

There are several possible explanations for combinations of similarities and interaction between these two species, four of which bear mention. 1, the situation could be a case of commensalism with only the chickadee benefitting. However, if this were the case, it is difficult to explain the similarities in plumage and voice in the warbler to those of the chickadee. These features suggest that the warbler has probably converged in plumage and vocalizations, as these types of coloration and vocalization are widespread in *Parus*. 2, commensalism could be operating, with only the warbler benefitting. This would explain the convergences, but is not borne out by the behavioral interactions. 3, the similarities could be due to chance. This seems unlikely in view of the multiplicity of features and because of the behavioral interactions. 4, the warbler and chickadee may exhibit mutualism. We think that this is the best hypothesis, based on our current state of knowledge. The activities of the warbler during spring provide the clearest case. The warbler is a migrant, and the chickadee is a resident. Presumably the chickadee utilizes the best feeding areas on its territory and also might be particularly aware of predators in the area. Thus, the warbler may benefit in these two regards by seeking out the chickadees. On the other hand, the chickadee gains access to buds opened by the warbler which it would otherwise have to hammer open. We suggest that the Golden-wing may not take all the insects available from buds because the warbler is rapidly displaced by the approach of the chickadee. Interactions during the breeding season are less obvious, although the two species seem attracted to each other.

Plumage similarities between birds may result from selection for similarity in aggressive releasers related to territoriality (Cody, *Condor*, 71:223-239; Cody and Brown, *Evolution*, 24:304-310, 1970), or they may be instances of "social mimicry," involving releasers facilitating interspecific flocking (Moynihan, *Evolution*, 22:315-331, 1968). The warbler-chickadee relationship described here seems more likely a case of social mimicry, as aggression between the two is uncommon while attraction is rather frequent. The interactions of these species deserve further attention to clarify the nature of the relationship and the selection pressures acting to produce it.

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Species-specific foraging behavior in some Hawaiian honeycreepers (*Loxops*).

—Four congeneric species of Drepanididae coexist without apparent competition in the native Ohia forests of the Hawaiian island of Kauai. The species are distinguished from one another by differences in the shape of the bill and in foraging habits. In 1970-71, I had an opportunity to observe these forms in the Kokee Forest of Kauai, and I also studied in detail the exploratory behavior of three of the species in captivity. The captive specimens were raised indoors from the nestling stage by A. J. Berger and C. R. Eddinger and never foraged for food in nature. This afforded an opportunity to test whether species-specific foraging behavior was innate, or whether it was learned in the face of competition with other closely related species.

I will briefly review the feeding habits of each species as an introduction to the behavior analysis in this study. The information is from Berger (*Hawaiian Birdlife*, Univ. Press of Hawaii, Honolulu, 1973) and my own field observations. For the purpose of this paper the type of substratum used and the postures and movements of the birds are of primary interest.

Loxops virens stejnegeri is perhaps the most generalized of the species. The bill is stout, moderately long, and slightly decurved. This species feeds on nectar and on insects gleaned mainly from the surfaces of leaves and branches. It seldom ventures onto the smallest branches, the tree trunk, or the ground, and it can be characterized as a crown forager, behaviorally similar to a vireo (*Vireo*) or a white-eye (*Zosterops*).

Loxops parva is similar to *L. virens* but is slightly smaller, with the bill much smaller and straighter than in *L. virens*. *L. parva* forages in the crowns of trees and also in the underbrush. Occasionally it forages like *L. maculata* on bark and dead twigs. On one occasion I saw one fly to the ground for a moment. Its movements are quick and agile; it goes through a variety of acrobatic movements and postures, moving rapidly through a bush or tree from branch to branch or along twigs, poking curiously among leaves and flowers. This species often uses the small tips of branches, sometimes hanging upside down by one foot. The other species generally bypass these small twigs. In general movements, agility, and active nature *L. parva* is highly reminiscent of a titmouse (*Parus*).

