Abstract
A common assumption is that communicative competence simply flows from some possibly innate by-product of vocal development. Understanding the dimensions of competence, or what in this chapter is called “communicative pragmatics,” can be summed up as answering the “wh” questions, the “who,” “what,” “where,” “when,” and “why” of vocal performance. This chapter shows that songbirds and infants have to (a) learn how to use their signals through social modeling and social operant learning and (b) learn to lengthen their attention span so as to be able to acquire critical feedback from social companions. Of particular importance is the convergence of directed attention and vocalizations because individuals are able to receive both vocal and visual feedback to their behaviors.

Keywords: communicative competence, vocal development, communicative pragmatics, songbirds, social modeling, social operant learning, attention span

Overview
The basic plan for a journalist writing a newspaper article is to assemble facts, beginning with “who,” followed by “what,” “when,” and “where,” progressing to “why” and ending with “how.” Here, we introduce the journalistic plan to define the major variable in this chapter, communicative pragmatics. The idea is simple—we are asking how an individual correctly identifies to whom to convey information in a timely fashion and in a correct context. Further, we ask what biological or psychological means facilitate the act of communicating. An effective communicative act, one that answers the questions cited above, can be compared to an effective newspaper article. We argue that many of the parameters of successful pragmatic performance are still unknown in even seemingly well-studied species. The consequence of the missing answers is that stories are formed that may sound good but are inaccurate, leaving the usually more complex account untold.

We have chosen two organisms, brown-headed cowbirds and humans, because much is known about their communication system, i.e., the structuring and meaning of information. The use of the information, the pragmatics, is less well studied than ordering or meaning because it is more difficult to measure and frequently taken for granted. The mode of communication is generally vocal, although we will see that dividing communication by reference to single senses does not always work. The time period of most interest is early in postnatal development, although one cannot ignore the life span. The function of the vocalizations (“why”) also are considered but not stressed as we have written about this topic often (King & West, 2002; West & King, 2001). And, we do not focus on the “how” in detail because the biology of the
Our research perspective originated in reaction to traditional views that development is guided by automated maturational programs. Studies of development during the 1960s and 1970s were guided by the simplified dichotomous view of nature (genes) dictating the end product with nurture (environment/experience) passively triggering the developmental process toward that predetermined end point. In this view, the developing organism and the environmental experience are separable entities. Traditional studies of vocal development in songbirds, for example, removed individuals from the natural developmental context and examined what experience was necessary to trigger the innate developmental program. Young males were housed in isolation to control their exposure to auditory stimulation and experimenters selected what the males heard and how much they heard to determine the influence of auditory experience on development. Or, alternatively, deprivation experiments were conducted to see what developed in the absence of any stimulation, thus revealing what was thought to be the innate blueprint for song (e.g., Marler et al., 1972). Although the research approach was well-intentioned—individuals were removed from their social environment to control external variables—it actually created a novel developmental environment because the absence of companionship introduced its own effects on development (Kuo, 1967). Comparable naturalistic studies of human vocal development at the time were those that examined infants with sensory impairments. Early babbling, when examined for phonetic properties of speech, seemed to be similar in deaf and hearing infants, thus suggesting that early experience had no influence on prelinguistic vocal development (Lenneberg, 1967).

A fundamental flaw of the false dichotomy of nature and nurture as separable entities is the implicit assumption that contributions of environment to development can be controlled like measurable quantities in a recipe. Adding or excluding certain experiences was thought to have predictable outcomes because the fluidity of the interaction of genes and environment was construed to be minimal at best: an environmental trigger of a predetermined genetic program (e.g., “reaction range” proposed by Gottesman, 1963; Scarr-Salapatek, 1976). Thus, environment was seen as a static influence rather than dynamically shaping the organisms’ development. However, rather than development being a passive unfolding of preprogrammed pathways through exposure to the environment, interactions with the environment, particularly the social environment, are key to directing behavioral development (Gottlieb, 1976; Lickliter & Gottlieb, 1985; Moore, 1984). Individuals’ early experiences have a cascading effect in structuring the pattern of further development, with a fluid interaction of what was traditionally viewed as “nature” and “nurture.” Therefore, there is no explanatory value in distinguishing the contribution of “nature” and “nurture” in development, as there is no boundary between the two—they are interdependent and inseparable. Furthermore, with the recognition of the inheritance of environments, the ontogenetic niche, one could no longer distinguish genes and environment on the basis of what is preexisting before development occurs (Oyama, 2000; West & King, 1987, 1988). The social surroundings and interactions of a young organism are part of its heritage just as are genes and proteins in the body.

In this chapter, our goals stem from this theoretical framework underscored at all times by the idea that communicative development is an interactive process involving social partners. Mere exposure to environmental or social variables is not sufficient; individuals must be active participants in their environment to learn. Organisms acting and behaving elicit social responses that shape an organism’s perception, affecting what there is to be learned (“performatory feedback”: Gibson, 1966). To exemplify this idea, we present evidence for a social gateway, which is the role of ecology in making stimulation available in the environment. Proximity to and interactions with social partners offer different opportunities for interactions, thus mediating the communicative behaviors that individuals produce and feedback they receive (West et al., 2003; White et al., 2002a). For example, for young individuals the degree of access to adults—a social gateway—predicts cultural guidance and thus what is available to be learned. Therefore, instead of considering exposure to all potential stimulation in the environment as relevant for development, we focus on the bioavailability of social stimulation: that portion that is accessible via the social gateway.

**Traditional Studies of Communicative Development**

Studies of early vocal development do not often focus on the development of pragmatics, that is, putting correct acoustic form into effective use; rather, most studies focus on the development of mature
acoustic forms of vocalizations or speech sounds, with the assumption that there is a predetermined linkage between producing the appropriate vocal forms and knowing how to use them. This assumption is a historic result of the widely held viewpoint that vocal development in humans and songbirds can be explained through the action of innate modules (Bloom, 1993; Chomsky, 1965; Konishi, 1965; Lenneberg, 1967; Marler, 1967; Marler & Nelson, 1992). Additionally, original comparisons made between birdsong and speech development focused on acoustic form rather than pragmatic use (Marler, 1970), as both were thought to be based on similar innate mechanisms. Included in such predetermination is the pragmatic component of communication, which is simply assumed to follow the development of functional vocalizations: once a bird sings, or a human produces their first protoword, correct usage comes in tow. A result of a reliance on innate explanations is that development becomes oversimplified because environmental influences are overlooked and underestimated.

However, a closer examination of the studies of communicative development (Payne & Payne, 1993), and many studies that have been performed in our laboratory, suggests that such simplistic views of development of acoustic form and usage cannot be supported. Studies of cowbirds have revealed that the development of song structure and communicative competence is dependent upon the nature of interactions between young males and their social partners. Females provide nonvocal social feedback that shapes fine acoustic structure of male song and that influences the rate of vocal development (King & West, 1988; King et al., 2005; Smith et al., 2000; West & King, 1988). Adult males provide the interactions through which males develop effective use of song (White et al., 2002b). Similarly, we have evidence in humans that differential responses to vocalizations may influence vocal development and usage similar to what we have seen in cowbirds (Goldstein et al., 2003; Goldstein & Schwade, 2008; Gros-Louis, 2006; Gros-Louis et al., 2006a, in preparation-b). Thus, in contrast to the view that early “babbling” in both songbirds and infants is merely motor practice (Bloom, 1993; Oller, 2000); contingent stimulation by social partners in response to early vocalizations actually drives development. The demonstration that social stimulation shapes developmental change makes it necessary to view the ontogeny of communication as part of a broader developmental ecology. The task that we face as researchers is to figure out the aspects of the social environment and social contingencies within that environment that operate to influence different components of communicative behavior.

