ADAPTIVE MODIFICATIONS AND ECOLOGICAL ISOLATING MECHANISMS IN THE THRUSH GENERA *CATHARUS* AND *HYLOCICHLA*

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CLOSELY-RELATED sympatric species, if they are to retain their sympatry, must develop mechanisms which enable them to surmount the detrimental effects of ecological competition. Lack (1949) and Gause (1934), for example, have expressed the idea that two species with identical requirements for existence cannot exist together in the same ecological niche. Experimental studies such as those conducted by Park (1948) on two species of flour beetles (*Tribolium*) support this idea.

When a species becomes divided by geographical barriers a certain amount of genetic change takes place in the then-isolated populations. What happens upon the subsequent contact of these populations depends upon the kind and amount of differentiation that has occurred. The two populations can continue to live side by side in the same habitat if the differentiation that has taken place is in the nature of a certain amount of preadaptation for ecological and reproductive isolation. The initial preadaptations, if sufficient, become reinforced in both forms by the selective pressures applied to each by the other. Since these phenomena have been discussed at length by Mayr (1942:147) and Lack (1949), they will not be pursued further here.

The following discussion is an attempt to describe and evaluate the ecological isolating mechanisms operating in two genera of forest-inhabiting thrushes, *Catharus* and *Hylocichla*. The reproductive isolating mechanisms developed by these species have been described elsewhere (Dilger, 1956a).

The species dealt with here are the Wood Thrush (*Hylocichla mustelina*) and four other species of forest thrushes which formerly were placed in the same genus. The four now are considered congeneric with the nightingale-thrushes (*Catharus*) of Middle America (Dilger, 1956b). They are the Veery (*C. fuscescens*) and the Hermit (*C. guttatus*), Olive-backed (*C. ustulatus*) and Gray-cheeked (*C. minimus*) thrushes. The distributional ranges of these five species are roughly allopatric, extending across the forested portion of North America. There are extensive areas of sympatry, and as many as four species may occupy certain areas in the northeastern United States and southeastern Canada (Fig. 1).

ACKNOWLEDGMENTS
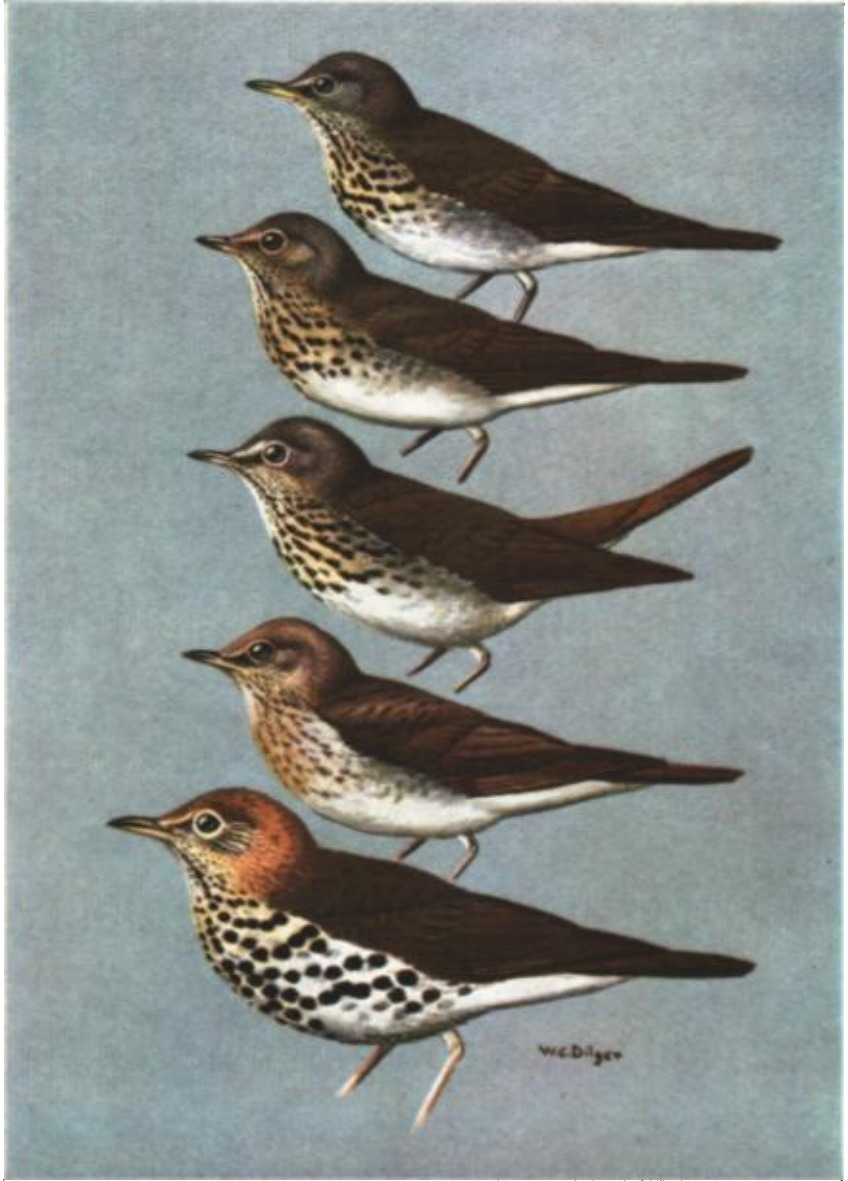
BREEDING MALES OF FOREST THRUSHES, from top to bottom:

Gray-cheeked Thrush *(Catharus minimus bicknelli)* from Essex County, New York
Olive-backed Thrush *(Catharus ustulatus swainsoni)* from Ulster County, New York
Hermit Thrush *(Catharus guttatus faxoni)* from Cattaraugus County, New York
Veery *(Catharus f. fuscescens)* from Essex County, New York
Wood Thrush *(Hylocichla mustelina)* from Tomkins County, New York

METHODS

The breeding seasons of 1952, 1953 and 1954 were devoted to field observation and to the accumulation of specimens. The field work was conducted in New York State, where all five of the forms breed. Two hundred and six skeletons representing *Hylocichla mustelina*, the four North American species of *Catharus* and the American Robin (*Turdus migratorius*) were examined and measured. Nearly one hundred other skeletons representing other species of *Catharus* and various additional turdine as well as saxicoline genera also were examined and measured. The collection of study skins at Cornell University was continually available.

Measurements of bones.—These were made with a dial caliper graduated in tenths of millimeters. The following are the measurements taken and the methods followed: The femur, tibiotarsus, tarsometatarsus, humerus, ulna, and manus (the entire hand from the proximal articular surface to the tip of the third digit) were measured across their greatest possible dimensions. This was accomplished by holding the bone perpendicularly between the faces of the caliper and sliding the caliper until it could go no further without damaging the bone. All the measurements listed above are believed to be reliable and free from instrumental error.
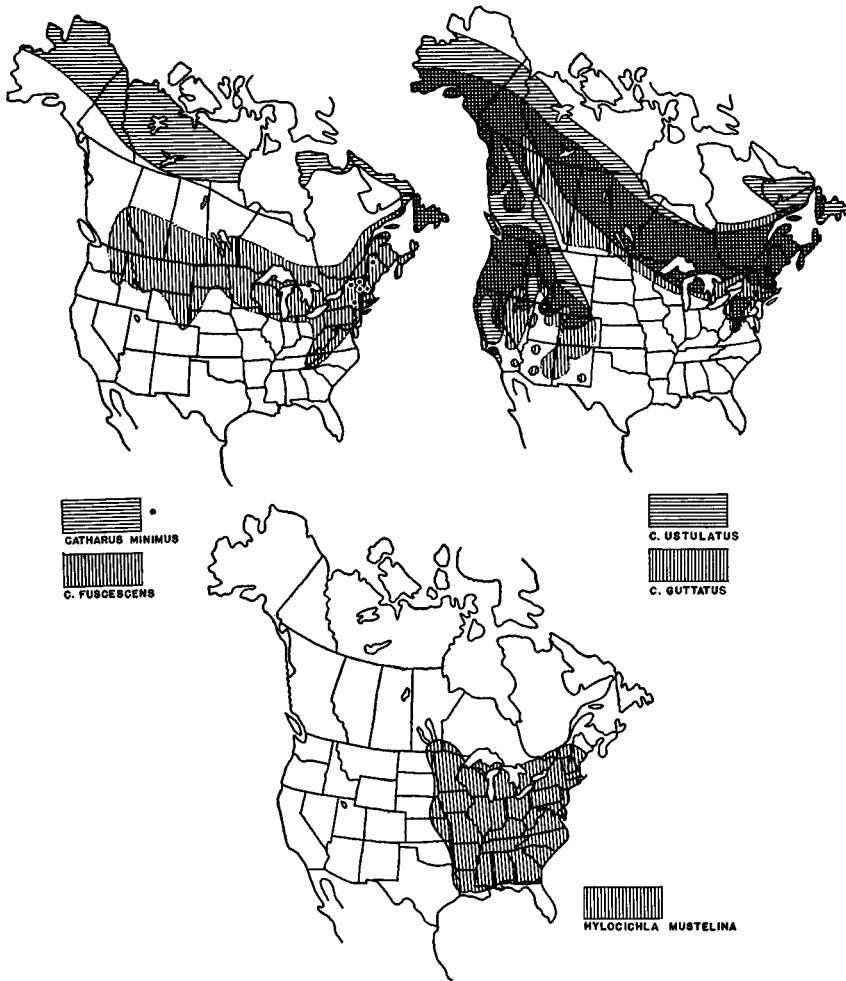
FIG. 1. Breeding ranges of *Catharus minimus*, *C. fuscescens*, *C. ustulatus*, *C. guttatus* and *Hylocichla mustelina*.