Loxops maculata bairdi is behaviorally and ecologically rather comparable to a nuthatch (*Sitta*). Its bill is fairly long and straight. This species forages for insects on the trunks and larger limbs of trees and bushes, and it can climb head first either up or down a tree trunk and along both upper and lower surfaces of horizontal branches. This is the only one of the four species which habitually forages on the ground, a habit in which it departs from its otherwise nuthatch-like behavior. Like nuthatches, but unlike many other trunk foragers such as woodpeckers or true creepers (Certhiidae), this species does not use retrices for support on vertical surfaces.

Loxops coccinea caeruleirostris forages for insects in the crowns of trees. The tips of the upper and lower mandibles are twisted in opposite directions as in the crossbills (*Loxia*), although not to the same extent. This specialized bill is used for opening leaf buds and seed pods containing insects, in a manner similar to that by which crossbills open pine cones. Richards and Bock (Amer. Ornith. Union, Monog. no. 15, 1973) analyzed the anatomical basis for this habit in *L. c. coccinea* of the island of Hawaii. My field observations of this species were limited, and no specimens were available in captivity; consequently, the following discussion will be limited to the first three species.

In a laboratory at the University of Hawaii, captive specimens of *L. virens stejnegeri*, *L. parva*, and *L. maculata bairdi* were maintained in large flight cages. There I was able to observe them almost daily for about one year, while also engaged in anatomical studies on the Drepanididae. I soon realized that each species spent much of its time exploring and moving about the cages in a manner similar to that of foraging behavior in nature. Each cage was provided with a variety of surfaces on which the birds could move about at will: a large vertical tree trunk, with smaller branches aligned at various angles; strings hung from the screen roof of the cage; and horizontal perches. The birds were not successfully foraging for food, on these surfaces, as no insects were present. This behavior was thus presumably merely exploratory and was never reinforced by a food reward. Actual feeding was possible only from dishes along the walls of the cages, and food could be had at will.

In order to quantify my somewhat subjective impressions of these exploratory activities, I spent about six hours recording a total of 572 movements. Each time a bird changed its position, I recorded whether it was on the ground, on branches, vertically climbing, or in a hanging posture. Although all three species used virtually all postural variations, the frequency varied between species in a way which corresponds closely to the foraging behavior of the three species in nature (Table 1). As this species-specific behavior arose in captivity without experience in nature and without food reward, the conclusion is

TABLE 1
ECOLOGICAL CHARACTERISTICS AND LOCOMOTOR PREFERENCES IN THREE SPECIES
OF HAWAIIAN HONEYCREEPERS

Species	Continental "ecological equivalent"	Main foraging substrate	No. of movements recorded	Substrate preferences in captivity (percent)			
				On the ground	On branches	Vertical climb- ing	Hanging postures
<i>Loxops virens</i>	White-eye (<i>Zosterops</i>) or <i>Vireo</i>	Medium-sized branches	171		68	10	22
<i>L. parva</i>	Chickadee (<i>Parus</i>)	Small branches and twigs	246	1	52	19	28
<i>L. maculata</i>	Nuthatch (<i>Sitta</i>)	Tree trunks, large branches, and on the ground	155	14	49	28	9

inescapable that it is innate or instinctive for each species. However, merely labelling a behavior pattern instinctive does not explain it. Indeed, the use of such terms, which may mask ignorance, has reached a point where some students of behavior are reluctant to use them at all. I would like to offer some brief speculations as to the nature of this "instinctive" behavior.

