efforts of P. J. Darlington, Jr., C. H. Lindroth, and G. E. Ball. Their scholarly works have served as models and their enthusiasm as stimuli for the present generation of students. Scores of professionals and amateurs continue to augment knowledge of carabids through taxonomic study and collecting. However, little detailed work has been done to date on the distributional patterns of our montane carabid species—those members of our fauna presently in the more obvious refugial areas. Ball's (1966) analysis of distribution patterns in species of subgenus *Scaphinotus* and Erwin and Ball's (1972) treatment of the *trifaria* and *ovipennis* species groups of *Nebria* stand out as pioneer examples of the kinds of analyses which should be attempted for the high-altitude fauna.

Although lack of comprehensive distributional data has precluded detailed analyses of this fauna in the past, concern for such studies began a century ago. LeConte (1878) professed interest in exploring phyletic relationships among the high-altitude species he described and called for more detailed knowledge of their present distributions as an essential prerequisite to reconstruction of a glacial history of the fauna. Van Dyke (1919, 1926) described (in general terms) distributional patterns of various montane carabids and discussed assumed phyletic relationships among them. Darlington (1943) studied the carabids of the Presidential Range in New Hampshire. His model survey of one local high-altitude fauna demonstrates the kind of study required for each of the many North

American mountain systems. Less detailed surveys of a montane region were those of Haubold (1951) and Armin (1963) for the Front Range (Rocky Mountains) in Colorado. Although Lindroth's (1961-1969) study of the fauna of Canada and Alaska contains no detailed analysis of distribution patterns, it still serves as the greatest single published data source on the Nearctic high-altitude carabid fauna. It has been an immeasurable advantage to me to begin study of *Nebria* after Lindroth brought reasonable taxonomic order to this and other Nearctic groups.

Alpha-level taxonomic work on our high-altitude carabid fauna is reasonably advanced, and, probably, few distinct species remain undescribed. For example, I now recognize 42 species of *Nebria* native to North America, including four presently undescribed. Lindroth (1961) also recognized 42 species, including four I do not regard as specifically distinct. My few conclusions at variance with his result from the study of material unavailable in 1961, from geographical areas not sampled prior to my study. Present need, therefore, in the study of our montane faunas is for additional faunal surveys of various mountain systems. Analyses must await additional collecting of specimens and data from geographically important areas. Although extensive carabid material is available for study in public and private collections at present, past collecting has been spotty, usually repeated in a few popular areas. Important areas which remain inadequately surveyed are the central Appalachian region, the Ozark Mountains and adjacent mountain systems, the Sierra Nevada of California and numerous distinctive subsystems of the Rocky Mountains.

Data on habitat distributions of montane carabids are even less available than data on their geographical ranges. Such information is of prime importance to an understanding of the nature of refugia and the geographical distributions of refugial species. Previously-mentioned works of Darlington (1943) and Lindroth (1961-1969) contain invaluable data on preferred habitats for some species but little on the limits of habitat ranges.

Environmental Tolerances of Taxa

Two approaches have been used to study the environmental tolerance limits of species. First is the quantitative method of testing tolerances of individuals to single environmental factors through the use of various simulator equipment. Manipulation of laboratory conditions and observations on the subsequent responses of individuals provide the required data. [Field studies, such as those which involve the recording of microenvironmental conditions at exact locations where individuals are found, may provide data on microhabitat preferences but not tolerance limits, unless sampling covers the full geographical range of the species as well.] This approach requires assumptions that (1) responses of individuals sampled reflect the full range of response for the species, (2) laboratory simulation accurately reproduces the appropriate environment, and (3) observational techniques do not alter individual response. Drawbacks to

this method include difficulty in establishing the validity of the assumptions and limits to the number of species that can be tested in a given period of time.