Several skull measurements were made as follows: the skull length was taken from the tip of the maxilla to the posteriormost portion of the cranium (just above the foramen magnum). The skull width was measured at the greatest width (between the auditory bullae). The skull width at lacrimals was taken as the greatest distance between the two lacrimals. The mandible was measured from its anterior tip to the posteriormost point of the condyle. The maxilla was measured from its anterior tip to the center of the crease of the naso-frontal hinge. The jaw width was measured between the

posterior points of the quadratojugals. The statistical analyses of these measurements are presented in Tables 1 to 5.

Weights.—Weights were accumulated for all of the species and subspecies in question. In order to minimize the error from seasonal fluctuations of weights only those of breeding males were utilized. The weights used were recorded to the nearest tenth of a gram and these data are summarized in Fig. 5.

Since the species being examined differed in absolute size, sometimes markedly, it was necessary to equate these measurements so that they could be compared directly. Body weight was used as an index to size and was employed as a measurement with which to equate the various bone measurements. The method proposed by Amadon (1943) was utilized. Since weights and measurements from the same individuals were not always obtainable, only the arithmetic means were compared. The procedure was to compute the cube root of the mean weight for each species and this figure was then divided into the mean skeletal measurements for each species. The various measurements thus were expressed as a proportion of body size. For ease of comparison these figures were further adjusted as percentages of the largest for each measurement of the same structure in different forms, the largest being regarded as 100 per cent.

Measurements of study skins.—Lengths of the tail and tarsus, and of the bill from the nostril were taken in the manner specified by Baldwin, Oberholser and Worley (1931). Measurements of the wing were taken as the chord of the closed (flattened) wing.

GENERAL BIOLOGY

Breeding Cycle.—The males arrive on the breeding grounds prior to the females and establish and defend territories against members of their own species. The females, upon arrival, seek out males of their own species and pair formation takes place (Dilger, 1956a). Nest building and incubation are performed by the female, but both parents help feed the young. The nests are typically rather bulky but neatly-constructed of twigs, grasses, mosses, leaf mold and leaves. Considerable mud is utilized by *H. mustelina*, the nests of which are similar to those made by the American Robin. All lay from three to five blue eggs, which are spotted with brownish in *C. ustulatus* and *C. minimus*. The eggs of *C. fuscescens* and *C. guttatus* are rarely spotted and, as far as is known, the eggs of *H. mustelina* are never spotted. The nests may be placed on the ground, as is typical of *C. guttatus* and *C. fuscescens* in the eastern part of their ranges, or they may be placed in trees or shrubs. Incubation requires about two weeks and fledging another two weeks.

Molts and Plumages.—The spotted young attain their first winter plumage

by a molt involving all but the flight feathers and a few pale-tipped scapulars or wing coverts. At this time the immature thrushes are indistinguishable from their parents except for the few remaining pale-tipped feathers. These are retained until the first post-nuptial molt. Once they are fully adult these birds are thought not to have any molt other than the annual post-nuptial, which is complete. There is a little evidence, however, that there may be at least a partial pre-nuptial molt. My captive thrushes had limited late-winter molts involving the crown, sides of the head and breast, back, rump and some of the wing coverts. This molt may have occurred because of the unnatural conditions imposed upon the birds by captivity. It is interesting to note, however, that these molts were symmetrical and always the same. It is also interesting that the breeding plumage in all these species is noticeably grayer than the warmer-toned winter plumage. The difference is thought to be due to feather wear. The new feathers acquired by these captives in the late winter or early spring were much grayer than the ones they had grown the previous autumn. Partial pre-nuptial molts have been described for several Old World species of thrushes (Witherby et al., 1943). The question of whether or not *Hylocichla* and *Catharus* have at least a partial pre-nuptial molt is still unsolved. Dr. Kenneth C. Parkes kindly examined specimens in the Carnegie Museum taken on their wintering grounds and found no evidence of a pre-nuptial molt.

Feeding and Food.—All the thrushes considered are forest inhabitants, feeding largely on the forest floor. Food is obtained by flipping aside the débris of the forest floor with the bill, and progression on the ground is by means of long, springing hops. The feet are not used for scratching aside the débris as in some other birds utilizing similar environments. All these thrushes eat considerable amounts of vegetable matter, principally small fruits. The animal food consists mostly of small invertebrates, such as beetles, ants, and spiders. Small vertebrates, such as tiny frogs and salamanders, are sometimes utilized. Quite a bit of flycatching and foraging in foliage also are done, particularly by *C. fuscescens* and *C. ustulatus*.

More detailed information on the general biology of these forms is presented by Bent (1949).

HABITAT PREFERENCES

Dr. Herbert Caswell and I, using Cole's (1949) method for the analysis of interspecific association, have arrived at some figures indicating the degree of association of these thrushes with various habitats. The results for the species under consideration are summarized in Figure 2. The sources of data for these computations were habitat-specific breeding-bird censuses taken mainly from *Audubon Field Notes*. About 500 censuses were utilized in this investigation. A scale of from minus 1 to plus 1 was used to

	UC	DC	FA	DD	UD
H	-.50	-.69	-.48	+.16	+.41
CF	+.06	+.24	-.90	+.12	-.01
CG	+.29	+.28	-1.0	-.07	-.31
CU	+.47	+.12	-1.0	-.41	-.56
CM	? +.80	? +.50	-1.0	-1.0	-1.0

	CM	CU	CG	CF	H
CM	+1.0	? +.30	? -.70	-1.0	-1.0
CU		+1.0	+.75	+.23	-.35
CG			+1.0	+.56	-.41
CF				+1.0	-.08
H					+1.0

Fig. 2. (Left) Coefficients of association of *Hylocichla mustelina* and the North American species of *Catharus* with habitats in eastern North America. H = *Hylocichla mustelina*, CF = *Catharus f. fuscescens*, CG = *C. guttatus faxoni*, CU = *C. ustulatus swainsoni*, and CM = *C. minimus bicknelli*. UC = undisturbed coniferous, DC = disturbed coniferous, FA = farmland, DD = disturbed deciduous, and UD = undisturbed deciduous. Plus 1 = complete association, zero = association expected by chance alone, and minus 1, complete negative association. See text for further explanation.

Fig. 3. (Right) Coefficients of association among *Hylocichla mustelina* and the four North American species of *Catharus*. These figures are based on the total range of each species in eastern North America. Key to species and the scale of values used are the same as in Fig. 2. See text for further explanation.

express these various associations. Minus 1 indicates that the form and habitat under consideration are found together the minimum number of times possible for the data available. Zero indicates the amount of association one would expect by chance alone. Plus 1 indicates the highest association possible. A detailed report of this work on these forms and others of North America will be published separately by Caswell.

Hylocichla mustelina.—An abundance of sapling growth is apparently associated with optimum conditions for this species. Wood Thrushes tend to avoid the drier habitats and are most abundant in edge situations associated with hardwood forests. Weaver (*in* Bent, 1949) mentions that this species is showing a growing tendency to occupy suburban areas, a trend that had its beginnings about 1890. The suburban areas occupied are mostly edges of hardwood forests and it is not surprising that this species is taking advantage of this type of man-made habitat, much as the American Robin did earlier. In addition to its beginning to expand into suburban habitats, the Wood Thrush is steadily pushing its range northward, but it is still weakly associated with coniferous situations (—.50 for undisturbed coniferous forests and —.69 for disturbed coniferous habitats). The Wood Thrush is most strongly associated with undisturbed deciduous woodland

($+$.41). It must be kept in mind that, for the most part, edge situations in these habitats are utilized.

Catharus f. fuscescens.—This subspecies of the Veery reaches its greatest concentrations in rather damp areas, either deciduous or coniferous. Moist bottomland woods with a lush understory of ferns and other plants seem to provide optimum conditions. The densest concentration of the Veery of which I am aware is one reported by Harding (1925). She found a three-acre area containing 12 pairs at Lake Asquam, New Hampshire. This area was a forested hillside fronting on the lake and covered with a dense understory of laurel (*Kalmia latifolia*). She does not mention the presence of any other thrushes. Our analysis showed that the greatest associations of the Veery were with disturbed deciduous ($+$.12) and disturbed coniferous ($+$.24) forests. The undisturbed habitats probably do not usually contain a dense enough understory for this species.

Catharus guttatus faxoni.—This subspecies of the Hermit Thrush is associated with edge type situations within forested areas. It is most often found along the margins of old burns, fire lanes, power line cuts, margins of lakes, and bogs, rather than the "exterior" edge situations inhabited by *H. mustelina.* The greatest concentrations of this species are associated with a rather dense, young, mixed coniferous-deciduous growth in the above areas. This thrush is much more tolerant of rather dry habitats than are its close relatives, although it is also frequently found in rather damp habitats. The Hermit Thrush is more closely associated with coniferous woodlands and mixed conifers and hardwoods than with pure deciduous woodland. It is most abundant in the proper habitats within coniferous woods, both disturbed ($+$.28) and undisturbed ($+$.29).

Catharus ustulatus swainsoni.—This form of the Olive-backed Thrush is most closely associated with undisturbed coniferous forests ($+$.47), although mixed forests appear acceptable, especially in the southern parts of its range. In mountainous areas in New York State it occurs from the mixed hardwoods (beech, maple, hemlock) upward into the mature forests of red spruce and balsam-fir. The presence of some conifers seems to be a necessity, for nest sites usually are located in them.

