

The Niche-Variation Hypothesis: An Examination of Assumptions and Organisms

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ABSTRACT: The academic and applied importance of conclusions resting upon the validity of the niche-variation hypothesis requires closer examination of Van Valen's seminal paper. Previous reviews of the niche-variation hypothesis have been **primarily** concerned with further tests using new data gathered on species different from those used by Van Valen (Soulé and Stewart 1970, Rothstein 1973a, Ashton and Rowell 1975). As has been stated previously (Rothstein 1973a), the niche-variation model is virtually impossible to invalidate. It does not follow, however, that lack of disproof constitutes proof (Popper 1968). While not invalidating the niche-variation hypothesis, an examination of the assumptions and biology of species used by Van Valen (1965) indicates several alternative hypotheses may account for the observed results. In addition, inappropriate mainland populations were probably used in calculating morphological variability of the species studied.

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INTRODUCTION:

The niche-variation hypothesis contends that the extent of morphological variation in a given population results in part from the size of that "organism's ecological niche." The variation can either be continuous or discontinuous, as in sexual dimorphism. In its broadest usage, the theory states that the variability of morphological structures is directly correlated with the width of the appropriate niche parameter. For example, species with wider feeding niches have more variability in trophic appendages than species with narrower feeding niches. Within species, the same process would be evident between different populations or subspecies which have different niche widths. No specific causal agent is called for; the mediating factor can be biotic, abiotic, or some combination of processes.

A number of assumptions are made concerning the examination of data when the niche-variation hypothesis is tested by comparison of mainland and island populations of the same species and interspecific competition is specified as the mediating process.

1. The width of the niche is considered to be determined by competition with congeneric or other similar species.

2. Areas with fewer species, such as islands, have less interspecific competition, while areas with more species, such as the mainland, have more interspecific competition.

3. If phenotypic variation is controlled by the size of the niche, then morphological variation of species in areas lacking congeneric competitors would be greater. (The reverse also holds.)

Van Valen compared museum skins assumed to represent island and mainland breeding populations of six bird species reported to demonstrate observable differences in the habitats they occupied. Using intrapopulation variance, he found that four of the species' island populations displayed greater variability of this bill measurement; and one species had more variable bill length on islands. Specifically, Parus caeruleus and Phylloscopus collybita have increased intrapopulation variance in bill size when compared to the mainland populations Van Valen (1965) measured, while Fringilla coelebs has decreased variation on Tenerife, Canary Islands. Fringilla coelebs, Montacilla

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cinerea, and Regulus regulus all displayed greater intrapopulation variance in the Azores than in the mainland areas measured. Mimus gilvus demonstrated greater bill length variability on Curacao than on the South American mainland areas used.

Van Valen (1965) treated each island as the locality of a single breeding population. The island subspecies of P. collybita and P. caeruleus were compared to British and German specimens. For M. cinerea, the island subspecies was compared to specimens from Britain and the entire European mainland west of Russia (excluding Scandinavia and Spain). Only British specimens were compared to island subspecies of R. regulus and F. coelebs. In each of the above, the maximum area used for a single breeding population was the county of Devon, England, except for M. cinerea in which all European specimens were treated as a single breeding population. The M. gilvus data were provided by Voous (1957). Van Valen made his own mainland measurements. Sexes were treated separately in each population comparison (Van Valen 1965).

The Canary Islands are the southern limit for the European birds' breeding ranges. Each breeding population exists as a subspecies in these islands (Table 1) and each subspecies demonstrates identifying character differences other than bill width (Meade-Waldo 1889, 1890, Hartert 1901, Lowe 1909, Lynes 1914, Bannerman 1920, Etchéopar and Hue 1964, Paynter 1967). Lack and Southern (1949) list five cases of habitat change for birds of the Canary Islands in addition to those mentioned by Van Valen (Table 2). A noticeable morphological difference from mainland subspecies was mentioned only for Parus caeruleus (Lack and Southern 1949).

