Johnston's work provides a fine example of the way in which concern with functional aspects of behavior can guide studies of proximate causation. In the first part of his chapter, Johnston discusses both flank-marking patterns and the vaginal-marking patterns of females. After describing each pattern, he discusses its proximate causation and function. It appears that flank marks advertise to others the presence of hamsters of a particular species, sex, and individual identity, and Johnston is able to relate the complex pattern of flank marking to a particular neurotransmitter functioning at a particular locus in the brain. Vaginal marking by females generates attraction from a distance, ultrasonic calling, elevated testosterone levels, and sexual arousal in males. Studies of the factors that affect vaginal marking suggest that the marks are directed primarily at males.

The remainder of Johnston's chapter is concerned with the olfactory control of behavior. He deals especially with flank marking, vaginal marking, ultrasonic calling, and individual discrimination. Using modern neurobiological techniques, Johnston unravels some of the olfactory influences on these behavioral patterns. Among the fruits of the chapter is a fine example of the progress that can be made with a systematic and integrated program of research on the immediate causation of behavior when guided by an understanding of the functional significance of the behavior under study for the life history of the organism.

Blanchard and Blanchard (Chapter 18) are concerned with social behavior, and in particular with aggressive interactions. The Blanchards' approach is focused on the use of biologically relevant, species-typical behavioral patterns studied in situations appropriate for their elicitation. They demonstrate the power of the experimental method used within such contexts.

The behavioral pattern on which the Blanchards focus is aggression in rats. They reveal the misunderstandings about behavior that can arise if one does not pay sufficient attention to the fine structure of the behavior of concern. In the present case, it is critical that the offensive and defensive aspects of agonistic interactions be distinguished. The key elements in aggressive interactions of rats are the attack toward and defense of the back. The various postures and movements in aggressive interactions can be seen as tactics on the part of the attacker to bite the back of the other animal and on the part of the defender to protect its back. This forces a reinterpretation of earlier work done before these distinctions were made. Thus, the much-used "pain-elicited aggression" test is seen not as eliciting aggression, but as a somewhat contaminated index of defensive behavior. Next, the Blanchards examine aggression in the contexts of the costs and benefits potentially accruing to the contestants in conflicts over limited resources. Consideration of the variables of which aggression is a function supports this economic interpretation. The results are relevant to analyses of stress and stress responses of the body and to the functioning of dominance hierarchies. The Blanchards' careful distinction between offense and defense has also proven useful in pharmacological and neural analyses.

Phrases such as "the human," "the animal," or "the rat" recur frequently in psychology textbooks, and are rightly regarded as innocuous scientific fictions. These phrases are needed to advance the reader to the more central concerns regarding the nature of psychological processes. But if the textbook is on comparative psychology, then phyletic liberties such as "the monkey" or "the bird" or "the carnivore" must be taken more seriously. At an organizational level, macrophyletic nomenclature causes few problems. But when it comes to the task of looking for mechanisms underlying species-typical adaptations, the use of such general terms may be misleading, leaving the impression that we know more about phylogenetic networks than is actually the case. Distinguishing primates from birds or rodents is easy, too easy, often amounting to nothing more than distinguishing the proverbial apples and oranges. Most contemporary comparative psychologists, however, face a harder task, because they tend to labor within small phyletic patches, studying the proverbial peas in a pod. By looking within narrow phyletic units, comparative psychologists hope to detect the kinds of variation that constitute the material of natural selection.

As an example of patch size, consider our own research. We work with birds, of which there are over 8,000 species, arranged into 29 orders and 155 families. If we specify the behaviors of interest to us, vocal communication by song, the
possible number of species of interest is reduced to around 5,000. We possess expert knowledge of only several populations of one species within one family of one order of one class. Can we then claim to be comparative psychologists? We believe we can, and hope to demonstrate why in this chapter by explaining analyses of intraspecific differences in avian communication.

We encountered the issue of intraspecific diversity while studying the ontogeny of song in cowbirds (Molothrus ater). After more than a decade of research, we find that even so specific a designation as “the eastern subspecies of the brown-headed cowbird” blurs distinctions in the very processes we want to study, i.e., relationships between song production in males and song perception by females. Here we review data illustrating the nature of the differences we uncovered. We then consider three psychobiological concepts that may facilitate the process of microphyletic comparison.

COWBIRDS: PROFILES IN DIVERSITY

If female cowbirds had calling cards, they would read: “Have eggs, will travel.” The female cowbird deposits her eggs in the nests of other species, delegating to them the duties of incubation and postnatal care (Friedmann, 1929). By allocating caregiving to other species, cowbirds create unusual ontogenetic challenges for their young. How will young cowbirds find other cowbirds? How will they acquire species-typical behavior? Cowbirds have long have been presumed to be ideal examples of closed genetic programs that reduce the need to acquire species-typical behavior through experience with conspecifics (Mayr, 1974). Our research confirms that naive males and females display impressive communicative competencies that should facilitate species identification. But the precise nature of the male’s or female’s communicative capacities depends on the population being described. To put the differences in perspective, we first review what we know about the nature of song communication in North Carolina (NC) cowbirds (M. a. ater), stating at the outset that we take our bearings from this population only because it is the one we know best.