Catharus minimus bicknelli.—This is the most habitat-specific of the forms studied. In New York State it is confined, as a breeding bird, to the cloud-drenched, stunted fir and spruce tangles of mountain tops. It occurs at lower altitudes farther north but the habitat is similar. The substrate, where almost all of the foraging is done, is composed of a deep tangle of limbs and trunks in all stages of decomposition, and the whole is clothed with a sodden blanket of *Sphagnum*, other mosses and small herbaceous plants. The dense coniferous tangles provide deep shade on

the ground even on the brightest days. Unfortunately the number of cen-
suses containing the Gray-cheeked Thrush do not permit a reliable statistical
analysis of its habitat associations. However, in view of the statements
presented above, its association with coniferous forests of this particular
type must be in the neighborhood of $+1$.

ECOLOGICAL ISOLATING MECHANISMS

It is apparent that the greatest competition should exist among individuals
of the same species. This seems logical because members of the same species
are most similar in their requirements. Various mechanisms that tend to
reduce the adverse effects of intraspecific competition have evolved. Behavior
patterns associated with territoriality (breeding territory, individual distance
and other hostile behavioral patterns) have evolved which permit an equable
intraspecific distribution throughout a favorable environment. Differential
adaptations of body size and/or size of the bill between the sexes may evolve,
and these differences may serve to reduce the amount of intraspecific compe-
tition (Rand, 1952). Such differences may also become secondarily involved
in sexual recognition. All of these adaptations permit maximum use of the
suitable environment by the species population and insure maximum abun-
dance and reproduction of individuals.

There is an ever-present tendency for animals to occupy more of the
immediately-available environment, and the range inhabited by a form at
any given time is the resultant between the forces tending to permit the
form to spread and the forces opposing its spread. The genetic variability
of any species tends to permit preadaptations to occur in varying degrees
and frequencies. These preadaptations may serve in multitudinous ways,
such as permitting higher reproductive rate, the utilization of different foods,
or greater tolerance for the various aspects of the physical environment.
The primary opposing factor is low genetic variability.

Likewise, the genetic variability of a species at any given time is mostly
the resultant between environmental selective forces making for more precise
adaptiveness to a particular niche (consequently reducing the variability)
and the selective forces permitting expansion into adjacent niches (which
tend to favor variability). Consequently, some species have narrower vari-
ability ("adaptive peaks") than do others. Among the forms presently
under discussion, the Gray-cheeked Thrush provides the best example of
a narrow adaptive peak, which is a reflection of its highly specialized
existence. The relatively small range of variability in the skull characters
studied may be a manifestation of this (see Table 2). On the other hand,
the Hermit Thrush is the best example, among those under discussion,
showing a rather wide range of variability in the skull characters studied.
This may be a reflection of its rather wide tolerances for habitats and food.

If the greatest competition is among individuals of the same species it follows that usually the next most serious competition would have come *originally* from individuals of a closely-related, sympatric form. These would have the next most similar genotypes and hence will have the next least differences in their requirements. Mechanisms must be evolved in these cases to minimize the effects of what must otherwise be rather severe competition, especially for food. The very existence of adaptive differences among closely-related, sympatric forms suggests that such forms usually do compete severely enough to initiate selective pressures bringing about adaptive differences. The selective pressures must be supplied by each of the different species to all of the others in competition with it. It would seem that these selective pressures must also be proportional to the amount of competition; the greater the competition, the greater the selective pressures. The selective pressures should gradually dwindle as the adaptive modifications become progressively more effective. Forms more distantly related may also tend to compete if a convergence in requirements is taking place. Here, again, isolating mechanisms must develop if the two forms are to continue to exist sympatrically.

Food is apparently one of the most important single factors involved in competitive situations. This has been borne out in ecological studies (such as that of Lack, 1949). Many of the adaptive differences arising between competing forms seem to have a direct bearing on allowing the differential taking of foods, either different kinds of foods in the same environment or similar foods in different environments. Many closely-related, sympatric forms have diverged markedly in size, enabling them to minimize the competition for food by permitting the taking of different foods because of this size difference. One of the most familiar examples of this phenomenon is provided by the relatively large Hairy Woodpecker (*Dendrocopos villosus*) and the smaller Downy Woodpecker (*D. pubescens*). These two species are very similar in appearance and habits but differ chiefly in body size and in the relative size of their bills. Another example is found in the hawks of the genus *Accipiter*, the larger Cooper Hawk (*A. cooperi*) and the smaller Sharp-shinned Hawk (*A. striatus*). These two species also differ mainly in size and, in addition, there is a strong sexual disparity in size which no doubt helps to reduce the intraspecific competition (Storer, 1952:284).

Another mechanism allowing the differential taking of foods is a divergence in the size and/or the proportions of the bill. A classic example of this may be seen in the Galapagos finches of the genus *Geospiza* (Lack, 1947). This mechanism, too, may work to reduce intraspecific competition. Many species of birds have a marked sexual difference in the size and/or proportions of the bill. Probably the most extreme case is that of

the extinct Huia (*Heterolocha acutirostris*) of New Zealand, discussed by
Lack (1947:155). The bill of the male was rather stout and short while
that of the female was very long, slender and decurved. The males foraged
by tearing open rotten logs for the invertebrate life within and the females
followed them, able to utilize the food found in the deeper burrows and
crevices by virtue of their remarkable bills. Of course, these are but a
couple of the mechanisms utilized by birds to avoid ecological competition,
but others exist and they undoubtedly exist in various combinations and
degrees of divergence.

There is evidence to show that the divergence, presumably partly in
response to competition, may be most marked in areas of sympatric occur-
rence and less evident in areas of solitary occurrence. Two species of rock
nuthatches studied by Vaurie (1951) furnish an example. The two species,
Sitta neumayer and *S. tephronota*, have rather wide distributions in western
Asia and with a considerable area of sympatry. *Sitta tephronota* has a
slightly larger bill than has *S. neumayer*, but in the area of sympatry this
size difference is greatly enhanced. These two species appear to be very
similar and this difference in bill size has been evolved, presumably resulting
in minimizing the adverse effects of competition for food in the overlap area.

The forms considered in the present study, except for *H. mustelina*, are
all closely related and demonstrate a high degree of sympatry. Since their
sizes, foraging behavior and general biology are so similar it seems likely
that there must have been a relatively great amount of interspecific compe-
tition for food during the period of initial contact of these forms. The
ecological isolating mechanisms which must have developed in this situation
are not immediately apparent.

It would seem likely that the amount of divergence that has taken place
must be in proportion to the amount of competition among the various
forms in the same environment. Dr. Herbert Caswell and I have measured
the amounts of interspecific association in a number of North American bird
species, including the present forms, by use of the method of measurement
of interspecific association proposed by Cole (1949). The resulting coeffi-
cients of association are shown in Figure 3. The figures are based on the
same scale as the species-habitat coefficients discussed earlier. These coef-
ficients are based on the total breeding ranges of the species as they occur
in eastern North America. If the coefficients were based on the overlap areas
only, the figures would be much higher. About 500 censuses were utilized
for this work. The above coefficients of association coincide very nicely
with the amounts of divergence found to be associated with ecological
isolating mechanisms.

An attempt was made to compute the coefficients of association for the

overlap areas but this was not feasible because of a lack of sufficient data
from many areas. Coefficients of association were computed, however, for
broad, roughly latitudinal bands which somewhat approximate the distribu-
tions of these thrushes (Fig. 4). These values give some interesting results
but break down, especially in the southern parts of their ranges, because
of the irregular distributions effected by the eastern mountains and by the
paucity of breeding bird censuses in some critical areas. With these limita-
tions in mind it may be seen that these latitudinal coefficients of association
are about what one would expect from an examination of the breeding
ranges and the total range coefficients.

The initial attempts to gain some knowledge of the ecological isolating
mechanisms that must be in operation consisted of watching foraging indi-
viduals of all five species on their breeding grounds. Aside from the quite
evident propensity of some forms for feeding largely at or near the edge
and of others for feeding largely in the interior of the woodland, different
strata appeared to be used in foraging. All the species fed commonly on the
forest floor but those that did so most frequently were the Wood, Hermit,
and Grey-cheeked thrushes. The Veery and, especially, the Olive-backed
Thrush fed more often in the foliage and engaged in frequent flycatching.
It is interesting to note that the three predominant ground feeders alternate
with the two arboreal foragers in a north-south sequence, and that the edge
foragers alternate with the interior foragers, except for *C. minimus* which
is an interior forager.

Others have noticed these apparent differences in foraging levels. Francis
H. Allen (*in* Bent, 1949:223) watched a Wood Thrush and a Veery foraging
in the same vicinity and noted that "while the wood thrush hopped along
in the manner of a robin, more or less, the veery was continually flitting
from a perch in a bush or tree (2 to 4 feet from the ground) down to the
ground, where he picked up an insect or something of the kind, and then
again to another perch." This seems to be very typical *fuscescens* behavior.
In addition, they are more frequently seen "flycatching" while foraging in
this manner than are the others with the exception of the Olive-backed
Thrush, the most inveterate flycatcher of them all. Bent (1949:176) says
of that species: "They come with the warblers and other late migrants, and,
like the warblers, they are often seen in the tree tops, feeding on insects
in the opening foliage." This tree-top foraging behavior, as mentioned above,
is by no means confined to migration but is the usual feeding behavior on
the breeding grounds as well. The colloquial names of "Flycatching Thrush"
and "Mosquito Thrush" reflect a general observance of this frequently-used
feeding method.

