The Oxbow Philadelphia Vireo

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In 1998 a Philadelphia Vireo (*Vireo philadelphicus*) was present during the spring and summer months in the Oxbow National Wildlife Refuge in Harvard, an occurrence that was unusual since Harvard is well south of the region where this vireo species normally breeds. In the spring of 1999, a Philadelphia Vireo, possibly the same individual that was observed in 1998, was again present from the middle of May until at least August. In 1999, however, the vireo sang a song that was similar to the song of the Warbling Vireos (*Vireo gilvus*) that commonly breed along the Nashua River. It sang this aberrant song, as well as the normal Philadelphia Vireo song, for about the first month after arriving. Later in the summer it sang the normal Philadelphia Vireo song exclusively. Except for a mimid or starling, this was the first time I had heard an individual of one passerine species sing the song of another. To my ear, the aberrant song sounded very much like an abbreviated Warbling Vireo song, but sweeter and not quite so throaty. Upon careful observation, the bird's plumage was consistent with that of a typical Philadelphia Vireo with dark lores, a yellow breast, a slightly less bright yellow belly and undertail coverts, and a gray crown grading into an olive nape and back. There was no visual indication that the vireo was a hybrid.

Bird song serves multiple functions including the establishment and maintenance of breeding and feeding territories, and mate attraction (e.g., Kroodsma and Byers 1991; McDonald 1989). Birders often observe territorial countersinging between males that sometimes escalates into physical aggression. Additionally, song is important for those species that share the same habitat and are interspecifically territorial. In the present example, this Philadelphia Vireo was defending a territory against a Warbling Vireo, which is a behavior not unusual for vireos (Rice 1978). Songs are also used for species recognition and mate attraction. Indeed, song can act as an ethological, or behavioral, isolating mechanism, which forms a highly effective reproductive barrier between closely related species (see Mayr 1963 for an excellent discussion of isolating mechanisms).

Since the acquisition of this Philadelphia Vireo's heterospecific vocalizations is so unusual, it is interesting to consider the circumstances that brought it about. Also, what is the likelihood that his aberrant song would attract a female of the other species? To address these questions, we must have an understanding of how passerines of the suborder Passeres, which are called oscines and which includes the vireos, learn their own species' songs and not the songs of other species. Additionally, a female bird's ability to recognize conspecific song will be examined.

Song Characterization Terminology and Sonograms

First, I'll discuss the terminology used to describe bird song. Figure 1 is a sonogram of the familiar song of a Song Sparrow. The abscissa represents the duration of song in units of seconds, and the ordinate represents the song frequency in units of kilocycles per seconds, or kilohertz. A continuous line on the sonogram

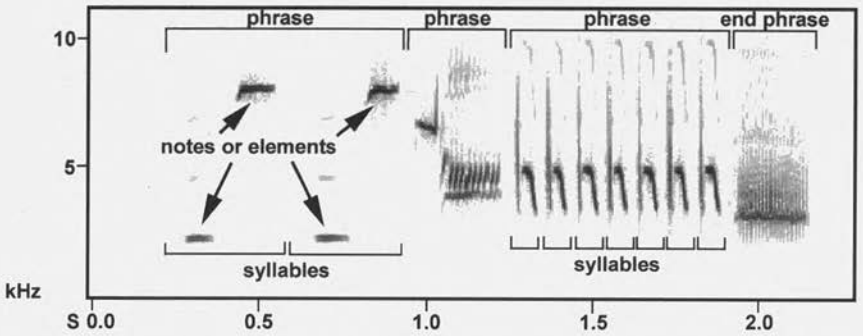

Figure 1: A sonogram representing one song type of a Song Sparrow. The y-axis or ordinate represents frequency, and the x-axis or abscissa represents time. See the text for a detailed description.

represents one note of the song. A horizontal line, such as the first note in the Song Sparrow song, is a pure tone. A vertical line represents a note that is made up of many different tones. A single note, or a series of notes that is repeated, is called a syllable. Finally, a distinct section within a bird song is called a phrase. Phrases may be constructed of repeated syllables, they may form a unique pattern of notes without repetition, or both. For example, the second phrase of the Song Sparrow song has a checkmark-shaped introductory note that is not repeated, followed by a series of vertical notes, which represent a buzzing sound. Some species, such as the Song Sparrow, produce a variety of songs, called song types, with an individual bird singing its own repertoire, or group of song types.

