Figure and Ground Squirrels

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DISSERTATION

Submitted in partial satisfaction of the requirements for the degree of

DOCTOR OF PHILOSOPHY

in

Psychology

in the

OFFICE OF GRADUATE STUDIES

of the

UNIVERSITY OF CALIFORNIA

DAVIS

Approved:

Committee in Charge

1998

Chris Thomas Tromborg

June 1998

Psychology

Figure and Ground Squirrels

Abstract

The influence of sound on antipredator vigilance in artificial settings was studied in California ground squirrels (Spermophilus b. beecheyi) as analogues for other laboratory and zoo animals. Wild-caught and laboratory-born squirrels were placed in an experimental setting with a naturalistic substrate and provisions for sound presentation. Data were unobtrusively video recorded from an overhead view for frame-by-frame analyses.

In the first of 3 studies, the vigilance behavior of 6 wild-caught squirrels from high elevations and 6 from low elevations was compared as they emerged from nest box refuges under 3 sound conditions: building, forest, and thunderstorm ambiences. Though behavioral changes were evident for all conditions, they did not reach statistical significance $\left(\alpha = .05\right)$. However, when conditions were collapsed, high elevation squirrels emerged from refuge significantly less frequently than the others. Under the thunderstorm condition, females emerged less frequently than males.

In the second and third studies, 6 wild-caught and 6 laboratory-born squirrels were compared over a 6-day period on the basis of differences in the orientation of visual scanning during their initial daily emergence. In the normative study, both groups exibited similar durations and frequencies of sideways and upward scanning. On the first day both groups displayed high levels of scanning in both directions; by the fifth day, all scanning had declined significantly. Groups did not differ significantly in any aspect of scanning behavior.

The third study, conducted 6 months later with the same subjects, examined scanning during emergence under building ambience, white-noise pulse, or ground squirrel antipredator vocalization conditions. Both groups increased scanning on days featuring the presentation of antipredator vocalizations. Wild-caught squirrels focused their scanning on the presumptive locations of avian and mammalian threats, as signified by antipredator vocalizations. Laboratory-born squirrels engaged in a more global assessment of their surroundings. These findings suggest that, though alarm calls might innately signify the presence of aerial or terrestrial predators, searching for them in specific spatial domains is developed through experience normally unavailable to captive animals.

Acknowledgments

I first wish to acknowledge my family and friends for their support and understanding throughout my academic career. I next wish to express my gratitude to the chair of my dissertation committee, Richard G. Coss, for his assistance in the acquisition and analysis of the data and with the preparation of this manuscript. Equally, I wish to express my gratitude to the other members of my graduate committee, Gary D. Mitchell, Donald H. Owings, and Hal A. Markowitz, for their suggestions regarding the execution of this project, the revision of this manuscript, and most importantly, for their infinite patience.

I am especially indebted to Nancy Bacon for her care and dedication in maintaining the research subjects. I am further indebted to my colleagues, Rosemary Babcock, Stan Bursten, Brad Dowd, and Ron Goldthwaite for their constructive criticism and assistance with the preparation and execution of this manuscript. Additionally, I wish to extend my gratitude to Josh Burke, Derel Hendricks, Tricia Tulapano, and Mat Wacker for their assistance with the decoding of an otherwise unmanageable number of videotapes. Moreover, I wish to express my gratitude to all of the staff and faculty of the Department of Psychology at The University of California, Davis, and the Department of Biology at California State University at San Francisco, from whom I received invaluable assistance. Finally, I must acknowledge the contribution of the squirrels, without whose participation this project would have been difficult. "Never has so much been owed by so many to so few."

This research was approved by the U.C.D.I.A.C.U.C. under protocol #UCD-5486 and partially supported under UC Research Grant 1016.

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CHAPTER ONE

The Sound and the Furry

The continual destruction of natural habitats probably relegates future representatives of surviving species to the protected, discontinuous remnants of their former habitats, the restricted habitats of wildlife parks, the artificial environments of zoological parks, or institutional animal-care facilities associated with biomedical research (Carpenter, 1983; Conway, 1974). All of these venues are likely to become acoustically more similar as they are impacted by the surrounding infrastructures of human societies. Nonetheless, they will have to function as reservoirs for populations of common, rare, and endangered species.

As the populations of some species continue to decline, managing them even in such compromised habitats will become increasingly important. Critical environmental factors that influence the reproductive success, long-term survival, welfare, and expression of species-typical behavior of captive animals should be discovered, described, and incorporated into husbandry routines as components of conservation programs (Burghardt, 1985; Markowitz, 1997).

