

(Zahavi, 1977; 1987), and little or no selection pressure on singers to use countermeasures to ranging exists. Indeed, selection has favored singers who use the ranging (assessment) ability of listeners against them: they threaten by producing songs rangeable to everyone in the population (Morton, 1986). These songbirds use song in the same manner that non-learning nonoscine passerines do. It is not accidental that dialect-songbirds share the same stable or tropical climates which host most of the nonlearning nonoscine species (Morton, 1986).

The ranging hypothesis offers an explanation for many, often disparate, functions of birdsong as well as the general trends already discussed. Playback experiments have supported several earlier predictions (Morton, 1986). For example, in addition to oscines, which are generally small species, evolutionary arms races should also produce song learning in other small-bodied, nonoscine taxa. This was confirmed for a hummingbird (*Calypte anna*) (Mirsky, 1976; Baptista & Schuchmann, 1990), which is energy limited (Stiles, 1971). The presence of song dialects in lekking hermit hummingbirds (e.g., *Phaethornis longuemareus*, *P. superciliosus*) suggests that song learning may be widespread in hummingbirds (Snow, 1968). Ranging has recently been shown in a nonoscine passerine, the dusky antbird (*Cercomacra tyrannina*), supporting the prediction that ranging evolved before song learning did in the passerines (Morton & Derrickson, 1996).

4

Mechanisms and proximate processes of vocal communication

This chapter is not divided as Chapter 2 is, into separate sections on assessment and management. Instead, it considers the integrated proximate functioning of these two processes, discussing the contributions of perception, cognition, motivation, and emotion to the interacting operation of assessment and management both within and between individuals. These multileveled interactions are most clearly highlighted in the last section of this chapter, in which the development of communicative abilities is explored. The adoption of an A/M approach has provided a framework for dealing with the dynamics of social interaction.

The material here may seem a bit off the point for those readers expecting a treatment dealing exclusively with vocal communication. Time is spent exploring broader issues, of how perception, cognition, motivation, and emotion work in general, not just during communication, and of how interactions between individuals not only result from management and assessment, but also influence those two processes. This latter point, that the dynamics of interaction among individuals is the arena of communication, is convergent with the same consistent theme in the writings of John Smith (1997), even though its source lies in a very different, noninformational starting point from Smith's. We share with Smith this message: if we are to continue progressing in our understanding of communication, we must return systematic descriptive research on the broader contexts of communicative behavior to its former high-priority position. With this theme, we ally ourselves once more with Tinbergen (1963), whose seminal paper on the aims and methods of ethology featured not only sections on his four questions, but also an initial section entitled 'Observation and Description.'

4.1 Perception

We all know that the fundamental function of perceptual systems is to support the actual pickup of cues. Without auditory systems, animals could not use acoustic cues because they could not detect sound. But the role of auditory systems is more subtle than that. As discussed briefly in Chapter 2, perceptual systems are designed, through both selection and proximate effects of interactions with the environment, to be selectively attuned to those features of the environment most important to the regulatory problems faced by individuals. So, we can use the response properties of auditory systems as clues to which features of vocalizations are the salient ones. Conversely, we can use the features of vocalizations as guides in our exploration of the tuning properties of the auditory system. Attunement of hearing to vocal systems has been discovered at multiple levels in vertebrate auditory systems, from the ear to central brain structures, and at multiple levels of complexity in sound structure.

The *audiogram* provides an example of tuning in part from a peripheral structure in the auditory system, the ear, and a simple feature of sound, its frequency. The audiogram is a measure of the auditory sensitivity of an individual to each of a range of sound frequencies. Audiograms typically reveal frequency tuning, that is, sensitivity peaks at one or more sound frequencies (Fig. 4.1). Correspondences have been discovered between these sensitivity peaks and the dominant frequencies of such important sounds as the vocalizations of conspecifics. The responses of female green treefrogs to male courtship calls illustrate selective sensitivity founded in part on the audiogram (Gerhardt, 1987). The inner ear of frogs has two separate receptor organs: the amphibian papilla, which is tuned to sound frequencies of 0.7–1.2 kHz in green treefrogs, and the basilar papilla, which is tuned to 3.0–3.6 kHz in green treefrogs. These peaks correspond approximately to the spectral peaks in the calls of average-size males. Females show a preference for those sounds that most stimulate their auditory systems, and the tuning of the inner-ear organs appears to play a role in mediating the selectivity of females' responses to male calls. The results of playback studies have been complex; nevertheless, when females have exhibited a frequency-related response, they have preferentially approached sounds with frequency characteristics that match the tuning of their ears. Such selectivity in the auditory system may be one mechanism whereby females avoid sexual approaches to males of the wrong species.

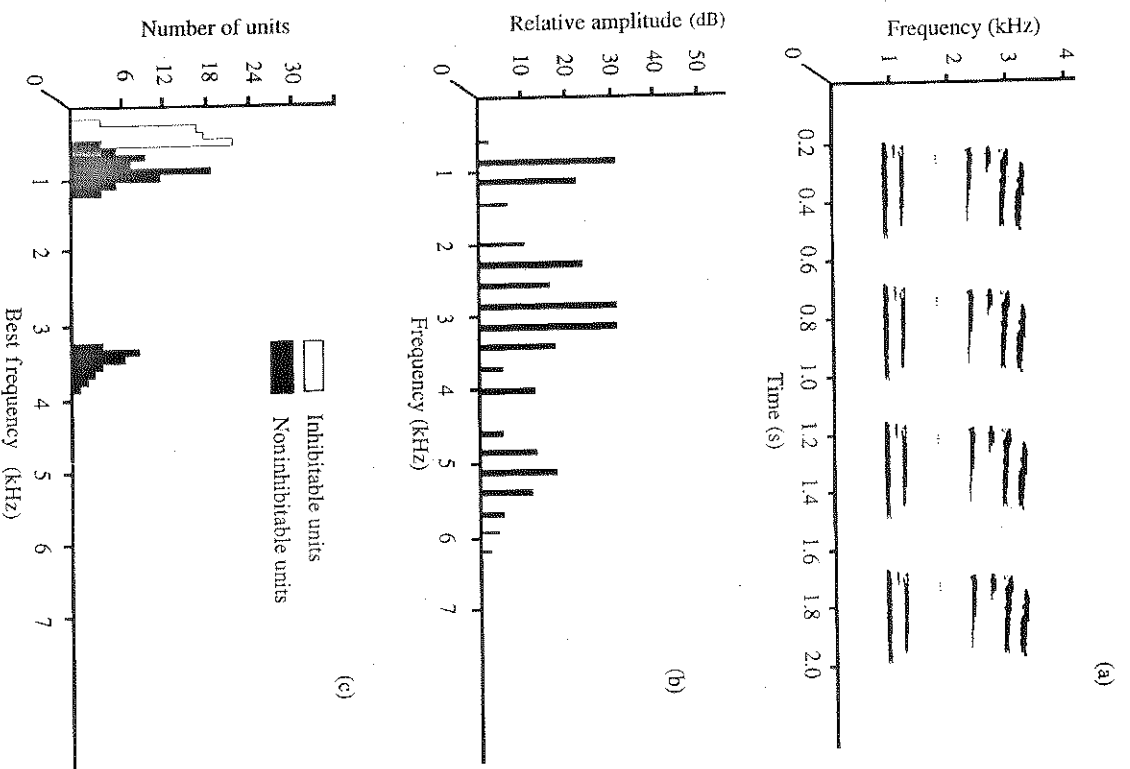


Fig. 4.1. An example of a match between the spectral structure of the calls of male green tree frogs and the spectral sensitivity of the auditory system of the target of these calls. (a) Four consecutive calls by a male. Note the concentration of the two clusters of call components around 1 and 3 kHz in the frequency spectrum. (b) This graph confirms the concentration of acoustic energy in two clusters around 1 and 3 kHz, respectively (as well as a third cluster around 5 kHz). (c) The selectiveness responsiveness of the green tree frog auditory system. The (noninhibitable) auditory neurons are most responsive to sound frequencies in the vicinity of 1 and 3 kHz. (Drawing (a) courtesy of Carl Gerhardt; (b) and (c) courtesy of Robert Capranica.)

Auditory systems may also be attuned to more complex patterns of acoustic stimulation. For example, male swamp sparrows and song sparrows differ in the complexity of the songs that they sing, and exhibit corresponding contrasts in their innate bases for distinguishing each other's songs (Marler & Peters, 1989). The songs of these species are structured hierarchically, consisting of *notes*, which are organized into *syllables*, that are assembled into *phrases*, which in turn constitute the *song* (Fig. 4.2). As can be seen from Figure 4.2, swamp sparrows sing relatively simple songs, consisting of a single phrase in which the same syllable is repeated. In contrast, song sparrows typically sing four-phrase songs, starting with a *trill*, a type of phrase that is alternated with *note-complex* phrases. As discussed in Chapters 1 and 3, all songbirds studied to date need to hear conspecific song in order to develop normal song themselves. As young swamp sparrows undergo the early perceptual-learning part of this process, they distinguish swamp sparrow song from that of song sparrows on the basis of syllable structure. Song sparrows at the same developmental stage, on the other hand, recognize conspecific song on the basis of the segmentation of the song into phrases. If swamp sparrow syllables are embedded in such songs, for example, they will be learned by the developing song sparrows.

We must not forget, of course, that auditory systems are used in many other contexts besides vocal communication, and that these other acoustic contexts also may have shaped the properties of these auditory systems through development, and natural and sexual selection. So, there are limits to the extent to which we can expect to find tight links between the response properties of auditory systems of a species and the structure of their vocal signals. For this reason, studies of an auditory system should explore its responsiveness to a broad area of acoustic space. Such research has provided not only a more complete understanding of perceptual systems, but also a bridge between the study of proximate and ultimate processes (Ryan, 1994).

The phenomenon of 'supernormal' stimuli illustrates how such proximate-ultimate bridging can be accomplished. Ethologists discovered long ago that stimulus objects that extend well above the normal range of variation in quantitative dimensions such as size can be unusually effective in evoking reactions (Tinbergen, 1951). Perhaps the most commonly encountered cases of supernormal stimuli in the literature involve preferences by birds for incubating very large eggs. Herring gulls, for example, look incongruous attempting to incubate a model of an egg as large as 20 times normal size (nearly their own body size!) and ignoring

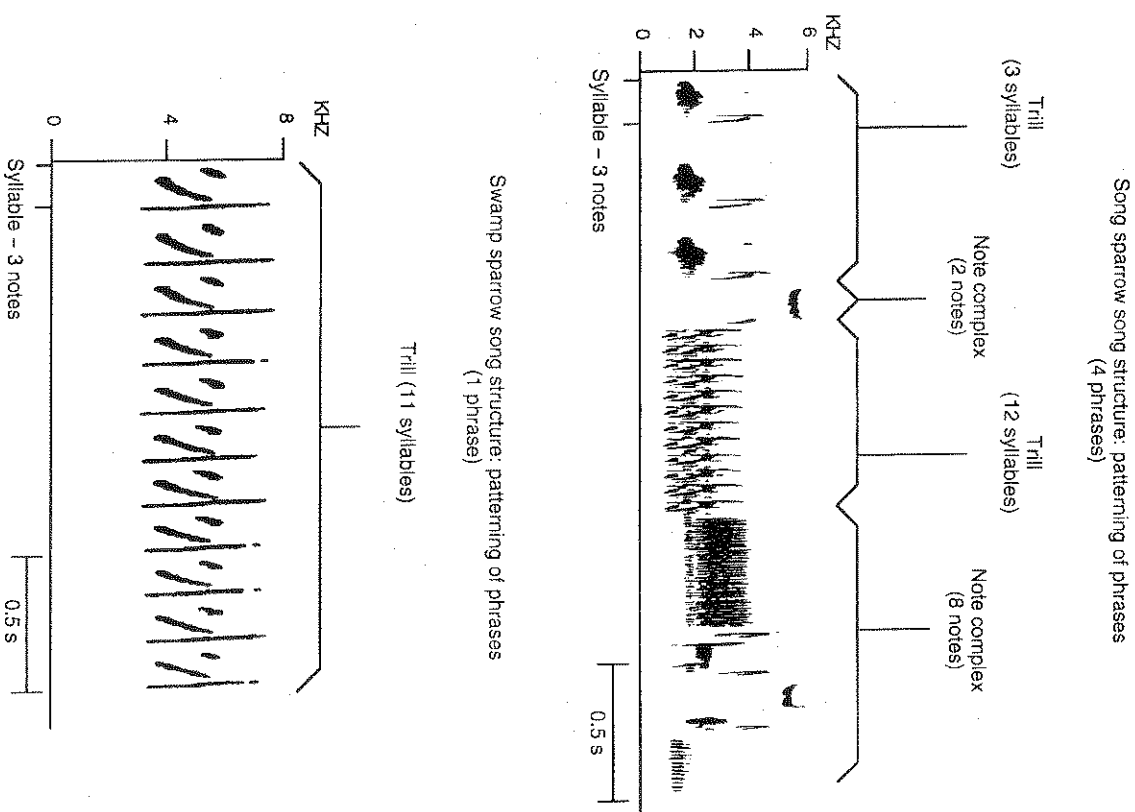


Fig. 4.2. Differences between song sparrows and swamp sparrows in the complexity of their songs. Song sparrows exhibit four organizational levels in their songs: notes, syllables (a set of notes), phrases (a set of syllables), and the song (a set of phrases). The songs of swamp sparrows involve only two levels, one phrase consisting of a string of similar notes. (Courtesy of Peter Marler.)

the model of normal size right beside it (Tinbergen, 1965, pp. 78–9). It is not clear why perceptual systems are so commonly hypersensitive to hyperstimuli, but this trait, whatever its origins, may be a source of selection on signals, shaping natural features of animals into exaggerated versions of themselves through a process of selection for signal value. For example, a number of species of cuckoos exploit other avian species by laying their eggs in the nests of those other species, thereby inducing them to care for cuckoo offspring. The eggs of these brood-parasitic cuckoos are accepted by their hosts in part because they have evolved to mimic the colour patterns of the host eggs. But, the cuckoo eggs are also usually larger than the host eggs, perhaps reflecting adaptation to act as supernormal evokers of incubation behavior, providing the parasitic eggs with an edge over the host's own eggs (Wickler, 1968). Supernormal responsiveness to exaggerated stimuli also appears common in the acoustic domain. For example, more than 150 studies have demonstrated female preferences for extreme values of optical and acoustic male traits important as cues in mate choice (Ryan & Keddy, 1992). Where such preferences exist, the overwhelming majority are for values above rather than below the mean. Females prefer more – more intense, more complex, and longer calls and songs, as well as vocalizations delivered at greater repetition rates. Perhaps these properties of female perceptual systems have been sources of sexual selection on the calls of males, favoring the evolution of extreme signals for use in courtship. It is only through detailed studies of such mechanisms that we can come to a more complete understanding of why evolutionary changes take the directions they do.

An A/M approach directs our attention to a set of cues that is more complex yet – feedback, or relations between output and input. We have already encountered the phenomenon of feedback. The ground squirrel in the Prologue, for example, assessed the level of risk she faced from the intruding rattlesnake by inducing it to rattle. She used the structure of the rattling sound to judge the snake's size and body temperature, two major determinants of the snake's threat to squirrels (see Fig. 2.11).

Such relational cues have traditionally not been available to the subjects of playback studies, the most popular type of experimental procedure in research on vocal communication (see Box 1.1; McGregor, 1992). As already mentioned, in a typical playback study, an audio tape is made of one or more vocalizations, and this tape is played to the subject irrespective of how it responds. As noted in Chapter 1, portable computers have made it possible to use interactive playback procedures, in which the choice of playback sounds varies, depending on how the subject is

responding. If relational cues are important, this should be revealed in different effects of traditional and interactive playback methods.

Work with European blackbirds supports the above prediction (Dabelsteen & Pedersen, 1990). Males of this species produce three structurally different types of songs – low intensity (LI), high intensity (HI), and strangled song (SS) – which are associated with low, medium and high probabilities of attack, respectively, on the part of the singer. When two males engage in a singing duel, they often adjust their singing to the behavior of each other in quite precise ways. Do such contingent adjustments make a difference? They can. The responses of males to song playbacks were compared under three conditions: (1) interactive shifts in song type, in which playbacks began with LI, were switched to HI if the target bird responded, and were escalated to SS if the subject approached the playback speaker to within 10 m; (2) noninteractive changes in song type irrespective of subject response; and (3) no change in played-back song type. Under all conditions, LI released the weakest aggressive responses, and HI and SS the strongest. But, HI and SS were distinguished only under the interactive conditions. So, the occurrence of feedback attunes interactants more precisely to the details of the other's behavior, perhaps making management more effective. It is in such interactive forms of perception that we see most clearly the links between assessment and management.

The effects of feedback on vocal communication have been studied systematically, most often in developmental time frames (e.g., Clayton, 1994). Nevertheless, many playback studies of animal vocalizations demonstrate the reality of immediate social feedback to vocalizing animals (e.g., McGregor, 1992): playbacks are used in studies of vocal communication *because* they have immediate social consequences. For example, male white-crowned sparrows respond to the playback of conspecific song by approaching the speaker, flying aggressively at it, and countersinging, even when they are only a few months old (DeWolfe, Baptista & Petrinovich, 1989). And, singing by these youngsters has the potential to evoke attacks by adult males. The developmental effects of such feedback are discussed later in this chapter.

Do animals adjust their communicative behavior to such consequences in more immediate time frames? Natural observations certainly make it appear so. The responses of other males to singing by young white-crowned sparrows typically is associated with a counterresponse by the young singer. But, do systematic experiments support this evidence? The data are not plentiful, but they indicate that immediate adjustments do

occur. Among songbirds, chaffinches (Stevenson, 1967) and zebra finches (ten Cate, 1991; Adret, 1993) treat the playback of conspecific song as rewarding; in laboratory experiments, they perform activities such as key pecking and landing on a perch more frequently when these activities are followed by song playback.