Sonograms of representative songs of the Oxbow Philadelphia Vireo, a Warbling Vireo, and a typical Philadelphia Vireo are displayed in Figure 2. All three songs have about the same frequency range (approximately two to six kilohertz). One of the two song types sung by the Oxbow Philadelphia Vireo that were similar to the song of the Warbling Vireo is illustrated. The two song types were usually alternated during an extended bout of singing. Typically, each song lasted about 0.8 seconds with a 3.7-second gap between songs. A Warbling Vireo song type lasts about 2.4 seconds with about 3.5 seconds between songs. The typical Philadelphia Vireo sings a series of short song types, each about 0.4 seconds long with an approximately 1.7-second pause between song types (Elliott et al. 1997). The Oxbow Philadelphia Vireo song is quite similar to that of a Warbling Vireo in terms of the pause between songs, but it is intermediate between the two species for song duration. Its song structure is analogous to that of a Warbling Vireo, with many notes having the same sort of frequency structure. The resulting songs sound remarkably similar to a typical Warbling Vireo and quite different from the normal Philadelphia Vireo song.

Part I: Song-learning

In order to understand how this Philadelphia Vireo may have acquired his aberrant song, the song-learning process in oscines will be examined. The general model of song development, evidence of song-learning preferences, and the role that

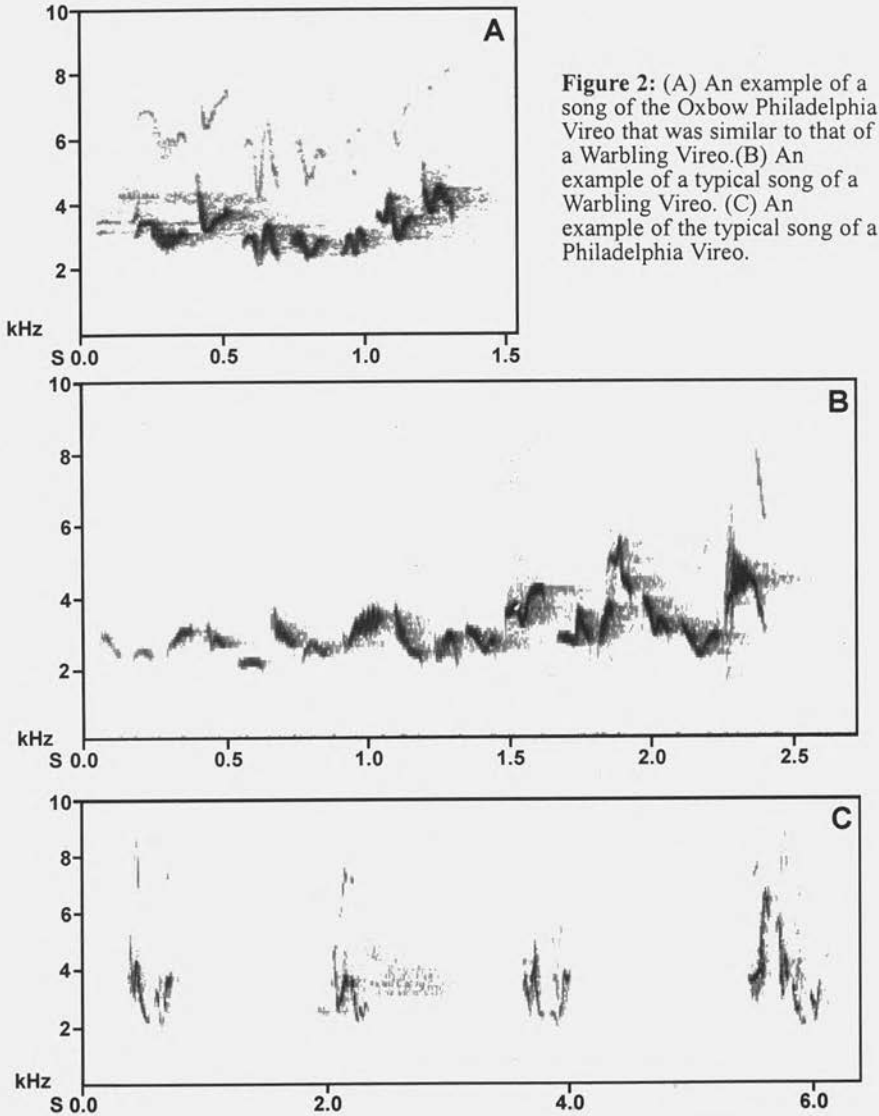

Figure 2: (A) An example of a song of the Oxbow Philadelphia Vireo that was similar to that of a Warbling Vireo.(B) An example of a typical song of a Warbling Vireo. (C) An example of the typical song of a Philadelphia Vireo.

social interactions play in song-learning will be presented. Where possible, specific information on vireos will be included. Also, situations in which wild oscines have acquired songs of other species will be discussed so that we might better understand how this vireo may have acquired his Warbling Vireo song.