Ideally, well-designed environments should reduce the occurrence of sterotypic behaviors while maximizing opportunities for animals to engage in appropriate interactions with their surroundings (Mason, 1991; Markowitz, 1982). Environments should, in fact, provide animals with challenging experiences that prepare them for ultimate reintroduction into their former habitats (Beck, 1991). Minimally, environmental modification procedures should be developed to immerse animals within environments featuring some relevant characteristics reminiscent of natural environments (Markowitz and Gavazzi, 1995; Tromborg, 1993).

Ultimately, the application of ecologically relevant procedures could minimize the divergence of captive populations from their ancestral forms. Divergence is most likely to occur if limited, inbred populations adapt to environments substantially different from those in which their species evolved (Boice, 1980, 1981; Frankham, et al., 1986).

All of these goals provide motivation to investigate environmental influences on behavior in the restricted conditions of captivity. The traditional belief that research conducted in natural settings has greater validity than that conducted in artificial settings is no longer completely tenable (Timberlake, 1990). Although illuminating research involving the influence of various environmental factors on behavior has been conducted in the field, this venue does not offer the degree of control over subjects and variables possible in the restricted conditions of the laboratory and zoological park (Schneirla, 1950).

Another reason for conducting research in artificial settings is to improve the conditions of captivity. Prior to the introduction of the concept of environmental enrichment (Markowitz, 1973, 1975; Markowitz and Stevens, 1978), most artificial environments were structurally simple and unresponsive to behavior. Typically, these environments did not provide animals with opportunities to interact with their surroundings in ways which promoted the development of their sensory and cognitive abilities.

As a consequence of this realization, over the past several decades scientists have developed strategies for improving the conditions of captivity. They have investigated the effects of modifying the structure, complexity, and interactivity of traditional and artificial environments on the behavior and health of captive animals (Erwin, 1979; Erwin, Maple, and Mitchell, 1979; Markowitz, 1982; Markowitz and Spinelli, 1986; Schmidt and Markowitz, 1977; Snyder, 1975; van Hooff, 1986; van Rooijen, 1984).

Contemporary methods for improving artificial environments include, but are not limited to, enhancing several abiotic parameters, such as enclosure size and substrate complexity (Carlstead, Brown, and Seidensticker, 1993; Erwin, 1979, 1986; Stricklin, 1995; Thomas, 1986). Elements from natural habitats have been introduced into zoo exhibits, imbuing them with an apparent naturalism for visitors and enhancing their ecological relevance to captive animals (Hutchins, Hancocks, and Crockett, 1984).

More complex, enriched environments offer greater opportunities for exploration and withdrawal from observation. Behavioral options allow animals to respond to adverse environmental conditions by managing confinement-related stress (Carlstead, Brown, and Seidensticker, 1993).

Finally, in some instances, interactive or automated technologies have been employed to increase opportunities for animals to engage in complex problem solving while contending with variation in the physical properties of their environments (R. G. Coss, personal communication, 1990; Markowitz, 1982; Markowitz and Stevens, 1978). In essence, intelligently managed zoological gardens attempt to preserve species-typical behavior (Markowitz, 1997).

Acoustics and Animals

While environmental enrichment strategies have undoubtedly improved the conditions of captivity (Erwin, 1979, 1986; Maple and Finlay, 1986; Sadleir, 1975; van Rooijen, 1984), they have tended to underemphasize the influence of artificial environments on the sensory behavior of captive animals. This is especially true for the auditory sensory modality, which, based on the amount of research focusing on audio-vocal behavior in nonhuman animals, is a critical feature of many of their natural histories (Byrne, 1982; Connor, 1982; Ehret, 1980, 1989, 1990; Klump and Shalter, 1984; Knudsen, 1984; Kroodsma, 1989, 1996; Snowdon, 1986).

Researchers studying acoustic phenomena have investigated the structure and function of vocal signals and the influence of habitat acoustics on their evolution and propagation (Bowman, 1979; Klump and Shalter, 1984; Marler, 1967; Morton, 1975; Owings and Morton, 1998; Richards and Wiley, 1980; Waser and Brown, 1984, 1986; Wiley and Richards, 1978). Others have investigated the influence of the acoustic dimension of social environments on the ontogeny and expression of vocal behavior (Cheney and Seyfarth, 1985; Cleveland and Snowdon, 1982; Green, 1975; Miller, 1994; Seyfarth, Cheney, and Marler, 1980; Snowdon, 1986). Still others have focused on the influence of laboratory noise on the genesis of acoustically mediated pathologies (Anthony, Ackerman, and Lloyd, 1959; Gamble, 1982). In a few instances, the influences of anthropogenic noise on wildlife has been investigated (Ames, 1978; Busnel, 1978; Shaw, 1978).