Innate or instinctive behavior patterns were in the past often regarded (or disregarded) as being somehow encoded into the central nervous system, where they developed during ontogeny under the control of genes. More recently, the analysis of such "instinctive" behavioral capacities as species-recognition and singing have shown that they involve specialized learning components, e.g. imprinting and the learning of species-specific songs. It is possible that some such learning activity is involved in the development of species-specific foraging behavior, such as that described above. The different species of honeycreepers probably vary slightly in their weight, limb proportions, muscle mechanics, or other factors modifying the mechanical properties of their locomotor apparatus. I do not have adequate anatomical material to examine this possibility, but I suspect that it is true in *Loxops*; it has been demonstrated in other avian groups, such as in the parulid warblers studied by Osterhaus (Amer. Midl. Nat., 68:474-486, 1962). If this is so, then certain postures and movements may be more comfortable or easily performed by one species than another. All of the *Loxops* species that I studied use all of the same postures, but in different frequencies. This means that each species is physically capable of every position, but *emphasizes* certain ones. Perhaps each individual has learned to do so by trial and error. In its early postfledging exploratory behavior an individual may find that it is more comfortable and efficient in certain postures and on certain surfaces, and hence will come to emphasize these in its foraging. In other words, the innate basis for species-specific foraging behavior may be determined more by the genes which control the development of the body and limbs than those which control the development of the brain. This would involve a simple type of learning via proprioceptive feedback from the limbs to the central nervous system. This is a simpler hypothesis than one which

postulates the existence of neural centers controlling the behavior in question, such as those postulated by proponents of theories of instinctive behavior which propose complex models of presumably inherited neural mechanisms which have no known physiological correlates in the nervous system.

This simpler hypothesis could be tested by carefully recording the movements and postures of young birds immediately after fledging and for a period of time thereafter, to see whether the species-specific locomotor pattern appears at once or only gradually.

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Foraging of Pine Warblers allopatric and sympatric to Yellow-throated Warblers.

—Pine (*Pinus* spp.) forests in the southeastern United States usually support a single nesting species of *Dendroica* warbler, the Pine Warbler (*D. pinus*). However, Ficken, Ficken, and Morse (*Evolution*, 22:307–314, 1968) described a case in which Pine Warblers and Yellow-throated Warblers (*D. dominica*) coexist in loblolly pine (*P. taeda*) forests on the Delmarva Peninsula of Maryland. They suggested that niche-partitioning is accomplished primarily through the ability of Yellow-throated Warblers to probe in pine cones for invertebrates, a behavior that the Pine Warbler cannot perform, because its bill is too short and its skull too large to reach to the stalk of the pine cones. In addition, Yellow-throated Warblers usually foraged somewhat higher than Pine Warblers, though overlap in this measure was high.

The present paper compares data collected upon Pine Warblers in a loblolly pine forest where no Yellow-throated Warblers occur with additional data from the Delmarva Peninsula. The primary purpose of these observations was to determine whether Pine Warblers in allopatry and sympatry forage differently. Unfortunately, I know of no pine forests occupied only by Yellow-throated Warblers, so it has not been possible to test the converse. In addition, I compare the foraging patterns of male and female Pine Warblers at both locations and relate these data to other studies.

If Yellow-throated Warblers affect the exploitation patterns of Pine Warblers, then Pine Warblers at the one-species site should forage more frequently in high positions than they do at the two-species site, for those were the parts of the habitat used most frequently by Yellow-throated Warblers. However, as the forest at the one-species site is somewhat shorter than the one at the two-species site, an absolute change in height might not occur. Further, it is possible that Pine Warblers might hawk for insects more frequently at the former location than at the latter location, as Yellow-throated Warblers in the latter hawked for insects much more frequently than did Pine Warblers.

Observations of Pine Warblers were made during March and April of 1967 and 1968 at Cedarville State Forest, Brandywine, Prince George's County, Maryland, and in March and April of 1967 at Shad Landing State Park, Worcester County, Maryland (the Delmarva site). Cedarville lies approximately 135 km WNW of Shad Landing, the study site for the two-species observations (Ficken et al., op. cit.), and is separated from it by the Chesapeake Bay. The forest at Cedarville, planted in the early 1930's, is somewhat shorter than the one at Shad Landing, averaging 15 m in height at the time of the study, approximately three m shorter than the one at Shad Landing. Other than this, the two areas are very similar, with only scattered deciduous trees and little underbrush occurring within the forest. Only a few Virginia pines (*P. virginiana*) grow on the main study area at Cedarville, although they are common in adjacent locations.