The Song-Learning Process

As a young oscine learns song, it generally goes through three stages of song vocalization that are intimately related to the song-learning process. The learning process underlying these three stages of song production is described by the "auditory

template model" (Catchpole and Slater 1995; Marler 1970; Konishi and Nottebohm 1969; Konishi 1965; Konishi 1964; Marler 1952). The young male begins by hearing song, and then by storing song to augment its own innate, but unrefined, auditory template. This early sensitive phase begins when the bird fledges and continues for the next few weeks (Marler and Peters 1987). During the later portion of this early part of the song-learning process, the young male may engage in subsong, the first stage of song production. During subsong the young bird produces notes that bear little resemblance to adult song and appears to be learning the mechanics of sound vocalization. During the next stage, called plastic song, memorized songs are recalled and rehearsed. Songs produced in this more advanced stage of vocalization are still highly variable, but they are characterized by the first signs of identifiable memorized song patterns. As an individual matures, it will often sing a wider variety of different song types during this period than after it acquires its final repertoire, a phenomenon known as overproduction. Usually, but not always (see DeWolfe et al. 1989), the vocalization of songs during the plastic song phase is induced by heightened testosterone levels, as the birds come into breeding condition.

The song-learning process culminates in song stabilization and crystallization, which results in the production of the stereotyped song characteristic of adult breeding birds of the species. During crystallization, the overproduction of song types present during the plastic song stage is subjected to attrition, and only one song or group of songs (depending upon the species) forms the stereotyped adult repertoire (Marler and Peters 1987). For some species, the production of a crystallized song is greatly facilitated by the interaction of a young bird with other individuals of its species. The process often involves song matching between the bird and one or more of his neighbors, called his tutor or tutors, during territorial bouts of countersinging, chasing, and supplanting behavior. These interactions usually take place during the first breeding season, when the yearling male tries to establish a territory. Songs that fail to match those sung by a neighbor are discarded. This interactive tutoring process is crucial to song-learning in several species that have been studied (Liu and Kroodsma 1999; Beecher et al. 1994).

Oscine songbirds demonstrate a high degree of variability in the timing of song-learning by young birds. However, four broad patterns are apparent (Slater *et al.* 1993). In some species, song is memorized in the fledgling and juvenile stage only: for example, Bewick's Wren (Kroodsma 1974), Song Sparrow (Beecher et al. 1994), Swamp Sparrow (Marler and Peters 1988), White-crowned Sparrow (Petrinovich and Baptista 1987), Chipping Sparrow (Liu and Kroodsma 1999), Field Sparrow (Liu and Kroodsma 1999; Nelson 1992), and Zebra Finch (*Taeniopygia guttata*, Eales 1985). In other species, song is memorized as a young adult during the first breeding season. Payne (1981) showed that yearling Indigo Buntings require social interaction with mature males in order to learn song and that these interactions take place early in their first spring as they establish territories and engage in territorial behavior. In other species, such as Marsh Wrens (Kroodsma and Pickert 1984a), Chaffinchs (*Fringilla coelebs*, Catchpole and Slater 1995), and Northern Cardinals (Kroodsma 1974), song is memorized during both the first summer and the first spring but not at any subsequent time. Finally, birds such as European Starlings appear to be able to continuously learn songs as adults; birds as old as two and four years are able to

extensively change their repertoires (Mountjoy and Lemon 1995). This is also true of the Village Indigobird (*Vidua chalybeata)*, an African Estrildid finch that displays in groups and sings a particular group song that may change from year to year. When an individual indigobird switches groups, it will modify its song to conform to the song of the new group (Catchpole and Slater 1995). One must be cautious, however, in interpreting the production of new song types in years subsequent to the first year as constituting the learning of new songs, since it is possible that the songs were memorized in an early sensitive period and are only crystallized as needed later in life (Slater et al. 1993).