Pragmatics Defined

To clarify the way in which we use the terms “pragmatics” and what we mean by “vocal usage” in this chapter, we provide a brief overview of three different analytic levels of communication that stem from early semiotic and linguistic theory (Chomsky, 1965; Morris, 1946) and its extension to ethology (Sebeok, 1962, 1965). The first two levels, syntactic and semantic, examine what message potentially could be contained in a signal or display rather than its use in the context of an interaction. Syntactic analysis abstracts signals from their communicative context to investigate their potential for communicating meaning alone and in combination with other signals, asking such questions as what constitutes a signal and how the potential meaning of a signal changes in combination with other signals (Chomsky, 1965; Smith, 1977). Semantics, on the other hand, investigates what kind of information is contained in a signal, asking whether a signal carries meaning through association with particular objects or behaviors; however, although semantics examine the predictable association of a signal and potential referents, this association is divorced from social context to strip away any potential contextual “cues” for meaning.

The pragmatic level of analysis considers use of signals in social interactions. Therefore, it is both the signal and the contextual production of it that results in a signal’s function. For this reason, the same signals in different contexts may have different meanings or functional outcomes (Smith, 1977). And, this leads us to an important point of comparison of pragmatics to syntax or semantics. Syntax involves specific structures, semantics involves specific meanings, but because of variation across contexts, pragmatics is not predictable and predefined in the same way as syntax or semantics. To illustrate this point, Dore states “The function of interrogative structures, for example, is to ask questions. But this tells us little about the experienced regularities of what, where, when, why, how, and with whom questions are used” (Dore, 1986, p. 6). The analogy in the present chapter is that although the function of birdsong or prelinguistic behaviors may be recognized, the development of the content of a signal is not predictive of the development of its pragmatic usage. Furthermore, pragmatic usage is essential for the functional effectiveness of signals.
### Table 33.1 Excerpts of Definitions of Communication from a Variety of Theoretical Perspectives of Different Academic Disciplines

<table>
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<tr>
<th>Academic Discipline</th>
<th>Definition</th>
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<tr>
<td>Behavioral ecology</td>
<td>“…signals or displays to modify the behaviour of reactors…” (Krebs &amp; Davies, 1993, p. 349)</td>
</tr>
<tr>
<td>Cognitive psychology</td>
<td>“…internal representation and symbolic behaviour that conveys that representa-</td>
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<td>tion…the interpretation of the symbolic behaviour.” (Johnson-Laird, 1990, pp. 2–4)</td>
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<tr>
<td>Ethology</td>
<td>“…the transfer of information via signals…between sender and receiver” (Hailman, 1977, p. 52)</td>
</tr>
<tr>
<td>Linguistics</td>
<td>“…vocal and nonvocal gestures as we interact…” (Lindblom, 1990, p. 220)</td>
</tr>
<tr>
<td>Neuropsychology</td>
<td>“…behaviors of one member of a species conveys information to another member of the species…” (Kimura, 1993, p. 3)</td>
</tr>
<tr>
<td>Sensory ecology</td>
<td>“…behavior generates a signal that mediates interaction…” (Dusenbery, 1992, p. 37)</td>
</tr>
<tr>
<td>Sociobiology</td>
<td>“…action or cue given by one organism to another…” (Wilson, 1975, p. 111)</td>
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Source: Adapted from Hauser (1996).

Although the early semiotic distinction of the three components of the communicative process included syntax, semantics, and pragmatics, an examination of definitions of communication from different theoretical perspectives indicates that definitions do not explicitly include pragmatics (Hauser, 1996; Table 33.1). Such an omission reiterates the fact that pragmatics are often inherently taken for granted, assumed to follow from the production of vocalizations (but see Dore, 1979 who argues that function precedes form and can derive from separate sources ontogenetically). Thus, the differential focus across academic disciplines is the structure or content of the signal but not the delivery of the signal. Ethology and sociobiology view signals as inherent in the behaviors of individuals (e.g., Smith, 1977; Wilson, 1975), whereas cognitive psychology views signals with discrete meaning and an underlying mental representation (Johnson-Laird, 1990).

In addition, in our view, definitions of communication provide the description for the end point, a successful communicative act, rather than the necessary precursors of communicative behavior or the process that results in a communicative act. For example, the “prerequisites” for describing vocal interactions in songbirds are indicated to be the “who,” “what,” and “why,” leaving out the “when” (Dabelsteen & McGregor, 1996).

Nonetheless, pragmatics are implied in the definitions of communication in that they either explicitly include a signaler and a recipient of a signal, or the premise that information is transmitted between two individuals. Definitions that focus on behavioral interaction as communication, rather than those that focus specifically on the content of signals, are most useful in comparative studies of communication across species. In particular, when comparing prelinguistic communication in humans to communication in other animals, an ethological perspective is a valuable approach, as both communication systems share more similarities with one another than human language: “information is a feature of an interaction between sender and perceiver” (Hauser, 1996) or communication is a “process of signaling and eliciting responses” (Smith, 1977).

It is probably no accident that definitions of communication and studies of communicative development lack explicit focus on the correct delivery or usage of signals. Popular experimental designs employed in studies of nonhuman vocal development involve solitary individuals. In such a design, pragmatics are inherently absent, as pragmatics involve social partners. Furthermore, there is no need to explain origins of behavior when relying on a nativist explanation: ghosts in the machine provide the blueprint for development and connect form with function. Thus, end points serve as a starting point from which researchers work backward to explain development rather than prospective studies considering the process to get to the end point. The danger in a retrospective approach is that it fails to capture the origins of behavior, as researchers have certain preconceptions of early behaviors and their potential plasticity (cf., Reddy, 1999). The use and significance of sounds, or their directness to a social partner (defined by visual gaze), are overlooked because they will be supplanted by mature song or words. We provide examples from
studies of both cowbirds and infants that demonstrate that understanding the origins of behavior is necessary to understanding its function and that communicative development needs to be studied in a prospective manner in order to appreciate the role of socially gated stimulation to construct behavior.

**Absence of Pragmatics in Developmental Studies**

**Birdsong Development**

Researchers have noted recently that although the historical emphasis has been on strictly auditory influences on song learning, the next few decades will be devoted to analyses of social factors (Beecher & Brenowitz, 2005; Beecher & Burt, 2004). An early consideration of social influences was rooted in the finding in the mid-1980s that live tutors could facilitate imitation beyond that seen with a tape tutor (Baptista & Petrinovich, 1984). At the same time, studies by King and West revealed that nonvocal social stimulation of females influenced vocal development in male cowbirds (King & West, 1983, 1988; West & King, 1988). The newly recognized role of social interactions in development ultimately led to a greater focus on the behavior of singers and recipients in the form of “action-based” learning (Marler & Peters, 1982). However, because of the strong hold of innate underpinnings in developmental theory, social influences were viewed as experiential contributions to divergent pathways of predetermined vocal end points. Song variants were winnowed during development via feedback between senders and receivers, rather than feedback contributing to song origins (Marler & Nelson, 1993; Nelson & Marler, 1994). Furthermore, social feedback was generally considered to be of an acoustic nature, such as song matching to a tutor or through interactions between neighboring males (Beecher et al., 2000). This is not to say that pragmatics is not part of birdsong, as birds must decide whether and when to match songs or repertoires with neighbors (Beecher, Burt, O’Loghlen, Templeton, & Campbell, 2007) and from whom to learn song (Kroodsma, 2004). However, an important point is that this research considers the role of pragmatics in vocal development rather than pragmatic development itself.

The focus on acoustic variables may account for the fragmented state of the field as a whole. Kroodsma (1996), in calling for more serious attention to the ecology of song, has characterized the field of song learning as composed of “myriad facts…largely unconnected, bits of a grand evolutionary picture” (p. 3). The fragmentation of the field of birdsong may be tolerable for those interested in only part of the communication process, e.g., the mechanisms of motor or hormonal control underlying song production and seasonal neuronal plasticity (Brenowitz, 2004). But for those seeking to understand the development and evolution of communication, knowledge about the dynamical nature of interactions between communicators is essential (McGregor & Peake, 2000; Nowicki et al., 2001; Payne & Payne, 1993). Acoustic variables are insufficient because they neglect the actual social interactions in which song use is embedded. Thus, research over the past decades on the development of acoustic structure of song in birds have made significant discoveries into the potential mechanisms of vocal development, ranging from neurobiological to external social influences, but the research has overlooked the fact that effective song may not bring with it effective use in social interactions.