First, a few remarks are required to explain some basic methods. To reveal naive male cowbirds’ vocal capacities, we raise males from the egg or from fledgling age in social environments that provide no opportunities to hear conspecifics sing. We provide avian companions, such as female cowbirds or other songbirds, to prevent a confounding of social and auditory deprivation. We analyze the males’ songs for structural parallels to the songs of normally reared or wild males. We also use two procedures to assess the functional properties of males’ songs. The first procedure consists of playing back songs to captive male-deprived females who are in breeding condition. This technique provides a measure of song potency, i.e., the percentage of playback trials on which a song elicits a copulatory posture from a female. The procedure also contains a double play: it allows us to probe females’ perceptual attributes. We can test the sensitivity of the females to the songs of different males or to different songs from the same male. If we find differences in potency, we can test which acoustic features are most crucial to female discrimination (King & West, 1983a).

The second test of the functional properties of songs comes from observing how song is used by males in captive colonies during courtship and mating. By recording vocal behavior, social relations, and courtship patterns, we can assess the “fate” of certain songs and validate the significance of females’ differential responsiveness to songs in playback trials. The contextual demands of life in a resident colony force males to attend to the dual obligations of male–male competition and courtship of females, and force females to assess singers as well as songs (West & King, 1980; West, King, & Eastzer, 1981). Although colony life cannot approximate many of the demands on free-living birds, it appears to elicit many behaviors similar to those observed in the wild. Captive females lay fertile eggs and parasitize nests; males and females show nonrandom polygamous patterns of mating, with copulations occurring after a period of active courtship; and residents maintain a diurnal cycle of early morning courtship and afternoon feeding (King & West, 1984).

By using these two methods, we have found that acoustically deprived NC males require no experience with adult males in order to sing effective songs, and that NC females need no exposure to conspecifics to discriminate cowbird songs from those of other songbirds or to discriminate among cowbird subspecies (King & West, 1977, 1983a, 1983c). Moreover, even juvenile males’ acoustically primitive precursors to song (often labelled “subsong” or “plastic” song) evoke species-typical copulatory responses from adult females (West & King, 1988b). However, although naive males can produce effective songs without ever having heard any male cowbird songs but their own, they proceed to alter the potent songs of their youth, with the nature of the alterations depending on their social surroundings. During interactions with other males, dominance relations are established that ultimately affect song production. Males learn that singing too effective a song can have deadly consequences, because dominant individuals may attack subordinates that sing highly potent songs (West & King, 1980). But singing cannot be avoided if reproduction is to occur. Females do not mate with a male unless he has sung to her for several days, a phenomenon also seen in wild populations (Rothstein, Yokel, & Fleischer, 1986; West et al., 1981; Yokel, 1986). Moreover, females are quite discriminating about the kinds of males they prefer, choosing the more dominant males that tend to sing the most potent songs (West, King, & Harrocks, 1983).

Social interactions with conspecifics prior to the breeding season affect more than song potency. Adult males sing two to seven song types, that is, distinctively different melodic patterns. The song types developed during a male’s first spring depend largely on social feedback from the singer’s audience, including females.
Although females do not sing and thus cannot serve as fellow performers, they can serve as social critics and conductors of the process of vocal composition. They do so by providing social feedback during the winter and spring, well before courtship begins.

To learn how females communicated about song, we videotaped males housed individually with females in late winter and early spring. This is the time (from mid-March through April) when wild birds from North Carolina return to their prospective breeding grounds and presumably begin to interact with the females with whom they may mate. We looked at what NC females did when NC males sang. Over 90 percent of the time, the females appeared to do nothing: an observer would not know by looking at the female that she had just heard a song sung a foot away. But the female’s apparent indifference served to call attention to the times when she did react. A particular form of reaction involved a rapid extension and retraction of one or both of the female’s wings, a behavior we term “wing stroking” (West & King, 1988c).

Changes in the male’s singing patterns suggested the importance of wing stroking. Instead of employing the species-typical pattern of cycling through two to seven song types in succession, with little or no repetition, the males repeated the song that had elicited a wing stroke as many as four times in the next eight songs produced. The repetition of that song type by males suggested to us that wing stroking represented positive feedback, i.e., that the females’ displays were responses to potentially potent songs. A playback experiment, using a new sample of females exposed to songs that had or had not elicited wing stroking, confirmed that the wing-stroke-eliciting songs were highly effective releasers of copulatory postures, as were the songs repeated after the wing stroke (West & King, 1988c). Thus, taken together, the studies suggest that in the NC population, song development is a synergistic process in which both males and females are active participants.

These data are exciting to us because they reveal concrete linkages between male production and female perception. Although conceptual linkages have long been acknowledged (Marler, 1976), the ontogeny of bird song has been studied too often and with too many species without ever permitting the major participants to meet, let alone mate. To learn more about the female’s role, we looked at female perception from several perspectives. First, as mentioned earlier, we documented NC females’ native song preferences, a bias found in both captive and wild females (King & West, 1983c). Second, we probed for modifiability of song preference by housing naive NC females with adult males from the second cowbird subspecies, M. a. obscursus, which had been collected in south Texas (TX). After a year’s social housing, the NC females responded to playbacks of NC song (which they had never heard) significantly more often than to TX song. Even an acoustically naive hybrid female (NC mother × TX father) preferred NC song.