Learning Preferences

The singing of heterospecific songs is very rare in nature, due in part to an innate preference for conspecific song that biases a young bird to copy conspecific, rather than heterospecific, song. This preference has been demonstrated for several species in laboratory experiments. For example, naive Marsh Wrens will preferentially learn conspecific syllables when they are exposed to Marsh Wren, Sedge Wren, Bewick's Wren, and Song Sparrow songs (Kroodsma and Pickert 1984b). Song Sparrows also have a clear preference for conspecific song; they are sensitive to several levels of song organization, including note and syllabic structure, as well as the temporal organization of the phrases (Marler and Peters 1988). Male Swamp Sparrows, on the other hand, prefer conspecific song, but they place greater importance on the syllables from which the song is constructed than on the overall temporal organization of the song (Marler and Peters 1977). In some species, learning appears to be unimportant for development of normal song. For example, Gray Catbirds raised in complete isolation are able to sing perfectly normal songs (Kroodsma et al. 1997). Innate preferences and abilities, therefore, strongly influence song development in oscines.

The Learning Process in Vireos

The song-learning process in vireos has not been well studied, and no studies have been performed for the Philadelphia Vireo. It is not known, for example, whether a Philadelphia Vireo will change its repertoire from year to year. Red-eyed Vireos, however, have been studied (Borror 1981) and, since Philadelphia and Red-eyed vireos are closely related, it is expected that their song-learning patterns are similar. Red-eyed Vireos develop large repertoires of songs. They appear to go through the normal sequence of song acquisition, progressing from subsong to song crystallization. During the plastic song phase, which may span the first summer and part of the following spring, syllables vary at first, but they become more stereotyped as song development progresses. Overproduction is evident with the final crystallized repertoire consisting of a subset of the overproduced repertoire. There is a tendency, demonstrated by both Red-eyed and White-eyed vireos, for males not to duplicate the songs of neighboring conspecifics (Borror 1981; Bradley 1981), a clear departure from the song behavior displayed by many of the oscines that have been studied.

Species Singing Heterospecific Song

In what situations do oscine, other than mimids, starlings, and lyrebirds, imitate heterospecific song? In the highly artificial conditions of the laboratory, ethological

barriers can be degraded or destroyed, making the production of heterospecific song much more common. Table 1 gives examples of birds singing heterospecific song in the laboratory.

There are a few examples of birds singing heterospecific song in the wild (Table 2), so apparently there is no physiological barrier to producing these songs; however, it is a rarely observed phenomenon. In each of these examples, the species involved are sympatric, often sharing habitats, and they may be in direct competition for resources. For example, in areas of sympatry for White-crowned and Lincoln's Sparrows, the two species exhibit interspecific territoriality, which rarely may lead to the acquisition of the other species' song (Baptista and Morton 1988). This is also the

Table 1: Examples of Heterospecific Song in the Laboratory

Species	Species imitated	Degree	Reference
Marsh Wren	Sedge Wren	entire song	Kroodsma and Pickert 1984 b
Marsh Wren	Bewick's Wren	entire song	Kroodsma and Pickert 1984 b
Chipping Sparrow	Field Sparrow	one syllable	Liu and Kroodsma 1999
Field Sparrow	Sedge Wren	some syllables	Liu and Kroodsma 1999
Song Sparrow	Swamp Sparrow	some syllables	Marler and Peters 1987
White-crowned Sparrow	Dark-eyed Junco	some syllables	Baptista and Petrinovich 1986
White-crowned Sparrow	Song Sparrow	some syllables	Baptista and Petrinovich 1986
White-crowned Sparrow	Strawberry Finch (*Amandava amandava*)	entire song	Baptista and Petrinovich 1984; Baptista and Morton 1981

case with Song Sparrows and White-crowned Sparrows, and Song Sparrows and Wrentits. In the laboratory, White-crowned Sparrows have learned Strawberry Finch song (Amandava amandava), probably during intense countersinging bouts when housed in adjacent cages, which supports the hypothesis of heightened interspecific interactions leading to heterospecific song-learning (Baptista and Morton 1988).