Summarizing these observations, it would seem that *H. mustelina* and *C.*

	CU	CG	CF	H
CU	+1.0	+.86	+.25	
CG		+1.0	+.20	
CF			+1.0	
H				

A

	CU	CG	CF	H
CU	+1.0	+.33	−.66	+.08
CG		+1.0	+.47	+.37
CF			+1.0	+.54
H				+1.0

B

	CU	CG	CF	H
CU				
CG		+1.0	+.73	+.57
CF			+1.0	+.47
H				+1.0

C

	CU	CG	CF	H
CU	+1.0	+.89	+.88	−.08
CG		+1.0	+.67	−.30
CF			+1.0	+.05
H				+1.0

D

A—
B—
C—
D—
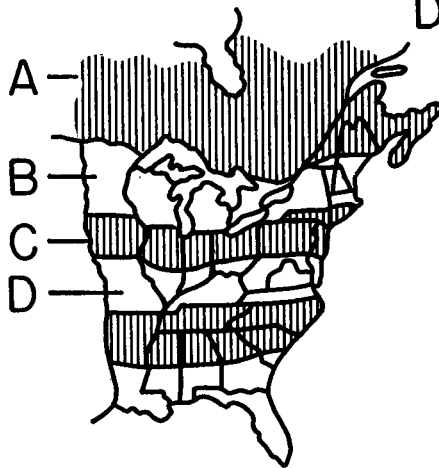
guttatus faxoni are mainly ground feeders at edge type situations, that
C. f. fuscescens and *C. ustulatus swainsoni* are primarily arboreal foragers
of interior situations and that *C. minimus bicknelli* is a ground forager in
the interior of the forest.

ADAPTATIONS FOR FORAGING

Some method of analysis was sought that would demonstrate any adaptive
differences and supply a test for the validity of these subjective field observa-
tions. Two methods of approach were considered. It was reasoned that if
this seeming difference between ground feeding and arboreal feeding were
a real one, then there should be detectable adaptive differences in the bills
and in the limbs consistent with the different habits. It was also reasoned
that a detailed analysis of the contents of a number of stomachs of the various
species should show something about the place of capture of the insects
they contained.

Stomach Contents.—Hundreds of stomachs of these species have been
investigated but, unfortunately, none ever was analysed carefully enough to
gain much insight as to the ecology of the food organisms it contained.
A notation of "beetles, 12 per cent" does not give one any idea whether
the beetles in question were arboreal or terrestrial forms. Beal reported
(Bent, 1949:152, 181) on the analysis of 551 stomachs of *C. guttatus faxoni*
and 403 stomachs of *C. ustulatus swainsoni*; these represent birds taken in
every month of the year. His data suggest that their foraging sites differ.
Diptera, for example, were represented as 3.02 per cent of the diet of *C.
guttatus faxoni* and 6.23 per cent of the diet of *C. ustulatus swainsoni*;
Orthoptera comprised 6.32 per cent of the diet of *C. guttatus faxoni* but
only 2.42 per cent of the diet of *C. ustulatus swainsoni*. Likewise, the per-
centage representation of spiders and millipedes for the Hermit Thrush was
7.47, while for the Olive-backed Thrush it was but 2.22. These figures are
certainly suggestive of where the birds did much of their foraging but a
careful detailed analysis of a large number of stomachs from all five species
would still be desirable in order to gain a more accurate impression of
their respective food habits.

Hind Limb Adaptations.—A number of skeletons of all five species con-
cerned in this study were examined and measured along with those of the
Russet Nightingale-thrush (*C. o. occidentalis*) and the American Robin.
Special attention was paid to features that were likely to demonstrate adaptive

FIG. 4. (opposite)   Coefficients of association among *Catharus ustulatus, C. guttatus,
C. fuscescens,* and *Hylocichla mustelina* based on mutual occurrence within each of four
latitudinal belts (A, B, C, and D). Open square in upper left of each box indicates that
figure is not statistically significant, while solid square indicates significance. Key as
in Figure 2. See text for further discussion.

modifications in respect to food getting, principally the bills and hind limbs. It was hoped that analysis might reveal some adaptive modifications consistent with what had been learned about the differential feeding habits of these forms. It is well known that limb lengths and the proportions of the component segments vary with the use to which they are adapted. Cursorial birds, for example have relatively longer legs than do arboreal ones. Not only do the relative lengths vary but cursorial forms tend to have relatively shorter femurs and relatively longer tarsometatarsi than do the arboreal forms. This is easy to demonstrate by the examination of two extreme forms; a ground-foraging thrush, such as *C. minimus,* and an aerial bird such as the Chimney Swift (*Chaetura pelagica*). Of course, extreme differences such as these were not expected upon examining the limb lengths and proportions of the forest thrushes but it was hoped that some detectable trend toward
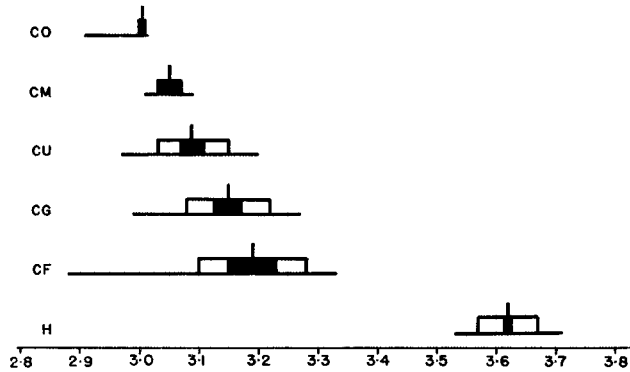
FIG. 5. Statistical analysis of the cube roots of weights in grams of breeding males of *Catharus* and *Hylocichla* species. CO = *Catharus o. occidentalis*; other symbols as in Figure 2. The horizontal line indicates the range, the vertical line, the mean, the black rectangle, two standard errors on either side of the mean, and the open rectangle, one standard deviation on either side of the mean.

arboreal proportions might be revealed in *C. fuscescens* and *C. ustulatus.* Indeed this is shown by the relatively-shorter tarsometatarsus in those two species (see Tables 1 and 2 and Figures 6 and 7).

The method used to equate the measurements of various appendages to body weight was discussed earlier. The weights of the several species of thrushes are compared graphically in Figure 5, and the various equated measurements appear in Tables 1 to 5.

In most cases the differences between the mean measurements of critical structures were readily evident without utilization of the equating procedure. However, it is felt that the equated measurements give a more

TABLE 1

MEASUREMENTS OF THE HIND LIMB ELEMENTS IN ADULT MALE
THRUSHES OF THE GENERA *Hylocichla, Catharus* AND *Turdus*

	Size of sample	Observed range	Mean with standard error	Standard deviation	Coefficient of variation	Equated value[1]	Per cent of largest
			FEMUR				
H. mustelina	21	22.60–24.60	23.50±.11	.51	2.17	6.4913	94.53
C. fuscescens	20	19.90–22.10	21.27±.13	.59	2.77	6.6750	97.20
C. guttatus	14	19.00–21.80	20.36±.19	.74	3.14	6.4565	94.02
C. ustulatus	21	19.50–21.40	20.28±.11	.51	2.51	6.5550	95.45
C. minimus	4	20.50–21.00	20.65±.12	.24	1.16	6.7691	98.57
C. occidentalis	4	20.20–20.90	20.48±.15	.31	1.51	6.8676	100.00
T. migratorius	12	26.50–28.20	27.34±.17	.59	2.16	6.3927	93.09
			TIBIOTARSUS				
H. mustelina	20	40.00–44.20	42.10±.25	1.09	2.59	11.6291	86.31
C. fuscescens	20	37.80–40.50	39.39±.29	1.00	2.54	12.3615	91.75
C. guttatus	12	37.70–40.60	39.04±.27	.94	2.40	12.3802	91.88
C. ustulatus	11	36.00–38.40	36.97±.20	.66	1.79	11.9497	88.69
C. minimus	4	38.60–38.90	38.78±.06	.12	.31	12.7122	94.35
C. occidentalis	5	39.20–41.20	40.18±.40	.87	2.11	13.4737	100.00
T. migratorius	12	45.50–49.10	46.98±.28	.98	2.09	10.9848	81.53
			TARSOMETATARSUS				
H. mustelina	22	29.70–34.10	31.10±.23	1.00	3.21	8.5906	78.22
C. fuscescens	18	27.50–31.50	30.04±.21	.88	2.93	9.4273	85.84
C. guttatus	12	28.80–32.00	30.08±.21	.75	2.16	9.5389	86.85
C. ustulatus	13	26.00–29.60	27.58±.21	.76	2.76	8.9146	81.17
C. minimus	5	28.80–30.90	30.04±.37	.83	2.76	9.8472	89.66
C. occidentalis	6	30.70–34.80	32.75±.67	1.67	4.89	10.9821	100.00
T. migratorius	12	32.00–34.80	33.05±.30	1.03	3.12	7.7277	70.36

[1]Actual measurement divided by cube root of body weight (see text).

accurate picture of the adaptive differences than do the unadjusted data.

All of the forms considered here are primarily adapted for ground foraging and the proportions and lengths of their legs are consistent with this mode of feeding. An apparent discrepancy is found in *H. mustelina*, which is terrestrial in habit although it has a relatively short tarsometatarsus (Fig. 7). The American Robin and other species of *Turdus* are mainly cursorial and also have relatively short tarsometatarsi as compared to *Catharus*. The limb proportions of *Turdus* and *Hylocichla* are clearly of the cursorial type but appear as if they both had been adapted from a common ancestor with a shorter tarsometatarsus than had the form from which *Catharus* was derived. In other words, a bigger step was involved in the selection for a more arboreally-adapted limb in *Catharus* than it would have been in the equally ground-adapted *Turdus* and *Hylocichla*.