The second approach was termed the "biogeographical method" by Lindroth (1965) in his paper on the Skaftafel, Iceland fauna. In this method, actual distributional (geographical and habitat) limits of the species are considered a reflection of environmental tolerance limits. If the range of a species is known in detail, an attempt is made to correlate the distributional pattern with climatic or other environmental patterns over the same area. In general, correlations should be observed between distribution and one or more synoptic environmental patterns. Minor deviations from these patterns should usually be correlated with local environmental anomalies (see Figure 5); but where even this correlation appears unlikely, local adaptation might be suspected. Assumptions required in use of this method for recognizing tolerance limits of species are: (1) that biotic factors (such as predation or competition) are not affecting distribution; (2) that local adaptations (changes in tolerance limits) are non-existent or at least minimal; and (3) that limits to species distributions reflect present environmental tolerance limits rather than simply an historical lack of opportunity for range expansion. Lindroth (1963) made effective use of this technique in his analysis of the Newfoundland carabid fauna using Hare's (1952) climatological data. As more detailed data on species distributions and climatic patterns for other regions accumulate, this approach should become more popular and quite useful. For example, Figs. 1 and 2 illustrate a possible correlation between the northern and northeastern limits to the distribution of *Nebria eschscholtzii* Menetries and mean monthly minimum air temperature for January [members of this species generally overwinter as larvae and probably require a mild winter for development].

Life Zone Concepts and Montane Faunas

Special problems are encountered, however, in applying the biogeographical method to studies on montane species. Combinations of geographical and altitudinal climatic variation patterns are difficult or impossible to represent on two-dimensional maps. Extreme local variation in topography, exposure, and microclimatic effects unique to montane regions (such as small-scale rain shadows, influences of glaciers, etc.) further complicate patterns, rendering synoptic climatological data almost useless. Fortunately (unlike Udvardy, 1969:247), I found **life zone** concepts (Merriam, 1894, 1898; and Marr, 1967) extremely useful in working with montane faunas. To some degree, recognition of correlation between one or more life zones and the habitat distributions of carabid species permits us to ignore local environmental anomalies and search for possible correlates among species distributions, distributions of certain life zones, and broader climatic patterns.