The idea of feedback sensitivity suggests a literature to consult for guidance in exploring the features of perceptual mechanisms in vocal communication; auditory mechanisms of echolocation are of necessity sensitive to feedback (Neuweiler, 1990). Indeed, from an A/M perspective, echolocation and vocal communication bear some striking resemblances (West & King, 1990; Tyack, 1997). In both cases a major source of assessment cues arises from attention to feedback from emitted sounds. In echolocation, the feedback is from the echo of the emitted sound. In vocal communication, the feedback is from the reactions of other individuals to the vocalization.

Can the literature on echolocation suggest design features to seek in vocal communication perceptual systems? Perhaps. For example, one of the problems faced in echolocation is interference between the auditory effects of the high-intensity emitted vocalization and the low-intensity echo; the effects of the emitted sound have the potential to mask detection of the echo (Neuweiler, 1990). The results of electrophysiological studies of auditory neurons in horseshoe bats are consistent with this expectation: neuronal response to a tone can be suppressed by a second tone. The evolutionary importance of such interference is suggested by the presence of adaptations in this auditory system that may function to reduce interference. A major frequency component of the returning echo for this species falls in the band 81–88 KHz. Neurons tuned to this band actually become *more* sensitive in the immediate aftermath of stimulation by the sound frequencies of a typical echolocation call (which are somewhat lower than the echo because of Doppler shift effects).

What sorts of implications do such findings have for vocal communication? When vocalizers are close, and especially when they also produce high-intensity calls, we might expect to find that animals avoid auditory interference by using some alternative to immediate acoustic feedback. Canary-winged parakeets may illustrate this point (Arrowood, 1988). Pair-bonded male–female couples sing antiphonal duets in which the male and female contribute alternating notes; these notes are produced so rapidly and coordinated with the mate's so precisely that they sound like a single, very loud, individual singing (Fig. 4.3). The precision of male–female vocal coordination is indicated by the fact that a pair may

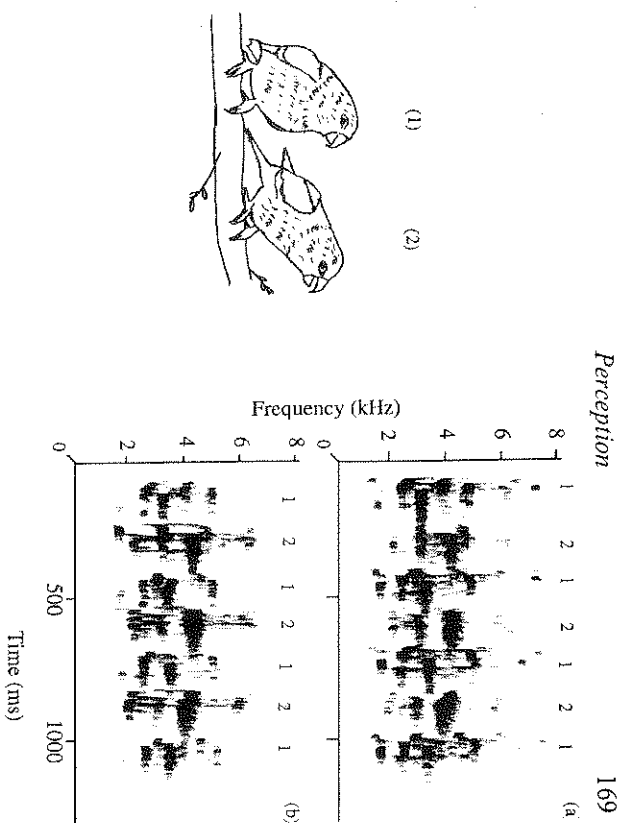


Fig. 4.3. Duetting canary-winged parakeets. The spectrograms show how easily this coordinated duet could be mistaken for the song of a single bird. The male has produced the notes numbered 1, the female has emitted those numbered 2. The two members of the pair are contributing alternating notes to the duet, in a tightly coordinated way. (a) For this recording, the microphone was closer to bird 1, the male, whose notes are consequently more pronounced than those of bird 2. (b) A recording of the same duet, but through a microphone closer to bird 2, the female, whose notes are therefore more pronounced. (Spectrograms and photograph of parakeets courtesy of Patricia Arrowood.)

produce notes at a pace of five to six per second, with neither overlap nor silent gaps between consecutive notes. They often stand within a few centimeters of each other while duetting, even touching at times, with their beaks 1–2 cm apart, and may even be confronting another loudly duetting pair. So, the potential for auditory interference would seem to be high. Consequently, an individual might not be able to time each note by responding to the mate's preceding note. Do they cue each other visually? Perhaps, but not always; sometimes they interrupt mutual allopreening to duet, keeping their heads buried in each other's plumage while singing (Arrowood, personal communication), leaving open only the option of tactile cueing. In addition, they often duet while confronting another pair, where the need to focus on the rival pair might limit visual attention to the mate. So, the coordination may actually be mediated auditorily, but perhaps not on a note-to-note basis, in which auditory interference would be most serious.

There is anecdotal evidence that the members of a pair of canary-winged parakeets may stay coordinated through a process of entrainment (see Section 2.3.2), in which each individual's notes are rhythmically driven by neural oscillators that are activated half a cycle out of phase with each other. Sometimes, for example, an individual produces a few notes in the absence of the partner, because the partner either started singing late or finished early. In those situations, the solitary singer may produce notes rhythmically, leaving silent spaces where the mate would have normally chimed in (Arrowood, personal communication). This persistence of rhythmicity without the partner may be loosely analogous to the persistence of circadian rhythmicity in the absence of the usual environmental entraining cycle. Many species of calling insects and amphibians, such as crickets and frogs, use this entrainment method to adjust their rhythmic calling to that of a vocalizing conspecific (Greenfield, 1994).

However, the parakeets do pick up on some relatively immediate cues; for example, they regularly make coordinated switches between duet types. So, there is some form of on-line monitoring, perhaps of one another's duet types. But, we must not slip into the trap of assuming that all or even most feedback to a vocalizing individual is acoustic. Canary-winged parakeets, for example, may also use visual or tactile cues as a way of coordinating their changes in duet types. Similarly, white-crowned sparrows, described above, not only countering to the song of a conspecific, but also approach, loom aggressively, and even attack the source of the song (DeWolfe *et al.*, 1989). Attending only to the acoustic dimension of interacting has the potential to 'de-contextualize' communication, deflecting our attention from major sources of insight into communicative behavior (West & King, 1996).

4.2 Motivation

Motivation stands in a two-way causal relationship with perception. The cues picked up by perceptual systems play a role in setting the individual's motivational state. Animals, for example, are often quite prepared to give up feeding to seek refuge when the antipredator calls of conspecifics ring out. At the same time, the motivational state of the individual establishes a context for assessment, focusing the individual's attention on some cues, for example, and deflecting attention from others. So, for example, the extent to which antipredator calls can disrupt an individual's feeding will depend on the implications of the threat of predation.

Female California ground squirrels with vulnerable young respond more strongly to playbacks of antipredator calls, with greater disruptions of feeding and other activities, than adult females without pups (Leger & Owings, 1978).

Motivational systems set the broad regulatory themes of an individual's behavior. As discussed in Chapter 2, these themes are the general life tasks that individuals face – acquiring food, reproducing, avoiding attack by predators and parasites, maintaining social status, and so forth. These broadly defined goals only loosely specify the content of lower levels of behavioral organization, that is, the more specific matters represented in the mode, module, and action levels of behavior systems discussed in Chapter 2 (see Fig. 2.10). When an individual evaluates an event in terms of content, it is judging the relevance of the event not only to major life themes (e.g., avoiding predation) but also to subthemes, modes, and modules (e.g., What exactly should I do about this snake?).

The above levels correspond to what has been called the motive aspect of motivation (Beer, 1982), in the sense of an individual's motives, the specifications in currently active managerial systems about preferred states of affairs. This can be contrasted with the motor aspect of motivation (Beer, 1982), which is most strongly linked to the importance dimension of evaluation, mentioned in the discussion of emotions below. Rather than dealing with content, motor refers to how strongly an individual's behavior is 'turned on,' e.g., how vigorously impelled it is to eat, mate, fight, etc. To speak of such matters in terms of importance, one would ask how much of an individual's time, energy, risk, and attentional budgets the activity can monopolize, e.g., how much injury it will risk in order to engage in the activity.

There is evidence that the motor and motive aspects of motivation affect different dimensions of vocal behavior. For example, both cotton-top tamarins (a small New World primate) and domestic chickens (Fig. 4.4) use specific calls in the presence of food, a particular motive context (Marler *et al.*, 1986; Elowson, Tannenbaum & Snowdon, 1991). Both also vary their rate of calling as a positive function of their motivation to feed (motor aspect), either in the presence of food of varying palatability, or as they vary in level of satiation. Less-sated animals, or animals in the presence of highly preferred food items, call at higher rates. It is of interest that these animals shift the rate of calling but not the type of call that is emitted as their level of motivation varies (Evans, 1997). The type of call seems pretty tightly linked to the motive context of presence or prospects of food, a feature that has led to the conclusion

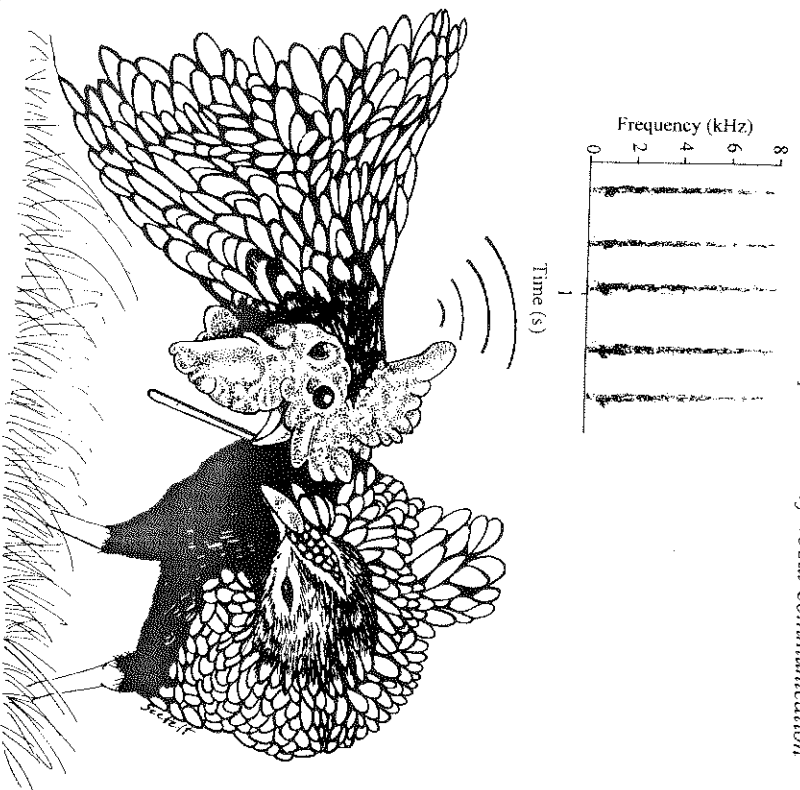


Fig. 4.4. A male domestic chicken attracting a female to court her by holding a piece of straw in his beak and food calling. (Spectrogram courtesy of Chris Evans; photograph from Peter Marler.)

by some that these calls convey information specifically about food. This topic is discussed under the heading of referential communication in the section on cognition below.

When we speak of an individual's motivational state, we are asking which theme(s) has priority, and how important the individual considers the theme to be. Motivational states are most clearly relevant to management because they deal with what an individual is attempting to accomplish, and how hard it is trying, but they are also relevant to assessment because they focus an individual's attention on the features of the environment most relevant to its current efforts. Cosmides and Tooby (1995) have explained why motivational mechanisms should have this attention-focusing effect. These mechanisms are shaped by selection for their potential to contribute to inclusive fitness. But, the connexions between the proximate details of behaving and inclusive fitness are quite complex

and indirect (Thompson, 1986). The fitness consequences of behaving are not immediate enough to guide behavioral decisions, so attentional mechanisms cannot be focused there. And, the consequences that are most relevant depend on the task at hand. The cues for 'moving in the right direction' in a task for acquiring a mate, for example, are often quite distinct from those for deterring a rattlesnake or coyote. So, attention needs to be redirected when motivation changes. From the perspective of communication, this means that the signal that is most salient depends on the individual's motivational state. When an individual is hungry, food-associated signals may be most apparent; when sexually motivated, sex-associated signals may be more salient, and so forth. Remember from Chapter 2, for example, that female laboratory rats are more responsive to the vocalizations of pups when they have been induced into a parenting state by parturition and care of young, than when they have not recently had that experience (see Section 2.3.1).

Is there additional evidence that an individual's response to vocalizations depends on its motivational state? Yes. Parenting often involves responding to cues more indirectly relevant to offspring, such as the acoustic signals of predators (Swaigood, 1994). As described in the Prologue and Chapter 2, rattlesnakes are an important source of predation on California ground squirrel pups, but not on adults. Adults confront these snakes, and maternal females spend more time in this activity than nonmaternal females and males, neither of whom contribute much to the care of pups. Rattlesnake confrontation by adults can be aggressive enough to induce the snake to rattle at the squirrel, and this sound incidentally includes cues about the degree of risk that the confronting squirrel faces. In playbacks of rattling sounds, maternal females respond more strongly, and differentiate more finely among these acoustic risk cues, than nonmaternal females and males (Fig. 4.5).

4.2.1 'Intentional' signaling

Exploring the motive aspects of motivation provides insights relevant to a recently visible issue in the study of animal communication: the interest generated by game theory in the extent to which animals signal their 'intentions' (e.g., Hauser & Nelson, 1991). This issue was touched upon in Chapter 2, noting that from a game-theoretic approach, intention is more a statistical than a cognitive concept. That is, signals about intentions are defined simply as signals that are statistically predictive of the signaler's subsequent behavior; no higher-order cognitive abilities are

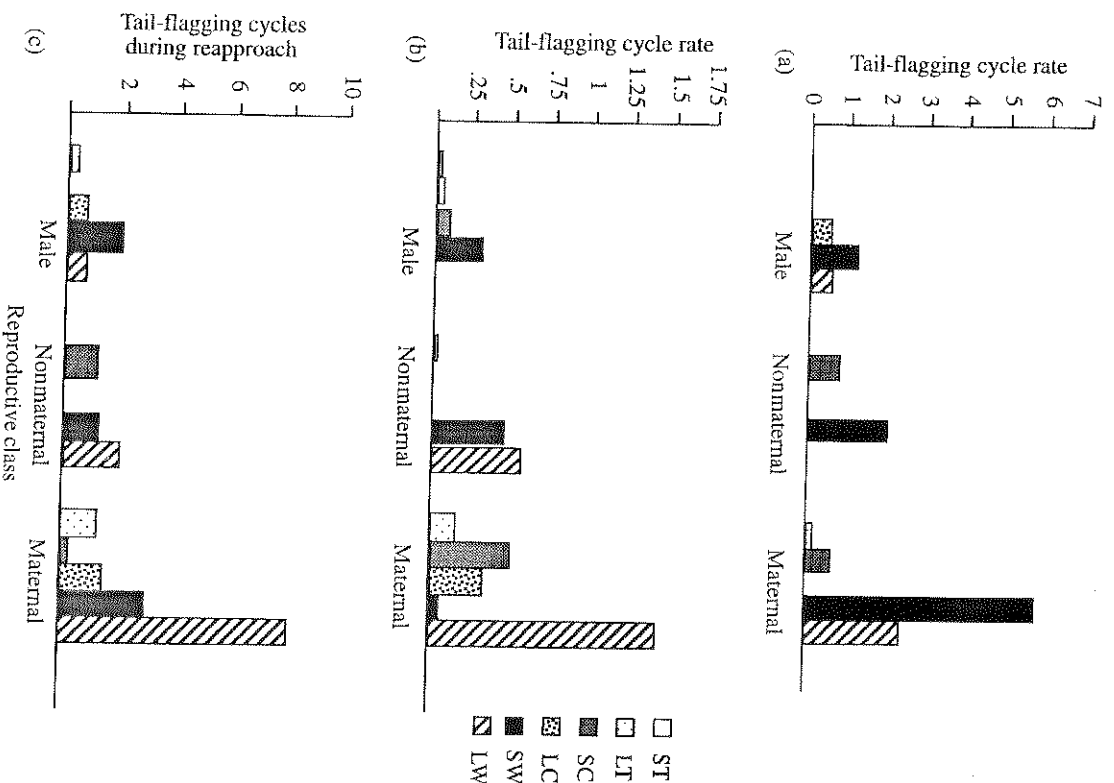


Fig. 4.5. Maternal female California ground squirrels (those with young pups) are much more responsive and risk sensitive in their reactions to playbacks of the rattling sounds of rattlesnakes than adult males and nonmaternal females are. For snakes and large versus small snakes were significant for all three measures (a-c). None of these six comparisons was significant for males, and only two of the six were significant for nonmaternal females. (a) The number of cycles of tail

implied. Therefore, they might more appropriately be labeled as predictive signals (Hauser & Nelson, 1991). As noted in Chapter 2, the discovery of such signals has been viewed as inconsistent with game-theoretic predictions that such signals should not be evolutionarily stable. However, an A/M approach led us to conclude, at least in the case of graded agonistic signals, that these are not signals of intent at all; they are graded probes, used to judge at minimal risk how much of the adversary's fighting capacity it is prepared to commit to the current encounter. The goal here is to extend the examination of the game-theoretic literature on agonistic signals, following the A/M prescription that insights about evolutionary processes can be gained from examining proximate processes. Our treatment is convergent with Hamilton and McNurt's critique of game-theoretic approaches (1997).

