THEY SANG IT THEIR WAY:
The Deviant Chickadees of Martha's Vineyard

by Bruce E. Byers and Donald E. Kroodsma

The island of Martha's Vineyard is a famous place. It's where Bill Clinton went to roost after his apology speech. And it's where the rich and famous of all stripes build gargantuan houses and post astonishing numbers of "No Trespassing" signs. For aficionados of bird song, however, the island's claim to fame is not its politicians, Wall Street wizards, or rock stars. Instead, lovers of bird song know the Vineyard as the place where chickadees sing weird songs.

The strangeness of Vineyard chickadee songs is especially noticeable to a well-traveled birder. A birder who has been around knows that across vast stretches of North America, the Black-capped Chickadee is easily identifiable by its distinctive whistle song. From Newfoundland to British Columbia to Minnesota to Missouri, a visitor can expect to hear the familiar two-tone whistle, which the National Geographic Society field guide describes as "a clear, whistled *fee-bee* or *fee-bee-ee*, the first note higher in pitch." Actually, if you listen closely to a Black-cap at reasonably close range, you'll be able to hear that, although the song sounds like *fee-bee* to the casual listener, the *fee-bee-ee* transliteration is more accurate. There is a barely perceptible pause, or break, in the second, lower-pitched whistle (Figure 1).

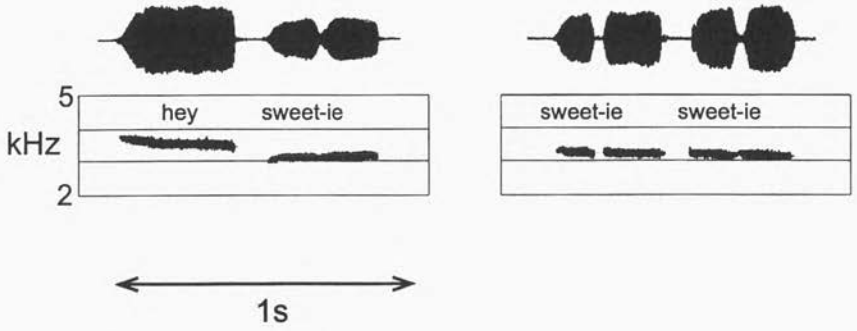

Figure 1. Visual representations of a typical mainland Black-capped Chickadee whistle song (left) and an example of a Vineyard song (right). For each song, the top display is an amplitude trace, which shows how the amplitude ("loudness") of the song changes over time, and the bottom display is a sonagram, which shows how the frequency (pitch) of the song changes over time. Note that in the mainland song the first whistle is higher in pitch than the second whistle, and the second whistle contains an amplitude break. In the Vineyard song (one of numerous different types on the island), both whistles are at the same pitch and amplitude breaks occur in each whistle.

But when our well-traveled birder steps off the ferry in Oak Bluffs on a fine May day, she immediately senses that something is not quite right in the world. Casting about for the source of her discomfort, she notices that the local chickadees are singing loudly. The songs are two-part whistles, just as they were on the mainland across Vineyard Sound, but something seems odd. The songs lack the two-tone sound of mainland songs. Instead, the local birds sing in a monotone, with both whistles on the same pitch.

Birders have long been aware of the odd, monotone songs of Martha's Vineyard, which were noted by Brewster as early as 1891 (see Griscom and Emerson 1959) and reported by Bagg (1958). Our personal obsession with the songs, though, began when, after making a few visits to the island, we began to suspect that the singing of the local chickadees encompassed more than just a small deviation from mainland singing. Intrigued by what we heard, we resolved to look more closely at the communication behavior of the island birds. So we returned to the island in May 1995, and this time we brought along a collection of tape recorders, plenty of microphones, a setup for computerized analysis of sounds, and (most importantly) a large and enthusiastic crew of fellow ornithologists. Guided and inspired by local birding legend Dolly Minis, our band of bioacousticians fanned out across the island. For the next five days, we recorded the whistle songs of every chickadee we could find. Invigorated by what we discovered, we returned periodically over the following two years.

As we learned more about singing by the Black-capped Chickadees of Martha's Vineyard, we were astonished. And as continued analysis revealed ever more details about the songs, our astonishment grew. It seemed that the singing of the island birds differed from the singing of mainland birds in every way imaginable. (For a detailed technical report, see our paper in *The Auk*, Kroodsma et al. in press). In addition to the monotone structure of most of the island songs, four other differences were especially striking.

Island songs are much more diverse than mainland songs. Mainland songs invariably contain an amplitude break (the brief pause in the middle of a whistle) in the second whistle, but in island songs the amplitude break may occur in the first, second, or both main whistles, or it may be omitted altogether. If we think of the standard mainland whistle as a two-tone *hey sweetie* (where "*hey*" represents the first, unbroken whistle and "*sweetie*" represents the second, broken whistle), then on the island we found birds singing *sweetie hey*, *sweetie sweetie*, *sosweetie sweetie*, and *hey hey* in addition to monotone *hey sweetie*. In fact, we found six different common song types and several more rare ones on the island, a sharp contrast to the single song type found over many thousands of square miles on the mainland.