TABLE 2

MEASUREMENTS OF THE SKULLS OF ADULT MALE THRUSHES OF
THE GENERA *Hylocichla, Catharus* AND *Turdus*

	Size of sample	Observed range	Mean with standard error	Standard deviation	Coefficient of variation	Equated value[1]	Per cent of largest
		SKULL LENGTH					
H. mustelina	23	40.70–44.20	42.30±.23	1.45	3.43	11.6844	93.62
C. fuscescens	15	35.60–38.60	37.21±.26	.99	2.66	11.6773	93.56
C. guttatus	13	35.30–40.30	38.04±.35	1.34	3.52	12.0631	96.65
C. ustulatus	14	35.00–37.70	36.66±.19	.70	1.91	11.8495	94.94
C. minimus	6	36.10–37.80	36.80±.25	.61	1.66	12.0632	96.65
C. occidentalis	5	36.60–38.70	37.22±.41	.91	2.44	12.4811	100.00
T. migratorius	12	45.00–49.10	46.93±.33	1.15	2.45	10.9731	87.92
		SKULL WIDTH AT LACRYMALS					
H. mustelina	23	10.50–11.60	10.90±.07	.35	3.21	3.0108	97.23
C. fuscescens	17	9.00–10.50	9.76±.12	.51	5.23	3.0629	98.91
C. guttatus	14	8.90–10.00	9.56±.07	.25	2.61	3.0316	97.90
C. ustulatus	13	9.00–10.10	9.58±.09	.35	3.65	3.0965	100.00
C. minimus	6	8.80– 9.30	9.05±.08	.21	2.32	2.9660	95.80
C. occidentalis	5	8.50– 9.50	9.02±.18	.40	4.43	3.0247	97.68
T. migratorius	11	11.60–13.20	12.44±.16	.54	4.34	2.9087	93.93
		JAW WIDTH					
H. mustelina	23	13.40–16.60	15.10±.13	.61	4.04	4.1711	93.67
C. fuscescens	17	13.60–14.80	14.19±.08	.35	2.47	4.4531	100.00
C. guttatus	13	12.60–14.10	13.40±.10	.39	2.91	4.2493	95.42
C. ustulatus	12	12.60–14.60	13.67±.15	.53	3.88	4.4185	99.22
C. minimus	6	12.50–13.80	13.00±.21	.52	4.00	4.2615	95.70
C. occidentalis	5	12.60–13.60	13.06±.19	.42	3.22	4.3794	98.34
T. migratorius	12	15.50–18.40	17.26±.21	.72	4.17	4.0357	90.63

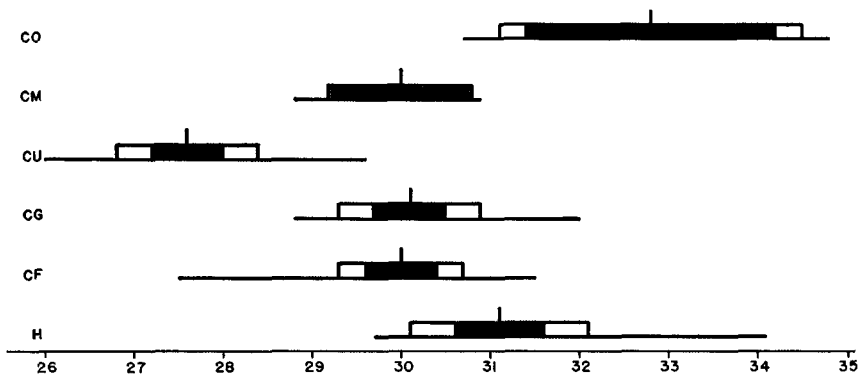[1]Actual measurement divided by cube root of body weight (see text).

FIG. 6. Statistical analysis of the length (in millimeters) of the tarsometatarsus in adult male *Catharus* species and *Hylocichla mustelina*. Key as in Figure 5.

There are two other factors that have a bearing on length of limb in addition to the degree of ground- or arboreal-adaptiveness. Everything else being equal, a larger bird will tend to have a relatively shorter tarsometatarsus than will a smaller one. This is merely a reflection of the greater weight of the larger bird and the need for proportionately greater support. Gustav Kramer (pers. comm.) has found that condition among the corvids: the Raven (*Corvus corax*) has relatively shorter legs than has the smaller Fish Crow (*C. ossifragus*). The depth of the debris on the substrate upon which a bird forages also has a bearing on leg length. The greater the depth of the "clutter" in proportion to the size of the ground-foraging bird, the longer its legs must be if the bird is to move about efficiently. Whether or not the ground has a certain depth and density of debris also has a bearing upon whether a particular species walks or hops. Those species that forage on substrates that are deep and densely-tangled in proportion to their sizes must progress by hopping (*Catharus, Pipilo, Dumetella, Hylocichla, Melospiza*). Ground-foraging birds of relatively uncluttered substrates (for their sizes) walk (*Sturnus, Molothrus, Quiscalus, Anthus, Alauda*). The relatively-shorter tarsometatarsus of *Hylocichla mustelina* is probably due to the fact that it is larger than the *Catharus* species to which it is supposedly closely related and because it forages over substrates which are actually and relatively less-cluttered than those used by the *Catharus* species. Also, the Wood Thrush is probably most closely related to the genus *Turdus*, which is characterized by a short tarsometatarsus. The hopping motions of *Hylocichla* are much like those of *Turdus migratorius*, while those of the *Catharus* species are rather long and springing; this suggests that a relatively-longer tarsometatarsus may be associated with a greater mechanical advantage for long, high hops.

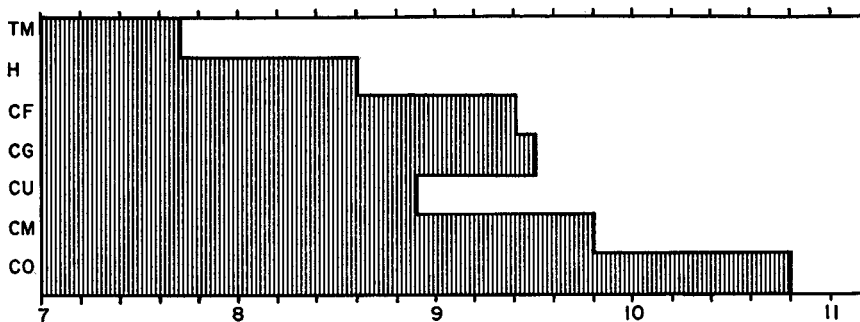Among the forest thrushes considered, the non-migratory and ground-

FIG. 7. Mean length of tarsometatarsus equated to mean cube root of the body weight in several species of thrushes. TM = *Turdus migratorius*; other symbols as in Figure 5.

dwelling Russet Nightingale-thrush (*C. occidentalis*) has the longest leg and also the longest segments of the leg. The next in order of modification for foraging on the ground is the Gray-cheeked Thrush, *C. minimus bicknelli*, and *C. guttatus faxoni* follows (see equated tarsometatarsus, Table 1). Observations in the field certainly bear this out. I have never seen *minimus* feeding anywhere but on the ground and it probably has to contend with a more-cluttered substrate, for its size, than does any of the others (see above under Habitat Preferences). The Hermit Thrush does some flycatching as well as foraging in trees and shrubs for small fruits, especially in the fall and winter. The remaining two species are the arboreal foragers and *fuscescens* is obviously not as highly adapted as *ustulatus* in this respect.

Apparently when a limb is becoming adapted for an arboreal mode of life the distal segment is the first to become shorter and the femur begins to adapt much later, or at least not as rapidly. The tarsometatarsus of the largely arboreal Olive-backed Thrush (*ustulatus*) has become more adapted for this mode of life than has the femur. The segment in most immediate contact with the environment is apparently the first one to experience modification due to selective pressures. It is apparent that the femur is becoming relatively longer both in *ustulatus* and *fuscescens*, but for some reason that of *fuscescens* is longer than that of *ustulatus*. I would have expected just the opposite condition. It may be that the limb proportions of *fuscescens* have had a different history than those of *ustulatus*. There is no reason to suppose that selection cannot proceed toward a more terrestrial-type limb, change to selection for an arboreal-type limb and reverse itself again, in various combinations of strengths and durations, depending on the vicissitudes of these selective pressures.

Perhaps the short tarsometatarsus of *H. mustelina* can be explained in a similar way, but it does not seem likely in view of the thoroughly-terrestrial habits of the Wood Thrush and the fact that *Turdus* and its close relatives are ground feeders for the most part and still have proportionately-shorter tarsometatarsi than do the species of *Catharus*. The femur is also relatively short in these latter forms. If there is a lag in femoral adaptation over tarsometatarsal adaptation, one would expect an arboreal form (with short tarsometatarsus and long femur), which is under selection favoring ground foraging, to develop a longer tarsometatarsus before the femur begins to shorten. This is not the case with the short-femured *mustelina*, which apparently was derived from terrestrial ancestors.

The long femur of *C. minimus bicknelli* can probably best be explained by taking into account the lengthening of the whole leg in response to the deeply cluttered substrate over which this small form feeds. The long femur of *C. occidentalis* can be explained in the same way.