These manipulations involved a level of discrimination not normally experienced by NC females, i.e., listening to NC versus TX song. Thus, we also looked for evidence of perceptual stability at a local level by measuring perceptual concordance of song preferences within and across local females. Did females from a given area perceive all variants of local song as equally potent, and if not, did females “agree” with one another about which songs are the most or least effective?

In answer to the first question, we found that not all males’ songs were equally effective. In general, dominant males, successful in courting females, possessed the largest repertoires of effective songs, although even these males included in their repertoire songs to which females responded infrequently. Thus, females were discriminating at a local level (West & King, 1986).

With respect to the second question, we found that local females showed high levels of agreement about which songs were most or least potent. To test concordance, we chose 12 NC songs previously played back to females, 6 of which had elicited many responses (high-potency songs) and 6 that had elicited few responses (low-potency songs). We asked whether a new group of NC females would “agree” with the previous group in terms of their relative responsiveness to the songs. They did, producing significant positive rank-order correlations with the playback preferences of the original cohort. A year later, after living with different NC males for 9 months, the females’ playback preferences for the 12 songs were retested, and again showed a comparable level of concordance (West & King, 1986; King & West, 1988). Thus, if NC females can be said to screen males (sensu West-Eberhard, 1983) on the basis of song, they appear to do so using shared criteria.

NORTH CAROLINA COWBIRDS: THE EXCEPTION OR THE RULE?

The data presented thus far hold two lessons for the understanding of behavior. First, the data demonstrate that the brood parasitic habits of cowbirds have not ruled out learning as a means of acquiring species-typical behavior. Second, the data suggest potentially new mechanisms of learning, mechanisms never before postulated for any songbird. The results show that cowbirds can learn by means other than imitation: males do not alter their songs by copying wing strokes, but by attending to their “meaning.” Thus, vocal imitation cannot be assumed to be “the” learning mechanism for “songbirds” (Kroodsma, 1982). The experiments also indicate that audition is not the only sensory pathway guiding song development. Thus, the data challenge current views of the role of underlying sensory templates, and call for the mapping of neural regions that receive visual information. As such, data from a single pea in one avian pod render many
textbook explications of “bird song” potentially misleading: clearly, there is more than one way to achieve vocal competence.

The emphasis on imitation and on vocal stimulation is, to a large extent, a methodological consequence of framing research questions about song from the male’s perspective. The singer-dominated approach is especially apparent in studies of geographic variation (Canady, Kroodsma, & Nottebohm, 1984; Krebs & Kroodsma, 1980). Although the functional significance of song variation is still the subject of active debate (Baker & Cunningham, 1985), until recently, few data existed on female variation in song responsiveness. Until playback procedures with females were developed (King & West, 1977; Baker, Spitler-Nabors, & Bradley, 1981), direct measures of female perception of song were scarce. Female perception has now become the topic of scrutiny in a number of songbirds and will eventually lead to a proliferation of theories of song acquisition (e.g., Baker, 1983; Baker et al., 1981; Baker, Spitler-Nabors, Thompson, & Cunningham, 1987; Catchpole, Dittami, & Leisler, 1984; Ratcliffe & Weisman, 1987; Searcy, 1984; Searcy & Marler, 1981, 1984; Searcy, Marler, & Peters, 1981).

It was our ability to ask females questions that provided the opportunity to study intraspecific variation. Once we had discovered linkages between NC males and females with respect to song ontogeny, we asked whether we could find evidence of this in other parts of the cowbird’s extensive range. The answer is a qualified “yes.” We qualify the answer for two reasons. We have yet to study other populations as thoroughly as the NC population, so many loose ends remain. But the songs of the two subspecies also differ (Figure 2). Males in the M. a. obscurus range include a cluster of notes before the terminal whistle which we term the midsong element (MSE). This song element is never found in the songs of M. a. ater males (sampled from 11 locations), making it a valuable acoustic marker of subspecies identity (King, West, & Eastzer, 1980). (The third subspecies, M. a. artemisiae, the sagebrush cowbird, occupies western North America and is not yet a topic of inquiry for us (but see Rothstein, Verner, & Stevens, 1980).