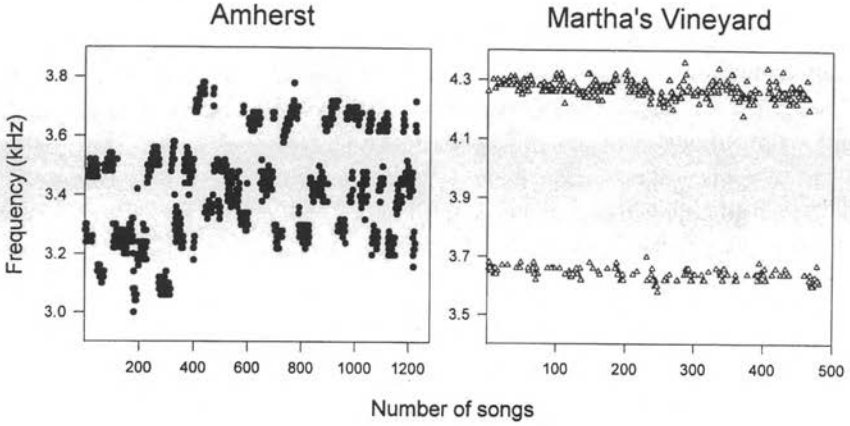

Figure 2. The frequency (pitch) of successive whistle songs sung by two birds, one from Amherst, Massachusetts, and one from Martha's Vineyard. Note that the mainland (Amherst) bird's songs occur across a continuous range of frequencies, but that the Vineyard bird's songs occur on two discrete, narrow frequency bands. For the Amherst song, the frequency is measured on the 'sweet' of the second whistle. For the Vineyard songs, the frequency is measured on the second of the two monotone whistles. On the Vineyard, high-frequency songs are usually at 4.2 to 4.4 kHz (just higher than the high C key on a piano), while low-frequency songs are at 3.7 kHz (roughly A-sharp below high C). Thus, with a little practice, any listener can readily distinguish the high and low songs of the Vineyard chickadees.

Island males often have repertoires of two different songs. On the mainland, each individual male chickadee uses only one type of song, the classic two-tone *hey sweetie*. In contrast, many individual males on Martha's Vineyard use two different song types, and even those birds with only a single type typically sing it at two different pitches (see below).

Island males don't "pitch shift." When a mainland male sings his single song type, he may vary its pitch as he sings, ultimately singing the whistle on a whole variety of different frequencies (Figure 2). This "pitch shifting" behavior is common to males across the mainland. But island birds don't do it. Instead, each male has a "high song" and a "low song," each of which is sung at only a single pitch. The high and low songs are usually of different types, but may be of the same type; the birds at Gay Head, for example, use *sweetie hey* as both high and low songs.

Song "dialects" occur on the Vineyard. The mainland *hey sweetie* song is remarkably stereotyped. Whether in Nova Scotia or British Columbia or Iowa, the song sounds the same. If you heard a tape-recorded two-tone whistle song, you couldn't guess the geographic location at which the song was recorded. On the Vineyard, it's a different story altogether. Particular idiosyncratic song types

are tied to particular, often very small, geographic areas. The result is a patchwork of song types, analogous to the regional dialects that are common in human language (Figure 3).

In summary, then, the Black-capped Chickadees on Martha's Vineyard sing in a manner that is distinctly different from mainland chickadee singing. The island birds use a variety of different songs that occur in well-defined song dialects, and individual males have multisong repertoires without pitch-shifting. This pattern of singing stands in stark contrast to that of the masses of Black-capped Chickadees elsewhere, which sing a single, widely distributed, highly stereotyped song type that is used in pitch-shifting fashion. Why do the island birds sing so differently?

The peculiar behavior of the island chickadees is in fact a mystery inside of a mystery. For in many ways, it is the singing of mainland chickadees that is surprising. In particular, very few songbirds use songs that are so uniform over such a wide geographic area. The reason for this general lack of uniformity is straightforward. Most species of songbirds must learn their songs; young birds acquire songs by memorizing and imitating the songs of adults. In general, this copying process can be expected to foster locally distinctive, diverse singing. (To understand why, think of how rumors or jokes spread in our own culture; by the time the story is repeated a few dozen times, it has changed considerably and may not even be recognizable as the original.) So it comes as something of a shock that mainland chickadees are able to keep their song so strictly stereotyped, especially since our laboratory experiments with young mainland chickadees have demonstrated that these birds have the ability to learn large repertoires of diverse sounds (Kroodsma et al. 1995).

It appears that mainland Black-capped Chickadees have developed some mechanism for enforcing stereotypy in whistle songs and singing behavior. We don't yet know what that mechanism might be, but it does allow us to restate our question about the island birds. How have the island populations been released from the pressure to maintain rigid stereotypy, and thereby freed to express the rich diversity of songs and singing behaviors that we have come to expect from typical songbirds?