The oversight of pragmatics in vocal studies has several root causes. First and foremost, investigators have simply assumed that evidence of the presence of a communicative signal is also evidence that its use will be appropriate. Second, the contexts studied, often isolates or small groups of songbirds, may not reveal the absence of pragmatic skills. Third, investigators may unwittingly substitute their own actions for the behaviors that animals must perform in nature. For example, in playback work, experimenters expose male-deprived females to recorded songs and measure whether she adopts a copulatory posture to the songs. The focus is on discovering song function and it has been used in diverse songbird species (Searcy, 1992). The appeal of this unambiguous response is its objectivity and quantifiability, but its simplicity can be deceiving because it completely obscures the realm of pragmatics. It is the investigator, not the singing bird, who determines what, where, when, and to whom recorded vocalizations are directed. In reality, however, males must not only know what to sing, but they must also know where, when, and to whom to sing.

Such an omission is critical when we consider the instrumental importance of pragmatics of singing behavior in natural contexts. By removing the playback context previously engineered by humans, a series of experiments revealed that the development of biologically effective song does not automatically result in the reproductive success that is suggested by song efficacy in playback experiments.
Young male cowbirds were housed first with adult female cowbirds or canaries and then were exposed to a new set of female cowbirds or canaries to provide a more “freestyle” social context of courting and mating behavior (Freeberg et al., 1995; West et al., 1996). The “where” component of communicating was varied by first having males meet their new companions in a flight cage and then in a large aviary populated by female cowbirds from three populations, canaries of different color morphs, and starlings, a novel species. In the flight cage setting, the male cowbirds, who had been housed with female cowbirds, looked normal: they sang to female cowbirds and ignored the canaries. But in the aviaries, the female-housed cowbirds sang primarily to themselves or one another, ignoring the often-solicitous female cowbirds. Even after observing the mating behavior of adult male models in the aviaries, the male cowbirds still ignored females of their own species. The data from the canary housed males was more dramatic. In both contexts, the canary-housed males courted new canaries and ignored female cowbirds.

Returning to the journalistic framework, males in these studies collectively showed deviations in “who,” “what,” “where,” and “when.” Males who developed effective songs, but not appropriate “pragmatic” skills, did not achieve copulations. These results provided experimental evidence for the idea that form and usage do not automatically develop concurrently. More importantly, it pointed to the need for researchers to consider the inherited environment of development and emphasized the need for multiple contexts for assessment of the end point of functional behaviors such as singing. Had the experiments stopped with playback experiments or with the flight cage test, male’s development would have appeared normal. And, in fact, these would have been potential stopping points for many researchers without access to the complex social context of a flock, the context where song is actually used.

**Infant Development**

Most studies of early infant vocal development, like those of songbirds, historically have focused on auditory influences on vocal learning, such as the influence of exposure to speech sounds of the primary language on structural variation in phonemes during the first year (e.g., de Boysson-Bardies & Vihman, 1991; Vihman et al., 1986). Thus, vocal behavior is examined to document and explain stage-like changes at the phonemic level rather than communicative use of vocalizations (Locke, 1983; Oller, 2000; Stoel-Gammon & Otomo, 1986). However, just as in songbirds, vocal development is not only about producing more phonologically advanced sounds, but is also about learning the pragmatics of communication: how to use vocalizations for effective social and communicative interactions (Dore, 1974). The social-pragmatic approach to language development recognizes the importance of pragmatic comprehension scaffolding language development toward the end of the first year (Akhtar & Tomasello, 2000; Baldwin & Tomasello, 1998; Tomasello, 1997). However, few studies examine the development of pragmatics of productive communicative behavior (Carpenter et al., 1983; but see Dore, 1983; Smith, 1998).

Studies more often provide descriptions of pre-determined pragmatic abilities, which are labeled “intentional communication” or “communicative intentions” rather than examining their developmental origins (e.g., Carpenter et al., 1983; e.g., Wetherby et al., 1988). By examining an expected end point, as suggested by the term “communicative intentions,” researchers fail to notice the potential communicative function of combined vocal, attentional, and gestural behaviors. Not all infants will develop similar pragmatic behaviors, as some infants will use more gesture, tone, or protowords (Dore, 1974) and thus it is important to study their convergent development.

One reason that few studies have explored pre-linguistic communicative development may be that there is often a conflation of language and communication (Golinkoff & Gordon, 1983). The designation of the term “pre” linguistic indicates that language is the end point rather than broader communicative competence. Thus, language researchers have often approached the study of the prelinguistic period in a retrospective manner, focusing on month-by-month or stage-by-stage changes to bridge the gap between babbling and first words by identifying precursors to formal language (e.g., Kent & Miolo, 1995 and references therein). Studies that do consider social influences on language development attempt to predict behavioral changes over many months, e.g., from 8 to 14 months. Often, infants’ abilities or behaviors at time y (14 months) are then retrospectively related to their abilities at time x (8 months) to determine the relative influence of particular communicative measures on developmental linguistic milestones (Bornstein et al., 1992; Tamis-LeMonda et al., 2001). The result is that the development of

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pragmatics is taken for granted just as in songbirds, in that development of a communicative signal (language) brings with it the development of its appropriate use. This may be a result of early views of not only innate behaviors, but also a “hereditary teaching mechanism” responsible for connecting behaviors to function (Lorenz, 1965). The machine supplies the pragmatic connection in an automatic fashion not requiring learning. Pragmatics is simply doing what comes naturally or nativistically. Development is of the “plug and play” variety.

Prelinguistic behaviors originally were identified relative to their mode of production, and thus viewed as distinct channels of communication (Stern, 1974): affective (vocal and facial expression), attentional (eye gaze, gestures), and vocal (babbling) (see also Barratt et al., 1992; Stern, 1974). A number of studies have explored the temporal relationship among communicative behaviors, such as visual gaze, vocalizing, and/or smiling (D’Odorico & Cassibba, 1995; Keller & Scholmerich, 1987; Schaffer et al., 1977; Striano & Rochat, 1999), although the perspective has been to study their co-occurrence or sequential nature. Thus the structural timing, rather than communicative significance, has been the focus of many studies. What is needed is a study that documents when and how phonologically different vocal behaviors converge with other modes of communication and how that results in broader communicative competency.

We propose that combining studies of vocal behavior with those of sociocognitive behavior is the starting point for understanding the development of communication because sociocognitive abilities contribute to the attentional components of prelinguistic communication. It is the integration of directed attentional focus (toward objects or social partners), vocal behaviors, and nonverbal gestures (though not considered in detail in this chapter) that gives rise to the pragmatic function of early communicative behaviors (cf., Bates, 1976; Ninio & Bruner, 1978). Bringing attentional and vocal behaviors together is a key, as suggested for later language and apt for our journalist metaphor: integrating gaze and linguistic channels tells a recipient the when, where, and what use to give the gazing activity in relation to language (Kasher & Meilijson, 1996; Schieffelin, 1983). Compounded behaviors are especially apparent in the second 6 months of life when infants bring together new skills: babbling, socially directed behaviors such as social referencing, establishing joint attention episodes, and attentional-sharing behaviors such as protodeclarative pointing. A quote from Bates (1976) exemplifies the communicative capacity of combined prelinguistic behaviors at the end of the first year: “…combinations of apparent imperative intention: stretching forth the arms with an open-and-shut gesture of the hand, pointing, reiterated and insistent vocalizations, and intermittent eye contact with the adult” (Bates, 1976, pp. 55–56; Bruner, 1975; see also Ninio & Bruner, 1978).

Also, a point alone may orient caregivers’ attention, but if the point is accompanied by a vocalization, there is more indication of the infants’ goal (Jones & Zimmerman, 2003). In particular, it is the coordination of behavioral and attentional focus on objects and people in interactions, i.e., joint attention or secondary intersubjectivity (Bakeman & Adamson, 1984; Trevarthen & Hubley, 1979), that is thought to form the basis of preverbal communication because it “encodes” infants’ intentions (Sugarman, 1984, p. 60).