TABLE 1

Distribution and Habitats of Birds in the Canary Islands cited by Lack and Southern 1949

Species	Subspecies	Islands	Habitat	Sources
<u>Parus caeruleus</u>	degener	Lanzarote, Fuerteventura	villages, gardens, trees from coast	Bannerman 1912
	teneriffae	Tenerife, Gomera, Gran Canaria	to upper limits of pine forests	Lack & Southern 1949
	palmensis	Palma	pine woods	Meade-Waldo 1890
	ombriosus	Hierro		Etchéopar & Hue 1964
<u>Montacilla cinerea</u>	canariensis	Tenerife	dry barrancos	Lack & Southern 1949
		All other islands	semi-desert, nests in towns	
<u>Fringilla coelebs</u>	canariensis	Tenerife, Gomera, Gran Canaria	laurel, tree heath, escobon above 2500 feet	Bannerman 1920
	palmiae	Palma		Lack & Southern 1949
	ombriosa	Hierro		
<u>Phylloscopus collybita</u>	exsul	Lanzarote, Fuerteventura	desert scrub, gardens, towns	Etchéopar & Hue 1964
	canariensis	All other islands	through cultivated and forest zones	Tristram 1889
<u>Regulus regulus</u> *		All islands	pine woods, laurel, tree heath zone, not cultivated land	Meade-Waldo 1893

* no special subspecies

Table 2

Niche Width Changes in Canary Island Birds Cited by Lack and Southern (1949).

- 1) Expansion of the Raven, Corvus corax, into woods and cultivated fields.
- 2) Occupation of shrubs by Phylloscopus collybita.
- 3) Use of pine forests by Parus caeruleus.
- 4) Nesting in town gardens by the Blackcap, Sylvia atricapilla.
- 5) Nesting by Monticola cinerea in towns.
- 6) Breeding of the Short-eared Owl, Asio otus, in semi-desert.
- 7) Absence of Fringilla coelebs from coniferous woodland.
- 8) Restriction of the Black Swift, Apus unicolor, to high altitudes.

The niche-variation hypothesis as stated by Van Valen (1975) is not supported by a species if it can be demonstrated in a comparison of island and mainland populations of the same species that: (case 1) niche width is not structured by interspecific competition but by other biotic or abiotic factors, or (case 2) morphological variability in the structure measured is the result of factors other than the width of the niche, or (case 3) the species used as support for the niche-variation hypothesis does not demonstrate a difference in niche width between areas of higher and lower congener number. Cases 1 and 3 are tests of the competitive interpretation of the hypothesis while case 2 is a test of the niche-variation hypothesis proper. I review the natural history of the avian species used by Van Valen (1965) and show that the above tests disqualify each of these bird species as support of the niche-variation hypothesis.

Factors other than competition that influence niche width size

The assumption that niche width is determined by the presence or absence of interspecific competition warrents investigation. Gibb (1954) in his studies on feeding behaviors in Parus species and Regulus regulus found that the only evident competition occurred in midwinter and was totally intra-specific. Niche width varied seasonally with distinct segregation of feeding habitat only observable in the winter and possibly during breeding territorially (Gibb 1954). Niche width boundaries in Parus species break down in spring and summer, in temperate latitudes, when temporary super-abundance of food occurs (Hartley 1953). Parus caeruleus tends to eat the same foods in the same habitats as other Parus species except when breeding or during severe winters (Betts 1955). The zonal niche distribution of P. caeruleus was equal throughout the year to that of P. major in host feeding site with overlap between the two species throughout the total vertical environment (Colquhoun and Morley 1943, Gibb 1960). It appears that the feeding niche as distinguished from habitat occupied is quite wide for both P. caeruleus and R. regulus even in the presence of congeners.

Disruptive environmental factors have a bearing on the niches occupied by these birds (Table 1). In the Canary Islands the laurel forests have almost completely disappeared. Large trees have been removed for the manufacture of charcoal and much of the undergrowth has been trampled or removed. The intermediate zone of tree-heath is now patchy. In replanting bare ground, "exotic" species have been introduced. The semi-desert zone below the forests is now completely under cultivation throughout most of Tenerife (Lack and Southern 1949). Clearly, if an avian species survives this drastic habitat disruption, its current presence in the altered environment does not constitute a habitat niche shift in response to competition. It is merely that a species remained at a geographical location while the environment was altered around it. Lack (1942) hypothesized that environmental disruption was responsible for changes

in niche in Fringilla coelebs, Parus caeruleus, and Regulus regulus on British islands. Alerstram et al. (1974) observed no change in niche width for P. caeruleus and R. regulus on Götland, Sweden, a relatively undisturbed island. Snow (1954) felt that changes in dominant vegetation were responsible for P. caeruleus' presence in pines in England. It may be plausible, then, that P. collybita inhabits the shrubs of Tenerife because trees have been eliminated by man, P. caeruleus is in pine forests because deciduous forests are all but gone in the Canary Islands, and Montacilla cinerea nests in towns because natural sites have been destroyed. Since niche is being defined here by habitat usage (Lack and Southern 1949), the absence or presence of congeners can have no effect on the niche width of a species when conditions preclude even the availability of an alternative.