Thus, to put the sites of Figure 1 into perspective, cowbirds in the center of the United States represent older and denser populations, whereas the NC and California (CA) populations represent some of the newest areas of expansion. Cowbirds have been breeding in North Carolina only for the last 50 years (Potter & Whitehurst, 1981), as opposed to hundreds of years in the central plains and prairies (Grinnell, 1909; Mayfield, 1965; Oberholser, 1920), and they have been breeding in southern California for 80 years and northern California for 50 years (Rothstein et al., 1980). We do not presume to know at this point how to organize the ecological and evolutionary variation subserved by these sites. But we present it to indicate the potential richness of microphyletic variation.
**Figure 2.** A sound spectrogram of *M. a. obscurus* song and *M. a. ater* song. The song components labelled are IS1 and IS2, introductory syllables 1 and 2; IPU, interphrase unit; MSE, midsong element. *M. a. obscurus* songs almost always contain MSE's, *M. a. ater* songs do not. The rhythm differences found in OK songs consisted of differences in the timing of peak-to-peak amplitude on the low and high voice notes in the first syllable. Specifically, the duration of the high to low voice interval (H2 to L4) was found to be a multiple of the previous low to high voice interval (L2 to H2). Differences in syllable diversity among TX *M. a. obscurus* populations referred to the number and arrangement of notes within IS1 and IS2.

**Perspective from the Prairie: Female Flexibility**

We begin the comparative tale with studies of cowbirds in Oklahoma (OK), the population closest to NC in phyletic terms, as both are classed as the same subspecies (*M. a. ater*). Even though the OK populations live in closer proximity to the *M. a. obscurus* subspecies, OK females, like NC females, respond selectively to their own subspecies' songs in comparison to *M. a. obscurus* songs (King, West, & Eastzer, 1986; King & West, 1987). Other similarities also exist. Acoustic examination of the songs of the two populations suggests common ancestry. On many measures of frequency, duration, and timing, it is difficult to differentiate OK from NC songs. Playback tests to NC females give the same impression. NC females respond as often to OK songs as they do to NC songs. But OK females do not show a comparable tolerance for NC songs. They clearly discriminate between OK and NC songs, preferring the former by a significant margin. Thus, NC and OK females possess different patterns of perceptual breadth, with the OK females displaying more specificity (West & King, 1988a).

Structural analyses of OK and NC songs reveal that OK songs are characterized by a higher degree of stereotyped rhythm in the introductory syllables (King et al., 1986). To study the relevance of this characteristic to the perceptual differences between NC and OK females, we selected a group of NC songs and manipulated the rhythm parameters to mimic those naturally found in OK songs. We played back the manipulated and unmanipulated versions to NC and OK females. The addition of the OK rhythm produced a significant increase in the response of the OK females to the NC songs, but had no effect on the NC females. The sensitivity of the OK females to this feature suggests that the vocal ecology of OK has led to the need for finer levels of discrimination. The greater density of males in OK may have led to this need, as OK females come into contact with a larger numbers of potential mates, which may confer an advantage on those females with very finely tuned discriminative abilities.

Two other differences are noteworthy. First, we looked at intra-populational concordance with respect to song potency in the OK population. We had found high levels of concordance among NC females, yielding rank order correlations greater than +.80 across multiple cohorts (West & King, 1988; King & West, 1988). In contrast, OK females showed considerably less concordance, producing nonsignificant correlations. Retesting of the same females after a year's social housing with OK males revealed a strong bias toward OK songs, but not necessarily to the same songs that had elicited the most responses in the previous year.

The relatively lower level of perceptual concordance in OK fits with a second finding. In an attempt to look at flexibility in OK females' perceptual preferences, we housed juvenile OK females for a year with *M. a. obscurus* TX males, repeating the procedures used with juvenile NC females, except that the TX males had been captured at different sites (see King & West, 1987). We found
that after a year's social housing, the females responded significantly more often to TX songs than did normally reared OK females (King et al., 1986). Thus, social housing apparently has different effects in OK than in NC, broadening the former group's tolerance for song to include variants characteristic of the second subspecies. In a subsequent year, we repeated the procedure of social housing with TX males using adult OK females as subjects. We obtained the same result—an equal tolerance for OK and TX song. 

The difference in flexibility between NC and OK females may relate to the evolutionary age of their respective populations, or it may be a consequence of proximate differences in their respective environments, or both. An explanation in terms of evolutionary age might be that the longer history of the OK population in their prairie setting has allowed an open system of perceptual learning in females to develop. The evolutionary odds that OK cowbirds would meet and learn from other cowbirds grew so high that postnatal learning became the more efficient strategy.

The proximate explanation might be that differences imposed by the physical expanse of the grasslands or the more populous social ecology led to differences in the fine structure of the males' songs. As stated earlier, the songs of OK males are more stereotyped in terms of their rhythm; they have differences too subtle for humans and for NC females, but not for OK females, calling for a flexible ontogenetic program to "tune" the female's perceptual system to tighter acoustic specifications. In any case, taken together, the data show that OK and NC females can be differentiated on several perceptual attributes, suggesting that dissimilar geographic addresses dictated the need for dissimilar perceptual capacities.

CROSSING THE SUBSPECIES BORDER: NEW DIMENSIONS OF DIVERSITY

The studies of NC and OK females revealed several dimensions on which to compare females: perceptual specificity, concordance, and flexibility. Our studies of females from the second subspecies, *M. a. obscurus*, have added another: female responsiveness to song. Despite the differences in perceptual selectivity and modifiability just detailed between NC and OK females, both populations appear equally responsive to native song in playback tests. In operational terms, this means that when NC or OK females hear native songs, they respond positively on 51 percent and 53 percent of all trials respectively (calculated as a mean percentage of positive responses per individual, with a maximum of one per trial, across all songs, divided by number of playback trials).

