

SONG DIVERGENCE IN HUMMINGBIRD AND JUNCO POPULATIONS ON GUADALUPE ISLAND

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Guadalupe Island is a true oceanic island of volcanic origin, lying about 240 km west of Baja California, Mexico. W. E. Bryant (1887) was the first naturalist to make a thorough survey of the island's bird fauna. He noted that the song and call of the resident junco, *Junco (hyemalis?) insularis*, differed from that of mainland populations of *J. hyemalis*. He suggested that the song resembled somewhat the trill of the Chipping Sparrow (*Spizella passerina*). Bryant also collected Anna Hummingbirds (*Calypte anna*), but did not comment on the song of this species.

Howell and Cade (1954) reported that juncos sang frequently during their visit to Guadalupe Island in June 1953, but they did not hear the slow trilling characteristic of mainland populations of *J. hyemalis*. They also noted that the call and song of both adult and immature Anna Hummingbirds sounded different from those of mainland individuals and suggested, "It is possible that the small insular population does have an established vocal difference, but future observations will be needed to substantiate this." In this paper I document this insular divergence for both the junco and the Anna Hummingbird.

MATERIALS AND METHODS

I spent 17 days on Guadalupe Island between 23 November and 26 December 1973. Songs of the island juncos and hummingbirds were recorded between 3–10 December among the wild tobacco (*Nicotiana glauca*) groves at the northeast anchorage. A Uher 4000-L tape recorder was used at a tape speed of 19 cm/sec with a Uher M514 microphone mounted at the focal point of a 24-inch parabolic reflector. In the laboratory, permanent graphic recordings were made with a Sona-Graph 6061-B audio-frequency analyzer using the wide-band filter. Recordings of Anna Hummingbird vocalizations also were made on the campus of the University of California at Los Angeles for comparison. Terminology follows Heck-enlively (1970).

GUADALUPE ISLAND ANNA HUMMINGBIRD

GENERAL BIOLOGY

For the years between 1885, when Bryant (1887:292) collected Anna Hummingbirds, and 1953, when Howell and Cade (1954) collected them, no certain records of this species on the island exist. Thayer and Bangs (1908)

and Anthony (1925) gave anecdotal accounts of presumed Anna Hummingbirds, but species identification was assumed on the basis of Bryant's prior record. The possibility that the hummingbirds were able to breed successfully and maintain even a sparse population on the island during the approximately 50 years between 1885 and the introduction of wild tobacco seems remote. The destruction of the once abundant endemic vegetation by goats began just prior to 1875 (Ridgway 1876) and proceeded rapidly. By 1906, barren conditions similar to those of the present day had already been reached (Thayer and Bangs 1908). Those native shrubs that remain are found only in areas inaccessible to goats. The scarce native flowering plants do not seem capable of providing enough nectar and supporting enough insects to have maintained a breeding population of hummingbirds on the island. Howell and Cade noted the establishment of the large shrub *Nicotiana glauca* in a restricted area at northeast anchorage. They suggested that *Nicotiana* was established no earlier than 1932 possibly only since 1941 (U.S. Office of Chief of Naval Oper. 1942 and photographs). No other hummingbird species has been positively recorded from the island, and we can only speculate on whether or not *C. anna* has been present continuously on Guadalupe Island.

The establishment of *Nicotiana* provided a year-round resource for the hummingbirds. At the time of Howell and Cade's visit it was present only at northeast anchorage, and they estimated the hummingbird population at between 15 and 20 individuals. The subsequent spread of the wild tobacco over much of the northeastern part of the island has allowed the hummingbird population to increase to about 100 individuals.