However, there have been few investigations focusing on the influence of typical background acoustics characteristic of research laboratories and zoological parks on the behavior of captive animals. There has been equally scarce research involving attempts to increase the ecological relevance of the acoustic environments of artificial settings. The few studies that have been conducted have yielded inconclusive results (Ogden and Lindburg, 1991; Ogden, Lindburg, and Maple, 1994; Tromborg, 1993).

The paucity of research focusing on the acoustics of laboratories and zoos is surprising, considering that many of them are located near or within urban centers. The acoustic surroundings of urban areas are characterized by chronically high levels of anthropogenic noise, including sounds emanating from transportation systems, communication systems, operation of the urban infrastructure, and vocalizations of other species, including human beings.

The scarcity of knowledge about the impact of environmental sounds on behavior extends to those involved with the detection of and defense against predators. In species targeted for reintroduction to the wild, it is critical that their current environments shape the appropriate development and expression of this essential category of audio-vocal behavior.

Compared with animals dwelling in relatively undisturbed tracts of nature, those housed in artificial environments either fail to receive a full range of appropriate acoustic experiences or are continually exposed to potentially deleterious noise. Laboratory-based research suggests that long-term exposure of animals to elevated levels of unnatural noise is correlated with increases in behavioral, physiological, and developmental anomalies (Anthony, Ackerman, and Lloyd, 1959; Ehret, 1980, 1989, 1990; Gamble, 1982; Snyder, 1975). Research also suggests that these deleterious effects can be reduced through the attenuation or elimination of noise. There has not been a parallel emphasis investigating the effects on behavior of improving the acoustic structures of artificial environments.

These not only possess unnatural noise but usually lack ecologically important acoustic features. Whether or not the ecological authenticity of artificial acoustic environments can be enhanced through the introduction of acoustic elements derived from or reminiscent of natural habitats remains unclear.

As envisioned here, naturalistic acoustic environments could possess features with which species have historically interacted. Their presence could foster normal developmental sequences (Lickliter, 1990). Such acoustic backgrounds could isolate animals from noisy surroundings by masking potentially provocative noise generated near animal enclosures. The perceived attenuation of unpredictable noise could reduce acoustically provoked behaviors, especially startle responses or reclusive behavior. Animals reacting less to unnatural noise and more to species-appropriate acoustic stimulation might express a more normal suite of behaviors.

Research on the influence of all facets of the acoustic domain that can shape the development and expression of antipredator behavior is essential in the design of better environments for captive animals. This is especially critical for species serving as normative populations in biomedical research, those serving as behavioral exemplars in educational exhibits, or for those targeted for reintroduction into natural habitats.

Decibels, Denizens, and Dens

Animals are continually confronted with the challenge of efficiently receiving, processing, interpreting, and appropriately responding to a constellation of potentially important information from their environments (Attneave, 1959; Shannon and Weaver, 1962). Managing this environmental information effectively can confer adaptive advantages in defense, foraging, and reproduction (Dusenbery, 1992). Potential environmental information may be available to animals through several primary sensory modalities, including olfaction, vision, and audition (Bradbury and Vehrencamp, 1998; Brown and MacDonald, 1985; Dusenbery, 1992; Eisenberg and Kleiman, 1972; Lythgo, 1979; Marler, 1977; Stebbens, 1983; Steiner, 1974; Stoddard, 1980; Webster and Webster, 1971). To extract relevant information from constantly changing combinations of environmental sources, percipients must continually adjust their attentional focus to attend to the sensory channels yielding the most immediately pertinent information (Dusenbery, 1992). The effectiveness of environmental information in influencing behavior is partially governed by the *psychological landscape* of percipients, the sensory appropriateness (*relevance*) of phenomena, the prominence (*salience*) of events functioning as signals, the intrinsic meaning (*semanticity*) of such signals, and the nature of contexts within which such phenomena are perceived (Coss and Owings, 1985; Guilford and Dawkins, 1991; Klump and Shalter, 1984; Markl, 1985; Marler, 1985).