But responsiveness to song is lower in populations of *M. a. obscurus* collected in TX and California (CA) and tested using the same procedures employed with OK and NC birds. The TX females responded to approximately 36 percent of native songs, the CA females to about 20 percent. We were especially curious about the lowered threshold for song in TX because we knew these females used song in many of the same ways as NC and OK females did. *M. a. obscurus* females from south TX, for example, respond preferentially to native song. Such females are also able to influence the song development of NC males. When NC males were housed with *M. a. obscurus* females, the males developed bilingual repertoires, composed of prototypical NC and TX songs. The major changes in the males' songs involved inclusion of a midsong element, a cluster typically not present in *M. a. ater* songs (Figure 2). It is a feature to which *M. a. obscurus* (but not *M. a. ater*) females appear especially sensitive in playback tests (King & West, 1983b). Moreover, when *M. a. obscurus* females are given a "choice" of males to mate with, they copulate most often with males whose repertoires contain the most songs with midsong elements (West et al., 1983).

Thus, the females from the second subspecies appear to be able to influence male song and to use male song to assess males. So, too, *M. a. obscurus* males, housed with NC females, alter their songs in ways that make them less effective to *M. a. obscurus* females, suggesting that they too are stimulated by communicative signals from females. Both subspecies therefore appear to be able to "read" each other's communicative signals, even though they prefer different song variants.

We were struck by the differences in absolute responsiveness between the two subspecies. Two lines of research offered a means of tying the differences in song perception to differences in song production. In extensive analyses of the acoustic structure of male song in the two subspecies in sites ranging from NC through TX, Eastzer (1988) documented a relevant difference within TX *M. a. obscurus* populations. Males in the TX *M. a. obscurus* range displayed more intrapopulational diversity with respect to the acoustic structure of the introductory syllables of their songs than *M. a. ater* populations did (see Figure 2). To be more precise, *M. a. obscurus* males included more diverse note clusters in the first two syllables than *M. a. ater* males did. Thus, TX *M. a. obscurus* males develop more diverse vocal material during song ontogeny. Are social responses by females responsible? Several leaps of faith are needed to connect Eastzer's data to such a conclusion, but we are prepared to make the leap in light of other knowledge about *M. a. obscurus*.

The first source of knowledge originates in observations across two breeding seasons of captive TX *M. a. obscurus* females being courted by TX *M. a. obscurus* males and by NC *M. a. ater* males (King & West, 1984). What was most striking was the passivity of TX females, compared to NC females, in response to song. While NC females terminated 88 percent of social interactions including a song after the delivery of only one song, the TX females departed before a second song during 50 percent of social encounters, permitting males to sing a second or third song during half of all song-related encounters. Males also
sang in closer physical proximity to TX females, delivering the majority of their songs while within six inches of the female. In contrast, males courting NC females sang the majority of their songs at distances greater than 1 foot, and often while flying. Courtship of NC females appeared to be a frenetic affair involving innumerable aerial pursuits and many brief encounters. Courtship of TX females occurred at a more leisurely pace, and involved less flight and more songs. The end result was that TX females received more song stimulation in absolute terms, although the number and rate of copulations observed did not differ for the two subspecies.

The second line of evidence comes from studies of the ontogeny of song of NC males housed with M. a. obscurus females, and includes acoustic analyses of over 10,000 songs (King & West, 1988). We have already described the major outcome of such housing: the NC males come to sing considerable amounts of prototypical TX song. But another striking effect concerned the rate of song development, i.e., the pace at which the males proceeded from the production of variable and diverse song precursors to crystallization of repertoires composed of two to seven song types. In contrast to NC males housed with other species or with M. a. ater females, NC males housed with M. a. obscurus females retained plastic, that is, noncrystallized, song longer. The same result was obtained when NC males were housed with TX females but tutored with NC song. The males housed with TX M. a. obscurus females retained plastic song longer than males tutored with the same NC song but housed with females of other species. So, too, the NC males with M. a. obscurus females sang less of the tutor song, developing more original and more diverse repertoires (King & West, 1988).

These data lead us to speculate that Eastzer's (1988) finding of greater heterogeneity in syllable content in TX M. a. obscurus represents the operation of female influence early in ontogeny, leading to vocal alterations on the part of the males to deal with the relatively lower level of female responsiveness to song. By including more variation in their songs, the males may give the songs more potential to arouse the less reactive females.

**COASTAL PERSPECTIVES: CHANGES IN COMMUNICATIVE FUNCTION?**

Data from a final geographic point are relevant to this hypothesis. As stated earlier, we have also tested the playback responsiveness of another M. a. obscurus population, females from southern California. Their playback responsiveness to CA songs was almost half that of their TX counterparts to TX song. Although our sample of males was small (5), we then looked for any possible associated differences in the songs of CA males.