Though the parallel development of vocal and sociocognitive behaviors are the basis of more complex communication, at present, there is a disconnect between studies of early vocal development and social and cognitive development. In contrast to a handful of studies in the 1970s and 1980s that examined the potential communicative function of combined behaviors (e.g., Dore, 1974; Sugarman, 1984), current studies of sociocognitive abilities focus on the ages at which these abilities emerge, rather than consider these abilities in combination with emerging vocal skills. This is tantamount to the documentation of phonological achievements in studies of early speech development and how they may contribute to language learning (Baldwin & Tomasello, 1998; Pruden et al., 2006). Often times, it is not until after a child has referential language that vocal behavior and skills such as joint attention are considered together for their communicative potential (termed “verbalizations”—Carpenter et al., 2002; but see Wetherby et al., 1988). Clearly sociocognitive skills play a role in language development, but we stress the need to consider the convergence of prelinguistic vocalizations and emerging sociocognitive skills during development as the beginning of communicative pragmatics. As infants begin to produce directed vocalizations in the context of social referencing, for example, caregiver responsiveness is likely to be influenced by both the phonological quality of the infants’ vocalization in addition to their attentional focus or activity (Rochat & Striano, 1999). A fruitful line of research would be to explore the
significance and effectiveness of “re-engagement vocalizations” and “re-engagement activities” that have been observed in dyadic interactions in which adults adopt a still face (Striano & Rochat, 1999). And, further, researchers should explore how caregiver responsiveness to such vocalizations shape pragmatic development.

The main studies that examine pragmatic development concurrently with vocal development are those of children with sociocommunicative disorders. In these cases, dissociations in the form and function of communicative behavior make the significance of pragmatics apparent. For example, most relevant to our comparative work with songbirds, children with autism spectrum disorder, in particular Asperger’s syndrome, may show deficits in the pragmatics of language although they show few deficits in vocabulary or grammar (e.g., Surian et al., 1996; Tanguay et al., 1998). In fact, high-functioning autistic children develop referential language, i.e. words, before they begin producing protodeclarative gestures, such as pointing or showing to share or direct (although they do produce protoimperative gestures: Baron-Cohen, 1989); thus, they can produce words before becoming communicatively competent, which is the opposite of typically developing children (Carpenter et al., 2002). Also, although apparent later in development, children with attention deficit hyperactivity disorder (ADHD) and Williams syndrome show deficits in pragmatic aspects of language rather than in other areas (Purvis & Tannock, 1997), such as inappropriate initiation of conversation and conversational rapport (Laws & Bishop, 2004). In cases where grammatical or semantic deficits are present, these are likely linked to pragmatic deficits that negatively impact learning (Camarata & Gibson, 1999).

In sum, the “why,” “when,” and “who” of communicative interactions are most impaired in children with social communicative disorders, while the “what” is less impaired. Although there are obviously other significant differences, through a comparative lens, we see a parallel with male cowbirds that lack the ability to sustain attention in social interactions, thus developing potent song but never engaging in successful pragmatics of song production (White et al., 2002b). Therefore, there is compelling evidence in both songbirds and human infants that the linkage between structure and function is not inherent in the system and that pragmatic development needs to be integrated with vocal development.

Mechanisms of Communicative Development

Contingent Stimulation and the Development of Attention

Our research has shown that from the beginning of vocal production, young songbirds produce variable vocalizations, akin to infant “babbling,” and nonvocal, social feedback is bounced back to them, a process termed “behavioral sonar” (King & West, 1988; Skoyles, 1998; West et al., 1990). This process is an extension of “performatory” feedback (Gibson, 1966) because young males can learn what notes to keep and what notes to drop by attending to feedback from females who cannot sing (West & King, 1988). This finding was provocative because prior research had assumed that auditory input and feedback was the necessary and sufficient experiential variable for song development. However, for behavioral sonar to work, males must produce directed song (oriented toward a social partner, in this case the female; see Figure 33.1) rather than undirected song (no song recipient) and attend to the consequences of their singing. The attention span of the singing male delimits the opportunities to receive social feedback that shapes acoustic form and connects form and function. Thus, the songs that receive feedback from females during development are those that elicit copulatory postures from those same females (White et al., 2006).

In the most extensive studies of the social shaping of avian babbling, Smith et al. (2000), West and King (1988), and King et al. (2005) found that the nonsinging female companions of immature male cowbirds provided different forms of nonvocal feedback that influenced the rate of vocal development and phonological quality of male song. Frame-by-frame measurements of male–female

Figure 33.1 Illustration from a single frame of a video recording of a male cowbird directing a song to a female cowbird.
interactions revealed that female wing strokes and gapes are performed in reaction to songs that are directed to females. A wing stroke is a rapid flick of the wing that by definition must occur coincident with song delivery and a gape is rapid opening of the beak accompanied by raising of the head (Figure 32.2A,B). These behaviors led males to repeat the sounds and behaviors that produced social responses from companions and eventually to drop sounds that did not produce reactions. Furthermore, social feedback shaped the attention span of the males, as measured by looking (King et al., 2005) and the length and content of social interactions (King, unpublished data). Directed song, a proxy for attentional focus, predicts the acquisition of articulate and attractive song, as wing strokes and gapes correlated with the earlier onset of stereotyped song and higher song quality as measured by playback (King et al., 2005). Greater social feedback led to a faster rate of development and faster progress toward stable articulation of the phonemic-like structures of their vocalizations. Males producing more directed song have an advantage entering the breeding season: having developed song at a faster rate and having better song repertoires, they court earlier and more successfully (Smith et al., 2000). Thus, proper use of directed song and accompanying attentional skills are a critical pragmatic dimension of communication in cowbirds and should be considered a “prelinguistic” milestone that drives further development.

Different social responses of females also affect neural development. Males housed with more socially interactive females, compared to those housed with less interactive females, had a greater volume and higher number of neurons in one of the visual nuclei located in the thalamus that is thought to process information about form and motion (Freeberg et al., 2002; Hamilton et al., 1998). As males were randomly assigned to conditions, the differences in their repertoires and neural structures must reflect the differential influence of their female companions’ social stimulation. Males learn to read visual signals from females to modify their own vocal signals and they do so on-line while interacting with females. Thus, it is likely that the neural differences between males housed with responsive compared to unresponsive females stem from the demands of males sustaining their attention in cross-modal tasks. Further indication that attention is a significant component of communicative interaction comes from research showing that differential ZENK gene expression is associated with the use of directed but not undirected song (Jarvis et al., 1998). Therefore, the attentional aspect of social interaction is important for communicative development from social, neural, and molecular perspectives. And, we believe, it is this attentional aspect that is the basis of the pragmatic dimension of communication.

Directed vocalizations in infants, just as in cowbirds, are the critical pragmatic dimension of communication between caregivers and infants and provide the opportunity for learning through responding by social partners. Similar to our findings in songbirds, there is an implied behavioral sonar mechanism in infant vocal development. Locke (2001) suggests that vocalizations and other expressive behaviors are part of a developmental system that necessitates that “signals be sent in order for information to be received” (p. 302). Infants produce variable vocal or social behaviors and feedback to these behaviors is “bounced” back to them, providing a potential source of information about the effectiveness of infants’ behaviors, a first step in learning what sounds to produce and how to use them. For example, at around 4 months of age, infants can shift their gaze and exhibit more varied vocalizations. Particular patterns of vocalizing, or
vocalizations occurring concurrently with attentional focus on an object, are initially coincidences rather than being under voluntary control (cf., Collis, 1979). Nonetheless, regardless of the intentionality on the part of the infant to communicate, the vocalizations elicit responses from caregivers (Bates et al., 1975; Locke, 1996). The responses can bootstrap the infant to behaviors that appear more “intentional,” thus connecting form and function, by commenting on or manipulating the object that the infant is vocalizing to (Collis, 1979; Halliday, 1979; Siegel, 1999).