The breeding biology and territorial behavior of *C. anna* on Guadalupe Island seems very similar to that on the mainland of southern California (Stiles 1973). At the time of my visit to Guadalupe in late November 1973, male hummingbirds had already begun establishing territories in the *Nicotiana*. Males were singing from exposed perches throughout much of the day, and they pursued any other hummingbird which flew over their ter-

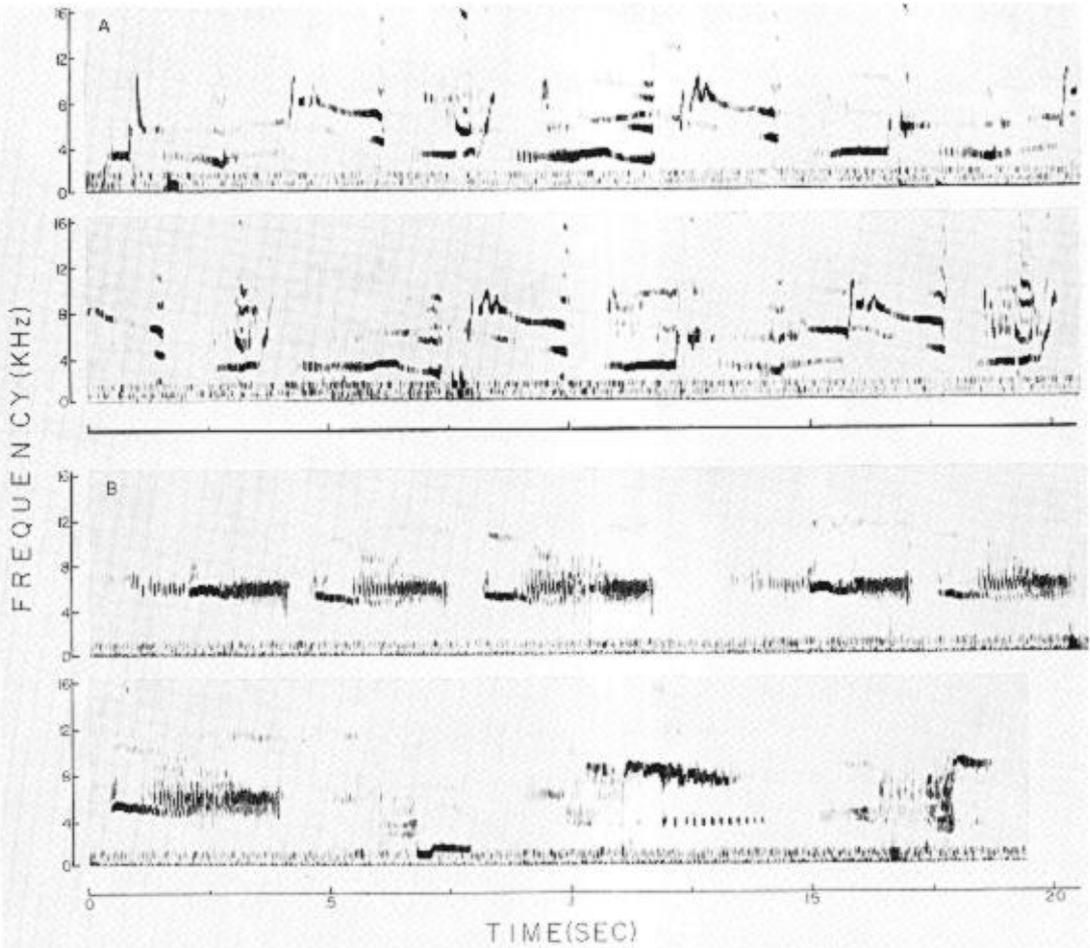


FIGURE 1. Audiospectrograms of songs of adult male Anna Hummingbirds. One song continues on two lines. (A) Guadalupe Island male song, characterized by several prolonged phrases with high frequency harmonics. Phrase one lasts approximately 0.6 sec and phrase two approximately 0.25 sec. Sets one and two last 1.5 sec each, and both contain three phrases. Set three contains only two phrases and lasts 1 sec. (B) Southern California male song consisting of three sets of three distinct phrases. The phrases of set one are repeated in sets two and four (not shown) of the song. The first phrase of set three is loud and of low frequency.

ritory. When a female entered the territory of a male, he immediately flew out and chased her. When the female stopped and perched, the male gave one or more dive displays in which he climbed to a height of up to 35 m and then dived nearly vertically, swinging up at the end with a loud squeak. No nests of hummingbirds were found.