The prediction that signals of intent would not be favored by selection can be understood better if it is compared with game-theoretic predictions about what agonistic signals *should* be about. Agonistic signals are constrained by active assessment to correlate with the true fighting ability, or the resource-holding power (RHP; Parker, 1974), of the signaling individual. The rationale for this prediction is as follows. The most commonly used index of RHP is body size, and this is a characteristic that may be difficult to exaggerate. In contrast, 'honest' signaling about intentions should never be evolutionarily stable because honest signalers put themselves at a disadvantage if their signals indicate their willingness to persist or escalate in a contest. Such honest individuals would be vulnerable to others who always bluff the highest level of aggressive motivation, thus taking advantage of assessing individuals who use these cues to decide when to back down. Once again, assessing individuals are selected to ignore such bluffs, but in this case it is the assessing individuals who are constrained. Because motivational processes are thought to be more covert than RHP, assessors should be less able to extract reliable information from tail flagging and remaining vigilant. (Courtesy of Ron Swaisgood.)

mation about intentions and thus should be selected to ignore all ritualized displays which seem to proffer information regarding motivation. Managing individuals, on the other hand, are assumed to be less behaviorally constrained by their motivational states than by their RHP, behaving in a way that is not consistent with one's motivational state is thought to be quite feasible. In other words, it is generally assumed that the signal 'I will attack' is more easily faked than 'I am risky to pick a fight with' (Maynard Smith, 1982, p. 3). That such assumptions are not necessarily valid can be illustrated by exploring two very visible examples from the animal conflict literature – the meral spread by mantis shrimp (Dingle, 1969), and the state of musth in male African elephants (Poole, 1987).

Mantis shrimp provide us with one of the more compelling examples of signals 'about' aggressive intent, albeit not involving vocal communication. They defend their home cavities against repeated intrusions by neighbors, in part through the use of a signal called a meral spread in which the dangerous claws are held up in display at the intruder (Steger & Caldwell, 1983; Caldwell, 1986; Adams & Caldwell, 1990). The effectiveness of this display in repelling intruders is maintained by following it with a potentially lethal smash with the claws. Such apparent Pavlovian conditioning of neighbors is intensified at a critical time, just prior to each shedding of the exoskeleton, during which the individual is very vulnerable because it has neither armour nor weapons. The result is that the meral spread remains effective as a bluff through the molt (15–20 percent of the individual's life), when a smash cannot be delivered. The feasibility of bluffing is further enhanced by the fact that the state of molt is not detectable either visually or chemically.

So, RHP can be as covert, and as abruptly changeable as motivation is often assumed to be. Assessing individuals are constrained in their ability to detect the precipitous drop in RHP that comes with each molt, not only because the molt is so cryptic, but also because of the danger involved; a challenged mantis shrimp can deliver a lethal smash during the 80–85 percent of its life that it has an exoskeleton. Other examples of rapid reversals in RHP can include physical exhaustion from fighting (Clutton-Brock & Albon, 1979), the breakage of horns and antlers used in combat (Geist, 1966), and changes in the body temperatures of ectotherms (Rowe & Owings, 1990). Similarly, additional cryptic determinants of fighting ability include condition (e.g., Prins, 1989), experience (e.g., Berger, 1986), and skill (e.g., Berger, 1981). Such factors set limits

on the extent to which assessment systems can force management systems to be sources of reliable cues.

The state of musth in African elephants has also been presented as an 'announcement of intent' (Poole, 1989a). Musth is a state of heightened aggressiveness and sexual activity in male elephants, analogous in many ways to the state of rut in other male mammals. Musth is accompanied by a dramatic increase in testosterone levels (Poole *et al.*, 1984), as well as other characteristic physical and behavioral manifestations (Poole & Moss, 1981; Poole, 1987), including visual displays, odor signals, and a low-pitched vocalization called a musth rumble (Fig. 4.6). Unlike rutting in deer, musth in male elephants is asynchronous, i.e., different males may be in musth at different times of the year. Although body size is a significant determinant of rank, and thus of mating success, small males in musth are dominant over larger males in nonmusth. But why? Poole (1989a) argues that an estrus female represents a more valuable resource to a sexually-more-active male in musth than to a sexually-less-active male out of musth; thus Poole interprets musth as a signal of a male's aggressive motivation to fight for a valuable resource.

But if musth contributes so directly to a male's reproductive success, and if intentions are easy to fake, why not always signal musth? If a male could stay in musth longer, might he not increase his fitness? A partial explanation may relate to changes in male body condition with musth. Because they eat less, walk more, and have elevated metabolic rates relative to nonmusth individuals, males in musth rapidly lose condition. In Poole's study, weight loss was significantly correlated with duration of musth, and two males that had the longest duration of musth one year failed even to enter musth the next.

The evidence discussed above suggests that musth is constrained by the physiological ability to sustain it. A male elephant's aggressive motivation, then, appears tied to his physical condition. Indeed, musth may be viewed as a suite of physiological adjustments that simultaneously increases fighting ability and lowers aggressive thresholds. In support of this argument are the known parallel effects of testosterone: not only does testosterone facilitate aggressive motivation, but it also increases muscle mass (at least in the short term), promotes growth of motor neurons, mobilizes energy, and enhances cardiac function (Dixon, 1980; Mainwaring, Haining & Harper, 1988). (For those who remain doubtful about the effects of hormones on physical ability, consider the prohibition of the use of androgens by athletes because of the unfair advantage in physical prowess that these steroids provide.) In addition,



Fig. 4.6. The state of *musth* in mature male African elephants is similar to the state of *rut* in other male ungulates. While in *musth*, elephants produce olfactory signals, such as the exudate from the temporal gland and the dribbling of urine from the penis, wave their ears in a conspicuous visual display, and emit a very low-frequency vocalization called a *musth rumble* (see spectrogram). (From drawings courtesy of Joyce Poole.)

if we assume that aggressive motivation is tied to expected probability of winning, *musth* may confer on an individual a preliminary self-assessment of superior fighting ability, thus reinforcing its aggressive motivation (Hamilton & McNutt, 1997). *Musth* may therefore be interpreted not as a simple announcement of intent, but as a state of altered RHP and motivational priorities which includes cues about both of these variables. Indeed, displays used during the period of *musth* may be designed merely to emphasize the elephant's heightened fighting ability. To the extent that fighting ability and intentions are correlated, the state of *musth* may also afford cues regarding broad motivational state (i.e., probability of escalating) and subsequent changes in the use of relatively discrete displays which predict attack.

This analysis illustrates the utility of the closer scrutiny of proximate processes prescribed by an A/M approach: fighting ability and aggressive motivation may not be as independent as theory has assumed. Although

similar points have been made before (Enquist, 1985; Markl, 1985; Turner & Huntingford, 1986; Adams & Caldwell, 1990), the caveat seems not to have had the impact it merits (Hamilton & McNutt, 1997). If an individual's motivation and ability to fight are correlated, it may be difficult or impossible to disentangle signals that capitalize on assessment of intent from those that exploit assessment of RHP. Although there may be utility in making a conceptual distinction between intentions and fighting ability, it does not necessarily follow that animals should have evolved separate signals for these two components of dangerousness (e.g., Neil, 1983). Constraints such as those proposed for African elephants may link the two variables causally, thus limiting the ability to capitalize on assessment of one without influencing assessment of the other. Indeed, from the perspective of assessment, all that matters is the product of RHP and motivation, i.e., how much RHP the adversary is motivated to use (Parker & Rubenstein, 1981; Markl, 1985). The managerial goal is only to deter the opponent by convincing him, by whatever means, that the signaler may inflict damage.

Finally, yet another dichotomy between RHP and intentions established by game theorists seems to be blurred by a consideration of proximate mechanisms. It is generally assumed that increases in RHP entail a cost, whereas intentions can be altered without any intrinsic cost (e.g., Maynard Smith, 1982). Thus signals indicating heightened aggressive intent are considered to be relatively inexpensive and therefore easily bluffed. However, to the extent that (1) motivational changes are mediated hormonally, and (2) hormones produce real physiological costs, this game-theoretical assumption that motivation entails no costs appears unrealistic.

4.2.2 *Pumping up: the self as target*

As discussed earlier, the behavior of 'lying about one's intentions' is generally considered to be easy because it entails little or no cost in terms of constraining underlying motivational states. It is assumed that animals can 'feel one way and act another.' Zahavi (1982) and Bond (1989b) have argued that behavior cannot be so easily decoupled from motivation because specific behavioral activities are often contingent upon particular physiological/motivational states. Bond argues that gradual escalation in conflict occurs as a result of self-regulatory processes in which engaging in a behavior provides feedback to motivational/physiological systems, thus priming them for the incipient need for heightened

physical activity. If such acts are necessary precursors, providing adjustment of physiological/motivational systems supporting aggressive behavior, then they need not be viewed as 'signals' at all in the sense of having been specialized to influence the behavior of others. Indeed, the role of these activities as sources of information may be better understood from the perspective of assessment than of management. Since these acts are necessary precursors to aggression, these unritualized behaviors leak information upon which active perceivers can capitalize.

This scenario provides an excellent example of a fundamental point in an A/M approach: the proximate bottom line in management is self-regulation. Although animals often meet their own needs by managing the behavior of other individuals, they just as often meet their own needs by operating directly on themselves. (For example, the young white pelican depicted in Fig. 2.3b regulated its body temperature initially only by squawking to evoke parental incubation activities, but not long after hatching was able to shiver as a more direct means of thermoregulation.)

Two examples support the idea that individuals may prepare themselves for important activities in part through self-stimulation. First, Hollis (1984, 1990) used a Pavlovian paradigm to condition territorial male blue gouramis to expect an intruder following the presentation of a light. This enabled these fish to prepare for the incipient intrusion by engaging in early aggressive signaling such as frontal display and threat posture (Hollis suggests the possibility that such preparation may be accompanied by an anticipatory release of testosterone). Subsequently, they confronted rivals in a 'pre-escalated' mode, winning more fights and delivering significantly more bites and tailbeats. So, male gouramis can gain a distinct advantage over interlopers if they can learn to respond to events which predict impending encroachment of rival males. Such predictive cues would be a part of natural interactions as well.

Cheng's work with ring doves deals with the *coo* vocalizations used by both sexes during courtship (Cheng, 1992). Reproduction in this species involves a cascading series of changes in male and female. Males typically initiate courtship by bowing and *cooing*, which is followed by the male's *cooing* over prospective nest sites. The female gradually comes to join the male in *cooing* over the prospective nest site, and ultimately engages in a long stint of solo nest-*cooing*, before the two join forces in the construction of a nest. When nest building reaches a threshold level, hormonal changes are triggered in the female which culminate in ovulation and copulation. What role do the female's *coos* play in this process? It has

seemed reasonable to identify the male as the target of these vocalizations. However, muting the female in several different ways leaves the male's courtship activities relatively unchanged, but blocks the hormonal changes in the female leading to ovulation. And, playbacks of *coos* to the female restore those changes, especially when the vocalizations used are her own (Fig. 4.7). Further playback studies indicate that the female is the target of the male's calls, but they have their effects on the female by stimulating her to *coo*, which in turn induces her to ovulate through a process of vocal self-stimulation.

The point of the preceding paragraphs is that evolutionary theorizing without dealing with the properties of the proximate mechanisms involved is likely to lead to mistaken or oversimplified models. Adaptive behavior is accomplished through mechanisms whose properties are major determinants of what works best.

4.2.3 Refining the concept of intentions

Poole's interpretation of much also reveals the potential confusion that can arise as a result of defining 'intention' as any behavior that predicts, at least probabilistically, what an animal will do in the future. This definition may incorporate a variety of motivational processes. Thus it may be useful to distinguish among processes which operate over different time frames or at different organizational levels (see Fig. 2.10; see Dennett (1983) for a different, more cognitive, formulation of levels of

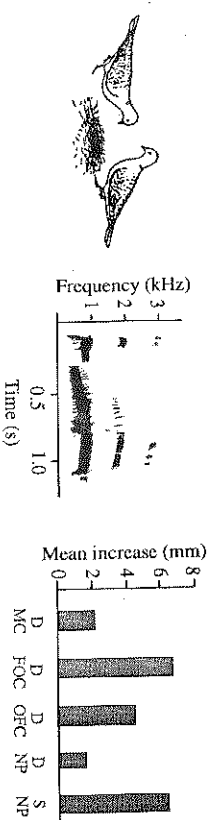


Fig. 4.7. Two ring doves courting at a nest site. The *coo* vocalization, depicted in the spectrogram, is emitted repeatedly by both male and female during courtship, and the female *coos* repeatedly in solo during the latter stages of nest-site selection. Playback studies demonstrate that the female's own *coos* are more effective in stimulating growth of ovarian follicles than any other source of vocal input. D = female devocalized; S = female sham devocalized; MC = male *coos* played back to female; FOC = female's own *coos* played back to her; OFC = other female's *coos* played back to female; NP = no playback to female. (Spectrogram courtesy of M.-F. Cheng; bar graph from Table 1 of Cheng, 1986.)

intention). Motivation is often thought of in terms of states (such as hunger and the phenomenon of mosh; the molar left end of Fig. 2.10) which influence the response probabilities of the organism (e.g., Wise, 1987). Such states are generally characterized by a certain amount of inertia. The concept of motivation, however, also subsumes moment-to-moment decision-making processes regarding what an animal will do next (the more molecular right end of Fig. 2.10, i.e., the everyday way of thinking of 'intentions').

In our view, the absence of a clear distinction among these organizational levels of motivation has given rise to some confusion regarding predictions from evolutionary analyses. Putative 'signals of intent' include both signals that say 'On my next move I will attack' and those which say 'I will persist in an escalated contest.' The former applies to the molecular level of motivation, but the latter may relate to molar adjustments in motivational state which prepare for and thus predict future actions. Compare, for example, demonstrations that an animal's next move can be predicted by its previous behavioral act (Dingle, 1969; Bossema & Burgler, 1980; Nelson, 1984; Waas, 1991), with evidence of the possibility of longer-term predictions (Riechert, 1978; Turner & Huntingford, 1986; Barlow, Rogers & Fraley, 1986; Poole, 1989b). Discussions of signals of intent rarely differentiate among these different kinds of intentions. Maynard Smith (1982), for example, appears to refer interchangeably to signals which indicate what an animal will do next, and to signals that indicate willingness to persist. As a result, empirical tests often do not clearly distinguish which prediction is being tested, in part because they do not address temporal/organizational dimensions of motivation.

The A/M approach deals explicitly with different levels of proximate influence on behavior. Moment-to-moment intentions, therefore, would be embedded in broad motivational states and in two-way interaction with them. Thus a shift in motivational state implies a changing distribution of motives, thereby potentially influencing behavior which predicts both immediately forthcoming actions and the patterning of behavior over a longer time scale. Such proximate considerations may prove useful in refining ultimate formulations because different levels of organization may be subject to different kinds of constraints. For example, it might be found that it is easier to fake or conceal intentions (what an organism may do next) than motivational state (a systemic adjustment reflecting preparation for certain kinds of activities, e.g., preparedness to escalate).

4.3 Emotion

Emotions ensure that high-priority life themes are taken care of. Positive emotions are sources of feedback that sustain the activities that produce them. Negative emotions are sources of feedback that disrupt ongoing activities, redirecting efforts to high-priority themes. In both cases, emotions provide partial answers to that most Darwinian of questions, 'What does this mean for me?' (Zajonc, 1980). Evaluation of the significance of events and conditions to the assessing individual is a critical aspect of the assessment process. Such evaluations can be said to have two general dimensions – importance and polarity (positive to negative). Emotional involvement increases as importance increases, but the specific nature of the emotion depends in part on whether the emotion is positive or negative.

An individual's behavior depends in part on these evaluative reactions to its experiences. Many of these evaluative reactions are linked to the well-being of the animal; painful inputs, for example, often involve tissue destruction, which can be detrimental to the animal's well-being. Animals exhibit many signs of finding painful stimulation aversive. They often work hard to limit painful stimulation, not only escaping from sources of such input, but also anticipating pain and avoiding activities and places previously associated with it (Bolles, 1970). However, not all evaluative processes have to do with well-being *per se*. For example, male rats find ejaculation highly rewarding (Agmo & Berenfeld, 1990), but there is no reason to believe that ejaculation contributes to a male's well-being. Indeed, the prerequisites and consequences of ejaculation, at least in the usual way through copulation, can be painful and detrimental to well-being. Males may exhaust and injure one another during sexual competition, females may injure males during copulation, and the surge of testosterone that can follow ejaculation can suppress the immune system (Herrndon, Turner & Collins, 1981; Zuk, 1994; Boellstorff *et al.*, 1994).

The key to understanding this apparent paradox is the logic of natural selection, which favors emotional systems that contribute to the fitness of individuals, selecting systems that promote well-being only to the extent that well-being contributes to fitness. Nevertheless, these evaluative systems exist, and need to be dealt with. For example, when animals need to contend with the possibility of pain in order to accomplish something adaptive, there are analgesic systems that are biochemically activated, for example through the release of internally produced opium-like substances

(Fanselow, 1991). The aversive motivational consequences of painful stimulation are inhibited in this way. Otherwise, the powerful motivating effects of pain might interfere with adaptive behavior.

As noted, these positive and negative evaluative reactions can become attached to cues of impending reward or punishment. Male rats, for example, are attracted to stimuli associated with locations where they have ejaculated (Agnio & Berenfeld, 1990) but avoid stimuli associated with locations where they have experienced painful stimulation (Bolles, 1970). So, human experimenters and animal trainers can manage the behavior of rats in part by using such signs, suppressing behavior by following it with stimuli associated with pain, or reinforcing behavior by following it with stimuli associated with positive consequences. We suggest that animal signals often work in an analogous way, i.e., through their association with positive or negative consequences. Of course, learning may or may not be involved; the 'discovery' of the association between the signal and positive or negative events no doubt usually involves natural or sexual selection. But, the effects are similar; vocal signals should affect the behavior of others in part by evoking emotional states and thereby motivating strong behavioral reactions. Indeed, the presence of these evaluative systems should create selection on managerial activities for effectiveness in capitalizing on them.