Within communication systems, (consisting of management systems, assessment systems, and signals), the effectiveness of signals is influenced by absolute amplitude, environmental attenuation, source signal-to-noise ratio, receiver signal-to-noise ratio, receiver discrimination ratio, the sensitivity thresholds of the receiver, and the information processing properties of the receiver. The information content of signals is usually greater at the source (broadcast information) than that arriving at the recipient (receiver information) (Attneave, 1959; Guilford and Dawkins, 1991; Klump and Shalter, 1984; Shannon and Weaver, 1962; Smith, 1977; Wiley and Richards, 1978). This relationship can be expressed as a ratio of signal to noise. The signal-to-noise parameter is determined by the intensities of signals relative to those of other sensory phenomena occurring simultaneously within the same sensory channel. Any noise operating within a sensory channel not related to the primarily relevant signal reduces the ratio of signal to noise (Fletcher, 1992). The ratio of signal-to-noise can limit the detectability, discriminability, and even the interpretability of important biological signals.

Of the major sensory modalities, the effectiveness of audition is particularly susceptible to degradation from environmental factors. Naturally occurring sources of noise include physical heterogeneities, atmospheric irregularities, and *zoogenic* sound (Waser and Brown, 1986; Wiley and Richards, 1978). Sources of noise can also be *anthropogenic*, originating with human beings and their activities (Shaw, 1978; Tromborg, 1993, 1994; Tromborg and Coss, 1995). This expanding source of signal degradation is of paramount importance for species whose survival requires an unencumbered acoustic channel. Research focusing on the impact of less than ideal acoustics on behavior is inconclusive. Consequently, more research in this area should be undertaken.

A more informed perspective on the influence of all forms of sound on behavior can be developed through investigations of organismic responses to sound in nature and to various environmental manipulations within the controlled conditions of the laboratory. From a theoretical perspective, this type of basic research in sensory behavior increases understanding pertinent to the functioning of sensory systems in a wide range of environmental contexts. From an applied perspective, due to accelerating rates of environmental degradation, there is an urgent requirement to understand the influence of compromised sensory environments on the behavior of both free-living and captive animals.

Developmental Effects

The sensory environments within which animals live, including the acoustic dimension, can exert profound influences on the development of behavior in a variety of ways (Ehret, 1980, 1989, 1990; Knudsen, 1984; Snowdon, 1986). A considerable body of research suggests that the range of these effects extends from the anatomy of the central nervous system to the organization of behavior (Kinoshi, 1985). These effects become particularly evident in animals housed under conditions devoid of adequate sensory input or the opportunities to act on it. Such simplified, unresponsive conditions are typical of the housing conditions in most laboratories and zoological parks. These barren surroundings usually fail to provide animals with problem solving challenges that foster neural development (Coss and Globus, 1978, 1979; Rosenzweig and Bennett, 1972; Rosenzweig, Bennett, and Diamond, 1973).

The implications of environmental inadequacy for synaptic stabilization in immature mammals has been well established (Coss, 1991b; Diamond, Rainbolt, Guzman, Greer, and Teitelbaum, 1986). Individuals not provided with adequate sensory stimulation undergo processes of synaptic loss that become increasingly irreversible with maturation (Black and Greenough, 1986; Hubel and Weisel, 1962). Many animals reared in simple (*deprived*) environments exhibit underdeveloped neurons with markedly reduced receptive surfaces, clearly indicating lower interneural connectivity. Conversely, animals reared in more complex (*enriched*) surroundings display enhanced neural complexity (Black and Greenough, 1986; Coss, 1991b; Greer, Diamond, and Murphy, 1982).

Deprivation effects have been observed in a wide variety of animals, including jewel fish (*Hemichromis bimaculatus*) (Coss and Globus, 1978, 1979; Coss, 1991b), rats (*Rattus norvegicus*) (Greer, Diamond, and Tang, 1982), and domestic cats (*Felis sylvesteris catus*) (Hubel and Wiesel, 1962). Similar research in birds suggests that the provision of spatial learning opportunities results in increases in neurogenesis in the ventricular zone of the avian brain (Pepatel, Clayton, and Krebs, 1997).

These effects become especially apparent in animals as they age, an important consideration for managers of zoo animals, many of which live far longer than their free-living counterparts (Connor, Beban, Melone, Yuen, and Diamond, 1982; Connor and Diamond, 1982; Greer, Diamond, and Tang, 1982; Soule, Gilpin, Conway, and Foose, 1986).