SONG

The song of the male Guadalupe Island Anna Hummingbird is altogether different from that of mainland birds (see below). Humans familiar with the latter do not recognize recordings of the island type song as that of *Calypte anna*. In a sustained bout of singing, a territorial male from Guadalupe Island typically delivers a series of prolonged phrases characterized by several high frequency harmonics

(fig. 1A). The individual phrases of the song are grouped into sets. As shown by the sound spectrogram, phrases and sets are sung in rapid succession and are connected by a low intensity sound, thus giving the auditory effect of a continuous buzz. Sets of phrases may be repeated up to six times (mode 3, $n = 50$). Each song lasts approximately four sec and is followed by a short pause of one to several sec before the next song of a bout begins. I detected only slight differences in the harmonic structure of the three songs of island males that were analyzed. Furthermore, while on the island I was unable to detect any distinctive differences in the more than 100 songs heard from about 30 different individuals.

The typical song of a mainland California male Anna Hummingbird consists of a series of three sets of three discrete phrases each,

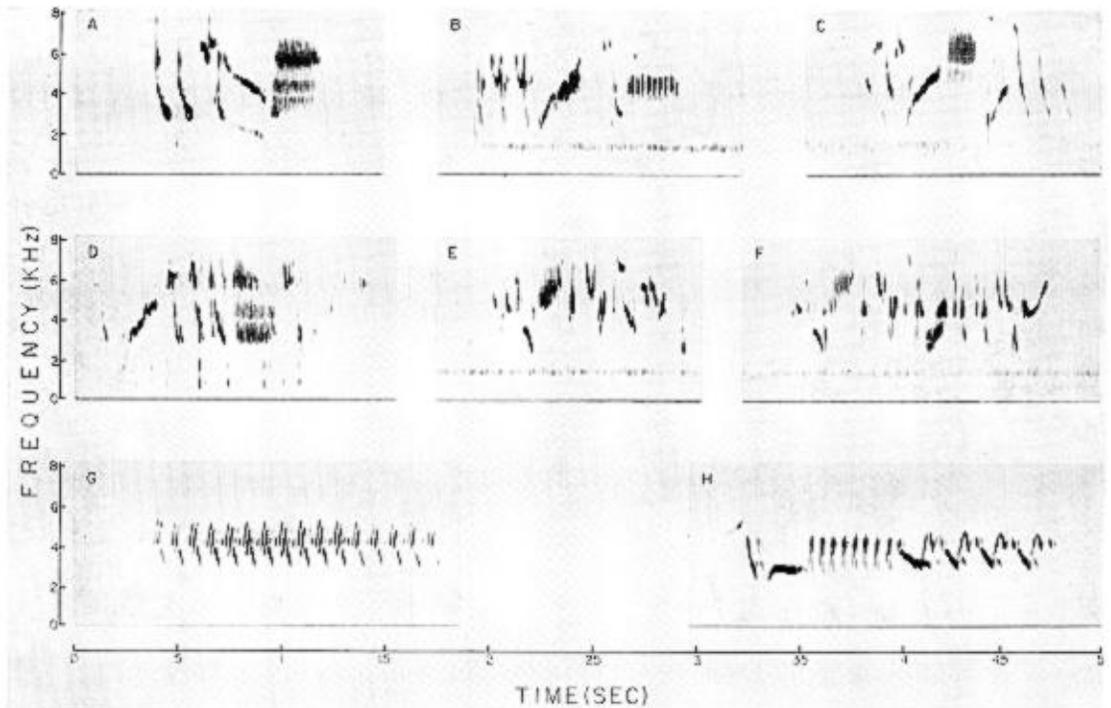


FIGURE 2. Audiospectrograms of complete adult male *Junco* songs. (A-F) Guadalupe Island junco. One song pattern from each of six individuals. (G) Dark-eyed Junco *J. hyemalis*. The song is a slow musical trill at one pitch. (H) *J. phaeonotus*. The song of this species also diverges from *J. hyemalis*. G and H were recorded from Peterson (1962).