What is the evidence that vocal signals achieve their effects on targets by influencing their emotions? There is a substantial history of interest in the extent to which emotions play a role in the *emission* of signals (e.g., Marler, 1984). Surprisingly, however, substantially less attention has been paid to the question of the emotional impact of signals on targets (Klinnert *et al.*, 1983; Scherer, 1992; Owings, 1994). Nevertheless, the beginnings of a story can be pieced together. As discussed in the Prologue and in Chapter 2, the prosodic features (melodies) of human speech work through the emotional systems of infants. A few months after exhibiting such emotional responses, these infants develop the ability to use social referencing during times of uncertainty, such as when they have been confronted with an unfamiliar object or person (Klinnert *et al.*, 1983). Social referencing involves taking cues from the emotional expression on the mother's face. Working hard to keep their mother's face in view, infants engaging in social referencing mirror the mother's emotions in their own facial expressions, and are more likely to make contact with stimuli about which they are uncertain if the mother's facial expression indicates a positive rather than a negative emotion. Such social processes are not unique to humans. Both rhesus monkeys and

European blackbirds catch the concern of conspecifics engaged in responding vocally and in other ways to a predator. If the object of the conspecific's concern is visible, the observer will develop a long-term fear of it (Vieth *et al.*, 1980; Mineka & Cook, 1988). The example of laughter by humans, discussed below, provides an especially compelling case.

The use of animal models of stress and anxiety indicates parallels between the sociophysiological mechanisms of human and nonhuman emotional responses. For example, when laboratory rats are subjected to electrical shock to the feet, they respond by vocalizing, jumping, struggling, defecating, and urinating. When other rats are allowed to observe these reactions, without experiencing pain themselves, the observing rats show signs of catching some of the stress that the shocked rats are experiencing (Kaneyuki *et al.*, 1991). Within ten minutes, the observing rats' adrenal glands release corticosterone, a sensitive hormonal index of emotional response to stress. After 30 minutes of such observations, chemical changes take place in the medial prefrontal cortex, a portion of the brain believed to play a role in control of negative emotional states, such as anxiety or fear. These changes in the prefrontal cortex are blocked by diazepam (Valium), a drug prescribed to humans for the reduction of anxiety.

It is reasonable to ask whether the construct of emotion adds anything to our understanding beyond what the concept of motivation provides (e.g., Fridlund, 1994). Berridge's (1996) work on the mechanisms underlying food reward indicate that both constructs are essential. Different behavioral assays are required to measure the two, and different systems of brain structures and neurotransmitters underlie them. It has been traditional to treat an animal's desire for food and its affective evaluation of food as essentially the same process. That is, animals are assumed to want what they like, and like what they want. However, Berridge's behavioral research indicates that wanting (motivation) and liking (affect/emotion) are separable systems, that do not always correspond in their impact on behavior. Wanting involves an active, instrumental 'reaching out' to reward, paralleling in many ways the ethological concept of appetitive behavior (and the levels of organization more toward the left side of Fig. 2.10). Wanting is assessed via a variety of instrumental procedures, many of which measure how hard the individual will work to gain access to the reward. Liking, on the other hand, parallels in many ways the ethological concept of consummatory behavior (and the levels of organization more toward the right side of Fig. 2.10). Liking is assessed by recording immediate behavioral reactions to the rewarding or aversive

input. Laboratory rats, for example, display distinctively different patterns of facial and forelimb actions to sweet versus bitter tastes that are similar in many ways to the reactions of human infants to the same flavors. Sweet tastes elicit rhythmic mouth movement, distinctive tongue protrusions, and prolonged lapping at the source. Bitter flavors evoke mouth gaping, rearing, shaking the head, facial wiping with the forelimbs, and shaking the paws. Most experimental manipulations that affect human perceptions of palatability also influence these affective reaction patterns by rats.

4.3.1 Emotional contagion

Peter Sellers was a master of cinematic comedy. As the son and daughter of the Owings family were growing up during the 1970–80s, the family enjoyed sitting down together to watch videos of Inspector Clouseau entangling himself in and miraculously extricating himself from yet another series of hilarious mishaps. Of course, it was not always possible to assemble the entire family, and one participant proved to be critical for maximum enjoyment; Ragon, the big brother, was the real connoisseur of the Pink Panther films. He would roll on the floor, almost helpless with laughter, and his laughter was contagious. The whole family laughed more and enjoyed the films more with the added stimulation of Ragon's laughter.

This infectious effect of Ragon's laughter is not unique. Laughter, a distinctive human vocal and visual signal (Fig. 4.8), typically induces others to laugh; and it is more than just the vocal pattern that is contagious. Laughter is also a means to spread a positive emotional state to

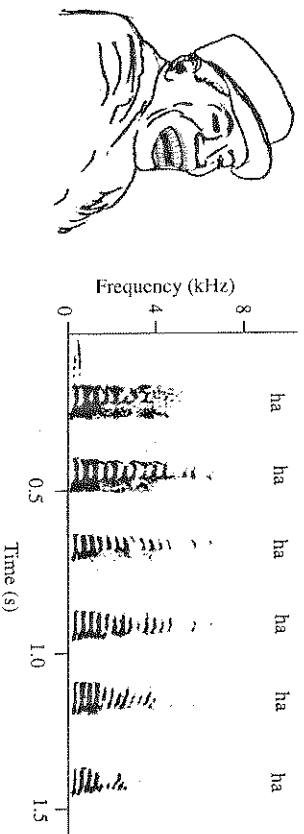


Fig. 4.8. Laughter, a species-typical human vocalization and facial expression. (Spectrogram courtesy of Robert Provine.)

others (Provine, 1996b). Broadcast radio discovered and applied this biological fact early on (Provine, 1996a). Ed Wynn's first live comedy performances on radio in the 1920s were seriously disrupted without feedback from a laughing audience, so he initially recruited the stage crew, and subsequently began to use 'laugh tracks' (recordings of laughter). Ultimately, broadcasters discovered that audiences enjoyed programs more with the laugh tracks, and continued to incorporate them for that reason. From the 1950s to the present, many television comedies have also exploited this playback procedure as a way of enhancing program ratings.

What are the processes underlying emotional contagion? Three general categories have been identified in humans – conscious cognitive processes, unconditioned emotional responses, and conditioned emotional responses (Hatfield *et al.*, 1994). (1) Conscious cognitive induction would include vividly imagining oneself in an emotionally charged situation currently being described by a companion. (2) Unconditioned emotional responses can be illustrated by the emotional responses of human infants to our distinctive ways of speaking to them, called motherese (see Prologue and Fig. 2.4). There is evidence that such processes are based in part on mimicry of motor patterns. Human infants, for example, mimic the facial expressions of adults from an early age, and the adoption of those expressions has the potential to induce the associated emotional state (Ekman, 1992; Hatfield *et al.*, 1994) (3) Conditioned emotional responses are readily induced through Pavlovian conditioning procedures in both humans and nonhumans (Fanselow, 1991). A common method is to pair electrical shock to a rat's feet with an initially neutral stimulus such as a tone; the rat quickly comes to anticipate the shock when it hears the tone, taking behavioral and physiological steps associated with the state of fear that can be instrumental in avoiding the shock. Actively assessing individuals should discover and use such predictive cues all the time in their natural circumstances, responding to the call of a conspecific in part on the basis of the behavior associated with that call type during past interactions with that individual (Hollis, 1990; Owren & Rendall, 1997).

4.3.2 An affect-conditioning model

Conditioned emotional responses have been proposed to play a central role in nonhuman primate vocal communication (Owren & Rendall, 1997). This model deals relatively little with the details of emotion, con-

centrating instead on the importance of individuality in vocal structure for natural Pavlovian conditioning processes. Since this form of learning is a basic cognitive process (Rescorla, 1988), it provides a good topic for bridging to the next section on cognition.

The affect-conditioning model from which this proposal was derived is consistent with an A/M approach. The model calls our attention to proximate issues other than the information conveyed by signals, including the fundamental role of emotional processes in communication, and the decisive importance of attention to call structure. The result is a novel way of thinking both about the significance of individual variation in vocal structure, and about the acoustic structural sources of individuality.

Some vocalizations of nonhuman primates vary among individuals (e.g., the *coo* calls of rhesus monkeys), and these cues about individuality make a difference in playback studies. In contrast, other calls by the same species (e.g., noisy screams) show little evidence of individuality (Rendall *et al.*, 1996; Rendall, 1996). From an informational perspective, the natural response to such data has been to focus on the differing information these calls make available about the identity of the caller. In contrast, Owren and Rendall begin their inquiry with the more basic, pragmatic position that signals are used to influence the behavior of targets; they then explore the structural bases of vocal individuality, and the significance of variation in individuality for emotional conditioning in communication.

Owren and Rendall note that mechanisms of Pavlovian conditioning are very widespread in the animal world, and that these mechanisms almost certainly play a role in social interactions. One of the most compelling demonstrations of the social role of Pavlovian conditioning can be found in the work, described above, on the use of the meral spread display by mantis shrimp (but Caldwell and his colleagues do not use the term 'conditioning'). The individually distinctive cues associated with a specific mantis shrimp's meral spread are paired with aggressive lunges and smashes, allowing that individual to rely on the meral spread alone as a conditioned stimulus during subsequent encounters with its neighbors. Although this might result in enhancement of the impact of meral spreads by all individuals, the fact of dominance relationships indicates that the conditioning effects also accrue selectively to the individual signaler/smasher.

Owren and Rendall note that the social interactions of nonhuman primates also involve the pairing of (vocal) signals with negative and positive emotional consequences. For example, in many primate species,

former opponents reconcile with one another after fights, engaging in friendly interactions at higher rates following aggressive interactions than at other times (Silk, Cheney & Seyfarth, 1996). Among adult female baboons in the Okavango Delta of Botswana, *grunt* vocalizations are regularly used by the initiator of reconciliation, and these calls seem to reduce the target's subsequent apprehension about aggression from the initiator (Cheney, Seyfarth & Silk, 1995). Owren and Rendall, in this case, suggest that the association between grunts and friendly interactions has given grunts the power to serve as a 'safety signal,' evoking a conditioned positive emotional reaction in the target individual. In fact, the grooming interactions that can follow grunting have the effect of inducing the release of endogenous opium-like neurochemicals, which are components of a mechanism that mediates the rewarding effects of friendly social interactions (Keverne, Martensz & Tuite, 1989; Martel *et al.*, 1995). Among rhesus monkeys, fighting can also be a very vocal affair. Individuals who are confident of their ability to win a fight pair their threats and aggression toward subordinate individuals with a roar vocalization (Rowell, 1962). Such pairing could make the dominant monkey's roars an aversive conditioned stimulus for the individuals who have experienced the juxtaposition of roar and aggression. Owren and Rendall conclude that the well-understood processes of Pavlovian conditioning, which are known to be effective in managing the emotional states of target individuals (Fanselow, 1989), provide a mechanism for the impact of individually distinctive primate vocalizations that is much more tangible than the metaphor of information exchange. These conditioned effects would be specific to the history of interaction between the individuals of interest, and would function in addition to the unconditioned effects expected from the evolutionary processes upon which, for example, motivation-structural rules are based (see Chapter 3).

The affect-conditioning model is useful in accounting for variation among primate vocalizations in the availability and form of individual cues. Two sources of such cues can be identified – one having to do with the transfer function of the vocal tract (Fig. 4.9), the other with distinctive temporal patterns. Transfer functions have to do with the shape and size of the supralaryngeal vocal tract, that is, the portion of the throat, mouth, and nasal cavity into which sound is projected by the vocal folds of the larynx. Even where the vocal folds of different individuals produce the same source sound, the different shapes and sizes of the tracts of different individuals can generate different resonance patterns, reinforcing and attenuating different frequency components (creating formants),

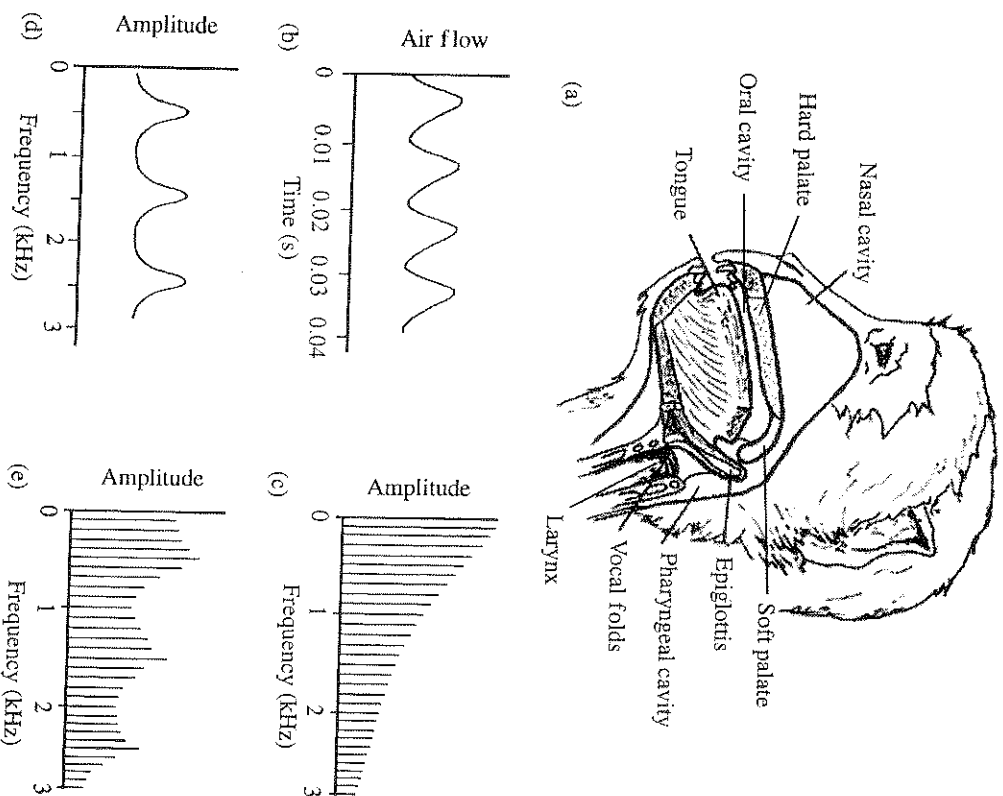


Fig. 4.9. Sources of variation in the structure of the vocalizations of primates, and of mammals in general. (a) A midsagittal drawing of the head of a rhesus monkey. The sources of vocal sounds are the vocal folds ('cords') in the mouth of the larynx. These sounds are projected into the supralaryngeal vocal tract, whose resonant properties filter the sound, by amplifying some frequency components of the source sound and attenuating others. This *source-filter* model of vocal structure is illustrated in b–d. (b) The vocal folds are opening and closing 100 times per second, yielding (c) a sound with a fundamental frequency of 100 Hz, and harmonics at integer multiples of 100 Hz, which decline exponentially in amplitude with increasing frequency. (d) The supralaryngeal vocal tract amplifies in certain source-sound frequencies, creating *formants* (regions of emphasis) around 0.5, 1.5 and 2.5 kHz. (e) These filtering effects (the *transfer function*) yield a final sound structure with a quality strongly influenced by both source and filter contributions. (Courtesy of Michael Owren.)

thereby making the calls of different individuals distinctive. This source of individuality of calls is not very flexible for a given source sound (in contrast to humans); it places an inevitable signature on calls. But, there is variation in the conspicuousness of such transfer-function signatures. They become more apparent where more sound frequencies are available over which to distribute the signature. These conditions are met by harmonically structured tonal sounds of lower fundamental frequency (*sonorants*, e.g., the *coo* in Fig. 4.10), and by impulsive sounds consisting of broad-band noise (*gruffs*). Transfer-function signatures become less apparent, both as the fundamental frequency of harmonically structured tonal sounds increases (such *shrieks* provide fewer harmonics over which to 'write' the signature), and as sound intensity increases beyond a certain point (such *screams* are produced with the mouth wide open, which reduces the filtering capacity of the vocal tract, e.g., the noisy *scream* in Fig. 4.10). The second source of individuality – distinctive temporal patterns of calling – can be used even for those sounds not individually stamped by the vocal tract. Temporal patterns can take a variety of

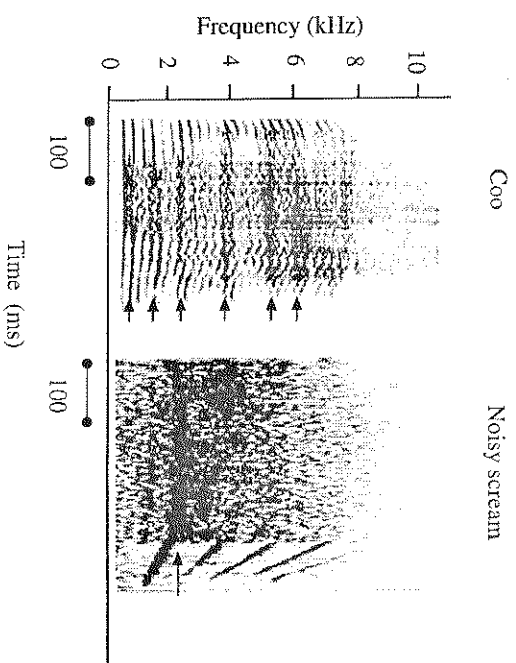


Fig. 4.10. *Coos* and noisy *screams* of rhesus monkeys. The *coo* illustrates the many formants (identified by the arrows) available as cues to the identity of the caller. These transfer-function cues are especially abundant here because the low fundamental frequency and moderate amplitude of the *coo* provide many harmonics to reveal the many points of resonance of the vocal cavity. The noisy *scream* reveals many fewer formants, because of its higher amplitude and fundamental frequency (the latter revealed by the arrow). (Courtesy of Michael Owren.)

forms, including frequency or amplitude contours, distinctive sequences of different call types, and so forth. These should be less obligate cues than those arising from transfer functions, and might therefore vary more in their availability.