When we housed CA females with juvenile CA males, by the late spring, when TX or NC males’ repertoires are in final form, the CA males were still singing highly variable song, with much of it not meeting a criterion of stereotypy sufficient to call it crystallized song. The nature of the acoustic variability was striking: most of the songlike vocalizations were fragments of songs consisting of recombination and duplications of individual song elements—vocal behaviors seen in NC or TX males in late fall or early winter, but never in the late spring. The simplest explanation appears to be that the CA males’ song development occurred at a very slow rate, with some males entering the breeding season possessing primarily plastic or variable song, fitting with observations by Rothstein et al. (1986) that some juvenile males do not breed in their first year.

The developmental data on CA birds are too scant to form many conclusions. But Rothstein and his colleagues have also studied this population’s vocal behavior and have found other lines of evidence to suggest that CA males possess a different vocal program than NC or TX males. Most notably, Rothstein has evidence that another male vocalization, the flight whistle, which is used to signal departures and flight movements, is quite modifiable through the male’s first breeding season (Rothstein & Fleischer, 1987). Evidence also exists to suggest that flight whistles may play a direct role in eliciting copulations in CA populations (Rothstein, Yokel, and Fleischer, 1988). While our aviary observations and other field observations suggest that copulations are always preceded by song in the eastern subspecies, CA females appear to copulate when immediately cued by only a flight whistle. Although Rothstein et al. find ample evidence of the use of courtship songs, the songs appear to occur in a different proximate relationship to the elicitation of copulatory postures in wild females.

Thus, the lowered responsiveness of CA females to playback of songs and the delayed development of song in CA males may reflect a functional shift in the use of vocal signals in the western part of the cowbird’s range. Rothstein et al. speculate that the larger ranges in the west may have favored increased use of long distance signals, such as the flight whistle, which transmit better across greater distances than the courtship song. Thus, the whistled vocalization may have come to have more salience in coordinating male–female interactions.

Rothstein has not yet tested CA females’ playback responsiveness to flight whistles. We have tested the responsiveness of TX females to flight whistles from four areas and have found no responses at all (West & King, 1989). We have more limited data on NC females, but we have never been able to elicit a copulatory response to a flight whistle. If Rothstein finds CA females to be responsive to whistles, it would represent significant converging evidence of yet another instance of interrelationships between female perception and male production in relation to differences in ecology.

**INDIVIDUAL DIFFERENCES IN RESPONSIVENESS**

Our travels from NC to CA have uncovered a number of perceptual variables on which females may differ. We have also uncovered ways in which such differences may be linked to male song production. We have recently completed
a study with NC birds in which we tried to test some implicit assumptions about interrelationships between female responsiveness and male song production (King & West, 1989). To do so, we exploited the range of individual variation among NC females in song responsiveness. In 15 years of playback testing of females, we have routinely recorded individual differences in playback responsiveness. Every year, we find a range of females, from those who respond on 80–90 percent of all trials to those who respond on 20–30 percent of all trials. Although, on a relative basis, the females prefer the same songs, some express their preference more frequently than others.

To see if individual variation in playback responsiveness produced local effects that paralleled populational effects, we housed several naive juvenile NC males each with an adult female of known playback responsiveness (King & West, 1989). We deliberately selected female companions who varied considerably in their level of responsiveness. One female had responded to only 7 percent of all playback songs, two had responded to fewer than 20 percent, three had responded to between 50 and 60 percent, and two to more than 75 percent. To introduce some standardization in acoustic stimulation, we tutored all the males with the playback songs on which the females had been tested. After allowing the males and females to interact from late August until the next breeding season, we looked at the nature of the males’ song production. We also retested the females’ preferences for the playback songs to see if social housing had had any effects.

As in all past work with NC females, we found no evidence of changes in the females’ responsiveness: the rank orderings of the females from high to low were unchanged a year later. But noteworthy differences were apparent in the vocal production of the males in relation to the “nature” of their female companions. In line with the populational findings, males housed with relatively unresponsive females developed larger repertoires and included more diversity in their introductory note clusters. In contrast, males with females who responded very frequently developed smaller and less diverse repertoires. And thus we were able to approximate in the laboratory what Eastzer (1988) had found in the field: an association between female responsiveness and syllable diversity.

We have also been able to trace the process one step further. Playback responsiveness is a measure of behavior during the breeding season—females do not adopt copulatory postures at other times of year. Could we connect playback responsiveness to other indices of song reactivity outside of the breeding season? In particular, is there a discernible relationship between playback responsiveness and wing stroking? Although our sample was small (8 females), we did find a positive correlation between playback responsiveness and wing stroking, suggesting that the wing stroke may be a behavioral precursor to a copulatory posture.

And thus we are back where we started—looking at the proximate dynamics of interactions between NC males and females. But we are doing so armed with many new questions. As stated earlier, we had noted individual variation in frequency of responding for 15 years, but it was only after the geographic comparisons that we developed a testable hypothesis. Every comparative psychologist who studies the same population and the same individuals knows that his or her animals have different “personalities,” but it is sometimes hard to know what to make of some of the differences—are they statistical noise or empirical signals? Looking at new populations but asking the same questions can put old data in a new light.