followed by one set of two phrases (fig. 1B). The phrases of set one are repeated in set two and again in set four of the song. The phrases of set three are distinct, particularly the first, which is loud and of low frequency. A male may include one or all phrases of set three anywhere in a song, or he may omit it. During a sustained period of singing, many songs, separated by pauses of less than 0.25 sec, are delivered in succession. Although I have not studied song variability in a mainland population of *C. anna*, inspection of sonagrammed phrases from several birds reveals that individual songs are variable in note structure, but easily recognized as belonging to that species.

Responses of five male *C. anna* on mating territories and five females in nearby areas to recorded songs of Guadalupe Island males were tested on 8 January 1974, in Old Topanga Canyon, Los Angeles, California. Three songs of Guadalupe Island males were played to each California bird five times in succession at one or two min intervals. Neither males nor females responded to these recordings. I waited one or two min after each series of Guadalupe Island male song, and then played locally-recorded songs of mainland *C. anna* in the same manner. Each of the five males responded immediately, flying toward the

speaker, hovering within 2 m of it, and then flying to a perch after the sound ceased. Mainland females showed no response to recorded songs of either Guadalupe Island or mainland males; this is consistent with the behavior of female *C. anna* in response to singing males (Stiles 1973).

GUADALUPE ISLAND JUNCOS

GENERAL BIOLOGY

The biology of the Guadalupe Island junco was summarized by Howell (1968). Miller (1941) discussed the possible origin and relationships of this form in considerable detail in his monograph on the genus *Junco*. Morphologically, the Guadalupe Island junco is distinguished from mainland populations principally by its relatively long bill, short wing and tail, and virtual absence of sexual dimorphism in color. Both sexes of *insularis* superficially resemble females of the pink-sided form, *J. h. mearnsi*.

The juncos inhabit the remains of the groves of pine (*Pinus radiata*), oak (*Quercus tomentella*), and cypress (*Cupressus quadalupensis*) at the higher elevations on the island. They also are found in the stands of wild tobacco around the northeast anchorage. Apart from

"insular tameness" their habits appear similar to those of other juncos, but the ecology and behavior of the island population have not been studied in detail.

SONG

I was able to record the songs of only six birds because the juncos were not singing frequently at the time of my visit. Thirty-seven songs were recorded (fig. 2A-F). In a bout of singing, a Guadalupe Island junco delivers a song of one pattern several times with little variation and then switches to a song of another (usually similar) pattern before returning to the first. Although the song may be about the same duration as that of mainland juncos, it includes several syllable types instead of just one (fig. 2G). The song may or may not include a trill. When a trill is present, it is made up of syllables with a wide frequency range. Most songs also contain a single buzz. The buzz may be found near the beginning, middle, or end of the song. A few songs contained two buzzes. No song started with a buzz. The total number of syllables in each song is also variable. In many cases the characteristic junco trill was replaced by a phrase accompanied by a buzz. Finally, the duration and temporal pattern of the song vary. Thus individuals within the population appear to show a remarkable amount of variability. Recorded songs of Guadalupe Island males were not played to mainland juncos.

DISCUSSION

In order to account for the observed differences in song between mainland and island populations of juncos and Anna Hummingbirds, we must consider learning, acoustical background, the "founder principle," genetic drift, and the amount of variability in songs of continental populations of these species.

The song of most wild male *J. hyemalis* in California consists of repetitions of identical syllables at constant intervals (fig. 2G). Only rarely does a song include two syllable types. In such a case, the syllables form separate parts of the song (Konishi 1964). Each male has a small repertoire of two or three song types. These songs show individuality in the structure and number of syllables (Marler et al. 1962, Konishi and Nottebohm 1969). An isolated junco population on Guadalupe Island, presumably established by a few individuals carrying only a small part of the genetic and behavioral information of the parental population, might be expected to possess limited song variability. Instead, the

Guadalupe Island juncos exhibit greater song variability than do southern California populations of *J. hyemalis*. The sound environment of a species is thought to affect the amount and kind of variability found in the song. Among the factors ultimately governing this is a song's distinctiveness from the song of sympatric species (Lack and Southern 1949). Marler and Isaac (1961) employed this concept as a factor contributing to the considerable song variability in a Mexican population of *Junco phaenotus* in an environment with a small number of bird species (fig. 2H). The same explanation may be applicable to the variability in the song of *insularis*.