Predictions of the model are largely untested, as yet, but provide a rich basis for future empirical test. Predictions by Owren and Rendall include the following. (1) If the pattern of formants in primate calls is as important as the affect-conditioning model suggests, we might expect to find that corresponding auditory systems are particularly sensitive to the positioning of formants. (In an A/M approach, this should be true because signals are said to be selected to capitalize on salient assessment dimensions.) Japanese macaque monkeys are indeed very sensitive to shifts in the positioning of formants, much more so than to changes in the fundamental frequency of sounds; this is just the reverse of the pattern exhibited by humans, who detect shifts in fundamental frequency much more acutely. (2) Where cues about individuality are unavailable in the structure of single calls, we might expect two patterns. First, we should find evidence of compensation for this loss via repetition of calls so that individuality can be replaced via the cross-call patterning of vocalizing. Consistent with this prediction, shrieks and screams, which lack rich formant structure, are typically emitted in bouts, rather than as individual calls (Gouzoules *et al.*, 1984; Gouzoules & Gouzoules, 1989). Second, the loss of conspicuous transfer-function-based individuality should be offset by some compensatory gain. In the case of shrieks and screams, the compensation appears to come in the form of strong unconditioned effects on targets. Shrieks and screams are certainly noxious sounds, in part because they are the loudest vocalizations, at least in the vocal repertoires of macaque monkeys. But they also share other structural features with crying by human babies – a set of vocalizations widely acknowledged to be aversive (Gustafson & Green, 1989) – including sound energy at relatively high frequencies and dysphonation (irregular movement of the vocal cords, resulting in a poorly defined fundamental frequency, as in the noisy *scream* of Fig. 4.10, relative to the *coo*). The repetition of these sounds also contributes to their noxiousness, in addition to restoring cues about individuality. So, shrieks and screams should be effective in deterring continued aggression by the adversary of the subordinate individual.

As discussed in Chapter 2, that we use 'cognition' broadly to refer to all input-processing activities beyond perception, including storing, retrieving, computing, and integrating as a basis for behavioral decisions (consistent with Mason, 1986; Dyer, 1994). According to this inclusive definition, even simple processes like Pavlovian and operant conditioning are cognitive processes. Consistent with the concern in this chapter about integrating management and assessment, it is also argued below that most or perhaps all cognitive mechanisms used in animal communication are parts of action systems, that judge objects and events in terms of what to do about them, not in terms of some abstract representation isolated from its functional context.

Cognitive scientists distinguish between 'data-driven' and 'conceptually driven' cognitive processes (Cohen, 1990). Data-driven processes are initiated and guided by cues coming in from the external world and currently being received by the sense organs. Such processes are perhaps most evident when external events are high-priority ones, such as when a source of danger threatens an individual or its offspring, or a very attractive, sexually receptive potential mate has just presented itself. At those times, current stimulation appears to be a dominant determinant of an individual's behavior. Conceptually driven processes are, for our purposes, more appropriately labeled 'state driven,' because of our concern with the role of motivational and emotional states in addition to cognitive ones in assessment.

The role of internal states is revealed in part through selective attention, and can be illustrated with the phenomenon of latent learning from the animal-learning literature (Simon, 1994). When a hungry rat negotiates a maze that contains food and water in different locations, it learns in relatively few trials how to travel directly to the food location with few wrong turns. However, if it is subsequently made thirsty instead of hungry, it will reveal that it also learned the location of the water, because it improves even more quickly in its travel to the water than it did originally for the food reward. Such findings were treated as evidence that learning, e.g., the location of water, can occur without motivation to acquire water. The learning simply remains latent until thirst motivates expression of it. However, subsequent research proved that this interpretation was too simple. A more modern view demands appeal to processes of attention. Rats learn whatever they *attend* to, but the direction of their attention depends on their motivational state. If hungry, but not too

hungry, rats note and remember where water was detected during their search for food. But if highly food deprived, their attention is not attracted by anything but food; water goes unnoticed and its location remains unlearned until it is exposed to the maze in a state of thirst.

The example of latent learning illustrates how cognitive processes such as learning are typically driven not separately by data or internal factors, but by both. An animal's cognitive representation of a maze is determined in part by its experience with the maze, but the details that are highlighted in the map depend in part on internal factors such as its motivational state. From an A/M perspective, an individual's cognitive processes could be said to depend on its current regulatory problems. A hungry rat has experienced a disturbance in the regulation of its nutritional state; a thirsty rat's water balance is disrupted.

4.4.1 Context

Animals are regularly faced with the question 'What should I do next?' and the answer, according to what we have said so far, is 'It depends on what the current regulatory problems are.' Superficially, this sounds straightforward; individuals simply need to identify their current regulatory problems, and then the next step should be self-evident. But life is more complicated than that. It is not always clear what problems an individual is facing. A predator may be nearby but undetected, because it is hiding in ambush. Or, another member of the group may be surreptitiously attempting to usurp the individual's position of social status. Even when such problems are uncovered, the solution may not be clear. If an individual discovers a social climber, it will usually be confronted. But, how assertive should the individual be? It depends on the climber's aggressive motivation and ability (Hamilton & McNart, 1997). One source of cues on those matters is the structure of the vocalizations that the climber emits (e.g., Davies & Halliday, 1978). But, vocalizations may not always be the most reliable source of cues (Markl, 1985), because they have been shaped by selection for effectiveness in managing the behavior of opponents, including bluffing when necessary.

Conditions such as those described above are important sources of selection for very active assessment. Problems are not always immediately evident, so active efforts may be required to uncover them. Once problems are identified, the need for a reliable foundation for behavioral decisions favors the supplementation or even replacement of cues from individual signals with contextual cues. The complexities of social assess-

ment and interaction place a premium on the cognitive ability to integrate cues from multiple sources.

What are the contextual sources available for more precise assessment? One important source consists of the patterning of signaling, a level of organization that is independent of the structure of individual signals. The red deer stags of Scotland make use of the rate of roaring as an assessment cue during conflict with other males for sexual access to groups of females (Clutton-Brock & Albon, 1979; Clutton-Brock, Guinness & Albon, 1982). A contest begins when a challenger approaches to within 200–300 metres of a harem-holding stag. The two usually roar at each other for several minutes, and the challenger typically then withdraws. If, however, the challenger approaches even more closely, the adversaries exchange an additional set of roars and then may progress to a parallel walk, in which the stags walk tensely, side by side, perpendicular to the direction from which the challenger approached. About half of the parallel walks escalate to actual fights, in which individuals lock antlers, pushing, twisting, and even stabbing the opponent if an opportunity arises. The consequences of losing a fight can be serious; about 23 percent of stags over five years of age show some sign of injury during the rut each year, and up to 6 percent are permanently injured. So, accurate assessment of opponents is important. Playback studies indicate that males attempt to roar more rapidly than their adversary in roaring contests, and observations of actual contests demonstrate that the male that peaks at a lower roaring rate is most likely to withdraw at that point, or to lose the fight if the encounter escalates that far. As we noted earlier, the fighting ability (RHP) of an adversary may not be at all straightforward to assess; probing and monitoring feedback may be the only way to uncover the patterning of behavior indicative of different levels of fighting ability.

Rate of signaling is one of several contextual sources that are data driven (as this term is used above). Data-driven sources can arise either from the signaler or from the setting (Leger, 1993). From the signaler, the signaler's concomitant nonsignaling behavior is a useful source in addition to rate of signaling. Concomitant behavior can include spatial factors, such as how close the signaler is and whether it is oriented toward the target, factors that can influence the target's behavior more than signaling does (Paton, 1986). Sources from the setting include the behavior and identity of other nearby individuals, both heterospecific and conspecific. In field playback experiments, for example, white-throated sparrows respond more strongly to playbacks of a stranger's song than

they do to playbacks of their own song. But this difference seems to be the result of the reactions of the playback subject's neighbors. The neighbors responded more strongly to the stranger's song than to the subject's (their neighbor's) song, approaching aggressively at the sound of a stranger (Brooks & Falls, 1975; Leger, 1993).

The assessing individual has also been identified as a source of contextual influence on the significance of signals (Leger, 1993). In the terminology used above, these are called state-driven contextual sources, a category of source that follows logically from the pragmatic approach to assessment developed here. That is, the significance of a perceived signal depends on the assessing individual's dominant regulatory problems at that time. Such influences have already been mentioned, e.g., the effect of nutritional state on Belding's ground squirrel responses to playback of antipredator vocalizations. Many of the identified sources of contextual influence on signal assessment undoubtedly also influence the individual's regulatory problems. These sources include the following.

1. *Stage of development.* For example, adult and juvenile California ground squirrels differ in how they differentiate among antipredator calls. Whistles are associated with high-urgency situations, and are most often elicited by raptors. Chatters are associated with less urgency, and are typically emitted while dealing with terrestrial predators, such as coyotes and bobcats. The reactions of adults to playbacks are consistent with this contrast in urgency. They spend more time out in the open and vigilant after chatters, and more time out of view and under cover after whistles. Juveniles reverse this difference, opting for more exposed vigilance after whistles, and more use of cover after chatters (Hanson, 1995). Developmental changes in the means and ends of regulation are discussed in Chapter 1, and are the topic of a later section of this chapter.

2. *Physiological (including motivational/emotional) condition.* For example, the regulatory problems of acquiring sufficient nutrition and avoiding predators can conflict with each other, in part because dropping the head to feed is incompatible with elevating the head to scan for predators. As discussed earlier, Belding's ground squirrels differ in the priority that they allocate to avoiding predators, depending on whether they are ahead of or behind schedule on weight gain in preparation for hibernation. When behind schedule, they take less time away from feeding to remain vigilant after playback of an antipredator call (see above).

3. *Previous experience.* For example, when vervet monkeys are exposed repeatedly to playbacks of a particular type of call by a particular individual, they become less responsive to such calls, but only to those from that individual. This suggests that they have come to interpret that individual as an unreliable source of cues (Cheney & Seyfarth, 1988).

4. *Relationship with the signaler.* For example, maternal northern fur seals alternate between two- to three-day nursing sessions and five- to twelve-day foraging trips during the four-month nursing period (Insley, 1996). These periods of absence from the pup are the longest of any pinniped, so each of the mother's returns is after an extended absence and to a crowded onshore colony containing many youngsters eager to suckle. Behavioral observations indicate that the effort to reunite is a mutual one. The mother begins calling as she comes ashore, and responds quite aggressively to suckling attempts by pups that are not her own. Her pup returns her calls with vocalizations of its own, and their reunions are remarkably quick, given the crowded, noisy conditions. Vocal playback studies demonstrate that mother-offspring recognition is mutual; both mother and pup vocalize significantly more to each other's calls than to those of other individuals in the colony.

4.4.2 Memory

When we speak of memory, we typically think of individuals retrieving information stored as a result of experience. However, animals also 'remember' things that they have never experienced (Coss, 1991). For example, laboratory-born California ground squirrels which have never experienced a snake before, seem to 'remember' what to do about snakes on first contact, tail flagging and substrate throwing at the snake, as well as apparently inferring that a snake who has been removed has crawled into a burrow (Owings & Coss, 1991). Such memories may persist for as long as 300 000 years in the absence of selection arising from snake predation (Coss, 1991). Qualitatively, this antsnake behavior is much like that exhibited by an experienced adult California ground squirrel. Similarly, the swamp sparrows and song sparrows discussed under *perception* above 'remember' some of the details of what conspecific song sounds like without prior experience with song (Marler & Peters, 1989). In both cases, these memories can contribute to the significance of vocalizations to assessing individuals. And, in both cases, these behavioral

systems do change as individuals mature, no doubt in part because of memory changes arising from the squirrels' experiences with snakes (see also Hersek & Owings, 1994), and the sparrows' experiences with conspecifics. The storage mechanisms and retrieval processes for these innate memories may be basically similar to those acquired through experience (Coss, 1991).

Memory can stand an individual in good stead during agonistic encounters. During aggressive interactions, the owners of territories have an advantage over intruders; owners typically win many more of these encounters than intruders do. It is widely believed that familiarity with the territory lies at the root of this advantage. Familiarity could make the territory more valuable to the owner than to the intruder because the owner would have more knowledge of the locations of resources. This greater value should provide greater motivation to the owner than to the intruder during confrontations. However, Stamps (1995) emphasizes that familiarity has another effect, too; owners may use a territory more efficiently than intruders during an encounter, and so fight more effectively. Most of the thinking about resident advantage has focused on information (e.g., knowing the layout, knowing where the resources are, etc.) But, Stamps' motor-learning hypothesis focuses more on pragmatic issues of using a territory, rather than information, and in this sense is consistent with the pragmatic approach prescribed by A/M.

The distinction that Stamps makes, between memory of the layout of an area and memory of how to use an area, parallels in many ways the distinction in the cognition literature between semantic and habit memory (Squire, 1994). Research with both humans and nonhumans indicates that similar distinctions between types of memory systems apply, and that these multiple forms of memory are supported by different brain systems and have different characteristics. Habit memories are about what to do about a situation, and are similar in many ways to what Jean Piaget has called sensorimotor intelligence (Piaget, 1971). Semantic memories, on the other hand, involve more detailed cognitive representations of the situation itself. These two differ in their flexibility; semantic memories can often be linked to more than one form of action, whereas habit memories are more tightly linked to specific ways of behaving. For example, when a person learns a motor skill, such as a complex dance or the swing of a squash racket, its form is often not consciously accessible (e.g., for verbal description), but only expressible through performance of the movements.

We suggest that much of the action in animal communication happens via processes much closer to habit than to semantic memory. This suggestion is consistent, for example, with the primary conclusions of an extensive program of research on the cognitive abilities underlying vocal communication by vervet monkeys (Cheney & Seyfarth, 1990). Vervet monkeys reveal considerable cognitive sophistication in their social maneuvering, but much of that sophistication is specific to the social domain, and not readily transferable to other domains, such as dealing with predators. Consistent with the pragmatic perspective of an A/M approach, the knowledge of assessment systems is pragmatic knowledge, about the implications of input for managerial action. Indeed, the process of developing social competence has been likened to a dance between the developing individual and its social companions (Kraemer, 1992). This topic is further explored later in this chapter with discussion of ontogeny.

4.4.3 Referential specificity in animal signals

From an informational perspective, a common way to think of signals is as 'standing for' or 'referring to' something else. It is primarily from this perspective that interest has originated in the possibility of referentially specific communication. A signal is deemed referentially specific when it conveys 'sufficient information about an event for receivers to select appropriate responses' without the aid of contextual information (Macedonia & Evans, 1993). Confident conclusions that a signal refers to a specific environmental event should be founded on study of both the management and assessment sides of the communicative process; that is, the relationship between eliciting events and signal structure must be described systematically (management side), and then the effects of variation in signal structure on target response must be studied through the use of playbacks (assessment side) (Evans, 1997). For example, one would need to demonstrate that the differing calls typically used by ring-tailed lemurs for aerial and terrestrial predators do not change with such factors as the proximity of the predators (Pereira & Macedonia, 1991), and then seek differences in response to these two classes of vocalizations in playback studies (Macedonia, 1990).

The possibility of high referential specificity in animal signals first achieved visibility because it was thought to indicate that animal cognitive abilities are more sophisticated than previously thought. Peter Marler and his colleagues initiated this inquiry (Marler, 1984). The ability

to engage in referential communication was said to indicate that animals are more than simple, mechanical entities. Instead, referential signaling seemed to suggest that animal behavior can be mediated by quite specific cognitive representations, and not just by diffuse internal states. Interest in referential animal communication is just a small part of the 'cognitive revolution' that has recently transformed the study of animal behavior (Dyer, 1994).

More recently, referential communication has become a topic of interest in its own right, and researchers have become more cautious about detailed inferences of cognitive sophistication based on such work (Marler, Evans & Hauser, 1992; Macedonia & Evans, 1993; Evans, 1997).

How is referential specificity treated in an A/M approach? First, an attempt would be made to link the idea to fundamental systems of animal behavior, avoiding excitement about a phenomenon simply because it is relevant to apparently special human abilities. In that spirit, we suggest that the ability to treat perceived stimuli as standing for relatively specific environmental events is widespread, as is indicated by the fact that so many species are capable of the form of learning that is induced by Pavlovian conditioning procedures. Pavlov's dogs, for example, behaved as though the sound of a buzzer stood for meat powder after the two were paired repeatedly. But it would also be necessary to be precise about what is meant by saying that a predictive event (e.g., a conditioned stimulus, or vocal signal) 'stands for' a predicted event (e.g., an unconditioned stimulus, or predatory attack). In neither natural signaling systems nor responses to Pavlovian conditioned stimuli do animals treat the predictive and predicted inputs as equivalent. They behave as though they anticipate the arrival of the predicted event, not as though it has arrived. Responses to playbacks of antipredator signals rarely match the intensity or details of the form of actual reactions to predators. In most cases, for example, responses to calls involve silent vigilance; the vigilant responder engages in vocalizing and other evasive activities only if it detects the predator itself (e.g., Leger & Owings, 1978; Cheney & Seyfarth, 1990; Weary & Kramer, 1995). Similarly, responses to conditioned and unconditioned stimuli are typically not identical (Fanselow, 1991).

In an A/M approach, the contrast between the processes of management and assessment in communication is fundamental in thinking about referential communication. Even though communication involves an interplay between these two processes, the specific mechanisms involved are not necessarily intricately coordinated or coevolved. This point follows logically from the idea that assessment systems are specialized for

many purposes other than communication, and so may bring pre-existing biases to a communicative context that shape the features of signals through feedback processes (e.g., Ryan, 1994). Nevertheless, the literature on referential specificity has, so far, assumed symmetry of the relevant mechanisms. While the need to examine both sides of the process has been emphasized (Evans, 1997), a referentially specific signal has been assumed, at least implicitly, to involve referential specificity in both the management system and associated assessment mechanisms of typical targets. Little consideration has been given to the possibility that a management system might meet the criteria for referential specificity, but not the associated assessment system, or vice versa (Owings, 1994). But this is probably a common mix. For example, we know from Cheney and Seyfarth's (1990) work on vervet monkeys that manager and assessor systems can function at different levels even within the same individual. The reactions of six- to seven-month-old vervets to call playbacks are indistinguishable from the responses of adults, but the emission of calls in adult-like fashion, confining each to a particular type of predator, does not develop fully for another 18 months. So, there is A/M symmetry when these juveniles respond to adult calls, but not in the equally likely case of adults responding to juvenile calls. Such asymmetry may be common in communication not only between different age classes, but also between different species.