The abundance of predators affects habitat selection. The sparrowhawk is an important predator of P. caeruleus, R. regulus, and Phylloscopus collybita (Morse 1973). These birds avoid the sparrowhawk, Accipiter nisus, by use of deciduous tree cover (Chaworth-Musters 1939, Gibb 1950, 1954, 1960, Morse 1973). A. nisus is rare in the Canary Islands (Bannerman 1912, Lack and Southern 1949, Etcheopar and Hue 1964), while the only prey of the indigenous kestrel is lizards (Tristram 1889). Lack (1958) includes weasels and squirrels as important predators of P. caeruleus nestlings in Britain. No mammalian or reptilian predators of birds were present in the Canary Islands until they were introduced by man. It is conceivable that the lack of predators in the Canary Islands could allow prey species to expand into habitats which would not provide adequate cover, such as shrubs for P. collybita on Tenerife. This form of niche width expansion does not require assumption of interspecific competition.

Van Valen (1965) uses the observed decreased niche width of Fringilla coelebs with a concurrent decrease in bill variability as an important example of his niche-variation hypothesis. On Madeira, F. coelebs is absent from laurel forests for no apparent reason (Meinertzhagen 1925) but does not inhabit the pine forests of that island. Many have construed the absence of F. coelebs from the pine forests of Tenerife and Gran Canaria to be the result of competitive exclusion by its endemic congener F. teydea (Lack and Southern 1949, Moreau 1966). This may be so on those islands but the absence of F. coelebs from pinewoods and restriction to deciduous forests in Sicily and Tunisia where a "competing" congener is not present (Whitaker 1894, 1895) indicates that F. coelebs is absent from pine forests in the southernmost portion of its range for reasons other than competition.

Factors other than niche width responsible for morphological variability

Davis (1954) found a vernal increase in the bill lengths of passerine birds that eat significant amounts of insects in the summer and are primarily granivorous in the winter. Parus caeruleus has this type of feeding pattern in Britain (Gibb 1954, Betts 1957, Smith and Sweatman 1974). P. caeruleus on Tenerife probably has the same consumptive ability, and may eat what is seasonally available. If resource availability is more variable in the Canary Islands, the increased variability in the bill measurements of the islands' populations may be a function of this increased fluctuation in food types.

Fringilla coelebs is at the end of a geographic cline in bill size, song, and plumage in the Canary Islands (Lack and Southern 1949). Parus caeruleus is also at the end of a geographic cline in wing length, tail length, beak length, tarsus length, and plumage that extends across North Africa to the Canaries (Tristram 1890, Lack and Southern 1949, Snow, 1953, 1954). Snow (1953) has measured a general increase in bill measurements with latitude,

with a greater range in bill and tarsus length in the mainland populations of P. caeruleus than in Canary Island populations, an observation contrary to Van Valen (1965). In all Parus species Bergmann's Rule, that homiothermal vertebrates in warm areas tend to be smaller than those from cool areas, and Allen's Rule, that projecting parts and appendages tend to be shorter in cooler areas than in warm ones, seem to hold with correction for latitude effects (Snow 1953). Lynes (1914) has data indicating a slight cline between Phylloscopus collybita of Tenerife and Spanish subspecies. Mimus gilvus rostratus also appears to be at the end of a geographic cline that runs from Granada to Curacao. Lowe (1907) remarks that M. g. gilvus on Blanquilla Island appears to be intermediate between M. g. gilvus on mainland Venezuela and the M. g. rostratus subspecies on Curacao in irides color, plumage, head width, body size, and bill width. The M. g. rostratus captured by Lowe (1909) all had larger bills than typical M. g. gilvus. Since the bill cline runs with increasing size from east to west (Table 3), there may be a correlation of body size with latitude, as has been demonstrated by Snow (1954) for Parus.