Sympatric species may also learn heterospecific song when isolated individuals of a rare species are underexposed to conspecific song but frequently hear a more common species' song. This is the case with House Wrens that have learned Bewick's Wren songs (Kroodsma 1973). In these instances of unbalanced sympatry, birds still rarely learn heterospecific song. Observations in the wild are supported by laboratory studies in which juvenile birds learn heterospecific song after being taken from the nest, underexposed to conspecific song, and tutored with the song of another species. Both direct competition, resulting in interspecific territoriality, and unbalanced sympatry result in heightened interspecific interactions and are probably requisite for heterospecific song-learning in the wild. (Table 2)

Table 2: Examples of Heterospecific Song in the Wild

Species	Species imitated	Degree	Reference
Red-eyed Vireo	Eastern Towhee	some syllables	Borror 1968
House Wren	Bewick's Wren	multiple songs	Kroodsma 1973
Eastern Towhee	Field Sparrow	entire song	Borror 1968
Bachman's Sparrow	Field Sparrow	entire song	Borror 1968
Chipping Sparrow	Field Sparrow	some syllables	Borror 1968
Chipping Sparrow	Clay-colored Sparrow	entire song	Tasker 1955
Field Sparrow	Chipping Sparrow	entire song	Short 1966
Field Sparrow	Prairie Warbler	entire song	Borror 1968
Savannah Sparrow	White-crowned Sparrow	entire song	Cooper and Murphy 1985
Song Sparrow	White-crowned Sparrow	entire song	Baptista 1988
Song Sparrow	Wrentit	some syllables	Eberhardt and Baptista 1977
Lincoln's Sparrow	White-crowned Sparrow	entire song	Baptista et al. 1981
White-crowned Sparrow	Lincoln's Sparrow	entire song	Baptista and Morton 1988
White-crowned Sparrow	Savannah Sparrow	entire song	Baptista and Morton 1988
Western Meadowlark	Eastern Meadowlark	entire song	Lanyon 1957
Chaffinch (*Fringilla coelebs*)	Canary (*Serinus canaria*)	some syllables	Knecht and Scheer 1968
House Finch	White-crowned Sparrow	entire song	Baptista 1972

How might the Oxbow Philadelphia Vireo have learned his aberrant song? This Philadelphia Vireo may have been exposed to the song of a sympatric Warbling Vireo during its early sensitive period and may, therefore, have memorized the Warbling Vireo song, as well as its own. Warbling Vireo song may have been expressed during overproduction in the plastic song phase, but the normal Philadelphia Vireo song was crystallized, explaining why the bird also sang the normal species specific song. If the Warbling Vireo song remained stored in memory, however, it could have been produced from memory in response to intense interspecific territorial behavior. Philadelphia Vireos are known to display interspecific territoriality with Red-eyed

Vireos (Rice 1978), so it is possible that they may also display interspecific territoriality with Warbling Vireos. The Oxbow Philadelphia Vireo was observed on one occasion during the 1999 breeding season chasing and scolding one Warbling Vireo, while being chased himself by a second Warbling Vireo. This observation suggests that he had intense interspecific interactions with Warbling Vireos that might have stimulated him to produce the Warbling Vireo song.

Part II: Song Recognition by Females

Since the Oxbow Philadelphia Vireo learned, at least to some degree, the Warbling Vireo song, is it possible that he may also be able to defend a territory and attract a female Warbling Vireo? Will she recognize his song as an imperfect copy, or will it be an acceptable imitation? If a male Warbling Vireo recognizes the Philadelphia Vireo's song as being similar to his own and defends his territory as he would against a conspecific, his error results only in the expenditure of energy in defense of his territory from an intruder that potentially could be a Warbling Vireo but is not. Also, it is possible that Warbling and Philadelphia vireos are in competition for resources and are normally interspecifically territorial in areas of sympatry. The female, on the other hand, has more at stake. If she mates with the Philadelphia Vireo and produces offspring, it is likely that they will be of reduced viability; they may also be reproductively incompetent or sterile. In that case her reproductive effort for the year would be wasted.

Distinguishing Conspecific and Heterospecific Song

Several studies have shown that female birds have a significantly greater ability to distinguish conspecific from heterospecific song than males do. Much of this evidence comes from laboratory tests. *Melospiza* sparrows, particularly Song and Swamp sparrows, and Red-winged Blackbirds are well-studied examples of species whose females demonstrate a heightened ability to differentiate birdsong.

In the lab, receptive female Song Sparrows show copulation solicitation displays in response to Song Sparrow song but not to either Swamp Sparrow or Chaffinch songs, demonstrating that they are able to discriminate between conspecific and heterospecific song. Studies indicate that female Song Sparrows are sensitive to both individual syllables and overall temporal pattern construction but that the specific syllables appear to be more important in song recognition. Male Song Sparrows, on the other hand, learned and reproduced both Song and Swamp Sparrow syllables, particularly if the Swamp Sparrow syllables were presented in a Song Sparrow temporal pattern. The males' ability to reproduce Swamp Sparrow syllables that were incorporated into a Song Sparrow song pattern, and the females' unresponsiveness to the same artificial song indicate a reduced degree of discrimination on the part of the male.