TABLE 3

MEASUREMENTS OF MANDIBLE, MAXILLA AND BILL IN ADULT MALE THRUSHES
OF THE GENERA *Hylocichla, Catharus* AND *Turdus*

	Size of sample	Observed range	Mean with standard error	Standard deviation	Coefficient of variation	Equated value[1]	Per cent of largest
			MANDIBLE				
H. mustelina	22	32.00–35.60	33.20±.30	1.41	4.25	9.1707	96.19
C. fuscescens	15	26.90–30.50	28.85±.25	.98	3.40	9.0538	94.97
C. guttatus	14	26.00–32.40	29.12±.43	1.66	5.70	9.2344	96.86
C. ustulatus	12	26.50–28.70	28.07±.17	.58	2.07	9.0729	95.17
C. minimus	6	27.70–29.60	28.65±.28	.69	2.41	9.3915	98.51
C. occidentalis	4	27.50–29.80	28.43±.50	1.00	3.52	9.5336	100.00
T. migratorius	12	35.20–39.50	36.84±.41	1.43	3.88	8.6139	90.35
			MAXILLA				
H. mustelina	23	16.70–20.00	18.40±.18	.88	4.78	5.0825	95.32
C. fuscescens	15	15.10–17.00	16.09±.14	.56	3.48	5.0494	94.70
C. guttatus	12	15.10–18.00	16.49±.28	1.00	6.13	5.2292	98.07
C. ustulatus	13	14.20–16.30	15.27±.15	.56	3.67	4.9356	92.57
C. minimus	6	15.50–16.50	15.83±.15	.38	2.40	5.1891	97.32
C. occidentalis	5	15.20–16.80	15.90±.29	.66	4.15	5.3318	100.00
T. migratorius	12	20.00–22.90	21.05±.29	1.00	4.75	4.9219	92.31
			BILL FROM NOSTRIL				
H. mustelina	16	10.50–11.70	11.23±.10	.41	3.65	3.1020	98.93
C. fuscescens	17	8.70–10.40	9.58±.13	.53	5.53	3.0064	95.88
C. guttatus	16	9.50–10.80	9.84±.09	.38	3.86	3.1204	99.52
C. ustulatus	19	8.00– 9.50	8.67±.09	.39	4.49	2.8024	89.38
C. minimus	9	8.60– 9.40	9.10±.10	.30	3.30	2.9830	95.14
C. occidentalis	4	9.10–10.00	9.35±.21	.44	4.70	3.1354	100.00
T. migratorius	11	11.20–14.40	13.00±.26	.86	6.62	3.0396	96.94

[1]Actual measurement divided by cube root of body weight (see text).

Jaw Adaptations.—The bill tends to be longer and more slender in ground-foraging forms and shorter and wider in forms that forage in trees. A long, slender bill is a much better tool for flipping aside the debris of the forest floor and for probing into the crevices and cracks of this feeding niche than a shorter, stouter bill would be. Conversely, a relatively shorter and, especially, a wider bill would be of greater use in flycatching and for foraging in the foliage. A cursory comparison of the bills of a number of species that forage in the foliage and also indulge in flycatching will demonstrate this very nicely. Compare, for instance, the bills of the ground-foraging *Catharus* species and of *Turdus migratorius* with the bills of such arboreal feeders or flycatchers as the Red-eyed Vireo (*Vireo olivaceus*), Scarlet Tanager (*Piranga olivacea*) or the Eastern Wood Pewee (*Contopus virens*).

Various skull measurements were made for the species of *Catharus* and for *Hylocichla mustelina* and *Turdus migratorius* in order to detect any
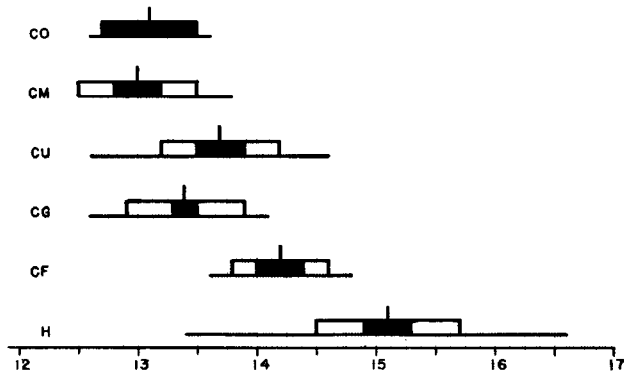
FIG. 8.   Statistical analysis of the jaw width in adult males of
Catharus species and *Hylocichla mustelina*. Symbols as in Figure 5.

drift toward shorter and wider bills in the more arboreal forms, *C. fuscescens*
and *C. ustulatus*. The results of this investigation are summarized in Tables
1 through 5 and further in Figures 8 and 9. These measurements also were
equated to the mean weights used as an index of body size. The necessity
for equating the jaw measurements is not as clear as it was for the leg
measurements. Bill proportions are not as intimately concerned with body
size as are the proportions of the limbs. In any case, both the equated and
unequated data (Table 2) show essentially the same pattern. The bills of
fuscescens and *ustulatus* are both wider and shorter than are the bills of
the more purely ground-foraging forms. Again, these differences in pro-
portions are not extreme but they are significant statistically and they are
consistent with what we know of the thrushes' feeding habits. The differences
are demonstrated most clearly by comparisons of the maxilla length to the
skull width at the lacrimals or the mandible length with the jaw width
(Fig. 10).

It is of some interest that *C. ustulatus*, which is more arboreal than *fusce-
scens*, has a slightly narrower mouth than has *fuscescens*. Again, this is not
what one would expect, but again we do not know the past history of
adaptation in these forms. It may be that *fuscescens*, instead of progressing
toward the arboreal feeding habit, is actually in the later stages of becoming
secondarily adapted for ground feeding. The fact that it has a slightly
longer femur, actually and relatively, than has *ustulatus* (see above) lends
some credence to this idea.

Wing Adaptations.—The lengths and proportions of the segments of the
wings follow the same pattern as was found in the hind limbs. Those forms
utilizing their wings to the greatest extent have the longest distal segments
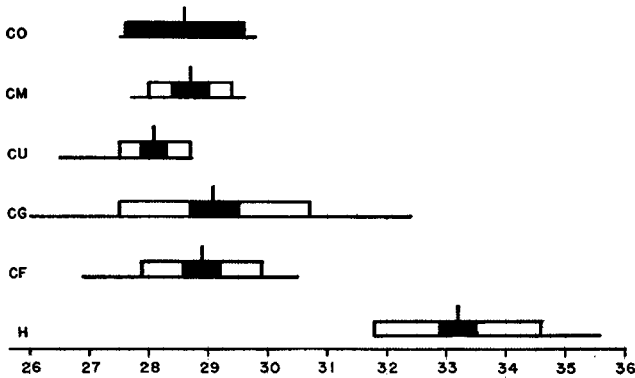(hands) and the shortest proximal segments (humeri). The converse is true

FIG. 9. Statistical analysis of mandible length in adult males
of *Hylocichla mustelina* and *Catharus* species. Key as in Figure 5.

for the forms which use their wings the least. This is again easy to demon-
strate by examining the wings of extreme examples, such as the wing of
the Chimney Swift and the wing of a flightless bird such as the Kiwi
(*Apteryx*). No such extreme differences as these are to be found among
the thrushes studied, of course, but again there is modification in the direc-
tion consistent with their specific habits. It is not surprising that *Catharus
occidentalis*, a non-migratory ground-forager, should have a wing least-
adapted for sustained flight. The ground-dwelling, moderately-migratory
Hermit Thrush also has a wing relatively poorly adapted for flying. The
longest manus and the longest wing (measured from the wrist to the tip of
longest primary) is found in *Catharus ustulatus*, a form which flies a great
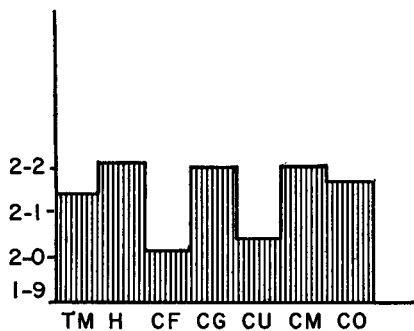

FIG. 10. Ratios of equated means of jaw width and mandible
length (equated mandible length divided by equated jaw width)
in several species of thrushes. The higher the ratio, the rela-
tively longer and narrower the jaw. Key as in Figure 7. See
text for further explanation.

TABLE 4

MEASUREMENTS OF THE WING ELEMENTS IN ADULT MALE THRUSHES
OF THE GENERA *Hylocichla, Catharus* AND *Turdus*

	Size of sample	Observed range	Mean with standard error	Coefficient Standard deviation	of variation	Equated value[1]	Per cent of largest
			HUMERUS				
H. mustelina	23	22.50–26.60	24.07±.16	.78	3.24	6.6489	98.50
C. fuscescens	18	20.70–22.20	21.24±.11	.46	2.17	6.6656	98.74
C. guttatus	16	19.40–21.80	20.59±.17	.69	3.35	6.5295	96.73
C. ustulatus	15	19.80–21.10	20.43±.09	.38	1.86	6.6035	97.82
C. minimus	5	19.30–20.60	19.92±.25	.55	2.76	6.5298	96.73
C. occidentalis	6	19.50–20.10	19.87±.10	.24	1.21	6.6630	98.71
T. migratorius	12	28.00–29.80	28.87±.19	.65	2.25	6.7503	100.00
			ULNA				
H. mustelina	23	28.30–31.10	29.76±.15	.75	2.52	8.2205	96.98
C. fuscescens	17	25.90–28.70	27.01±.19	.77	2.85	8.4763	100.00
C. guttatus	13	25.10–28.90	26.64±.27	1.08	4.05	8.4481	99.66
C. ustulatus	12	25.30–26.60	26.08±.11	.38	1.46	8.4298	99.45
C. minimus	5	23.30–26.00	24.22±.51	1.14	4.71	7.9394	93.66
C. occidentalis	5	23.50–23.70	23.56±.05	.11	.47	7.9004	93.20
T. migratorius	12	34.70–37.20	35.88±.27	.91	2.59	8.3894	98.97
			MANUS				
H. mustelina	21	24.70–27.40	26.16±.17	.81	3.09	7.2261	93.53
H. fuscescens	16	23.50–25.70	24.40±.15	.62	2.54	7.6573	99.12
C. guttatus	10	22.50–24.20	22.95±.10	.53	2.31	7.2778	94.20
C. ustulatus	11	22.40–24.90	23.90±.27	.91	3.81	7.7251	100.00
C. minimus	5	21.10–24.10	22.14±.52	1.18	5.33	7.2575	93.94
C. occidentalis	6	19.20–20.50	19.80±.19	.47	2.37	6.6396	85.94
T. migratorius	12	31.70–34.30	32.69±.21	.71	2.17	7.6435	98.94