A further explanation for the observed song differences between mainland and island populations of juncos is lack of opportunity for learning (Thielcke 1973). Marler et al. (1962) demonstrated that young male juncos model their songs on those of adult males. Hand-reared males lacking the opportunity to learn the song of adult males conformed to the adult male song in overall pattern but differed in having less diversity of syllable structure. They had a somewhat longer song with fewer long syllables, and a larger proportion of their songs consisted of two or more syllable types. Therefore, if in an isolated founder population on Guadalupe Island no opportunity to learn the song of adult males existed, young male juncos would be expected to develop a divergent song with increased variability.

I suggest that a similar explanation may account for the differences between mainland and island populations of Anna Hummingbirds i.e., from lack of opportunity in a founder population to learn the songs of mainland adult males.

Geographic isolation may be reversed and does not, by itself, lead to the formation of species. It simply permits natural selection to act on the newly isolated population producing adapted individuals with maximum "inclusive fitness" (Hamilton 1964). Indeed, it is not safe to infer reproductive isolation solely from differences in morphology or song. Genetic and behavioral barriers must be considered. If, as is likely, the Guadalupe Island junco and hummingbird populations were derived from a few individuals, the genetic information possessed by the founders would be but a fraction of the total variability of the parental population. The variability would be reduced further by genetic drift, the shift from an open to a closed population, and

adaptation to the narrow range of environmental heterogeneity of the island. Drastically reduced and subsequently expanded populations may acquire isolating mechanisms as a consequence of the ensuing genetic reconstruction (Mayr 1954). It is possible that a breeding population of Anna Hummingbirds has been present on Guadalupe Island throughout its known history. If so, two drastic limitations of genetic variability have occurred—initially with the small number of founders, and again after the destruction of most of the suitable habitat by goats.

Behavioral barriers are among the most important isolating mechanisms in birds (Mayr 1969). Individuals of all bird species respond during the breeding period to signals, some of which probably are genetically determined. Unfortunately, it is not known whether a female junco or hummingbird recognizes a conspecific male by just one signal or a combination of signals.

Male Guadalupe Island juncos differ from related continental males in coloration, morphology, and song. These differences presumably indicate considerable genetic differences between mainland and island populations. I support, therefore Miller's (1941) suggestion that the Guadalupe Island junco be given species status. The Guadalupe Island hummingbird population, although morphologically indistinguishable from mainland populations, may prove to be reproductively isolated from them as a result of vocal or genetic differences. The possibility of experimentally testing for genetic reconstruction and intrinsic barriers to genetic recombination remains.

SUMMARY

Both the Anna Hummingbird and the junco population on Guadalupe Island differ in song from mainland populations. Using playback experiments, I demonstrated that differences between the songs of island and mainland males of *C. anna* are sufficient to evoke different overt responses in mainland males; females fail to show an overt response to either island or mainland male songs. Male Guadalupe Island *C. anna* show no apparent difference in color or external morphology from mainland populations.

The song of the insular junco population is both different from and highly variable compared to the song of mainland *J. hyemalis*. The Guadalupe Island junco also differs from related continental populations in coloration and morphology. Such differences presu-

ably indicate considerable genetic difference between mainland and island populations which could result in reproductive isolation and specific distinctness. I propose that the observed divergence in song of both *C. anna* and *J. hyemalis* on Guadalupe Island may have arisen from lack of opportunity in a founder population for learning the song of mainland adult males. A further explanation, particularly applicable to *J. hyemalis*, is that in an environment with a small number of bird species present, selection for distinctiveness in song may be reduced, leading to increased variability and ultimately to song divergence.

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