An example of behavioral sonar in infants comes from Lawrence’s 1986 study of 20 mother–infant pairs when the children were 9 months of age. Lawrence (1986) found that different dyads produced different combinations of communicative gestures, tones, or protowords (see also Dore, 1974). These gestures, tones, and protowords are the initial behaviors emitted as “sonar.” The mother’s decisions about which behaviors were communicative led to differential feedback and thus her reactions represent a potential source for vocal shaping (Papousek, 1992). Infants may, therefore, take different developmental pathways and progress at different rates in their communicative skills due to individual variation in early vocal and attentional behaviors and caregiver responses to these behaviors. Such variability has been shown to predict the development of language and coordinated joint attention in the second year (Markus et al., 2000), indicating that infants’ behaviors drive their own development through interaction with the environment as in other domains such as locomotion (Thelen et al., 1996; Thelen & Ulrich, 1991) and as we have seen in cowbirds.

Contingent responses during social interactions provide the mechanism for infant phonological development similar to the social shaping that we discovered in cowbirds (King et al., 2005; West & King, 1988). Specifically, differential feedback from caregivers provided in moment-to-moment social interactions plays a central role in creating developmental pathways. The intonational quality of infant vocalizations, in addition to their acoustic structure, influences how caregivers respond (Beaumont & Bloom, 1993; Bloom et al., 1993; Gros-Louis et al., 2006a; Papousek, 1989). The timing and nature of feedback has now been shown to be important in both vocal and pragmatic development (Goldstein et al., 2003; Goldstein & Schwade, 2008; Gros-Louis & Ables, 2006; Gros-Louis et al., in preparation-b). Goldstein et al. (2003) documented a significant increase in infants’ well-formed, speech-like syllables (“canonical syllables,” Oller, 2000) when mothers provided contingent, nonvocal social feedback (smiles, touches) in response to their infants’ vocalizations. Furthermore, infants continued to increase production of these vocalizations after the period of structured maternal responding. By contrast, infants who received the same amount of noncontingent stimulation did not increase their production of speech-like syllables.

To follow up on Goldstein et al.’s (2003) experimental evidence of social shaping, we examined uninstructed maternal responsiveness during freeplay interactions in 10 mother–infant pairs (Gros-Louis et al., 2006a). Mothers responded to infant vocalizations with more vocal responses than nonvocal, interactive responses, such as making eye contact and smiling or touching the infant. Of these vocal responses, mothers delivered significantly more differentiated feedback to vocalizations that were acoustically more mature. Mothers responded with more imitations and acknowledgements (“oh really?”, “mmm-hmmm”) to phonologically advanced, syllable-like sounds (“bah”) compared to vowel-like sounds (“ah”). Mothers’ differential, contingent feedback may shape the structure of vocalizations, in addition to their usage, as acknowledgments provide a conversation-like framework for vocalizing.

To explore the relationship between contingent stimulation and the development of communicative behaviors, we conducted a longitudinal study of 12 infants over a period of 6 months starting when they were 8 months of age. Infants showed variation in their attentional focus in relation to caregiver responses when they vocalize, similar to males directing songs to females in cowbirds (Gros-Louis et al., in preparation-b). Directed vocalizations included those produced to a parent or a toy (defined by direction of visual gaze), while undirected vocalizations occurred when infants appeared not to be focused on any person or object, such as when looking around the room. Mothers showed variation in how they responded to their infants’ vocalizations, with most offering information about the object of infants’ attentional focus but many also ignoring a fairly large proportion of vocalizations. Mothers whose responses focused on infants’ attentional focus had infants who scored higher on vocal comprehension and gesture on the MacArthur Communicative Development Inventory (Gros-Louis et al., in preparation-b). Similar associations have been found for following
of infants’ attentional focus and language development (Dunham et al., 1993; Rollins, 2003; Tomasello et al., 2001; Tomasello & Farrar, 1986).

We also found suggestive evidence that maternal responsiveness to prelinguistic vocalizations influenced the development of infants’ pragmatic behavior. Infants who received more responses to their vocalizations from their mothers showed a larger relative increase in vocalizations that they directed toward their mothers between 8 and 14 months of age than infants who received fewer responses (Gros-Louis et al., in preparation-b; Figure 32.3). Therefore, infants who received more contingent feedback increased their pragmatic use of vocalizations.

Results from our prelinguistic infant studies suggest a bidirectional influence on communicative development that is embedded in real-time social interactions, just as we have documented in developmental studies of cowbirds. Bidirectional effects of infant–caregiver interactions on development, often termed transactional processes, have been suggested previously (Bruner, 1977, 1983; Papousek & Papousek, 1975; Sameroff, 1975; Vygotsky, 1962), but not at the level of identifying the specific mechanism whereby feedback shapes structural form and pragmatic force. Our research demonstrates that infants learn about the relative effectiveness of different behaviors through social interactions in which they are embedded (cf., Bruner, 1978; Gibb Harding, 1983; Papousek, 2007), suggesting a dynamic process of social shaping, where infants modify their behaviors in keeping with changing feedback from their ecology (e.g., Locke, 1993, 1996). At the heart of the social interactions are the behavioral contingencies that the infant receives to particular behaviors or joint behaviors (vocalizing and attentional focus). It is this contingent feedback that leads the infant to produce behaviors with more specificity in terms of their production, thus resulting in more precise pragmatics in terms of the “when,” “who,” and the “why” of communicative interactions.

**Not Too Much, Not Too Little: the Perfect Level of Contingent Responding**

The finding that socially contingent responding leads to infants producing sounds with more complex phonological features suggests that, as in studies of social, emotional, and cognitive development (Rochat & Striano, 1999; Stern, 2000; Watson, 1985), contingency may play a role in vocal development (see also Locke, 2001; Papousek & Bornstein, 1992). This fact is not surprising given the early sensitivity that infants show to perfect contingency, which later shifts to a preference for imperfect or “social” contingency (Bigelow, 1999; Bigelow & DeCoste, 2003; Gergely & Watson, 1999) and forms the basis for social expectations in interactions with people compared to objects (Ellsworth et al., 1993; Legerstee et al., 1987). Studies indicate that just the right amount of contingent responding is necessary to be effective in driving development (Bigelow & Birch, 1999), a suggestion that is supported with our studies of cowbird and infant vocal development (Gros-Louis et al., in preparation-b; Miller et al., 2008). In particular, variable contingent responding rather than predictable delivery of responses is likely to be more powerful for shaping behavior based on basic mechanisms of operant conditioning (cf., Neuringer et al., 2000).

In cowbirds, females differ substantially in their level of responsiveness, although group trends are reliably present. For example, local females respond more to local than distant song and permit more directed songs to be sung by local males because they remain in close proximity to the singing male (King et al., 2005). Female cowbirds also range considerably in their degree of responsiveness to song playback with some females showing much more choosiness than others (King & West, 1989). The variation in female behavior suggests that the

**Figure 33.3** The relationship between maternal responsiveness and relative change in the proportion of vocalizations that infants directed to their mothers from 8 to 14 months old (n = 11).

A negative change in directed vocalizations indicates a decrease over time. Maternal responsiveness of 0.1 = response to every sixth vocalization; 1 = response to every vocalization.
birds may display different communicative phenotypes, with parallels to different styles of maternal responsiveness in humans (discussed below).