Table 3

Average culmen length in Caribbean Mimus gilvus*

Island(s)	Average length of the exposed culmen (mm.)
Grenada	17.5
Margarita	19.0
Los Testigos	19.2
Blanquilla	20.0
Curacao	23.0

*after Lowe (1909).

Although absolute differences in bill length are not the issue, the variance in a morphological structure is often correlated with its mean (Snedecor and Cochran 1967). Until rigorous analyses are performed, it is not possible to discern whether increased variance in bill measurements is the result of absolute size, latitudinal gradient, or niche width, even when the difference in means is weighted by the variance statistic. For a specific example, Parus caeruleus, we find a rather continuous distribution across North Africa with distributional gaps in Spain, Sicily, and Egypt (Figure 1). The morphological difference in the ultramarinus and Canary Island subspecies from European P. caeruleus subspecies is incidental to the different habitats they occupy since coloration is correlated with climate. The bill is longer, in comparison, because of increase in relative beak length, not a decrease in relative beak depth (Table 4). The latter would have indicated a different diet or different foraging techniques in northwest African subspecies (Snow 1954). Since beak length is correlated with winter temperature (Snow 1953) and the Canary Islands are the warmest part of this species' range, one would expect Canarian P. caeruleus to have longer beaks regardless of habitat. That P. c. degener has the same beak length and shape as the P. caeruleus subspecies of the western islands even though Lanzarote and Fuerteventura are desert islands that contain no pines, demonstrates the beak shape is not related to the conifer habitat of P. c. teneriffe. So it appears that the geographical cline in bill and body size is a more important factor in determining bill morphology than niche width, as defined by habitat utilization.

Table 4

Beak Measurements in Parus caeruleus in Europe, North Africa, and the Canary Islands*

Country or Island	Habitat	Culmen (mm.)	Beak-depth (mm.)	Depth/ Culpen
S. Scandanavia	broadleaf	9.2	4.8	0.52
N. Portugal	broadleaf	9.1	4.2	0.46
N.W. Africa	broadleaf	10.1	4.1	0.41
(4 populations)	and conifers			
Lanzarote and Fuerteventura	tamarisk	10.4	4.3	0.41
Gran Canaria and Tenerife	broadleaf and conifers	10.9	4.1	0.38
Palma and Hierro	mainly pine	10.9	4.0	0.37

*after Lack (1971) from Snow, D.W., 1953, Systematics and Comparative Ecology of the Genus Parus in the Palaerctic Region. (D. Phil. Thesis, Oxford Univ.)

It is possible that the previously mentioned lack of predation on Tenerife (Lack and Southern 1949) allows more viable birds to survive since culling pressures are less than on the mainland, permitting more variability within populations of island birds. This would be evident from bill measurements, with the resulting pattern of island-mainland character variability indistinguishable from that predicted by the niche-variation hypothesis.

In the oft-cited case of decreased variability in an island bird, bill measurements of these populations of Fringilla coelebs might be less variable because of the disjunct distribution of deciduous forests in North Africa and Sicily. This limits local population size, resulting in small gene pools with limited variability.

Cases not susceptible to testing

Lack and Southern (1949) considered the use of pine forests on Tenerife as an expansion of niche width for Parus caeruleus. However the use of pine forests for feeding and breeding by P. caeruleus and Regulus regulus in Britain is well documented (Gibb 1960, Lack 1955, 1958, Smith and Sweatman 1974). Alerstam et al. (1974) noted the same use of pine woods by both species on the island of Götland and mainland Sweden. Pine forests are part of P. caeruleus' niche in North Africa (Bannerman and Priestly 1952). It appears, then, that the use of pine forests in the Canary Islands is not a niche width expansion peculiar to those P. caeruleus populations. Since there is no real niche width expansion, Parus caeruleus cannot be used in testing the niche-variation hypothesis.