Research focusing on the neural correlates of environmental enrichment has tended to concentrate on aspects of environments improved through enhancing the opportunity for locomotor behavior, social interaction, and visual or tactile stimulation. Research on the influence of environmental complexity in the auditory domain has been less extensive. Nonetheless, the peripheral and central components of the auditory system have evolved to develop under constant stimulation. Neonatal sensory research typically involves deprivation via induced conductive deafness or lesioning of auditory neural pathways (Clopton and Sneed, 1990; Coleman, 1990; Coleman, Blatchley, and Williams, 1982; Kitzes, 1990). For example, Mongolian gerbils (*Meriones unguiculatus*) surgically deprived of normal perinatal auditory stimulation exhibit a general reduction in soma size and altered spine density in neurons of the auditory cortex (McGinn, 1983; McGinn, Coss, Henry, and Williams). The research that has been completed suggests that neonatal acoustic restriction results in deficits in both central and peripheral auditory systems.

Irrespective of the effects of deprivation on the nervous system, its impact on behavior is well established. Animals not provided with the opportunity to interact with crucial environments featuring the complexity representative of historic conditions frequently exhibit developmental patterns different from those of free-living animals.

For example, animals not provided with the opportunity to engage in interactions with conspecifics and their vocalizations during early development frequently fail to exhibit adequate patterns of social behavior as adults (Fox, 1968; Mason, 1965; Mellen, 1991; Mitchell, Maple, and Erwin, 1979; Mitchell, Raymond, Ruppenthal, and Harlow, 1966).

Deprivation effects extend to the auditory realm. Infant rodents unable to perceive the vocalizations of their littermates or dams frequently fail to develop adequate orienting, searching, or contact behaviors (Clopton and Sneed, 1990; Coleman, 1990; Ehret, 1989, 1990; Kitzes, 1990). In species which rely on audition to detect the presence of predators, the maturation of appropriate antipredator behavior is almost certainly compromised when developing animals do not experience biologically relevant acoustic phenomena in the predator context. These phenomena include sounds generated by predators directly as they vocalize or move around in their environments. Another critical class of sounds are the vocalizations of conspecifics, which can be important in exchanging information about the location and status of resources, conspecifics, or predators (Byrne, 1982; Morton, 1986; Schere, 1985; Smith, 1977, 1981; Snowdon, 1986; Zahavi, 1982).

There are differences between species in the relative contributions of internal and external factors in the acquisition of the ability to produce, perceive, interpret, and deploy effectively species-typical signals. In species demonstrating lability in audio-vocal behavior, the experience of perceiving and deploying vocal signals in social contexts is necessary for the acquisition of normal patterns of adult communicatory behavior (cf. Baptista, 1996; Gould and Marler, 1987; Green, 1975; King, Freeberg, and West, 1996; Kroodsma and Miller, 1996; Marler, 1977; Snowdon, 1986; West and King, 1985, 1996).

Unfortunately, because of a traditional perspective that has viewed mammalian vocal behavior as relatively inflexible, most research on the ontogeny of vocal behavior has traditionally focused on avian taxa at the expense of other groups (Burghardt, 1977; Kroodsma and Miller, 1996). Neural processing is probably sufficiently different in mammals and birds to warrant caution in comparative treatments of vocal development in the two groups. The systems associated with vocal behavior are probably sufficiently divergent that they should be treated only as functional analogues (Sachs, Woolf, and Sinnott, 1990). The literature on avian vocal development and behavior is extensive and reviewed elsewhere (Baptista, 1996; Baptista and Morton, 1981; Baptista and Petrinovich, 1994; Ball and Hulse, 1998; Blaich, Miller, and Hicinbothom, 1989; Greenewalt, 1968; King and West, 1983, 1996; King, Freeberg, and West, 1996; Kinoshi, 1985; Kroodsma, 1982; Kroodsma and Miller, 1996; Marler, 1970, 1977; Marler and Tamura, 1996; Miller, 1994; Miller and Blaich, 1988; Miller and Hicinbothom, 1991; Nottebohm, 1972; West and King, 1985). The undoubtable richness of mammalian vocal behavior remains to be investigated.