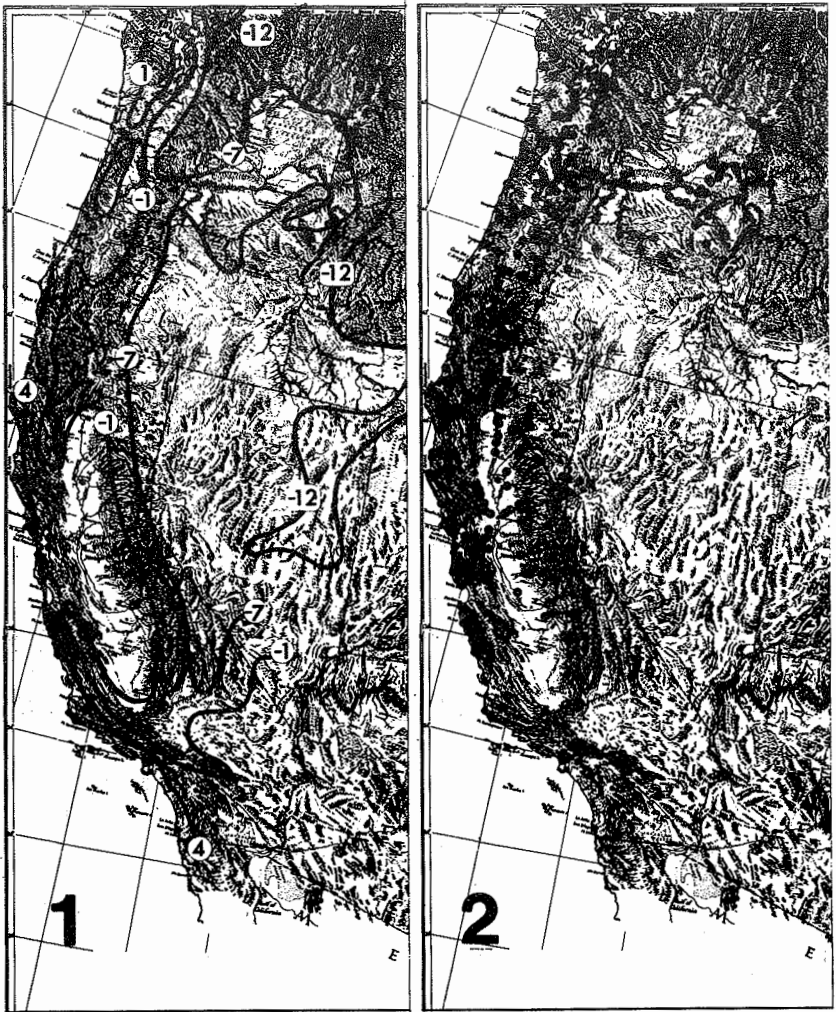


Fig. 1. January mean monthly minimum air temperature ($^{\circ}\text{C}$ isotherms) for western United States (redrawn from the National Atlas of the United States of America, U.S. Geological Survey, Washington, D. C., 1970).

Fig. 2. Map of known geographical distribution of *Nebria eschscholtzii* Menetries (copyrighted map reproduced with permission of E. Raisz).

Life zone concepts emphasize abiotic environmental similarities between latitude and altitude, especially in temperature variation patterns. Mani (1968:17) illustrated a relationship between altitude and latitude for temperature (specifically the 10°C and 0°C isotherms, corresponding to treeline and permanent snowline, respectively) (see Figures 5 and 6).

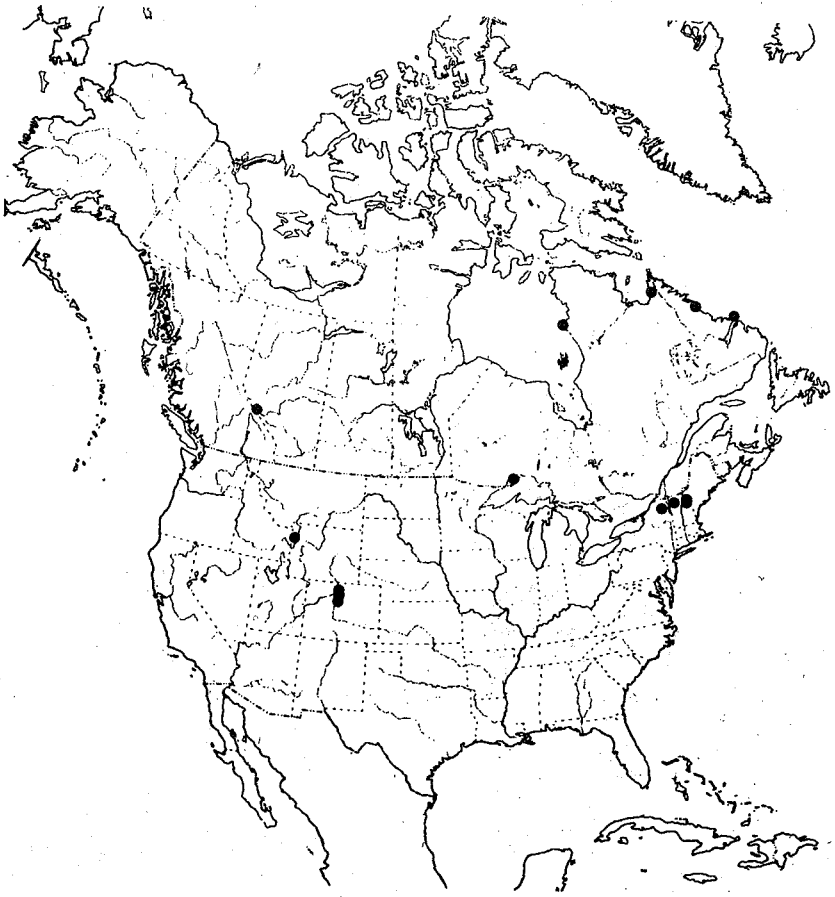


Fig. 3. Geographical distribution of *Nebria suturalis* LeConte.