An additional point is important regarding referential specificity from an A/M approach. The term *referential* specificity would be modified, to the less interpretive one of *situational* specificity. From the perspective of management, signals do not *refer* to anything; they are pragmatic acts emitted to produce an effect of variable specificity. This would lead us to treat the idea of referential specificity as important primarily as a subset of the broader topic of the relationship between signal structure and situations of use. As previously noted, according to A/M, relations between signals and situations arise from the shaping effects of situational constraints. A minimum requirement for situationally specific signals of the 'referentially specific' sort might be the possession by signal targets of the cognitive ability to deal with specific categories of entities, such as 'aerial predator,' and 'terrestrial predator' (Fig. 4.11). Such a cognitive ability would set the stage for managing the behavior of others through the use of signals with that level of situational specificity. Thus, the cognitive abilities of targets of management comprise one class of constraints on the specificity of the relationship between signal structure and situation. This class of constraints is the one most compatible with an

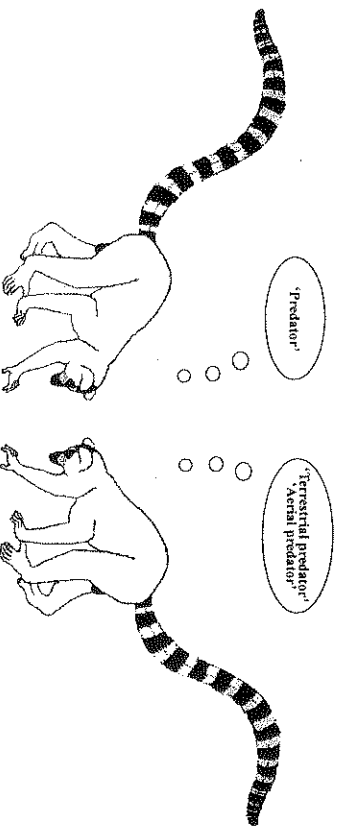


Fig. 4.11. Constraints of the cognitive categories of assessment systems on the potential predator specificity of antipredator vocalizations. These are ring-tailed lemurs. The assessment system on the left (a single, undifferentiated cognitive category for predators) would not select for different calls to aerial and terrestrial predators, but the assessment system on the right would.

informational view of signaling, i.e., 'if my conspecifics can understand about terrestrial predators, then I can signal to them about terrestrial predators.'

The above cognitive source of situational specificity offers little guidance regarding the expected structure of signals. (Chris Evans (in press) has converged with our thinking on these matters.) Macedonia and Evans (1993) have discussed sources of selection for contrasts in signal structure in an essay on the meaning of mammalian antipredator vocalizations. They begin with two simplifying steps, to make their task more tractable. First, they set aside the difficult question of underlying cognitive mechanisms, and explore 'functionally referential' signals, i.e., signals that are confined to specific predators and evoke predator-specific responses, whatever the associated cognitive mechanism. Second, they argue that the judgment of functional referentiality is least ambiguous when dealing with qualitatively different signals, rather than with different variants of the same signal type. (A signal that exhibits graded variation might be more likely to convey information about graded changes in motivational states.) Such qualitative differences in the structure of antipredator signals, they propose, might be favored by selection where the escape responses required to avoid the different classes of predators are incompatible with each other (e.g., vervet monkeys climb trees to evade leopards, but leave trees to deal with eagles). The rationale for this hypothesis is not entirely clear. Perhaps they mean that telling another individual to engage in conflicting activities might most effectively be

accomplished with signals of conflicting structures; the contrast in structure would then supplement the contrast in meaning.

An A/M approach would also lead us to seek more pragmatic constraints. Acredolo and Goodwyn's (1990) work on communicative gesturing in normal human infants provides an example of this sort of constraint. Prior to developing verbal proficiency, human infants not only use nonverbal vocal signals such as crying and laughing; they also develop and deploy communicative gestures in their interactions with parents. The form of gestures for objects typically arises either within interactive routines involving the parent (e.g., mimicking the mother's puffing sound of blowing on a fish mobile as a general symbol for fish), or through the child's own interaction with the object (e.g., a throwing motion to symbolize ball). Thus, the forms of these signals are not arbitrary; they emerge from the interactions that the infant typically has in association with the objects. This proximate process of creating signals is analogous to the ultimate process of evolving a signal from an intention movement (Tinbergen, 1952; Smith, 1977). Regarding the origins of form differences in antipredator calls, these results would lead us to explore how, for example, different evasive maneuvers might differentially distort the vocal cavity during calling; that is, how call structure emerges from interactive routines with the predator. Ohala (1984) has made an analogous 'byproduct' argument regarding the origins of the appeasing 'grin' and aggressive 'o-face' in primates (see Chapter 1). These visual displays, he hypothesized, were originally simply the facial adjustments needed to raise voice pitch in appeasement (shortening the vocal tract with the grin), and to lower voice pitch in a threatening growl (lengthening the vocal tract via lip protrusion in the 'o-face'). These facial expressions subsequently became emancipated from sound production, serving as signals in their own right.

Finally, M/A's focus on the broad issue of constraints can direct our attention to sources of situational specificity that would not appropriately be called referential even in an informational perspective. (Again, see also Chris Evans' convergent proposals, Evans, 1997). For example, Macedonia and Evans' hypothesis, described above, would lead to the prediction that California ground squirrels should have what they call functionally referential antipredator signals. Incompatible antipredator responses are required for two types of predator; the burrows in which these squirrels live are sources of refuge from most mammalian predators that threaten them (not counting mustelids), but are sources of danger from rattlesnakes. Consistent with this hypothesis, the squirrels use very

different signals for the different types of predators, chatter calling for mammalian predators, but waving their fluffed tail back and forth (tail flagging) for snakes (Owings *et al.*, 1986). By their operational definition, then, this is a functionally referential signaling system. However, the term seems inappropriate, for the following reason. The most likely reason for the structural difference in signals is that the predators themselves are targets of these signals (Hennessy & Owings, 1988; Hersek & Owings, 1993). The switch to visual signals with snakes apparently has been favored because, unlike mammalian predators, the snakes apparently cannot hear the calls of these squirrels. The specificity of signal structure to predator type arises from the properties of the signal target, not what is typically called the referent. Extending Macedonia and Evans' argument, in our terminology, we might say that qualitative differences in constraint on signal structure arise from a variety of sources, which can, for example, include the sensory specializations of signal targets.

4.4.4 Deception

On the day that a female Formosan tree squirrel becomes sexually receptive, 9–17 males assemble near her home range to attempt to mate with her (Tamura, 1995). During her approximately eight hours of sexual activity that day, she consorts with about eight males in succession, copulating once or several times with each. After mating with the female, most males initiate a series of 'postcopulatory calls,' loudly barking repeatedly for about 17 minutes. Other squirrels in the vicinity respond to these calls with apparent alarm, retreating from the ground to tree canopies and remaining immobile there for the duration of the calling bout. By calling, the consorting male may delay the next male's access to the female, which may increase the proportion of the female's litter that the consorting male sires. It is known that in some squirrels the proportion of a litter that a male actually sires depends in part on how quickly the female copulates with the next male (Schwagmeyer & Foltz, 1990).

Why do other squirrels seem to respond with alarm to these postcopulatory calls? Perhaps it is because they sound like the pattern of barking used when mammalian predators are detected. Indeed, statistical comparisons of the form and patterning of these calls revealed no significant differences between those emitted after copulation and those evoked by feral cats. And, playback experiments found that recordings of calling in the two contexts did not differ significantly in their effectiveness at inducing flight to trees and immobility.

Are these males deceiving other squirrels by using alarm calls to achieve their own selfish ends? We suggest that this is not the most scientifically valid question to pose. Similarly, we would argue that it is a misdirection of scientific inquiry to ask whether animals are *really* managing the behavior of others. In both cases, a more legitimate approach would be to ask how useful the concepts of deception and management are for making sense of the communicative patterns that we discover. This whole book explores the utility of the concept of management (and assessment). So, the focus here is on how useful the idea of deception is.

The considerable recent interest in the idea of animal deception (Hauser, 1996) has two sources: (1) recognition that natural selection can lead to exploitative behavior toward conspecifics (Burghardt, 1970; Dawkins & Krebs, 1978); and (2) an anthropocentric emphasis of concepts created to describe human behavior (Owings & Morton, 1997). We concur with source one, but resist anthropocentrism. The concept of deception is anthropocentric, in that it has been applied primarily to human interactions. This anthropocentrism is compounded when deception is defined as conveying false information or withholding true information. The primary goal here is to explore deception without appealing to information exchange. The concept of deception will be critically evaluated, retaining it but applying it in a more restricted way than is typical.

What are the phenomena that we often call deception? A mismatch occurs between our perception of how an individual *should* be behaving with regard to communication, and how it *is* behaving. The Formosan tree squirrels described above provide an example. Once we know the kind of calling that is used to deal with mammalian predators such as cats, we are surprised to discover the same kind of calling in the very different context of the aftermath of copulation. Such deceptive mismatches between our expectations about an animal's communicative behavior and the individual's actual behavior can take two general forms. The animal may emit a signal that we do not expect in the observed context, or fail to signal where we expect it. In informational terms, the former is said to involve the provision of false information, and the latter is labeled withholding information.

The decision that the animal is behaving deceptively is an onerous one. That is, we need to evaluate critically our assumptions about what the function of the signal is; this can be done in part by acquiring solid data on the norms of use of the signal before concluding that the norms have been violated (Smith, 1986a; Smith, 1997). Such steps are not always

taken. Male barn swallows, for example, have been reported to use anti-predator calls deceptively as a means of disrupting copulation between the caller's mate and another male (Moller, 1990). But, no quantitative normative data are available that would permit us to judge whether these calls really do function primarily as an antipredator warning. A much richer data set is available for Formosan tree squirrels; the distinctive pattern of repetitive calling is the norm both during encounters with cats, and in the aftermath of copulating. Such data complicate efforts to judge which context of calling is the original or normative one. Logic seems the primary guide; it is clearer how males would benefit from using antipredator calls after copulating, than how they gain from using post-copulatory calls to deal with predators. And, the cautious reactions of squirrels to playbacks of these calls seem more appropriate for an anti-predator context than for a mating one.

Foregoing signaling has been proposed to be a safer way to behave exploitatively than emitting a signal in an atypical situation, because foregoing leaves the individual less conspicuous and therefore reduces its chances of being 'caught' (Cheney & Seyfarth, 1985). According to this hypothesis, foregoing calling should be more prevalent and therefore easier for biologists to discover. The food-associated calls of rhesus monkeys may provide an example; they often call when they discover food, but are also frequently silent (Hauser & Marler, 1993b). When noncallers are discovered with food, their chances of being the target of aggression are greater than if they had called. The absence of food calling has been described as a case of deception about possession of food, and the increased incidence of aggression where calling did not occur has been interpreted as punishment for cheating (Hauser, 1992). Although this is an intriguing example, the case that not calling is deceptive will require additional scrutiny. For example, calling becomes more likely when the discoverer of food is hungry; so, a noncaller may simply be sated. Also, not calling was actually more common (55 percent of trials) than calling. It would normally be expected, from models of Batesian mimicry, that cheating would be effective primarily when rare; if cheating becomes the norm, the associated signal should lose its capacity to influence the behavior of others (Harper, 1991).

Hauser (1997) has made headway in building a case that not calling is deceptive, in part by distinguishing among different sources of the absence of calling. He has discovered that not all cases of failure to food call are appropriately labeled as deception; during experimental exposures to food, peripheral males (in contrast to regular members of

troops) never called. Since calling is not the norm, then not calling could hardly be considered deceptive. And, when other monkeys discovered peripheral males with food, they did not behave aggressively toward them. It is primarily calling by troop members that is the norm, and predominantly these members who experience elevated aggression when they do not call. This pattern makes sense; punishing peripheral males may not be useful, because the punisher may not encounter the victim again, and so may not benefit from the effects. But, punishing a member of the same troop could generate benefits that exceed costs, because of the high probability of future contact between punisher and punishee (Clutton-Brock & Parker, 1995).

The rhesus monkey example draws us back to several themes that are central to this book: the importance of distinguishing the perspectives of management and assessment, and the critical role of assessment in communicative processes. The idea of deception seems less useful from the perspective of management, given the pragmatic emphasis of this perspective. An individual that foregoes calling where it is the norm to do so may simply be protecting itself from the self-interested actions of others, in a way similar to the efforts of a camouflaged animal to limit its conspicuousness to a predator (Mitchell, 1986). Indeed, food calling by rhesus monkeys does attract others who are likely to take some of the food, and individuals get to eat more when they forego calling and go undetected than under any other conditions (Hauser & Marler, 1993b). When discussed in this way, foregoing calling does not seem like 'cheating' where are the 'rules' being violated by such behavior?

An interpretation in terms of camouflage has also been applied to 'deceptive' efforts by male pied flycatchers to mate bigamously (Dale & Slagsvold, 1994). Males of this European species of songbird sing to attract their mates to the nest cavities that they defend. After mating with one female and producing a clutch of eggs with her, they travel to a nest hole a considerable distance from their current territory (an average of about 200 m) and attempt to attract a second female. When they are successful, they produce a second clutch of eggs with her, but then leave her on her own, returning to their primary female to assist in rearing those young. The reproductive success of the primary mates of bigamous males is close to that of monogamously mated females, but the deserted, secondary females are significantly less successful (Alatalo *et al.*, 1981). Are these males deceiving their second mates, establishing a distant second territory to attract a second mate by hiding the fact that they are already mated? Perhaps not; maybe their move to a distant territory is a

pragmatic tactic to minimize disruption of the second mating effort by the first mate (Dale & Slagsvold, 1994). As we have argued from an A/M perspective, the best way to understand why animals use the signals they do, and in the ways they do, is to appeal to the constraints of the signaling situation, such as the impact of first mates on efforts to acquire second ones. This example, like the case of rhesus monkeys who forego food calling, highlights the limitations of anthropocentric terms like *deception* and *cheating* when applied to the behavior of nonhumans. The concept of cheating especially implies the violation of a set of rules or laws. Is it useful to think of nonhumans as guided by rules of conduct like the rules and laws of human cultures? We suggest that such concepts can distract us from exploring the constraints of communicative situations, generating controversy instead over whether animals are *really* being deceptive.

Dale and Slagsvold (1994) extend their thinking about pied flycatchers in ways that are also consistent with an A/M approach, noting the importance of considering the question of deception from the perspective of the assessing females. Their treatment of the females' assessment processes is consistent with signal-detection theory (Getty, 1996), a model of decision-making under uncertainty that psychologists adopted from engineering several decades ago (Tanner & Swets, 1954). The general idea of signal detection theory is illustrated in Figure 4.12. Male pied flycatchers vary in the amount of time they spend singing on their territories, but unmated males spend more time on average singing on their primary territories than mated males do on their secondary territories (Dale & Slagsvold, 1994). The uncertainty that a female faces in discriminating between mated and unmated males is indicated by the overlap in these two hypothetical distributions. Because of this overlap, the female's decision as to whether to mate with a particular male or not becomes a statistical matter; that is, she must always deal with the possibility of making a 'mistake,' either by rejecting an unmated male, or by accepting an already-mated male. Notice that, for a given level of difference between mated and unmated males, reduction in one type of error leads to an increase in the other. So, where her criterion for mating should be placed depends on the relative importance of the two types of errors. For example, in the short breeding season available to these birds in northern Europe, rejecting an unmated male could be fairly serious because another might not come available until it is too late to complete a cycle of reproduction. So, the female might be expected to set her acceptance criterion relatively low, at point *a* rather than *b*, to reduce her risk of

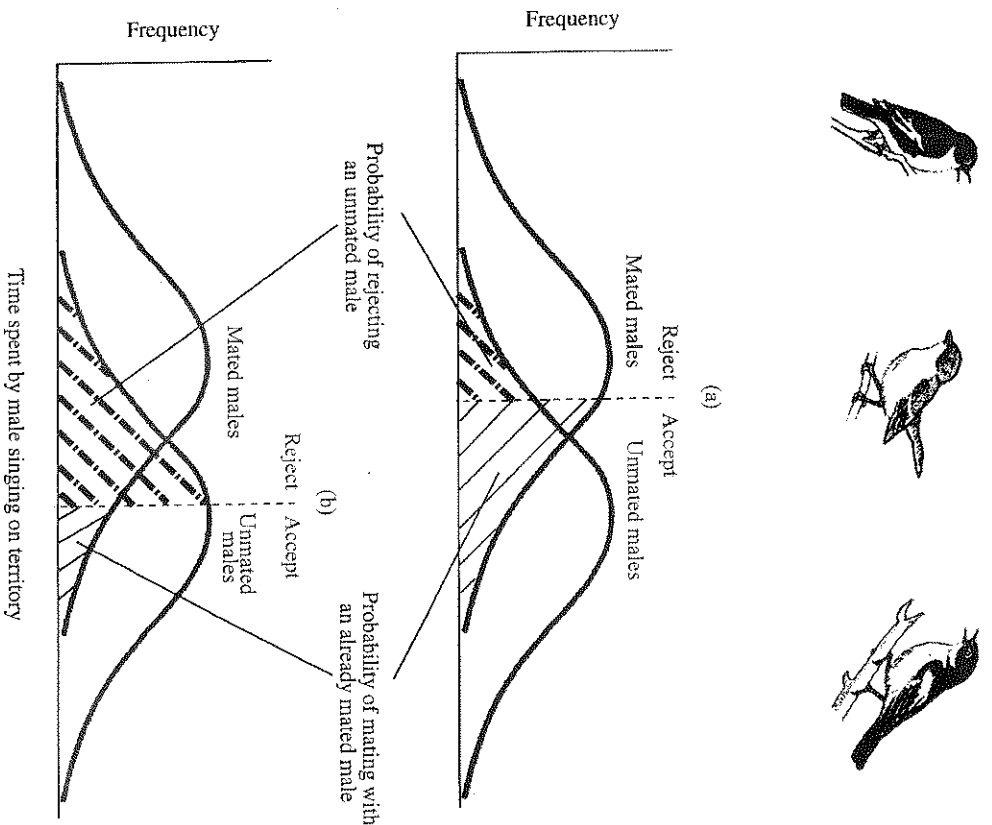


Fig. 4.12. A signal-detection theory approach to mate choice by female pied flycatchers. Females reproduce more successfully as primary or only mates. So, females face the task of choosing unmated males over males on a secondary territory who are already mated with a female on their distant primary territory. Mated males are known to be potentially distinguishable, because they spend less time on average singing on their secondary territories (left-hand distributions) than unmated males do on their primary territories (right-hand distributions). But, discriminating the two categories of males involves uncertainty in proportion to the degree of overlap of the two distributions. Decision criterion (a), at the top, minimizes the mistake of rejecting an unmated male, but at the cost of a greater risk of mating with an already-mated male. Decision criterion (b), at the bottom, minimizes the mistake of accepting an already-mated male, but at the cost of a greater risk of rejecting unmated males. See text for additional details.

rejecting an unmated male. Notice the bind she is in, though, by lowering her criterion, she has increased her risk of mating with an already-mated male. Such constraints on potential mate assessment by females probably account as much for 'deception' in pied flycatchers as devious managerial activity by males does.