Taxon notwithstanding, signals are associated with several important qualities including (a) syntax (structure) (b) semanticity (meaning) and (c) pragmatics (effectiveness). Interestingly, in mammals, syntactical lability in the development of vocal signals is indeed rare (Andrew, 1962; Salzinger, 1973). However, there are many examples of semantic and pragmatic development in mammals (cf. Cheney and Seyfarth, 1985; Cleveland and Snowdon, 1982; McCowan and Reiss, 1997). The differences in the development of audio-vocal behavior in various mammals range from those species that apparently possess nearly immutable innate syntactical and semantic capabilities

(Jurgens, 1990; Newman and Symmes, 1982) to those mammals demonstrating developmental flexibility in the acquisition of semantic and pragmatic competency (Cleveland and Snowdon, 1982; Marler, 1985; Snowdon, 1986).

Typical of the first group are squirrel monkeys (*Saimiri sciureus*), which exhibit little capacity for syntactical development or extensive vocal learning. Newborn Roman-arched and Gothic-arched squirrel monkeys, two distinct subspecies, emit correctly formed, subspecifically distinct isolation peeps even if deafened at birth. Hybrids born of parents representing each subspecies produce isolation peeps that are structurally intermediate between those produced by either parent. Isolation-reared infants possess the ability to discriminate correctly between vocalizations produced by females of their own and other subspecies, even during the initial presentation (Newman and Symmes, 1982; Snowdon, 1986). These findings suggest that the perceptual apparatus for these vocalizations is innate (Jurgens, 1990; Newman and Symmes, 1982).

The other group might be exemplified by pygmy marmosets (*Cebuella pygmaia*), mustache tamarins (*Saguinus mystax*), and cotton-top tamarins (*Saguinus o. oedipus*), which appear to exhibit a degree of developmental and behavioral plasticity in the syntactical, semantic, and pragmatic aspects of communication. They require interaction with conspecifics in contextually appropriate social milieus in order to develop competency in adult patterns of audio-vocal behavior (Cleveland and Snowdon, 1982; Snowdon, 1986; Snowdon and Pola, 1978; Snowdon and Hodun, 1985). Individuals of these species, prematurely removed from natal social groups and prevented from interacting vocally with other troop members, often fail to develop a complete adult vocal repertoire (Snowdon, 1986).

Experience with conspecifics and their vocalizations emitted when predators are detected can provide contexts for the refinement of audio-vocal behavior. For example, immature vervet monkeys (*Cercopithecus aethiops*) may exhibit an improvement in the perceptual specificity with which they respond to specific antipredator vocalizations through experience with appropriate responses by mature members of their troops (Cheney and Seyfarth, 1985; Seyfarth, Cheney, and Marler, 1980).

Many species of ground squirrels (*Spermophilus spp.*) are highly responsive to conspecific antipredator vocalizations (Owings and Hennessy, 1984). These vocalizations are differentially evocative, eliciting evasive behavior from juveniles and adults. However, the orientational, locomotor, and vocal responses of young squirrels are less well organized than those of more experienced squirrels (Hanson, 1995; Mateo, 1996a, 1996b). Developing California ground squirrels (*Spermophilus b. beecheyi*) exhibit increasing adult-like qualities in their responses to antipredator vocalizations, as revealed by their responses to chatter and whistle antipredator vocalizations (Hanson, 1995; Hanson and Coss, 1997; Leger and Owings, 1978; Leger, Owings, and Boal, 1979; Owings and Leger, 1980). These findings suggest that, for these species, the referential specificity of different classes of antipredator vocalizations is developed over ontogeny through repeated interactions with the environment. Specific antipredator vocalizations are emitted within distinct contexts, defined by the class of predator, its speed of attack, or possibly even its location in space (Hanson, 1995; Hanson and Coss, 1997; Leger and Owings, 1978; Leger, Owings, and Boal, 1979; Mateo, 1996a, 1996b; Owings and Leger, 1980). Related research suggests that some species, e.g., golden-mantled ground squirrels (*Spermophilus lateralis*) and yellow-bellied marmots (*Marmota* *flaviventris*), can learn to respond to heterospecific antipredator vocalizations (Shriner, 1995, 1998). In other species, important perceptual and locomotor skills are developed when immature animals orient sensory arrays as they attempt to localize nonstationary sources of sound, especially those produced by predators or prey (Ehret, 1980, 1990; Knudsen, 1984). Obviously, learned responsivity is facilitated most effectively in acoustic environments which are interactive and biologically relevant.