[1]Actual measurement divided by cube root of body weight (see text).

deal while foraging in the tree tops and which has a very long migration
route (Fig. 13). The other species also show the correlation between wing
length and proportions when their flying habits are taken into consideration.
One thing to keep in mind is that the wing length and manus length are
not always perfectly correlated. All else being equal, a larger bird will have
a proportionately longer manus in relation to the wing length than will a
smaller bird. Gulls of the genus *Larus* have been investigated in this respect
(Gustav Kramer, pers. comm.) and it has been found, for instance, that the
Great Black-backed Gull (*L. marinus*) has a relatively longer manus than
has the Herring Gull (*L. argentatus*). Equated wing length, therefore, prob-
ably is a better index of the amount of flying a bird does than is the manus
length. Values for the equated wing lengths of a number of thrushes are
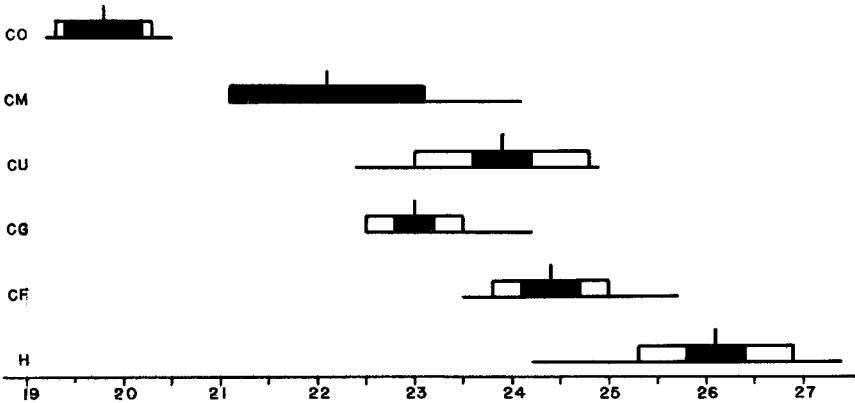presented in Table 5 and in Figure 13, and those for equated manus lengths

FIG. 11. Statistical analysis of the length of the manus in adult male *Catharus* species and *Hylocichla mustelina*. Key as in Figure 5.
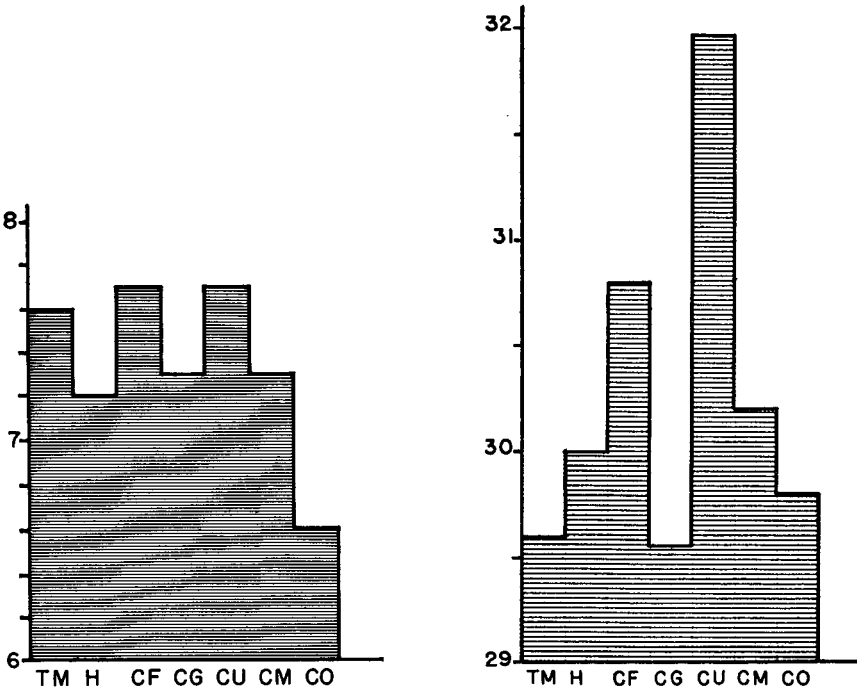

FIG. 12. (Left) Equated length of the manus in adult male *Turdus migratorius*, *Hylocichla mustelina* and *Catharus* species. Key as in Figure 7. Values were obtained by dividing the mean length by the mean cube root of the body weight.

FIG. 13. (Right) Equated wing length (wrist to tip of longest primary) in adult male thrushes. Key as in Figure 7.

TABLE 5

MEASUREMENTS OF THE WING, TAIL AND TARSUS IN ADULT MALE THRUSHES
OF THE GENERA *Hylocichla, Catharus* AND *Turdus*

	Size of sample	Observed range	Mean with standard error	Standard deviation	Coefficient of variation	Equated value[1]	Per cent of largest
			WING				
H. mustelina	16	105–112	108.75± .53	2.12	1.95	30.0400	94.07
C. fuscescens	17	93–102	98.24± .60	2.51	2.55	30.8300	96.54
C. guttatus	16	88– 97	93.19± .88	2.79	2.99	29.5520	92.54
C. ustulatus	20	94–103	98.80± .51	2.28	2.31	31.9340	100.00
C. minimus	9	86– 97	92.20±1.23	3.70	4.01	30.0000	94.63
C. occidentalis	4	85– 91	88.80±1.32	2.60	2.93	29.7780	93.25
T. migratorius	11	123–132	126.64± .87	2.91	2.30	29.6110	92.72
			TAIL				
H. mustelina	16	64.30– 77.00	69.69± .78	3.13	4.49	19.2503	74.15
C. fuscescens	17	66.30– 73.50	70.13± .57	2.35	3.35	22.0084	84.78
C. guttatus	15	65.00– 71.50	68.23± .49	1.92	2.81	21.6369	83.35
C. ustulatus	20	62.10– 71.50	66.20± .57	2.55	3.85	21.3976	82.42
C. minimus	9	60.30– 69.30	64.88±1.08	3.24	4.99	21.2679	81.92
C. occidentalis	4	70.70– 81.50	77.40±2.34	4.68	2.93	25.9548	100.00
T. migratorius	11	92.50–101.90	96.81± .87	2.90	2.99	22.6361	87.19
			TARSUS				
H. mustelina	16	28.70–32.30	30.84±.25	1.00	3.24	8.5188	75.88
C. fuscescens	17	27.50–30.80	29.35±.32	1.32	4.50	9.2107	82.04
C. guttatus	16	28.40–30.80	29.78±.20	.82	2.75	9.4437	84.12
C. ustulatus	20	25.30–28.70	27.10±.16	.72	2.66	8.7594	78.02
C. minimus	9	27.00–30.70	28.90±.11	1.10	3.81	9.4735	84.38
C. occidentalis	4	32.60–34.60	33.48±.42	.84	2.51	11.2269	100.00
T. migratorius	11	31.50–33.60	32.57±.25	.82	2.52	7.6155	67.83

[1]Actual measurement divided by cube root of body weight (see text).

appear in Table 4 and Figure 12. Figure 11 contains a statistical comparison of the unequated manus measurements.

It is clear from this examination of characters of the wing that the proportions and lengths are as completely associated with the habits of the birds as are the lengths and proportions of the leg. Wing length, then, may be a poor index of general body size, even among closely-related forms. There also seems to be a tendency toward a more pointed wing in the better flyers and toward a more rounded one in birds whose flights are relatively infrequent and of short duration. The tenth primary in the *Catharus* species of South and Central America is much longer than that of the migratory forms breeding north of the Mexican border. Among the forms under consideration here, *C. guttatus* has the longest tenth primary and, as mentioned above, is the least migratory. Another genus of thrushes which has

both northern, migratory forms and southern, sedentary forms is *Turdus*. Northern, migratory species, such as *Turdus migratorius* and *T. iliacus*, have short tenth primaries and the southern, sedentary *T. nudigenis* and *T. jamaicensis* have longer ones. It appears that a shortening of the tenth primary is associated with the amount of flying done.

Habitat Association and Ecological Isolation

The coefficient of breeding-habitat association of *ustulatus* with *guttatus* (Fig. 3) is plus 0.75. Its association with *minimus* must be high, but the number of habitat-specific breeding-bird censuses that included *minimus* was too small for analysis. My own field observations indicate a high association of *ustulatus* with *minimus*. In all of the areas occupied by *minimus* there was a broad overlap with *ustulatus*. The only other species which has a positive association with *ustulatus* is *fuscescens* but this is slight, being plus 0.23.

The coefficients of association of *guttatus* with its near competitors are *guttatus* to *ustulatus*, plus 0.75 and *guttatus* to *fuscescens*, plus 0.56. There is some association of *guttatus* with *mustelina* but it is low, minus 0.41. This is less than one would expect from chance alone.

As mentioned above, we have no significant data on the association of *minimus*, but *ustulatus* is the only related species with which it is in regular contact.

The coefficients of association of *fuscescens* with its near relatives are *fuscescens* to *guttatus*, plus 0.56; *fuscescens* to *ustulatus*, plus 0.23 and *fuscescens* to *mustelina*, minus 0.08.