The area between these two “lines” is equivalent to the “arctic/alpine” life zone. If definitive temperature data were available and plotted, other life zones would be represented on the graph by similarly-shaped areas below and left of the arctic/alpine zone. Plotting the altitudinal and latitudinal coordinates of known localities throughout the geographical range of a species directly on this graph illustrates relationship between its distribution and certain life zones (and temperature extremes). Although Mani’s graph is an extreme simplification (assuming continental climate and equal massiveness, exposure and slope of mountains), a rough estimate of thermal tolerance limits for the species can still be obtained (at least for mid-continental species). Figures 3 through 6 demonstrate this technique with two *Nebria* species as examples (see Figure captions for details).

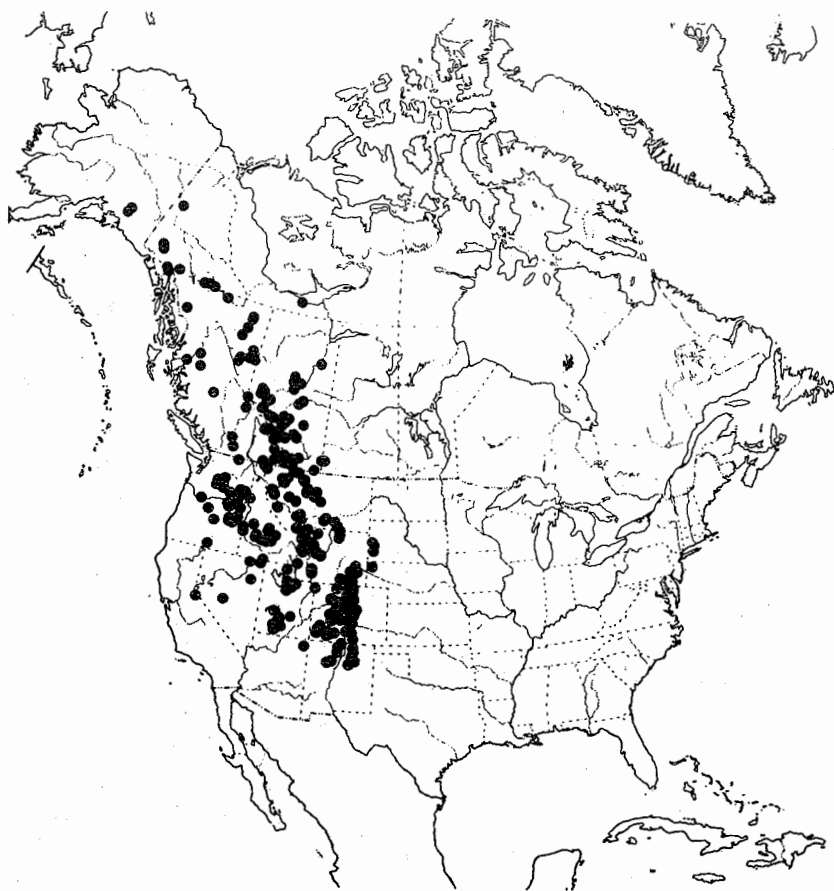
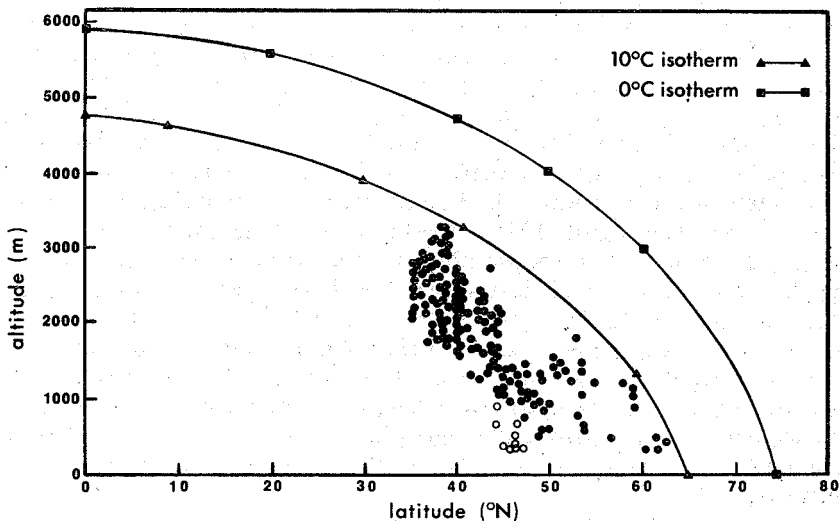
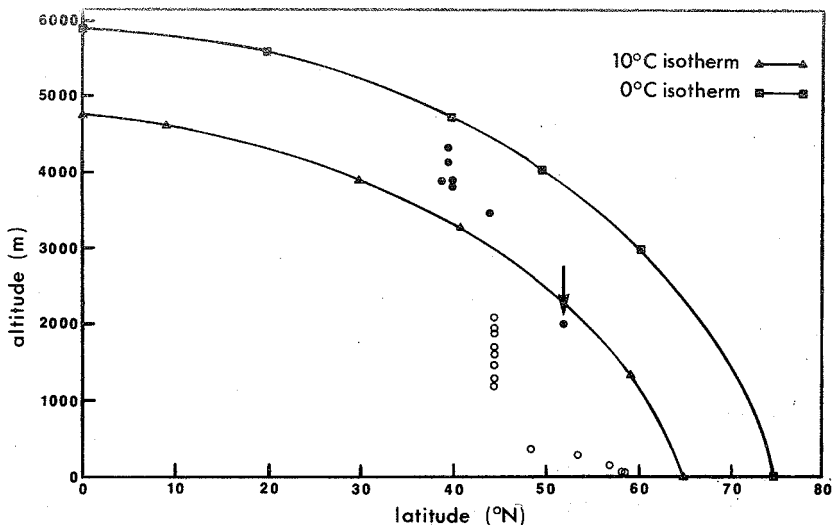