The effect of variable female responsiveness on male vocal development is highlighted in a recent study, with levels of contingent stimulation correlating with improvisation (Miller et al., 2008). Young males were more likely to improvise and develop variable songs when they were housed with adult females who were more discriminating in their interactions, and thus less responsive. By contrast, young males were more likely to copy one another’s song and showed less diversity in their song repertoires when they were housed with juvenile females who interacted indiscriminately and were therefore extremely responsive. Furthermore, when the males were switched between aviaries, they showed a new pattern of vocal development consistent with the responsiveness of the social environment: juvenile males who had been with extremely responsive juvenile females showed a dramatic increase in the number of note clusters that they produced in songs compared to when they were placed with less responsive adult females (Miller et al., 2008; Figure 32.4). Furthermore, the juvenile males now housed with adult females showed an increase in improvisation, likely related to the combinatorial possibilities introduced by the increase in note clusters in their repertoires. Although individual variation in female responsiveness to different song variants exists (White et al., 2006), it cannot account for the results of this study, as the level of interactivity of juvenile females and adult females with juvenile males showed distinct, nonoverlapping distributions (Freed-Brown et al., 2006). Clearly, females cannot be entirely unresponsive, as there would be no feedback available to males when they sing; however, these results indicate that the level of contingent stimulation can be too high. If any and all vocalizations receive feedback, the pattern of contingent stimulation is not informative, thus losing some efficacy in the ability to elicit variable vocal behavior.

The findings of the important role of female feedback in male vocal development are consistent with studies in other songbirds. Generally, there is a relation between variable vocal behavior and variable social contexts, which we propose may be related to the level of predictability of social partners. For example, nomadic sedge wrens show improvisation, whereas marsh wrens who are site faithful do not (Kroodsma & Pickert, 1984). In addition, male zebra finches show different strategies for song learning relative to the group size they are in during development (Liu et al., 2004). And, directly related to our findings, male zebra finches improvise more when they are housed with deafened females compared to hearing females, suggesting that males are sensitive to feedback of female companions (Williams, personal communication). Thus, our research fits with theoretical and experimental studies that have recognized the role of variability in female preferences in the development of male traits and behaviors (Coleman et al., 2004; Jennions & Petrie, 1997). Furthermore, it can be speculated that the prevalence of markings and color patterns in many avian species—wing-bars, eye-rings, stripes on the face—are likely effective in providing contextual information about body posture, head orientation, direction of gaze, etc., which are exactly the sorts of signals that would be useful in providing social feedback.

Similar to the patterns observed in female cowbirds, early during development human mothers sometimes ignore sounds or behaviors altogether because they do not infer communicative intent or simply are not attending closely to their infant. Mothers’ ignoring of signals, like the adult female cowbird’s selective inattention to song, may make infants more aware of what needs to occur for their
behavior to be taken seriously. Thus, infants’ vocal repertoire development and variability may be tied to caregiver responsiveness. At this point, we do not have a clear idea of what proportion of infant acts is treated as communicative and how this varies across individuals. However, results from our longitudinal study of 12 infants indicate wide variation across caregivers. Mothers verbally responded to 17%–83% of their infants’ prelinguistic vocalizations. Similar to the findings in the cowbirds, there is probably a level of contingent stimulation that is ideal. For instance, we know from studies of depressed mothers that too little feedback is detrimental to multiple aspects of communicative development. Depressed mothers may show less affect in their voices, with fewer temporal and intonational patterns of infant-directed speech to which infants attend (Kaplan et al., 2002). These infants are exposed to fewer of the important prosodic cues available in infant-directed speech that are thought to assist language learning (Kemler Nelson et al., 1989) and they experience fewer contingency-based interactions or less appropriately timed responses (Cohn et al., 1986; Field, 1998). As a result, these infants show communicative disorders in the first year of life, exhibiting less optimal interactive patterns and becoming withdrawn (Field et al., 1988; Jones et al., 1997). Furthermore, these infants show differential frontal lobe activation and neurotransmitter levels (Dawson & Ashman, 2000; Jones et al., 1997), which is reminiscent of neural differences in male cowbirds housed with females that differed in their levels of responsiveness. Although we do not have parallel evidence for extremely responsive caregivers, the findings for the extreme example of low levels of responsiveness of depressed mothers indicate that optimal levels of contingent stimulation within social interactions are necessary for communicative development from social and neural perspectives.

Caregivers differ not only in their level, or frequency, of responses, but also in their style of responding. One of the primary characterizations of caregiving styles identified in studies of infant attachment, maternal sensitivity, may be familiar to many readers. Measures of maternal sensitivity bring together a wide variety of maternal characteristics, including maternal warmth and appropriate responding to emotional, attentional, and communicative aspects of infants’ behavior using a numbered scale (Ainsworth et al., 1974, 1978). Here, however, we use terms that focus on one dimension of maternal sensitivity that refer specifically to how caregivers respond to infants’ attentional focus. Caregiver responses range between two extremes, which have been labeled “directive” and “follow-in” (Baldwin et al., 1996; Tomasello & Farrar, 1986). “Directive” behavior involves caregivers attempting to lead or direct infants’ attention away from their current attentional focus (i.e., introducing or commenting on a toy that is not the infant’s current focus). “Follow-in” behavior involves caregivers following in to the infants’ attentional focus (i.e., commenting on or labeling a toy that the infant is currently engaged with). There is experimental and observational evidence that follow-in responses that are sensitive to infant’s attentional focus facilitate vocabulary learning and language development, whereas directive responses that redirect infants’ attention to objects outside of their current focus have a negative impact on language learning (Baldwin & Tomasello, 1998; Baumwell et al., 1997; Tamis-LeMonda et al., 2001; Tomasello & Farrar, 1986).

Recent studies in our laboratory revealed the impact of these different response styles on infants’ prelinguistic attentional and communicative behaviors. The first study explored short-term effects of infants’ interactions with unfamiliar adults who either followed-in to or redirected the infants’ attentional focus (sensitive vs. directive responses). Infants shifted their attentional focus more often in the directive condition than in the sensitive condition not only to toys that the experimenter introduced, but also more frequently to toys that the experimenter had not introduced. Also, in the directive condition infants focused their attention on their social partner or the toy with which they were interacting for shorter amounts of time than in the sensitive condition. This difference in duration of attentional engagement was also apparent when infants were looking away from their social partner or to other toys in the room. Thus, when interactive with the directive individual, infants had shorter attention periods of attentional engagement both during social interaction and outside of the social interaction. The results indicate that the style of social partners’ interaction can shape infants’ attentional engagement, which could have effects not only on communicative development, but also on exploration and information (Miller et al., in press; Figure 32.5).

The second, longitudinal study revealed that over time, such different response styles can impact vocal usage, possibly related to infants not sustaining attention in social interactions. For illustrative
purposes, we provide examples from two mother–infant pairs, representing the two extremes of responsiveness: “follow-in” and “directive.” The infant whose mother displayed the most follow-in behavior at 8 months, responding to her infant’s vocalizations by attending to her attentional focus, increased her percentage of directed vocalizations by 14 months more than the infant whose mother was most directive, leading her infant’s attention away from her current attentional focus. Specifically, the infant of the mother who followed-in more increased vocalizations directed to her mother by 39%, whereas the infant whose mother was directive decreased vocalizations directed to her mother by 63%, thus appearing disengaged in interactions with her mother (Gros-Louis, unpublished data). These data suggest that caregiver responses early in the prelinguistic phase influence the development of communicative behavior, including pragmatics, prior to the advent of language.

Gating Contingent Stimulation

Given that feedback in social interactions lies at the heart of learning about both acoustic structure and pragmatics, West, King, and colleagues have examined the effects of different social environments, particularly the availability of social partners, on development. It was discovered that wide variation in singing behavior of young male cowbirds was dependent on the social contexts in which they were housed (e.g., Smith et al., 2000; White et al., 2002a, 2002b). Young males showed very different outcomes in their singing behavior (including song structure, song usage, repertoire size and rate of development) that varied consistently with the age and sex of individuals housed with them. Different environments resulted in different patterns of social associations and singing interactions, which in turn led to different facultative developmental trajectories of young males in their vocal production and communicative competency (vocal usage) as measured by reproductive success. These results led to consideration of a mechanism termed the “social gateway”: different social environments offer different opportunities for interactions, thus metering the communicative behaviors that individuals produce and the feedback they receive (West et al., 2003; White et al., 2002a). The existence of a social gateway is consistent with the observations in several songbird species that indicate a relationship between social responsiveness of the environment and vocal and social learning. More specifically, access to and interactions with experienced individuals at specific points in development are key to acquiring communicative competence (Beecher, 1996).