The obvious starting point for explaining the distinctive singing on the islands is the nature of islands themselves. Island populations tend to be isolated, and some observers (e.g., Bagg 1969) have noted that chickadees are reluctant to cross open water. Perhaps the birds on the Vineyard are simply cut off from the influence of mainland social structures. On the mainland, young chickadees often move over great distances in winter (Bagg 1969, Smith 1991). The net effect of these movements is that mainland chickadee populations are subject to

Chappaquiddick
Wasque Reservation
Edgartown
Katama
Felix Neck Refuge
Edgartown Great Pond
West Chop
Vineyard Haven
State Forest
Airport
Lake Tashmoo
Tisbury Great Pond
New Lane
South Rd
West Tisbury Center
Menemsha Hills
Gay Head

Figure 3 (*facing page*). The distribution of three common song types on Martha's Vineyard. Open squares represent high "*sosweetie sweetie*" songs; filled circles represent high "*sweetie hey*;" x's represent high "*sweetie sweetie*." The Vineyard also holds low-frequency versions of each of these song structures. Low "*sosweetie sweetie*" is found mainly near Edgartown in the east; low "*sweetie hey*" is widely distributed across the entire island (but not on Chappaquiddick); low "*sweetie sweetie*" is generally restricted to the eastern half of the Vineyard. A few of the Vineyard's high frequency songs also occur on Chappaquiddick, but entirely different high frequency songs predominate there.

regular, wide-scale mixing. This mixing ensures that young chickadees seeking a mate for the first time will conduct their search among individuals of diverse and unpredictable geographic origin.

In such circumstances, it is possible that young mainland males would gain a reproductive advantage by learning and singing a standardized song that can be easily recognized by females from any part of the mainland range. The mainland females may in turn enforce male performance of the standardized song by responding only to the highly stereotyped *hey sweetie*. In contrast, Vineyard birds have little or no opportunity for long-distance movements, and so perhaps are freed from social pressures to learn, sing, and respond to only the stereotyped mainland songs. A male Vineyard chickadee, breeding for the first time, is likely to encounter only females from his own neighborhood, and is under no pressure to produce a song that would be universally recognized. Under these conditions, Vineyard chickadee songs would be free to diverge from the communicative conformity observed on the mainland.

This explanation for the unique and distinctive songs of Vineyard males is appealing, but leaves us wondering why some other island chickadee populations (e. g., on Monhegan and other islands off the coast of Maine) adhere to mainland singing conventions. Although island isolation may be part of the explanation, it is certainly not the whole explanation.

Other aspects of the Vineyard may have contributed to deviant chickadee singing. One is the history of the island's forests, which, like many in New England, were almost completely cleared before regrowing over the past century. If tiny remnant populations of chickadees survived in isolated pockets during deforestation, each isolated band of birds may have developed its own song variant. A pocket of birds in Gay Head, for example, might have developed a high-frequency and low-frequency *sweetie hey*, even as isolated birds near Edgartown began to sing high and low *sosweetie sweetie*. Today, the dialect boundaries we find may simply be the outcome of restored contact among descendants of the original deviant singers.

Why do we not find dialects in the mainland areas with similar histories of deforestation and habitat fragmentation? Perhaps the "stranded" mainland populations were not as tiny as those on the Vineyard, or were not separated long enough for dialects to develop. Or perhaps mainland dialects did develop in

the past, but have subsequently been swamped and eliminated by the population mixing process described above. In the end, however, the absence of dialects in mainland habitats with Vineyard-like vegetation histories suggests that while forest fragmentation on the Vineyard may have contributed to dialect formation, some other distinctive feature in the history of Vineyard chickadee populations must also have played a role.

The exceptionally high density of Black-caps on Martha's Vineyard is another aspect of island chickadee ecology that may influence the birds' singing behavior. Crowded conditions may have created competitive pressures that led to the song repertoires of island birds (recall that each mainland bird sings only a single song type). Studies of other species have shown that larger song repertoires can increase a male's ability to defend a territory and/or attract a mate; when population density is high, competition for these resources might be expected to intensify. More intense competition, in turn, could increase pressure on males to increase the potency of their competitive "weapons," including songs. Natural selection for song diversity might therefore be stronger on the Vineyard than it is in other, more sparsely populated locales.

At this point, our explanations for the Vineyard chickadees' distinctive song forms, unique signing behavior, geographic dialects, and song repertoires are mainly informed speculation. We have identified some intriguing features of the island's geography, history, and ecology that may well have had an impact on the evolution of chickadee songs there, but our account of the origin of anomalous chickadee singing on Martha's Vineyard remains fragmentary and incomplete. Stronger explanations await further investigation and more evidence.

In the meantime, the weird singing of the island chickadees represents an opportunity for you to enrich your birding experience. Take a breeding-season trip to the Vineyard and listen carefully to chickadee songs. How many types can you discern by ear? As you travel around the island, can you detect the disappearance of some song types and the appearance of new ones? Are dialect boundaries still as we found them (see Figure 3), or have they shifted with time? The Mystery of the Deviant Chickadees serves as a reminder that even the most common, everyday birds can surprise us with behaviors that engage the ears and minds of curious birders.

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