Fig. 4. Geographical distribution of *Nebria obliqua* LeConte.

Preliminary Findings and Directions for Future Efforts

My studies on Nearctic *Nebria* distributions suggest that seasonal (and/or non-seasonal) temperature patterns are the main environmental features limiting ranges of species. Moisture patterns may have a secondary or associated role. I have tried to sample significant portions of montane carabid faunas wherever I've collected; but, to date, only *Nebria* material has been adequately studied. I suggest, however, that further studies will indicate that distributions of most other refugial montane carabids are also temperature-limited. If this is true, then paleoenvironmental (especially temperature) data from diverse sources can be used in formulating hypotheses on past distributions of these refugial carabid species. In addition, data reflecting past limits to and changes in the altitudinal and latitudinal distributions of life zones can be used as further evidence for



Figs. 5, 6. Latitudinal and altitudinal coordinates of localities for species superimposed on graphs relating altitude to latitude for mean annual air temperature (redrawn from Mani, 1968). Solid circles represent localities with continental climate, open circles for localities with (or in part influenced by) maritime climate.

5. *Nebria suturalis* LeConte. All samples (except those from Black Bay, Ontario and Athabasca Glacier, Alberta) are from areas north of or above treeline; but only Rocky Mountain localities appear in the "Arctic/Alpine Zone" on this graph because of maritime climatic influence on eastern localities. Arrow denotes sample from toe of Athabasca Glacier, which descends well below treeline—represents an example of local climatic anomaly rather than local adaptation of a population to life at lower altitude.