MANAGING INTRASPECIFIC VARIATION: THREE CONCEPTUAL TOOLS

Thus far, we have studied only a half-dozen populations in any depth, and we have uncovered 10 communicative variables. In females, perceptual selectivity, specificity, concordance, responsiveness, and reactivity may differ. In males, the rate and content of vocal production, sensitivity to female signals, modifiability, and imitative ability can vary. And how the five female parameters interact with those of males is another level of possible variation. We are in the process of attempting to negotiate our way through this array of differences. We have locked onto three concepts to help navigate the forest and the trees. We describe them below because we believe they may provide guidance to other investigators as well.

Communicative profiles

In attempting to compare the behavior of 45 different rodent species, Dewsbury (1988a) developed “adaptive profiles” to contrast the “personality—motivational structure of a given species” (p. 24). We have opted for a similar strategy, constructing communicative profiles of males and females from different populations. The aim is to find suites of behavior that seem to be natural units, such as low responsiveness in females and high modifiability in males. In such a way, we hope to be able to identify the mechanisms that couple male and female communicative traits so that the desired outcome, mating, is obtained. Adherence to a profile also helps us avoid the tendency to view bird song or vocal communication as a unitary concept. Among the behaviors embedded within bird song are the motoric skills necessary to articulate sound, orienting and attention mechanisms, trial-and-error learning, rehearsal of vocal material, long-term memory, vocal imitation, improvisation, and invention. And then there are the receptive capacities of listeners detailed earlier. Learning how all these behaviors are joined is similar to learning how the various compartments within a honeybee hive serve to create a society. The physical presence of a hive,
however, is a constant reminder that, in the end, everything fits together. It is
more difficult with bird song, because the physical signal does not encapsulate
the underlying phenomenon of interest: communication.

**Inherited niches**

After creating profiles, the next step is to look more carefully at the habitats
inherited by different populations of the same species. Elsewhere we have
proposed the concept of inherited niches to represent the ecological and social
legacies transmitted to the young (West & King, 1987). We deem a formal name
necessary to give exogenetic inheritance equal status with its genetic cognate.
The term *niche* captures the physical requirements necessary for the existence of
a species, as well as the particular role or occupation of that species within the
broader ecological community. If profiles describe capacities, then niches reveal
possibilities for translating capacities into capabilities.

For example, in cowbirds, some of the differences between populations may
be explained by focusing on variation in their physical and social ecologies. For
example, in field studies of CA cowbirds, Rothstein, Verner, & Stevens (1984)
documented a distinctive diurnal pattern: CA cowbirds engage in parasitism and
mating in the morning, then fly considerable distances in the afternoon to feed
in large pasture lots, during which time minimal, in any, courtship is seen.
Females may thus be separated from males for many hours each day, especially
while the females are engaging in egg removal, egg laying, and surveillance of
potential host nests, activities in which the male does not participate. Such
naturally occurring deprivation of the sight and sound of a mate could alter the
salience of cues from him. In particular, as these daily experiences may lower the
female’s threshold for mating, they might render the details of specific song
structures less important to the elicitation of copulation, although still making
song essential to the original choice of the male as her consort. In contrast, in a
prairie population in the Midwest, Elliott (1980) described feeding and mating
taking place in the same locale. In areas where feeding and courting are not
physically separated, especially in dense populations, females may become over-
stimulated, and thus males may need to outdo one another vocally to compete for
a female’s attention. Thus, in OK, for example, it may be important for females
to be maximally sensitive to fine differences in song structure, a sensitivity
improved by postnatal tuning of perceptual preferences.

Another source of niche variation in cowbirds is migration, a variable linked
to differences in learning opportunities in other songbirds (Kroodsma, 1983). The
M. a. obscurus populations we have studied the most tend to breed and over-
winter in the same vicinity, whereas more northern and eastern M. a. ater
populations may travel a thousand or more miles to wintering roosts. One impact
of migration may be in the amount of time males have to “work” on their songs
when they return to breeding sites. So, too, females may have more or less time
to influence or become sensitized to local songs. NC males and females are
migratory, returning to their breeding sites in mid-March, the time at which we
have found captive females reactive to song and males capable of modifying their
song in response to social cues (West & King, 1986).

The above scenarios are just that—possible sequences of events predicting
different relationships between male production and female perception depend-
ring on the properties of the niche. We provide them to illustrate correlations
between ecological heterogeneity across the range of cowbirds and heterogeneity
in the ontogeny of vocal communication.