H. mustelina, despite its recent range expansion into more northerly regions, has no positive associations with any of the four species of *Catharus*. As might be expected, it is most weakly negative with *fuscescens*. Study of Figure 3 will help to summarize the information on coefficients of association among these species.

An examination of the above data, augmented with what we know of the ranges and habitats of these species, indicates that the two species with the strongest positive associations with near competitors are *Catharus ustulatus* and *C. guttatus*. Each has strong association with another adjacent form, *guttatus* with *fuscescens*, and *ustulatus* with *minimus*. The selective pressures toward adaptive modifications to minimize ecological competition must be strongest in these two forms. The results of this adaptive divergence are well marked at this time and these two forms are the most widely separated, as to niche, of the competing forms; *guttatus* is a bird of interior edges and forages on the ground while *ustulatus* is a bird of the forest interior, feeding largely in the trees. All four of these species of *Catharus* have achieved a maximum amount of adaptive radiation with a minimum of

biological "effort." All vary principally in whether they inhabit interior or edge situations, and whether they are arboreal or forage on the ground. By an alternate expression of these few variables, along with their intergrading habitat preferences, the four species have achieved a rather high degree of ecological isolation from one another (Table 6).

Apparently *ustulatus* has become adapted for a more arboreal foraging niche in response to selective pressures brought to bear upon it by *guttatus* and *minimus*. As has been pointed out, it now forages largely in the forest canopy where it seemingly is beginning to enter into some competition with the other arboreal foragers, such as the Scarlet Tanager (*Piranga olivacea*). The evidence for this is indirect. First, both of these species commonly feed in the canopy, are of about the same size, and take about the same types of food. Secondly, both species have a hostile call (Dilger, 1956a) which is very similar (the "chuck-burr" note). This would function as a "spacer" in this stratum much as do the intraspecific hostile displays characteristic of any species. These calls are very much alike in both species and it seems likely that innate releasing mechanisms have developed in both that permit response to either. Considering the great variety of vocalizations of which birds are capable it seems highly unlikely that two such similar calls would have developed in these partially-sympatric forms without some reciprocal selective pressures being responsible. When the degree of foliage-foraging in *ustulatus* is finally stabilized it seems likely that it will be the resultant between the pressures from above, from already long-established foliage foragers, and the pressure from below supplied by *guttatus* and *minimus*.

Since hostile movements and vocalizations that are mutually "understood" are of value in insuring an equable intraspecific distribution it would seem highly plausible that the degree of similarity and "understanding" of hostile displays in interspecific situations might provide clues as to the amounts of existing interspecific ecological competition. An investigation into this subject would be a worth-while contribution that a behaviorist might do well to conduct.

It would be of interest to make a quantitative study of the adaptive differences among these various species of *Catharus* both in areas of sympatry and in areas of lone occurrence. It would seem likely that these adaptive differences are enhanced in areas of contact and to a lesser extent in areas of lone occurrence, much after the fashion of the nuthatches studied by Vaurie (1951). Many more specimens than I had available would be required to demonstrate this. My material was collected from areas of sympatry and probably represents the extreme conditions of adaptive divergence in these forms. I would expect a clinal type of distribution in these

TABLE 6

SOME RELATIONSHIPS OF SPECIES ASSOCIATION, BILL STRUCTURE, FEEDING STATION AND
HABITAT PREFERENCES IN THE THRUSH GENUS *Catharus*

Species	Coefficient of Species Association (see Fig. 3)	Difference Between Percentages of Equated:		Feeding Station	Habitat
		Maxillae	Jaw Widths		
minimus				Ground	Undisturbed stunted
	+.30	4.75	3.52	(forest interior)	coniferous (+.80?)
ustulatus				Largely arboreal	Undisturbed coniferous
	+.75	5.50	3.80	(forest interior)	(+.47)
guttatus				Ground	Undist. conif. (+.29)
	+.56	3.37	4.58	("interior edges")	Undist. decid. (+.28)
fuscescens				Somewhat arboreal	Dist. conif. (+.24)
				(forest interior)	Dist. decid. (+.12)

The species are arranged from top to bottom as they replace one another from north to south or from the top of a mountain to its base. The amount of actual association (overlap) is indicated by the association coefficient (see text). It is interesting to note that the two species with the highest association coefficient (*ustulatus* and *guttatus*) have the greatest differences in the percentages of equated maxilla length.

Species	Coefficient of Species Association (see Fig. 3)	Difference Between Percentages of Equated:	
		Maxillae	Jaw Widths
minimus			
	—.70	.75	.38
guttatus			
ustulatus			
	+.23	2.13	.78
fuscescens			

The species have been arranged according to the least amounts of overlap and hence the low coefficient of association figures. Since these species do not overlap very much, their similarities are greater. Note the little difference between the percentages of equated maxillae and jaw widths. Even here, however, the species pair with the most overlap (*ustulatus* and *fuscescens*) have the greatest differences between the maxillae and jaw widths.

characters to occur, the regularity of which would depend on the quantitative abruptness of occurrence of competing forms.

This study was conducted in eastern United States where *Hylocichla mustelina* and all four North American species of *Catharus* occur. In the extreme western United States, only two species occur commonly, *ustulatus* and *guttatus*. Here they have apparently solved the problems of ecological competition in a somewhat different manner. I have insufficient data from these areas and was unable to borrow sufficient anatomical material for

critical comparisons. A study of the interrelations of *Catharus* in these areas would be interesting in comparison to the work reported here.

SUMMARY

The very similar, roughly-allopatric, forest-inhabiting species of the thrush genera *Catharus* and *Hylocichla* often are found living beside one another in the areas of geographic overlap. Although each species differs somewhat in habitat, these habitats are shared with adjacent species, and differences in feeding niches have developed in response to selective pressures presumably stemming from competition for feeding areas.

The typical order of overlapping replacement from south to north or from lower altitudes to higher ones is *Hylocichla mustelina, Catharus fuscescens, C. guttatus, C. ustulatus* and *C. minimus*. The differences in feeding niches involve both the height at which foraging takes place and the location with respect to forest-edge or forest-interior sites. By a simple alternation of these places of foraging a maximum amount of ecological diversification is accomplished with a minimum amount of biological "effort" (Table 6). Adaptive modifications of the bill, hind limbs, and wings enable each species to occupy its specific feeding niche. A broader, shorter bill is associated with arboreal foraging and shorter legs accompanied by longer femurs and shorter tarsometatarsi are associated with arboreal feeding. Conversely, a longer, narrower bill and longer legs with shorter femurs and longer tarsometatarsi are associated with ground foraging. Longer, more pointed wings are associated with a greater amount of flying than are wings that are relatively shorter and more rounded. The Olive-backed Thrush, the most arboreal of the forms considered, has the longest wing in apparent response to the long migration route and also to the fact that it spends much of its time foraging in the foliage and in flycatching. The amounts of adaptive difference, in these respects, between the various pairs of species tend to be in direct proportion to the amounts of association between them. Coefficients of association were computed for the species by using habitat-specific breeding-bird censuses with Cole's (1949) method for the computation of interspecific association.

It is presumed that these species have achieved their ecological isolation by coming "rough sorted" as to habitat by virtue of their largely allopatric distributions and by developing differences in their feeding niches which allow them to occur sympatrically in the broad overlap areas.

LITERATURE CITED

AMADON, D.
    1943 Bird weights as an aid in taxonomy. *Wilson Bull.*, 55:164–177.
BALDWIN, S. P., H. C. OBERHOLSER AND L. G. WORLEY
    1931 Measurements of birds. *Sci. Publ. Cleveland Mus. Nat. Hist.*, 2:x + 1–165 pp.

BENT, A. C.
    1949   Life histories of North American thrushes, kinglets and their allies. *U.S. Nat. Mus. Bull.* 196:vii + 1–454 pp.

COLE, L. C.
    1949   The measurement of interspecific association. *Ecology*, 30:411–424.

DILGER, W. C.
    1956a The hostile behavior and reproductive isolating mechanisms in the avian genera *Catharus* and *Hylocichla*. *Auk*, 73:313–353.
    1956b Relationships of the avian genera *Catharus* and *Hylocichla*. *Systematic Zool.*, (in press).

GAUSE, G. F.
    1934   The struggle for existence. Baltimore; Williams and Wilkins.

HARDING, K. C.
    1925   Semi-colonization of veeries. *Bull. Northeastern Bird-Banding Assoc.*, 1:4–7.

LACK, D.
    1947   Darwin's finches. Cambridge Univ. Press.
    1949   The significance of ecological isolation. *In* Genetics, paleontology, and evolution. Princeton Univ. Press.

MAYR, E.
    1942   Systematics and the origin of species. New York; Columbia Univ. Press.

PARK, T.
    1948   Experimental studies of interspecies competition. I. Competition between populations of the flour beetles, *Tribolium confusum* Duval and *Tribolium castaneum* Herbst. *Ecol. Monogr.*, 18:265–308.

RAND, A. L.
    1952   Secondary sexual characters and ecological competition. *Fieldiana Zool.*, 34:65–70.

STORER, R. W.
    1952   Variation in resident sharp-shinned hawks of Mexico. *Condor*, 54:283–289.

VAURIE, C.
    1951   Adaptive differences between two sympatric species of nuthatches (*Sitta*). *Proc. Xth Internat. Ornith. Congr.*, 163–166.

WITHERBY, H. F., F. C. R. JOURDAIN, N. F. TICEHURST AND B. W. TUCKER
    1943   The handbook of British birds. Vol. 2. London; H. F. and G. Witherby.

LABORATORY OF ORNITHOLOGY, CORNELL UNIVERSITY, ITHACA, NEW YORK, JANUARY 15, 1956.