6. *Nebria obliqua* LeConte. Various data indicate that this species is restricted to the "Transition" and "Canadian" Zones (Merriam, 1894). Temperature equivalents for this life zone range are not established at present but could be inferred roughly from the graph if data were available from any localities at the range extremes. Samples from the Columbia River Basin of Oregon and Washington were taken at low elevations, suggesting a maritime influence in this area (see also Figures 1 and 2).

past distributions of species (if present distribution/life zone correlations are recognized) (see Lowe, 1961, 1964; Martin, 1958; Martin & Mehrlinger, 1965; and Morrison, 1965).

Future studies of montane Nearctic refugial areas should investigate their age, integrity and role in speciation. Properly dated paleoenvironmental data can be used to determine the ages of refugia if present relationships between the distributions of climatic features and species are known. Present montane refugia, at least in the Southern Rocky Mountain Region, have probably served as such throughout post-Wisconsinan time (over 12,000 years); but additional data are required to better document fluctuations in extent and degree of isolation of refugia during this period. For example, geographical variation patterns in several *Nebria* species (in Colorado) suggest that distributions (and, therefore, refugia) were considerably more restricted in some previous post-Wisconsinan time than at present; however, timing and duration of this presumably warmer period are unknown. [This evidence supports the existence of the so-called post-Glacial "altithermal" period (see Antevs, 1948, and Smith, 1965), at least in the Southern Rocky Mountain Region.]

The **integrity** of a montane refugium (i.e., the proportion of the resident fauna for which the area is actually a refugium) can be determined by analysis of data from detailed faunal surveys. Such a measure is of interest because it suggests the degree to which invasion by (and attendant adaptations in) species from the surrounding lowland fauna has occurred. Montane faunas of southern (especially tropical) areas are characteristically non-refugial, derived mainly from adjacent lowland faunas (see Darlington, 1971). Northern montane faunas, however, demonstrate horizontal (geographical) rather than vertical (altitudinal) phyletic relationships and vicariance patterns. The species composition of these montane areas has been determined mainly by past fluctuations (expansions, contractions, and linear shifts) in the ranges of cold-adapted species. Integrity is, therefore, inversely proportional to the number of species added to the refugial fauna (i.e., newly adapted to the montane environment). Comparisons of integrity in faunas of various refugial areas should indicate relative rates of faunal change (such as increased faunal diversity).

The role of refugia in speciation is generally assumed to be significant. Typically, past refugia are invoked in historical interpretations of present variational and vicariance patterns. Studies of organisms in present refugia are few; and, unfortunately, conclusions concerning the role of present refugia in speciation may be premature because, apparently, little speciation has occurred (among carabids) in post-Wisconsinan time (Kavanaugh, manuscript in preparation). Studies of present infraspecific geographical variation patterns correlated with refugial distributions may, however, provide insight into some details of the process of speciation.

Summary

Climatic refugia serve as sanctuaries for organisms adapted to habitats with restricted distributions. Interest in refugia springs from their presumed role in preservation of biotas and in providing conditions assumed favorable for rapid speciation. Studies of present climatic refugia in North America, especially those in montane regions, can provide insights into the nature of past refugia, past distributions of species, environmental features limiting present and past distributions and details of processes leading to speciation. Carabid beetles are considered model organisms for the investigation of present refugia. Present knowledge of Nearctic montane carabid faunas is reviewed. Guidelines and methods for acquiring relevant data for (and the orientation of) future studies are discussed. Additional faunal surveys are needed before analyses of most montane faunas can proceed. Use of "life zone" concepts is considered valuable in dealing with montane faunas and the habitat and geographical distributions of refugial species.

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REPRINTED FROM:

CARABID BEETLES

their evolution, natural history, and classification

Proceedings of the
First International Symposium of Carabidology

editors: Terry L. Erwin, George E. Ball,
Donald R. Whitehead