Deception: proximate contexts and mechanisms

It was noted earlier that the idea of deception is typically applied when a discrepancy is discovered between what animals should be doing, in our opinion, and what they are doing. However, not all such mismatches are considered deception. Some have been labeled mistakes, especially when the individual is young. An infant vervet monkey, for example, is said to be mistaken, not lying, when it responds to a warthog by barking, a call that adults generally use only for dangerous mammalian predators such as leopards (Cheney & Seyfarth, 1990). Reservations about treating such actions by infants simply as mistakes were discussed in Sections 1.2.9–1.2.11, and it was suggested instead that infants might be using barks as a means of evoking immediate parental feedback and assistance, if needed. This point highlights the importance of critically evaluating our assumptions about the functional organization of the individual's behavior. Youngsters are not 'trying' to act like adults, but falling short; they are behaving under the distinctive constraints of their current developmental stage. And, they are not applying correct versus incorrect, or true versus false labels to events; they are taking care of themselves, in part by making use of resources extractable from the parent. More generally, signals are not most usefully thought of as statements of fact that can be judged to be true or false; signals are more like the human speech acts discussed below – outputs that serve to achieve some effect on targets.

The vervet monkey developmental example above highlights the importance of understanding the mechanisms and proximate contexts of communication. That is, when one understands that young animals use signals appropriately for their ontogenetic niche, one is less disposed to treat them as mistakenly applying vocal labels to the wrong animals. Similarly, when one understands the proximate constraints that male and female pied flycatchers work under, the concept of deception becomes less useful. The knowledge structures that proximately underlie animal communication are discussed in Section 4.4.2, and it is proposed that they are much more similar to what has been called procedural memory than to semantic memory. That is, the evidence of domain specificity even in the relatively sophisticated cognitive systems of such species as vervet

monkeys (Cheney & Seyfarth, 1990) suggests that their knowledge is tied to particular action systems, rather than being applicable more broadly as some aspects of human knowledge are. This indicates that animal knowledge structures are fundamentally pragmatic, i.e., about what *to do* about objects, events, and states, a finding consistent with the stance specified by an A/M approach. According to this approach, signals are not statements of fact, that can be judged to be true or false, but are efforts to produce certain effects.

Even human language, that most semantic of communication systems, has this pragmatic quality, according to the *speech-act* literature (Horn, in press). Many human speech acts are not true or false statements of fact, but efforts instead to accomplish specific goals. The following examples illustrate this point.

1. 'Get out!'
2. 'Take your hands off of me!'
3. 'I now pronounce you husband and wife.'
4. 'Please make yourself comfortable and tell me what's on your mind.'
5. 'If an emergency arises, line up single file and walk quietly and quickly to the shelter.'

Those who offer analogies to human language in animal communication should attend to the speech-act literature at least as much as to the literature on cognitive representation.

A dedicated proponent or devil's advocate of information exchange might respond that even the above examples of speech acts need to correlate with conditions important to assessing target individuals in order to be effective. Statement 3, for example, is valid only if issued by a Justice of the Peace, or ordained minister. If issued by a person on the street, the man and woman do not legally become husband and wife. Similarly, statement 5 will continue to be effective only if marching quietly in line to shelters proves to be an effective way to deal with emergencies. Are these correlates, an information advocate would ask, not the information made available by these signals? No; this question confuses time frames of causation. Such correlates *validate* the cues as useful to assessing individuals (Horn, 1997), but are not the immediate cause of the assessing individual's reaction to the statement. Note that Horn's proposal turns the usual view of the role of information on its head. The correlates of signals ('information') are not immediate causes of the behavior of targets of signals, they are instead long-term validators of the signal's utility.

4.5 Development

According to an A/M approach, individuals are complete A/M systems within their natural developmental niche even at birth. In other words, their behavior must be understood in terms of how it meets their needs now, and not just how it contributes to maturation. These complete individuals are born into an environment consisting of other animals that are at least as complex and actively self-interested as the developing individual. So, from the outset, effective management necessitates negotiation and even competition with companions.

These managing/assessing companions are often very reliable sources of feedback about which managerial tactics are most effective, and under what circumstances. This feedback does not necessarily arise from teaching; it is often a product of the other individuals' pursuit of their own interests. Without this daily give and take of life with companions, individuals develop only limited effectiveness, at best, in managing the behavior of others (Mason, 1979c; West, King & Freeberg, 1997). Such developmental effects of companions can be illustrated by West, King and Freeberg's work on the ontogeny of competence as a singer in male brown-headed cowbirds. If young males are reared with the opportunity to interact only with older conspecific females, but not with older males, they develop songs that are actually *more* effective than those of normal males at evoking copulatory postures in females during playback studies. How could 'deprived' males develop more potent songs? Doesn't this contradict the statement above that social feedback is essential for the development of social competence? Only apparently. It is important to note first that these young males were not deprived of feedback from females; the selective responses of females to particular song structures did in fact play a role in shaping the potent songs that the young males came to sing (West, King & Freeberg, 1994). But, the absence of feedback from older males had a profound effect on the competence of these young males. Even though they had very potent songs, they did not deploy them effectively. Normal males sing as part of energetic efforts to court females, approaching them, maneuvering to get in front of them, fluffing their feathers as they get close, and mounting when the female invites it. In contrast, the male-deprived males did sing at females and even occasionally mounted them, but they lacked the normal males' enthusiasm and focus, quickly lapsing into a state of disinterest, perching, and 'vocalizing in a manner closer to hiccupping than interacting.' Despite their

more potent songs, deprived males achieved many fewer consorts than normal males did.

Such results indicate that the development of individuals is channeled by two inherited sources of influence. When we think of inheritance, we usually think of inherited genetic programs. However, genetic programs are selected to induce only those developmental outcomes that are not reliably generated by the environment. Developing individuals also inherit the environments with which they must negotiate (West *et al.*, 1994).

At any age, other organisms play key roles in an individual's fundamental regulatory processes. These other organisms may be sources of food or competitors for it, cues about the presence of predators, refuge from predators or sources of predatory threat, warmth to huddle with in the cold, collaboration in bringing up offspring or infanticidal threat to young, and so forth. Such contributions by one individual to the regulatory processes of another are perhaps most conspicuous in parent-offspring relationships. For example, the role that the mother plays in a rat pup's thermoregulation has already been discussed. The mother's huddling with and retrieval of her pups plays a critical role in the pups' maintenance of body temperature. And, of course, the pups orchestrate such maternal contributions with their ultrasonic vocalizations. It is only at later ages and larger sizes that pups become more self-sufficient in their thermoregulatory abilities (Ryan & Rand, 1993b).

A conspecific constitutes a package of influences on a developing individual (Lorenz, 1970). Discovery of the contents of this package has required much careful experimentation. For example, a long period of separation of a rat pup from its mother (18+ hours) induces an initial period of persistent retrieval calling by the pups (see above), and a later phase involving a complex of other changes that seem superficially like the 'despair' exhibited by human infants during long-term separation. However, detailed analysis of the properties and sources of these longer-term changes illustrates the mother's many separate contributions to the pup's regulatory processes, and the inapplicability of the despair concept (Hofer, 1987). The separately regulated processes in the pup include its gross motor activity level, sucking behavior, oscillation between sleeping and waking, and release of growth hormone. Different kinds of maternal stimulation produce increases and decreases in the level of these various processes. For example, activity level in a novel environment increases in pups isolated from their mothers but artificially maintained at appropriate nest temperatures. This increase

begins approximately four hours after separation and reaches an asymptote after about 18 hours. It is not nutrient levels that normally limit activity levels; contact with the mother blocks this increase, for example, even when she cannot nurse her pups. It is the olfactory and tactile stimulation provided by the mother's periodic visits to the nest that tends to keep activity down to normal levels. On the other hand, if pups are not artificially kept warm during these long-term separations, their activity undergoes a decrease rather than an increase. This suggests that the thermal stimulation provided by the mother tends to increase activity levels, and that the opposing effects of thermal and tactile/olfactory stimulation tightly maintain pup activity levels within a narrow range.

Such maternal contributions to young mammals' management of their own situations does not cease once youngsters become more mobile and thermally self-sufficient. As four-week-old Belding's ground squirrels first begin to emerge from their nursery burrows, they face serious danger from predators (Mateo, 1996): 13–27 percent of them will disappear during their first two weeks above ground, primarily as a result of predation. So, they would benefit from being able to respond appropriately to evidence of a nearby predator. Playbacks of the antipredator calls of this species indicate that the pups rely on their mother initially, but quickly become more self-sufficient. On the first day of emergence, pups are more likely to respond to playbacks if their mother is present than if she is absent. When they do respond, they typically bolt into their burrow, leaving the job of surveying for predators to their mother. By day five, pups react to playbacks whether or not their mother is present, and they remain outside their burrow, standing tall on their hind legs as they survey for the source of alarm themselves. (This rapid development of self-sufficiency may be in preparation for independence only four to six weeks after emergence, at about ten weeks of age (Holekamp & Sherman, 1989).)

Infant vervet monkeys also appear to use adult guidance. If they look toward adults before responding to an antipredator call, their behavior is more likely to be appropriate for the call's typical predatory elicitor than if they do not glance at an adult first (Cheney & Seyfarth, 1990). There is evidence that infants actively solicit this adult guidance, rather than simply using it when available (Owings, 1994). Infant vervet monkeys emit antipredator calls at a much wider variety of disturbances than adults do (Cheney & Seyfarth, 1990). Calls by infants at harmless species have been treated as mistakes (Cheney & Seyfarth, 1990), but there is evidence in

this same research program that calling infants receive immediate adult guidance and assistance (Owings, 1994). If the animal eliciting the infant's calling is a dangerous predator, then adults call, too; the infant, in turn, responds by fleeing to its mother, who protects it. If, on the other hand, the infant has called at a relatively harmless species, others are less likely to call, and the parent even occasionally punishes the infant (see also Caro & Hauser, 1992).

What are the developmental effects on the youngster of such maternal influences on regulatory processes (and paternal and peer, too, where there is regular contact with these types of individuals)? This question can be posed in two time frames – relatively immediate and longer term. With regard to relatively immediate effects, one can explore how these processes contribute to the individual's effectiveness as a manager/assessor while it is still young. With regard to the longer-term, one can ask how maternal regulatory processes lead to eventual development of adult levels of self-sufficiency.

4.5.1 *Immediate effects*

Relatively immediate effects can be illustrated with the copious research on filial imprinting in domestic chickens and their wild progenitors, Burmese red jungle fowl (for reviews see Bolhuis, 1991; Bolhuis & Van Kampen, 1992). Chick embryos first respond to sound at about 14–15 days gestational age (six to seven days before hatching). Two-way vocal interaction between the embryos and their mother begins on the day before the chicks hatch, and the rate of calling by both mother and offspring increases as the time of hatching approaches. When the embryo emits distress peeps, the hen calls or moves to the nest, and the embryo becomes silent or begins to emit pleasure notes.

During the first one to two days post-hatching, the chicks remain mostly in the dark under their mother, but very much in vocal contact with her. If they do become separated from their mother during this time, young chicks do approach and follow her and their siblings. Their readiness to follow is intensified by the *chicks' chicks* that the mother emits repeatedly as she walks along with ruffled feathers. As a result of this association, the chicks develop a visually based attachment to these individuals, and the stimulation produced by the mother's *chick chucking* enhances their subsequent attraction to her (Van Kampen & Bolhuis, 1993). Soon, when the chick is close to its mother and siblings, it will attempt to snuggle up, frequently emitting *whew* or *trill* vocalizations. If

the chick becomes isolated from its family, it will switch to loud *peeps* as it searches to reunite, but will avoid approaching a strange hen.

Early on, the clutch of siblings sticks together tightly and rarely strays more than a meter from the mother. Such attraction of a chick to its family has great utility; the mother is a remarkable resource for the chicks during this time. With regard to their nourishment, for example, the chicks respond to their mother's food pecking by pecking at objects on the ground, and they learn to peek at the same kinds of food items that she does (Suboski & Bartashunas, 1984). The mother also uncovers food for young chicks, breaking food items up if they are too large, and passing them directly to her chicks. As they grow older and wander more distantly, chicks respond quickly to the mother's *duk duk duk* food calls, approaching and eating the food items that she points to with her beak (Stokes, 1971). Chicks also cope with predatory threats through their mother (Palleroni & Marler, in press). When alone, chicks have only one response to initial evidence of predatory threat: they freeze and go silent. In the presence of their mother, however, they adjust their behavior more appropriately for the form of predatory threat. Cueing on their mother or on a nearby cock, chicks scatter and take cover at the adult *screams* that aerial predators evoke. In contrast, the mother's *duk, duk, duk, kaahs!* to terrestrial predators prompt the chicks to move away from cover and assemble about her, *peeping* repeatedly.

Social companions also have subtle and unexpected influences that fall outside the realm of what might be called 'guidance.' As noted briefly above, chicks begin distress *peeping* when socially isolated, and the arrival of either siblings or the mother is a source of feedback to the calling chick, reducing its calling. The chick's *peeping* is an effective means of helping to restore contact with its family; *peeping* increases maternal efforts such as calling to reunite with her young (Hughes, Hughes & Covalt-Dunning, 1982). In mallard ducklings, the tactile stimulation that comes from close association with the mother and siblings has a powerful calming effect that initiates a period of malleability, during which preferences develop for the vocalizations heard regularly during that time. In a natural context, these vocalizations are the maternal calls of the ducklings' mother, and the tactile stimulation comes from her and other ducklings. However, experimental work indicates that exposure to playbacks of heterospecific maternal calls, of a domestic chicken rather than a mallard, can induce a preference for the chicken calls as long as the requisite tactile stimulation is present. In addition, this tactile stimulation can be provided mechanically rather than by other ducks (Gottlieb,

1993). Thus, some kinds of stimulation come as parts of the social-companion package, and can contribute to learning during development without providing specific cues about what is to be learned. This process of creating a state conducive to learning, in contrast to processes of (incidentally) 'instructing' the developing individual, provides an example of motivational effects on the ontogeny of assessment systems.

The above discussion indicates that management and assessment processes within the same individual become linked to each other through their reciprocal influences on each other during development. It has been seen that tactile stimulation from family members sets the stage for development of such fundamental assessment abilities as recognizing conspecifics through their vocalizations. But, it has also been noted that developing individuals are not simply passive recipients of such tactile stimulation. Contact with others comes about in part as a result of the developing individual's own efforts; distress calling by a youngster, for example, attracts family members into contact with it. So, individuals play a significant role in orchestrating their own development, but they do so in part through the social consequences of their managerial activities (West *et al.*, 1997). These social consequences include incidental 'instruction,' in the sense that specific patterns of stimulation are learned and subsequently influence the individual's behavior. But, motivational effects are also important, in the sense that social consequences can influence development and learning, but do not become part of what is learned.

The motivational effects of social stimulation seem to be especially linked to its contingent properties, that is, to the parts of social input that are responses to the individual's own behavior. Young Japanese quail chicks, for example, develop a preference for an object that they see during their period of imprinting (ten Cate, 1986). The strength of this preference depends on certain properties of the object. If the object moves rather than remaining stationary, the chick becomes more attached to it, and if the object's movement is produced by the chick's distress calling, the attachment is especially strong. So, the chicks are most likely to become attached to the individual who most consistently responds to their calls, and, in the natural context, that individual usually happens to be the chicks' mother or siblings.

4.5.2 Longer-term effects

As discussed above, the neural representations of companions acquired early in life play a relatively immediate role. They are used by the devel-

oping individual to recognize and maintain an attachment to specific adults and peers. These same stored images of companions can also play a role later in life in the development of preferences for sexual partners (Bischof, 1994). This process of sexual imprinting involves two stages – the acquisition of the neural representation of companions, and the consolidation of sexual preference, in which this recognition system becomes linked to the executive neural system for the production of sexual behavior (Bateson, 1987; Bischof, 1994). The idea of two stages may sound familiar; as discussed below and in Chapter 1, a songbird's development of the ability to sing species-typical song also involves a two-stage process in which an early stored representation of normal song becomes linked to the vocal output system through a process of feedback-based practise. Sexual imprinting and song learning share the additional feature that social interactions significantly influence the outcomes of those processes (ten Cate, 1994; Bischof, 1994; Clayton, 1994). The ontogenetic processes underlying sexual imprinting and the development of song will provide the core for our exploration of longer-term developmental processes.

Zebra finches are one of the few species in which both song learning and sexual imprinting have been studied in some detail (see Clayton, 1994). This is an Australian species that exhibits a prolonged breeding season each year, extending for as long as seven months (Zann, 1990). Young become nutritionally independent at about 35 days of age, shortly after which their parents begin to re-establish their nest for another brood. At this time, the young often maintain their association with their natal colony, but join in flocks with adults for foraging and drinking sorties outside the bounds of the colony. Unlike many species of songbird (Baptista & Gaunt, 1994), female zebra finches do not sing. Therefore, the following survey focuses on males, the sex emphasized in studies of song development and sexual imprinting.

The processes of maturation of song structure and sexual preference follow apparently independent schedules. Neural storage of the relevant representations occur during restricted periods of the individual's lifetime, but at different times for the two processes. For sexual imprinting, storage is completed for the most part during the period from 13 to 19 days of age, but may under some conditions be extended (Bischof, 1994). The storage phase for song learning hardly overlaps at all with this dominant period of storage for sexual imprinting, occurring as it does from about 35–65 days of age (Slater, Eales & Clayton, 1988). Both

sexual preference and song structure crystallize as individuals become sexually mature, at about 80–100 days of age (Zann, 1990; Bischof, 1994).