Behaviors associated with predator detection and defense, in most cases, can be expected to possess long evolutionary histories. For the majority of individuals, antipredator behaviors develop most effectively when animals are confronted by predators throughout ontogeny (Fentress, 1983). Complete behavioral expression is potentiated in natural contexts in which a complete range of normal experiences occurs—or in experimental settings where they are replicated. That is, ontogeny proceeds most effectively in environments where events unfold in a manner concordant with the *expectancies* of developmental systems. If environmental conditions deviate substantially from expected norms, ontogenetic progress can be impaired or completely thwarted. Thus, captive animals presented with antipredator vocalizations of their own and other species are more likely to develop a full range of behaviors associated with predator detection and defense. Conversely, individuals unable to respond to such salient sources of stimulation will probably fail to fully develop antipredator behaviors.

In summary, the acoustics of artificial environments are frequently inappropriate, often inadequate, and, in fact, usually overlooked. These environments are inappropriate when they are characterized by incessant, excessively intense unnatural noise. They are inadequate when they are devoid of historically predictable, ecologically relevant sounds. Adequate acoustic environments feature spatial and temporal elements which allow animals to develop a full range of sensory capabilities and species-typical behaviors as they interact with sensorily appropriate sounds in ecologically relevant surroundings.

Modification of Behavior

Developmental state notwithstanding, the behavior of both free-living and captive animals can be directly influenced by acoustic stimuli. In the otherwise simplified conditions of captivity, most animals respond to a wide variety of acoustic provocation (Caine, 1984; Tromborg, 1993; Tromborg, personal observation, 1991). Research on the behavior of a variety of free-living sciurids and primates reveals considerable responsivity to the territorial and antipredator vocalizations of conspecifics (Leger and Owings, 1978; Leger, Owings, and Boal, 1979; Leger, Owings, and Gelfand, 1980; Seyfarth, Cheney, and Marler, 1980; Shriner, 1998; Strusaker, 1967), and to other important heterospecific acoustic signals (Rowe, Coss, and Owings, 1986; Rowe and Owings, 1978; Tromborg, personal observation, 1991). Acoustic reactivity is especially evident in prey species that emit vocalizations when they detect predators and in predators that exploit sound to locate prey. In both cases, survival depends on rapidly assessing the urgency of contexts within which vocalizations occur (Caine, 1987; Cheney and Seyfarth, 1985; Owings, Hennessy, Leger, and Gladney, 1986). Similar responsivity has been demonstrated in captivity by a variety of primates, including agile gibbons (*Hylobates agilus*), white-handed gibbons (*Hylobates lar*), and siamangs (*Symphalangus syndactylus*) (Maples and Haraway, 1982; Haraway, Maples, and Tolson, 1985; Raemaekers and Raemaekers, 1985; Shepherdson, Bemment, Carmen, and Reynolds, 1989).

There is also anecdotal evidence that many species respond to heterospecific vocalizations and other acoustic events. For example, siamangs (*Hylobates syndactylus*) have been observed to emit loud vocalizations in response to chimpanzee (*Pan troglodytes*) vocalizations, while black-and-white ruffed lemurs (*Varecia variegata variegata*) and red-ruffed lemurs (*V. v. rubra*), respond with roar choruses to provocation (Pereira, Seeligson, and Macedonia, 1988), including the vocalizations of polar bears (*Ursus maritimus*) and amplified human voices (Tromborg, personal observation, 1991).

In both nature and captivity, California ground squirrels respond to sounds such as conspecific vocalizations, heterospecific vocalizations, and to nonvocal sounds such as the rattling of rattlesnakes. Respondents exhibit a wide range of orienting, locomotor, and vocal behaviors (Fitch, 1948; Leger and Owings, 1978; Leger, Owings, and Boal, 1979; Owings and Virginia, 1978; Rowe, Coss, and Owings, 1986; Tromborg, personal observation, 1992). Differentiation varies with population and thus may be experience dependent. Ground squirrel responsiveness to acoustic phenomena suggests that they could serve as subjects in research focusing on the effects of sound on the development of behavior in captivity.

Acoustics, Artificial Environments, and Arousal

The anthropogenic noise in laboratories and zoological parks is particularly effective at provoking reactions from animals, even when responding is maladaptive. Captive animals are often subjected to unnatural sounds at high intensities (Anthony, Ackerman, and Lloyd, 1959; Gamble, 1976, 1982). Sound intensities in some zoological parks sometimes exceed 70 dB (SPL) within enclosures and approach 85 dB adjacent to them (Tromborg, 1993, 1994; Tromborg and Coss, 1995). The reflective nature of the materials used in the construction of most artificial habitats exacerbates the noise problem. This unnatural noise is generated by personnel and machinery during operations related to feeding, cleaning, maintenance, construction, transportation, or even entertainment (Pfaff and Stecker, 1976).