We propose that a social gateway provides a useful construct for examining how social interactions between infants and social partners (caregivers, parents, siblings) affect vocal development and vocal usage. We believe that human infants interacting with different social partners in different environments are vulnerable to influences on development, just as we have observed in songbirds. The structure of social interactions serves a “gatekeeping” function, modulating the information available to infants through differential attention and feedback. Future studies in our laboratory aim to document the variability of social contingencies available in interactions with different social partners and how these impact infants’ communicative behavior.

Research that demonstrates that the social gateway is the critical predictor of pragmatic competence bears on the nature–nurture question that often accompanies research in cowbirds. As brood parasites, the young are never raised by their own species but instead by over 200 different species and subspecies, leaving the question of ultimate outcome open: how do they recognize their own species and what if they mistakenly mate with the wrong species? This circumstance has led many theorists to suppose the hardwiring of directed behaviors such as singing to females or males serves as a genetic safety net. What better species to have innate modules than a brood parasite, as relying on
postnatal learning experience to guide development could have disastrous consequences?

Cowbirds were thought to be the model species for a closed developmental program (Lehrman, 1971; Mayr, 1974, 1979), but research by West and King has found precisely the opposite: lack of social experience leads to communicative and reproductive incompetence. Even if isolate birds learn songs that are effective in eliciting copulatory postures of females in playback experiments, there is no endogenous connection between form and function. These same birds cannot successfully mate even if their songs elicit copulatory postures. Thus, given that social experience is necessary to develop proper usage of vocalizations, the safety net is external to the individual, rather than existing in innate developmental programs. The social interactions that an individual experiences during development are the safety net that ensures correct pragmatic function of communicative behavior. It is possible that cowbirds, being brood parasites, are unusual in their reliance on social feedback as juveniles in part because they lack early conspecific experience. Unfortunately, to our knowledge, there is no evidence available from other avian species that confirms the importance of social feedback in shaping the pragmatics of vocal communication because the research has not been done.

Coordinated Communicative Behaviors

Thus far, we have been discussing relatively simple communicative behaviors such as the act of singing or babbling. Can we see the role for pragmatics in more complex behaviors? An example of such a behavior is countersinging (CS) in male cowbirds, i.e., exchanges of directed songs by males (Figure 32.6). CS highlights another dimension of the journalistic frame of questioning as two males must simultaneously make the same decision about to whom and when and where to sing. This behavior can only be studied when males live in flocks, as it requires at least the cooperation of two males and sometimes more. Adult males differ in how much they CS, varying from very frequently to not at all. The data show an underlying pragmatic dimension that differs as a result of early experience with or without adults (White et al., 2002b).

To examine how early interactions shape development, we conducted two studies which revealed that the level of CS can be culturally transmitted, representing an excellent example of a cultural trait that is not genetically controlled, but sustained through learning (White et al., 2007). In the first study, we exposed two groups of juvenile males to adults who had exhibited different levels of male competition via CS in the prior year. In the second study, we gave two new groups of juvenile males either social access to competitive males or only visual and auditory access to them. In addition, the juveniles in the second study were exposed to the competitive males only for a brief period in the fall months when CS is not occurring. In both studies, juvenile males developed behaviors that matched that of their adult “models,” but only if they had social access, that is, housed in the same flock within an aviary. They also exhibited other behavioral differences regarding courtship even though they had no opportunity to witness adult males performing courtship behaviors in either study.

The form of social influence on behavior depicted here for pragmatic forms differs from traditional concepts of cultural transmission where a behavior is directly copied. Because juveniles in the second study learned to CS even when they were with adult males not engaging in CS, it is clear that the juveniles were not merely copying an observed behavior. How had the juvenile males come to exhibit behaviors of “models” whom they did not see perform the target behaviors? We propose that the juveniles had learned to sustain their attention span via social interactions. Learning what to attend to, rather than observation of model behavior, shaped future interactions, resulting in the compounded behavior of CS later in development. Adults’ behavior set the early conditions for the group’s pattern of social engagement (see also White et al., 2002a), which put juveniles on a different developmental pathway.
This study highlights the importance of considering how learning occurs in a social environment. These data tell us that cultural transmission occurs for pragmatic dimensions and that it happens within a group network where individuals may influence one another in nonobvious ways. The importance of the group dynamic must be emphasized. Males needed physical contact, not just visual and acoustic stimulation, in order to learn adult behaviors. This is suggested from further findings in aviary studies: birds in adjacent aviaries, who can see and hear one another, do not share song types, something that occurs routinely within aviaries and in the wild (White et al., 2007). Males appear to need first-hand experience within interactions, receiving reactions to their own behavior rather than just observing other males' interactions. Through particular interactions information becomes accessible. In our words, the bioavailability of information is metered by the social gateway.

A rough parallel to CS in cowbirds is early protoconversation in caregiver–infant interactions. Infants primarily must learn when to respond in interactions, and later in development, they must learn to whom to respond when they start to engage in triadic interactions with multiple social partners or caregivers and objects (Striano & Rochat, 1999). Protoconversations develop in the first 2–3 months of life and involve the exchange of mutual gaze and affect (Bateson, 1975; Trevarthen, 1979). Although protoconversations often focus on socioemotional aspects of interaction, such as affect attunement (e.g., Stern, 2000; Stern et al., 1985), a key component important to our discussion here is the coordinated timing of infants and social partners. The rhythm of vocal exchanges is a key predictor of attachment and cognitive development in the first year (Jaffe et al., 2001) and, we propose, turn-taking within interactions forms the initial pragmatic basis of communication.

As with CS interactions in cowbirds, infants do not learn by observation, but by being an active social partner. It is the structural aspect of early interactions, not their content per se, that contributes to infant learning by modulating infants' attention (Menyuk et al., 1995; Papousek, 2007). In particular, early games and social routines contribute to learning about the pragmatics of conversational exchange, because infants learn turn-taking and turn-giving in social interactions (Bruner, 1979; Mayer & Tronick, 1985; Ratner & Bruner, 1978; Snow, 1984; Watson, 1972). Studies that show that infants become sensitive to the timing of social responses within games such as peekaboo at about 4 months of age (Rochat et al., 1999) indicate that infants are learning about the temporal patterning of social exchanges (see also Ninio & Bruner, 1978). “Communicating about communicating” in these early interactions (Bateson, 1956) thus provides information about the structuring of social exchanges, a first step in learning about the effectiveness of communicative behaviors.

It is after infants learn to sustain attention in interactions that specific feedback between caregivers and infants gives infants feedback about the effectiveness of their own behaviors. “Shared meaning” develops in caregiver–infant dyads, which contributes to learning the significance of particular behaviors (Halliday, 1975; Newson, 1979). Differentiated responses to variable behaviors across contexts can provide the infant with information about the communicative function of behaviors in social interactions (e.g., Gros-Louis et al., in preparation-a). Communication thus shifts from “communication by action to communication by symbol” (Camaioni, 1993, p. 161). What is needed is a study that investigates the contributions to this shift during development. Therefore, in addition to the many studies that investigate the temporal coordination and sequencing of behaviors in infant–caregiver exchanges (e.g., Hsu et al., 2001; Stevenson et al., 1992; Yale et al., 2003), studies must explore the development of pragmatic significance of conversational exchanges (e.g., Dore, 1979).

**Pragmatics and Evolutionary Implications**

In our laboratory, we have looked at evolutionary consequences by studying reproductive outcomes of different developmental trajectories and associated social skills. Parentage analysis of 1071 eggs from ten flocks (32 males and 57 females) documented longitudinal reproductive histories over a 4-year period as birds experienced different social contexts (unfamiliar males and females). We were surprised to discover that dominant males who are characterized by aggressive behavior (e.g., displacements, fights, etc.) sired only 1/4 as many eggs as the most successful males. The dominant males typically sing the most potent songs, a finding we have replicated numerous times. This leaves social pragmatics in the form of song use to distinguish individuals. Thus, traditional measures of song quality or status are misleading in understanding reproductive success because they leave out many pragmatic dimensions. The most successful males
may be more attentive to their potential mates or rivals and know they must integrate their behavior, not dominate another’s behavior.