**Ecological clocks**

Whereas ontogeny is often measured in terms of time or age, ecology is often
appraised in terms of physical resources. But an animal’s ecology also has tem-
poral dimensions, and thus we come to the final concept, ecological clocks.
Temporal readings of a population are in and of themselves triadic entities,
recording the passage of phylogenetic, ontogenetic, and individual time. For
many species, phylogenetic time estimates are, however, too crude to be direct
value to the comparative analysis of behavior. Only minuscule movements of
evolutionary time can be accurately tracked. In the case of cowbirds, however, we
can trace in general form the species’ radiation throughout North America. By
following humans’ efforts to clear land for pasture and livestock, the ancestral
path of cowbirds from South America becomes visible. And, as birdwatchers are
also a venerable lot, as quick with their pens as with their eyes, records exist to
mark cowbirds’ exploitation of the deforestation of the United States (Friedmann,
1929; Grinnell, 1909; Mayfield, 1965; Oberholser, 1920). As stated earlier, the
ancestral part of the cowbird’s range lies in the central United States; records of
their presence date back to the earliest European settlers (Friedmann, 1929). In
contrast, cowbirds have resided in North Carolina for only half a century (Potter
& Whitehurst, 1981). Cowbirds are also new to California and the Far West
(Rothstein et al., 1980). Thus, our studies of cowbirds span populations whose
ecological clocks register discernibly different evolutionary times. The signifi-
cance of this may be considerable in light of work on other animals suggesting
that “older” and “newer” populations may possess different ontogenetic mecha-
nisms (Mayr, 1982).

A recent theory concerning human diversity at microphyletic levels may
illuminate the use of ecological clocks in comparative analyses (Plomin, 1986).
Consider a common question about humans: Why are children in the same
family so different (Plomin & Daniels, 1987)? Given genetic relatedness and
physical proximity, why is it that parents readily remark on personality differences
among siblings that to them seem as conspicuous as they are intractable? Plomin
and Daniels argue that siblings may share parents and genes and homes, but they do not share environments. Systematic environmental differences include family composition, sibling interactions, parental treatment, and extrafamilial resources. Nonsystematic variation arises from birth spacing and gender differences, accidents, illnesses, divorce, physical and economic traumas, and exposure to peers, teachers, and television. Thus, children within the same family, by virtue of age differences, run on different ecological clocks.

If we extend the concept of the nonshared temporal environment to the life of a species, it is possible to think of the ancestral populations as firstborns and recent settlers as later-borns. Thus, NC cowbirds attempting to colonize North Carolina in 1930 faced different selection pressures than did their OK counterparts, which have now been settled in their "home" for hundreds of years. NC cowbirds are new kids on the evolutionary block, afforded neither the same opportunities nor the same obstacles.

Students of development are perhaps most used to noting the passage of intragenerational time, especially the portion spent as an infant or child. As important as experience early in ontogeny may be for understanding development, the nature of such experiences may have caused developmentalists to ignore later, equally influential periods. When considered in terms of timing, cowbirds may not be as different from nonparasitic songbirds as one might think. Although they do not experience conspecific parental care as nestlings, they interact with conspecifics at all other times of year. And, since adult male cowbirds do not cease to sing at the end of the breeding season as many other songbirds do, juvenile cowbirds can experience species-typical stimulation naturally once they are settled, at 50-60 days of age, into cowbird flocks. Thus, although stimulation from adults may be "time-shifted" relative to some other songbirds, it is not necessarily less effective. There is considerable evidence to suggest that song learning is not restricted to the natal period as much as previously thought for nonparasitic songbirds (Petrinovich, 1988b). Many songbirds leave the nest and parents at about the same time cowbirds do, and appear to learn many of their songs from unrelated neighbors the following spring. So, too, female songbirds' preferences may not be directly attributable to natal experience: knowing the songs of a female's father or brother may not be sufficient to explain later mate choice (Petrinovich & Baptista, 1984). Thus, the hours most important for cultural transmission must also be considered in a less age-limited manner, rendering the cowbird's pattern of development potentially less idiosyncratic.

In summary, we have proposed three activities necessary to the interpretation of intraspecific variation: preparation of profiles, knowledge of niches, and calibration of clocks. We suggest that they serve to make microphyletic differences especially fertile ground for the formulation of principles of behavioral adaptation. We are hardly the first to emphasize the need for such studies, but we feel compelled to repeat the call, because the question of the value and meaning of psychological comparisons between humans and other animals is still a current topic.

We suspect, judging from our own experiences, that simple inertia also impedes the pace of intraspecific comparisons. Once a phenomenon is settled into a home, thoughts of uprooting it may provoke anxiety. In our case, some of the anxiety stems from insecurity: How should we manage the diversity uncovered to date? We empathize with the New England homeowner, who, in organizing his attic, set aside a box filled with tiny pieces of string. The inscription on the box read: "String too short to be saved" (Hall, 1983). As we sort through data, it is sometimes difficult to know which bits and pieces will ultimately hang together and which ultimately should be set aside. But, for the present, we save them all. With threads of knowledge from many sources, a fine enough net may be woven to hold even the smallest of fruits from microphyletic patches.

**SUMMARY**

In this chapter, we describe variation in the perceptual and learning capacities of female cowbirds with respect to discrimination of and responsiveness to male song. We also present evidence to suggest that differences in the acoustic structure of males' songs within and across populations represent vocal adjustments to female cues. We attempt to relate these patterns of diversity in female perception and male production to differences in the natural history of cowbirds across their extensive range.

We propose three concepts to help organize evidence of intraspecific diversity: communicative profiles, inherited niches, and ecological clocks. We argue that the study of microphyletic variation is essential to understanding the responsiveness of ontogenetic systems to naturally occurring changes in a species' habitat.