For tests of the niche-variation hypothesis it is best to use populations with close genetic affinity, so that factors other than niche width which influence morphological variation are minimized. In a comparison of island and mainland birds, the mainland birds measured should be from the population which provided the island colonizer's source pool. It may be that a measurable difference in bill variability exists between the birds of Tenerife and the mainland populations Van Valen (1965) measured. It is very probable,

however, that the wrong mainland populations were examined by Van Valen. For Parus caeruleus and Phylloscopus collybita, British and German skills of the mainland populations were examined, not individuals from adjacent mainland populations. According to Tristram (1890), the Canary Islands have derived birds from the African coast. P. collybita of Tenerife is most closely related to Iberian subspecies and possibly originated there (Lynes 1914). Although it often tends to breed optimally in broad-leaved forests, P. caeruleus appears to be a very catholic species that makes use of whatever habitats are available to it (Lack 1958). Indeed, this ability to adapt to rigorous, unusual habitats is most fully exemplified in North Africa, the region which is the most likely source for the Canary Island subspecies (Meade-Waldo 1889, Hartert 1901, Lack and Southern 1949, Snow 1953, 1954). Distributional gaps between European populations and the Canary Islands may indicate that variability in gene pools more isolated from each other than a simple mainland/island situation was measured (Lynes 1914, Paynter 1967).

CONCLUSIONS

Even when "niche" is defined purely qualitatively, island and mainland populations of most species examined are indistinguishable in niche width (Van Valen 1965); only certain species fit the assumptions of the niche-variation model. Willson (1969) in her study of bird size and morphological variation in 55 North American species found no evidence of greater variation in morphology in regions of low species number (e.g., islands). Crowell (1962) in a specific attempt to demonstrate reduced interspecific competition in island birds found no relationship between bill variability and change in niche width. Attempts to find a morphological variation/niche width correlation in this and other systems have met with limited success (Rothstein 1973a, 1973b, Grant 1976, Hamilton and Johnston 1978) and conspicuous failure (Soulé and Stewart 1970, Alerstam et al. 1974, Partridge and Pring-Mill 1977, Ashton and Rowell 1975).

The hypothesis that variability in morphological characteristics of an organism is related to its ecological niche size has been the subject of much discussion and controversy (Crowell 1962, Soulé and Stewart 1970, Rothstein 1973a, 1973b). Van Valen's (1965) initial statement of the niche variation hypothesis has been adopted uncritically by ecologists in texts (Colinvaux 1973), monographs (MacArthur and Wilson 1967), and journals (Fretwell 1969). That continuous variation within local populations is adaptive in itself may well be true, but evidence to support this notion is far from compelling. When we examine the natural history of the species examined by Van Valen (1965), we must disqualify one species, Parus caeruleus, from consideration. Several alternative factors affecting the niche width and morphological variability of the birds in question cannot be excluded from consideration (Table 5). The niche-variation hypothesis does not uniquely predict patterns of niche width and morphological variation in these species.

Since Van Valen's (1965) work constituted the best evidence for the niche-variation hypothesis (Rothstein 1973a), the acceptance of the theory must be questioned. The majority of bird species show no measurable niche width/morphological variation correlation and closer examination of the supportive examples raises questions concerning their validity. The use of the niche-variation hypothesis as a unifying, general rule should be carefully qualified or discontinued.

Summary of Results from Examination of the Natural History of the Bird Species Studied

TEST and FACTOR/	SPECIES					
	<u>P. caeruleus</u>	<u>P. collybita</u>	<u>F. coelebs</u>	<u>M. cinerea</u>	<u>R. regulus</u>	<u>M. gilvus</u>
Case 1						
a)no difference in feeding niche from congeners	+				+	
b)altered environment	+	+	+	+	+	
c)release from predation	+	+			+	
d)restriction to habitat in absence as well as presence of congener			*			
Case 2						
a)seasonally variable diet	+					
b)at end of a morphological cline	*	+	+			+
c)small gene pool			+			
Case 3						
a)no niche width change between island and mainland	*					
b)wrong mainland populations used	*		+			

* strong evidence for exclusion from list of species supporting the niche-variation hypothesis,
 + possible evidence which either excludes the species as support of the niche-variation hypothesis or would predict the same results as the niche-variation hypothesis.

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Legends for Figures

Figure 1: Geographical distribution of *Parus caeruleus* subspecies in southern Europe, North Africa and the Canary Islands: 1: *ombriosus*, 2: *palmensis*, 3: *teneriffae*, 4: *degener*, 5: *ultramarinus*, 6: *cyrenaicae*, 7: *balearius*, 8: *oglaistratae*, 9: *caeruleus*.
 After Bannerman, 1920; Etchécopar and Hüe, 1964; Hartert, 1901; Meade-Waldo, 1890, 1903; Paynter, 1967; Snow, 1952; Tristram 1890; Wallis, 1895; Whitaker, 1895; Witherby, 1905.