An example of a critical constructor of successful reproductive behavior is the behavior of staying or leaving when approached by another individual male. Juvenile males tend to leave when adults sing to them whereas adults tend to stay. The juveniles must learn not to leave so that social negotiations such as CS can develop, which is correlated with increased levels of reproductive success (Gros-Louis et al., 2006b; King et al., 2003; West et al., 2002). Juveniles learn the pragmatic aspect of staying versus leaving through interactions with experienced males. For example, in White et al. (2007), direct social experience with competitive adults led juveniles to interact socially more often. Under these conditions, juveniles experienced different learning environments where different types of information were available and different contingencies connected their behaviors. For example, early in the fall when housed with adult males, these juveniles sang to adult males who, in turn, rarely left in response to the juveniles’ songs. As a result, the first significant difference between the two groups of juveniles after adult males were removed from physical or visual and acoustic proximity was in the behavior of leaving to song. Juveniles who had been housed with adult males, and thus had experienced direct contact with adults, learned to respond to song by staying, whereas juveniles who could only observe adults in another aviary, seemed by default to leave to a song directed to them and thus rarely experienced the consequences of singing. In effect, these observer juveniles constructed a condition of self-imposed social isolation. They rarely engaged in male social interactions, rarely showed the development of CS with other males, and in turn developed higher potency song, which is a characteristic of males developing in experimentally imposed male social isolation (West & King, 1980).

Until we discovered the role of pragmatics we were led to conclude, as many researchers do, that males with high-potency songs, as tested by playback, would be the most successful in an aviary setting. Although females are attracted to potent song, only some males can withstand the social pressure that comes with singing such songs, in particular, aggression from other males. Thus, they must learn that what they sing depends on to whom they direct their song and that the conditions for potent song may be rare, whereas the conditions for moderate song sung repeatedly to males and females may take them farther. The story about playback song potency is an example of a de-pragmatized narrative. The result is a good story but an inaccurate one. We initially assumed that playback potency always correlated with copulatory success but we were using the female’s copulatory posture as a proxy for copulation, an assumption we do not now make. One of the biggest lessons is that males with good songs as judged by playback may not use their song in an effective manner. Males have to learn song content but this learning is inadequate without understanding the social conditions in which to sing it.

Similar to our identification of cultural transmission in cowbirds that differs from the traditional view, Tomasello (2001) has indicated a similar process in language development in infants that he terms cultural learning (see also Trevarthen, 1988). Though he focuses on learning within an individual, he points out implications for evolutionary origins of communicative behavior. The parallel with the mechanism that we identified in the development of CS behavior is that children do not learn by directly emulating behaviors of caregivers or attending to specific associations that are made clear to them by their caregivers; rather, they learn through ongoing interactions with their caregivers. For example, most of the words learned by children do not come from direct attentional focus and labeling by a caregiver. In fact, this could only work for concrete nouns and some action verbs. Therefore, it is through social conventions and being a participant in an interaction that infants can learn the meaning of words by attending to nonverbal and paralinguistic cues (Tomasello & Barton, 1994; Tomasello et al., 1996). And, most importantly, similar to what we have concluded from our research on cowbirds, children inherit ontogenetic niches that bring with them patterns of interactions and contexts of learning that ensure cultural transmission.

**Conclusion**

Our research with both human infants and songbirds provides us with a comparative framework from which to examine communicative development. Songbirds provide a good parallel to infants because of similar developmental stages, and social and neural influences (Doupe & Kuhl, 1999; Kuhl, 2003). Until recently, the conspicuous period of production termed “babbling” in both systems had been considered to be motor practice for the goal of stereotyped song repertoires or speech
with limited or no social/communicative function (Bloom, 1993; but see Locke, 2001 where a “relational” function of babbling is proposed; Oller, 2000). However, our experience with vocal development in birds and infants demonstrate a strong social interactive component of early vocal interactions that influences communicative development (Goldstein et al., 2003; King & West, 1988).

Both animal studies and human communicative pathologies indicate that different mappings between vocal and pragmatic development can occur (Locke, 1993). Vocal learning (of birdsong or referential language) can progress without correct usage of vocal forms in social interactions. The emergence of directed attention while producing vocalizations provides a platform for pragmatic learning in both human and avian communicative development (Miller et al., 2006). We believe that the emphasis on the innate basis of vocal development, and the focus on the role of copying signals, has obscured the importance of pragmatic development. For example, although most of the focus in bird song learning is on imitation, improvisation is also a documented route, and one used by cowbirds. Improvisation occurs not only with song content, but song use. Thus, in the studies of CS, the young birds exposed to adults in the fall could not copy appropriate adult courtship behavior because they never saw it. But those with social contact ended up pragmatically competent because their social development created a pathway toward knowing how to respond to song, i.e., by staying and responding to social partners.

In both birds and babies, the use of copied versus improvised vocalizations coupled with directedness creates different learning opportunities. Specifically the use of directed improvised vocalizations may accelerate learning the relationship between vocal structure and its function because it provides varied contingent feedback to a range of vocalizations. Preliminary data support this view in cowbirds: in two flocks where we have followed juvenile males that were high or low improvisers, the high improvisers sang more directed song to males and females during the fall than the low improvisers and 6 months later were more successful courting females during their first breeding season (Miller, unpublished data). Thus, to return to the theme of the journalistic practice or reporting “who,” followed by “what,” “when,” and “where,” progressing to “why” and ending with “how,” we propose that vocal improvisation may represent an important engine of pragmatic learning, which informs about these issues. Because vocal development in nonmimicking birds is rooted in copying (Beecher, 1996; Nordby, Campbell, & Beecher, 2007), improvisation is often treated as copying errors and thus obscures the possibility of programmatic adaptive learning.

With respect to human vocal development, contrary to early views that imitation is the primary mechanism of development, it is through contingent stimulation in interactions that communicative behavior develops. Starting in the 1970s, researchers began to recognize the potential extent of the relationship between vocalizations used in social exchanges and the development of language (e.g., Bates et al., 1979; Bruner, 1977). It is the basic functional understanding of early prelinguistic communicative behaviors that is thought to provide the sociocognitive structures necessary for the development of language. An important point in prelinguistic infants and nonlinguistic species is that it is through the responses of social partners that behaviors are shaped and acquire functionality (Dore, 1979; Halliday, 1975). There need not be intentional on the part of a young organism to communicate but, through interactions, functional communication emerges (Cheney & Seyfarth, 1996; Smith, 1977; Sugarman, 1984). For example, as noted previously, infants will begin to disengage their gaze and look around the room at about 4 months of age. Caregivers view this as intentional or communicative and respond accordingly, providing feedback to the infant about the function of gazing (cf., Siegel, 1999). Thus, throughout development, infants’ production of novel vocalizations or actions provides new opportunities for caregivers to respond and to respond differentially, thus potentially providing potent feedback about the effectiveness of infants’ behaviors (Papousek, 1992; Snow, 1984).

The overarching purpose of our comparative research program is to discover principles of development through the investigation of the ontogeny of experience. We define the ontogeny of experience as the process by which an organism progressively creates and selects stimulation from a rich ecology. We believe that by maximizing the extent to which the organism can select information from its ecology, the opportunity to uncover common denominators of developmental systems becomes apparent. For example, understanding the role for attentional development to filter stimulation will be predictive of both social and cognitive outcomes across taxa. Our studies of the cowbird
demonstrate the limitations of a reliance on innate modules to predict functional outcomes and suggest the even supposedly “closed” developmental systems are inherently sensitive to developmental ecology. The avian work has been predictive of our human prelinguistic work, as similar processes appear to be functioning. Thus, the evidence suggests that developmental explanations of communicative behavior will rely on an understanding of the recurring opportunities for social experience, and the role of contingency-based learning within interactions, to understand the role of the developmental ecology to shape functional outcomes.

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