Since male Song Sparrows often sing several different song types in the wild, female Song Sparrows were further tested to determine if they were sensitive to the use or order of multiple song types. Female sparrows were significantly more responsive to song bouts that contained multiple song types, as opposed to those containing only one song type. Male Song Sparrows also tend to repeat a particular

song type several times before switching to another type, a pattern which elicits a stronger response from females than when one song is immediately followed by a different song without repetition. Therefore, female Song Sparrows are able to discriminate syllables, temporal pattern, and song type order, and they are most responsive to songs that match what is heard in the wild (Searcy and Marler 1981; Searcy et al. 1981).

Other species have been shown to demonstrate a similar level of discrimination. Female Swamp Sparrows are able to distinguish conspecific from heterospecific song on the basis of both syllables and temporal pattern (Searcy et al. 1981); male Swamp Sparrows, on the other hand, are sensitive to syllables but not to temporal pattern (Marler and Peters 1981). Female, but not male, Red-winged Blackbirds are able to distinguish between the Red-winged Blackbird's song and a Northern Mockingbird's imitation (Searcy and Brenowitz 1988; Brenowitz 1982). Female Red-winged Blackbirds are also able to distinguish different Red-winged Blackbird dialects, and they demonstrate a clear preference for their local dialect (Searcy 1990). It is clear from these examples that female passerines possess highly developed abilities to distinguish song types.

Even though there is considerable variability in conspecific songs of vireos, I suggest that a female Warbling Vireo's refined ability to distinguish conspecific from heterospecific song would have enabled her to identify the Oxbow Philadelphia Vireo's Warbling Vireo song as being foreign. A female that scrutinized the several singing males in the area and made a comparative choice would almost certainly have selected a conspecific mate. Conspecific song recognition in mate selection is an extremely effective ethological isolating mechanism that would prevent interspecific hybridization between this male Philadelphia Vireo and a female Warbling Vireo. These factors make it highly improbable that the Oxbow Philadelphia Vireo was able to attract a female Warbling Vireo as a mate.

The Oxbow Philadelphia Vireo provided an interesting example of a rare occurrence in nature when one of the behavioral differences that help to reproductively isolate one species from another is degraded. This is all the more remarkable in light of the song-learning process that most oscines go through. As we have seen, even though the process varies greatly from species to species, very seldom does an individual in the wild learn heterospecific song. It is also interesting to speculate about the effect of this male's aberrant song on female Warbling Vireos. Studies of female song recognition suggest that, even though the Oxbow Philadelphia Vireo produced a song similar to that of a Warbling Vireo, it is unlikely that a female of that species would have been enticed to pair with him. In the end, the mechanisms that serve to maintain the distinct character of each species were probably effective in this case too.

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Beauty On The Wing: The Double Lives of Butterflies

On September 29, 2000, the Harvard Museum of Natural History will present a new exhibition entitled ***Beauty on the Wing: The Double Lives of Butterflies.*** This exhibit is from the vast collection of butterflies at the Museum, one of the most historically significant in North America. This will be a rare opportunity to see so many of these beautiful insects up close.

Specimens of every size, shape and color will be on display. One wall of the exhibition will be covered with butterflies from all over the world, from the giant blue Morphos of tropical America to the huge Birdwing butterflies of Papua New Guinea. The specimens will be accompanied by images by Darlyne Murawski, a National Geographic photographer who has captured these butterflies on film in the wild. The exhibit will also feature a live display of interactions between caterpillars and ants.

There will also be two lectures on butterflies to complement the exhibition. On October 24 at 6 p.m. Robert Michael Pyle will present "Vladmir Nabokov and the Blues," and on December 5 at 6 p.m. Maraleen Manos-Jones will present "The Spirit of Butterflies: Myth, Magic and Art." Both these lectures are free and open to the general public and will be held in the Geological Lecture Hall at 24 Oxford St., Cambridge, MA.

The Harvard Museum of Natural History is open from 9 a.m. until 5 p.m. with an admission charge of $6.50 for adults and $4.00 for children. The Museum offers free admission on Sunday from 9 a.m. until noon and on Wednesdays from 3 p.m. until 5 p.m. The entrance is at 26 Oxford St., Cambridge, MA, and the telephone number is 617-495-3045.