4.5.3 *Sexual imprinting*

Evidence that adult sexual preferences in male zebra finches are founded upon early social learning comes from cross-fostering experiments, in which zebra finches were reared by Bengalese finches (Immelmann, 1969). When tested as adults, such cross-fostered males exhibited a preference for female Bengalese finches over females of their own species. This preference is founded primarily upon the learned visual features of the foster mother (Bischof, 1994). For example, males were foster reared by zebra finch parents. In some foster-parent pairs, the fathers were of normal plumage and the mothers were an all-white domesticated form; in other pairs, mothers were normally plumaged and males were white. The fostered males subsequently preferred a female with the same plumage as the foster mother's (Vos, 1994)

The early learning in sexual imprinting is influenced by the frequency of social interaction, including vocalization, between the developing individual and its foster parents (Bischof & Clayton, 1991). The male within each litter that begged and called for food most from its Bengalese finch foster parents and that was fed the most by them developed the strongest preference for Bengalese finch females when given a choice between these and female zebra finches. However, this latter study indicated that a second phase of social interaction, the first courtship, was important in stabilizing the males' sexual preference. These males were reared with their Bengalese finch foster parents until 40 days of age and then isolated until day 100. After that, half of the males were exposed to a Bengalese finch female for one week and a zebra finch female during the next week, and the other half received similar exposures but in the reverse order. These highly sexually ready males actively courted these females. Finally, all males were tested for their sexual preferences in a simultaneous choice between Bengalese and zebra finch females. Those males exposed first to Bengalese females after day 100 unanimously preferred Bengalese females in the preference tests, singing almost exclusively to these females of the same species with which they had been fostered earlier. In contrast, those males exposed first to zebra females exhibited much more variation in the preference tests, some preferring zebra females, others Bengalese females. The importance of the first courtship after sexual maturity in the development of sexual preferences reflects the operation of a second stage in

this process (Bischof, 1994). In the natural context, the species first courted would be the parental species, and the experience would simply consolidate the sexual preference. Two kinds of evidence indicate that this second phase is one of consolidation rather than additional learning. First, other males in the above study (Bischof & Clayton, 1991) were reared by zebra rather than Bengalese finches. In contrast to the males fostered with Bengalese finches, these males exhibited a preference for zebra females irrespective of which species they were exposed to first after day 100. Second, actual exposure to a female need not occur at this time in order for consolidation of the sexual preference to take place. If a male's sexual motivational system is simply aroused, e.g., through exposure to a nest box and nest, this is sufficient to stabilize his sexual preference for the parental species, whether they were heterospecific or conspecific (Oetting, Prove & Bischof, 1995).

Bischof has hypothesized that this consolidation process does not involve the storage of additional details about the perceptual features of preferred mates. Consolidation is instead the establishment of connections between the recognition system in which preferred perceptual features are stored, and the executive neural system that regulates the expression of reproductive behavior (Bateson, 1987; Bischof, 1994). In other words, the effects of consolidation are more motivational than cognitive. However, the experimental creation of a mismatch between the features of the currently courted conspecific female, and those of the heterospecific foster mother can initiate the establishment of a second neural representation, of the features of this second type of female. In this situation, the interaction with this second type of female has the potential to consolidate links between the executive system and the representation of both the foster mother and the current female.

The extent to which the second representation 'captures' any input sites depends on the number of sites that the representation of the foster mother is able to dominate. There is reason to believe that the number of these input sites is limited, so that strong connexion by one representation can 'competitively exclude' another (Bateson, 1987). Consistent with this idea is the finding that the half of the males that begged from and were fed most frequently by their Bengalese foster mothers exhibited very little shift in preference to zebra females as a result of exposure to them (Oetting *et al.*, 1995). In other words, their foster-mother representations occupied most of the available connexions during consolidation. In contrast, the half of the males fed least frequently by their Bengalese foster mothers exhibited a significant shift on

average toward a preference for zebra finch females after exposure to them. The less-fed males varied in their preference shift, depending on their motivational state at the time of exposure to the zebra female. The higher the male's arousal during exposure to the zebra finch, the stronger his subsequent preference for the zebra female. According to Bischof's hypothesis, higher male arousal while with the zebra finch female generated capture of a larger proportion of inputs by the representation for zebra females during consolidation, and therefore a stronger shift toward preference for the zebra female.

In summary, to communicate competently during courtship, a male zebra finch must be able to direct singing and other activities toward the appropriate species of female. This is important, since zebra finches are known to associate in mixed-species flocks during the breeding season (Zann, 1990). The developing male's own social initiatives generate many of the experiences necessary for development of this ability. Prior to fledging, the male's visual and vocal signaling during food begging stimulates feeding by the parents; these experiences yield a neural representation of the mother in the fledgling that can subsequently guide selection of a target for courtship. But the assembly of the courtship system into a functional mechanism depends on additional initiatives by the developing male. The first efforts at courtship generate connexions between the previously established recognition system and the neural systems that regulate expression of courtship behavior. This consolidates the mechanisms underlying male courtship behavior and sets the stage for effective deployment of courtship signals.

Of course, this summary represents only a small part of the whole developmental story. For example, some of the components of the courtship executive system are similarly dependent on the give-and-take of social interaction for their normal development. The ability to sing normal song is one example, which is the topic of the next section.

4.5.4 *Song learning*

When Immelmann (1969) cross-fostered zebra finches with Bengalese finch parents, the zebra finches not only preferred Bengalese over zebra females, but also sang songs that resembled those of Bengalese finches. The processes involved in development of song have since been explored in some detail.

As noted above, young zebra finches become nutritionally independent of their parents at about 35 days old. They form small, inconspicuous

groups within the colony at this time, but begin to flock with other adults around day 40 for feeding and drinking forays away from the colony. While in the nesting colony, immature birds remain relatively inconspicuous, but males begin their first efforts to sing around fledging time, and solitary males can be heard singing loud bouts of subsong from the tops of bushes (Zann, 1990). If we can extrapolate from observations of other species (West & King, 1985; DeWolfe *et al.*, 1989), these early singing efforts are associated with involvement in social interactions, including aggression. Songs mature when the zebra finch is about 80 days old, and might be placed into use for courtship shortly after, since males mature sexually at about the same age and this species has a breeding season that extends over about seven months. An estimated 65 percent of males learn songs from their father.

What is the nature of the developmental process leading to the ability to sing normal zebra finch song (see Slater *et al.*, 1988; and Clayton, 1994)? It is restricted in time; males typically 'memorize' the songs that they will subsequently copy between 35 and 65 days of age. If separated from a singing adult male at 35 days of age and exposed to another male, a developing male will not incorporate elements from the first male's song into his own. But, if allowed to remain with an adult male until 65 days old, young males will make extensive use of the adult's song elements. Even though youngsters have fledged by the beginning of this learning phase, their continued association with their father is apparently sufficient to allow a fair amount of song learning from him (Zann, 1990). This sensitive phase for song learning does not begin and end abruptly; it varies, depending on the developing individual's circumstances. For example, males do remember the songs that they heard prior to 35 days of age, but typically do not incorporate elements from them into their own song. However, elements from early songs may be used if the social stimulation available after 35 days of age is sufficient to stimulate song development, but insufficient to stimulate song learning, e.g., because visual access to the 'tutor' is not available, or the subsequent male is a different species from the father.

The sensitive phase for song learning by zebra finches involves two separate learning processes – song memorization and learning to produce that song. However, zebra finches were not conducive to the discovery of these separate processes for two reasons: they do not readily learn song from noninteractive playbacks of recorded song, and their two stages of song development overlap in time. White-crowned sparrows differ from zebra finches with regard to both of these traits: they readily learn from

playbacks of recorded song and temporally separate the two stages more than zebra finches do (e.g., see Nelson, Marler & Pallarini, 1995). As noted in Chapter 1, these sparrows have contributed significantly to the understanding of song development.

White-crowned sparrows sing one, stereotyped song. Their songs are, however, variable in another way; white-crowned sparrows exhibit dialects, in which local populations share a particular variant of the song, which is structurally distinguishable from the songs sung in adjacent populations. Figure 4.13 provides spectrograms of several white-crowned sparrow songs, and illustrates some of the differences among three identified dialects. Even though the dialect differences are evident among song pairs, the similarities among the pairs are equally conspicuous. All begin with whistles, progress to a buzz, and continue to a warbling series of note syllables or clusters. (Many also finish with another buzz, but this is soft enough to be lost in many field recordings; a terminal buzz is faintly visible in the spectrogram in Fig. 4.13c.) The variation among dialects provides a useful means to assess the extent to which vocal copy-

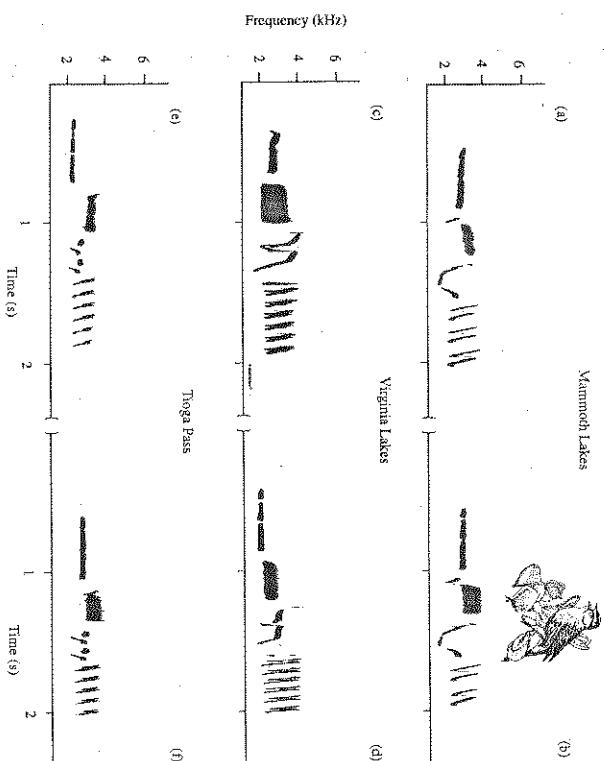


Fig. 4.13. Dialects of white-crowned sparrows from three different regions of the high Sierra Nevada mountains of California. See text for additional details. (Spectrograms and drawing courtesy of Luis Baptista.)

ing occurs; different individuals can be exposed to different dialects, and their subsequent songs can be compared to those of different dialects.

According to the early work on song development in white-crowned sparrows (Marler, 1970), memorization occurs only if males are exposed to recordings of songs during a critical phase, from 10 to 50 days of age. Delay of exposure to song playbacks until after that phase may have a general 'normalizing' effect on song structure, but the details of the training song are not copied by the male. In addition to being restricted in time, song memorization appears to involve an 'own-species' bias. White-crowned sparrow songs heard at this time become models for song production later, but the songs of other species do not. Males begin to produce song-like sounds as early as their second month post-hatching, but these subsong vocalizations are a far cry from the song of a normal adult male; no adult syllables are recognizable (Fig. 4.14a). It is not until the male makes a transition to plastic song at about 150 days of age that the effects of the memorized song begin to be evident. Plastic song is much more variable than mature song, but is divisible into introductory whistles and terminal trills, as mature song is, and contains recognizable elements of mature song (Fig. 4.14b and c). So, the memories of songs heard during the critical phase are stored without visible effect on song structure from about 50–150 days of age. This second phase appears to involve the singer comparing its actual vocal output to the structure of the memorized song, and adjusting its vocalizations to match this preferred song structure. If males are deafened after memorizing but before this 'practise' stage, then highly abnormal song is produced (Konishi, 1965). Song structure stabilizes at about 10–12 months of age (Fig. 4.14d), and little further change in vocal structure occurs.

Subsequent work indicated another, more social level of specification in the developmental systems involved in the ontogeny of song. The above work deals with specifications about song structure, indicating that the stored representations of song structure can serve as the *preferred value* in a regulatory system in which the *actual value* consists of the sounds that the bird is actually producing. Development in this case involves matching actual value to preferred value, that is, the song sung to the song memorized. But, the existence of social specifications is indicated by the fact that many species, including zebra finches, will not use noninteractive song playbacks as models in song development (Slater *et al.*, 1988); they need a singing bird to interact with. Furthermore, both the own-species bias in song structure specifications and the limitations on timing can be at least partially overridden by social circumstances.

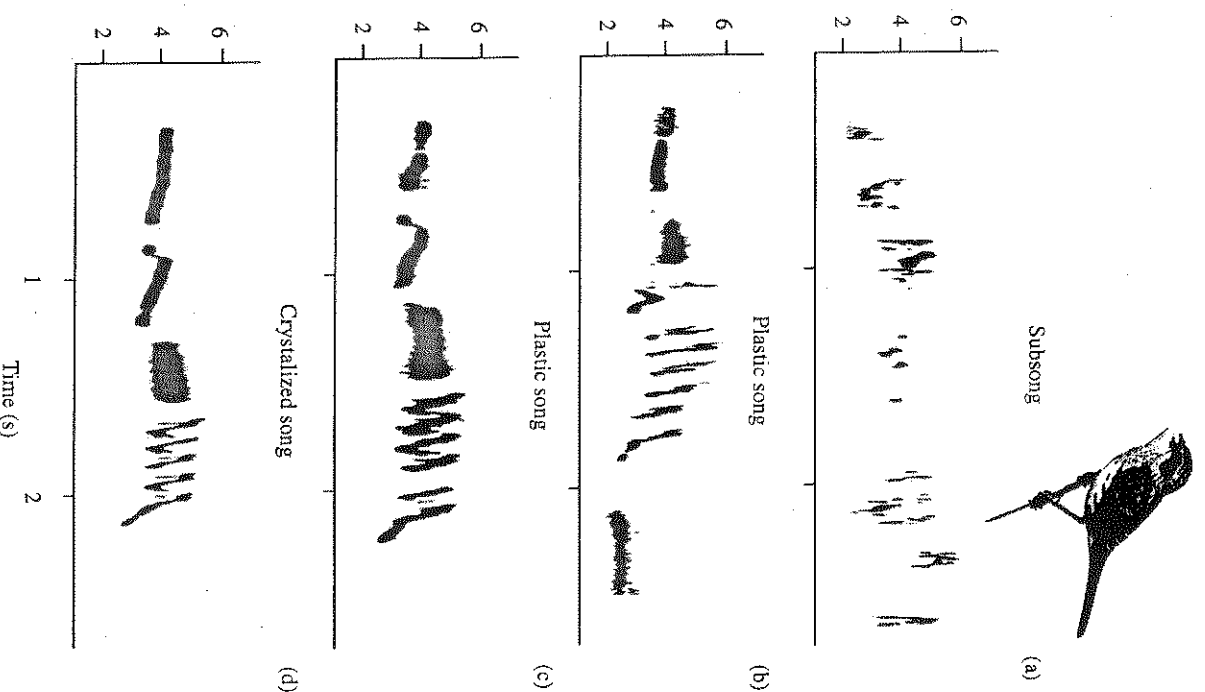


Fig. 4.14. The stages of development of song structure in white-crowned sparrows. See text for additional details. (Spectrograms courtesy of Doug Nelson.)

For example, even though zebra finch males do not typically sing the songs that they have heard prior to 35 days of age, they do remember those songs and will sing them under unusual circumstances (Clayton, 1994). If the only source of song input after 35 days is of a different species from the male who reared him, the developing male is disposed to incorporate elements of the earlier song into his own, even if the 'father' was a Bengalese finch. Similarly, if the only source of song input after 35 days is out of view, the developing male is disposed to incorporate elements of the earlier song into his own. What is deficient about input when the singer is not in view? One missing ingredient is the opportunity for social interaction. Indeed, when a young male has access to more than one singing adult, he is more likely to copy the song of the male that is more aggressive toward him. Even a tape recording of song can become a model for song learning if its playback is interactive. Male zebra finches who can turn on song playback by pecking a key copy more of the song than other males who can simply hear the playbacks but have no control over them (Adret, 1993).

Song development is typically embedded in the give and take of a social context. If we think of song and singing behavior as acts specialized to manage the behavior of others, then it is to be expected that social feedback should influence the structure of songs or the patterning of singing, or both. Developmental systems should be selected to induce ways of behaving socially that are effective in meeting the developing individual's needs.

The results of later research on song development in white-crowned sparrows were consistent with this pragmatic approach. Observations of singing behavior in natural populations revealed that some juveniles begin staking out territories in September and October, only three to four months after hatching (DeWolfe *et al.*, 1989). These intense social interactions are associated with accelerated song development, so that song crystallizes much earlier than in hand-reared birds (as early as 90 days, compared to 250 + days). Intriguingly, even prior to song crystallization, males use plastic-song in aggressive interactions, and these evoke aggressive responses by adults. Even more intriguingly, variation in plastic-song structure takes the form of singing up to four different song types. Juvenile males typically winnow such repertoires down to the one crystallized song that matches that of the males with whom they interact most. And, finally, there is evidence that plastic song is not just a developmental stepping stone to crystallized song. Young males singing plastic song will at times switch to crystallized song if challenged

by another male. So, plastic song may serve a social function that is different from that of crystallized song.

Even within the species white-crowned sparrows, the details of development differ among populations in ways that appear adaptive to local conditions (Nelson *et al.*, 1995). The results described immediately above were from a nonmigratory population of the subspecies *nuttalli* living in the moderate climate of central coastal California. Other populations breed in more strongly seasonal climates, such as the subspecies *oriantha* in the high Sierra Nevada mountains of California, and they are migratory, spending only the late spring and summer in the Sierra Nevada. In laboratory studies using song playback for tutoring, *nuttalli* memorize song later on average than *oriantha* do, a possible adaptation that allows matching of song to local singers as territorial behavior begins as early as the first autumn. In contrast, *oriantha* busy themselves with migrating in the autumn, feed in flocks during the winter, and only become territorial in the next breeding season back in the mountains. Correspondingly, they produce more varieties of plastic song than *nuttalli* do, and continue in plastic song for twice as long as *nuttalli*. These *oriantha* specializations may allow yearling males better to match local songs via selective attrition of song types long after memorization is done. Such an ability may be particularly important for the males of a subspecies who move farther from their region of birth, and therefore face more uncertainty about the local song types that they will encounter.