Elevated noise levels can become problematic when they interfere with important acoustic phenomena by masking or jamming them (Busnel, 1978). This is especially true for species using low-intensity vocalizations to maintain group cohesion in visually unpredictable habitats (Snowdon, 1986). It might also be a problem for species employing ultrasonic vocalizations in social, reproductive, or parental behavior (Brown, 1976; Brunelli, Shair, and Hofer, 1994; Haney and Micvek, 1993; Sales, 1972; Sales and Pye, 1974). Acoustic interference with reproductive performance has been demonstrated in highly endangered mouse lemurs (*Microcebus* spp.) (Cherry, Izard, and Simmons, 1987).

The noise problem becomes obvious when wild animals, many of which have more sensitive hearing than their inbred laboratory counterparts, are brought into captivity (Brown, 1976; Brown and Pye, 1975; Whitney, Coble, Stockton, and Tilson, 1973). A considerable body of research has determined that sound can function as a primary stressor (Broom and Johnson, 1993). Stress can be operationally defined as the totality of the adaptive response patterns employed by an organism (behavioral and hormonal) which effectively act to alleviate the stress-producing condition (Anthony, Ackerman, and

Lloyd, 1959). Stress-producing arousal is frequently indicative of the presence of environmental conditions over which animals have no control and from which they cannot escape. Perhaps constant physiological arousal is a product of an animal's continuous efforts to avoid aversive contingencies while chronic stress is the psychological consequence of its realization that it cannot escape from them (R. G. Coss, personal communication, 1997).

This perspective is supported by a novel view of stereotypical locomotor behavior. Traditionally, because of their repetitive performance, morphological invariance, and absence of function, they have been considered maladaptive responses to invariant environments (Mason, 1991). However, since unresponsive environments offer no extrinsic means of modulating or redirecting behavior, confined animals might counteract this deficit internally by emitting self-reinforcing patterned behavior (Carlstead, Brown, and Seidensticker, 1993; Mason, 1991). Thus, stereotypical behavior may actually constitute an adaptive response to invariant surroundings that moderates stress. It can also provide a means for monitoring arousal level and assessing environmental adequacy.

While many animals can cope with intermittently elevated intensities of noise, many continually exposed to intense noise frequently exhibit behavioral and physiological symptoms indicative of discomfort and stress (Ames, 1978; Anthony, Ackerman, and Lloyd, 1959; Bell, 1974; Broom and Johnson, 1993; Gamble, 1982; Snyder, 1975; Stoskopf, 1983). Rhesus macaques (*Macaca mulatta*) exhibit a decrease in locomotor activity while showing an increase in clasping and huddling after only one hour of exposure to the sounds of jackhammers (*Primate Record,* 1973). Lactating tree shrews (*Tupaia glis*) exhibit a marked reduction in milk production in response to excessively loud noise

(D'Souza and Martin, 1974). Finally, animals recently introduced into novel surroundings are particularly likely to exhibit high levels of reactivity to noise until they have become acclimated to their surroundings (Meyer-Holzapfel, 1968).

Compared with chronic background or repetitive noise, high amplitude punctate, aperiodic, or unpredictable noise is particularly effective at provoking responses (Cottereau, 1978; Belyaev, Plyusnina, and Trut, 1984; Gamble, 1982; Stoskopf, 1983). This type of reactivity is especially evident in easily aroused species, especially those which are targets of predators in nature (Fox, 1968; Meyer-Holzapfel, 1968; Stoskopf, 1983). Animals continuously subjected to intense noise manifest stress responses by exhibiting elevated levels of arousal (Gamble, 1982; Snyder, 1975). Aroused animals usually demonstrate behavioral vigilance or engage in elevated levels of startle responses. An artifact of the fight-or-flight syndrome, elevated arousal and its associated alertness are important in free-living animals that must engage in frequent predator detection and antipredator defense. In artificial settings, however, repetitive provocation can result in potentially injurious, chronically elevated levels of stress (Broom and Johnson, 1993).

Vigilance, along with its underlying arousal, persists even in the relatively benign environments of laboratories and zoological parks. For example, red-bellied tamarins (*Saguinus labiatus*) continue to exhibit vigilance in the form of visual scanning even in the absence of natural enemies (Caine, 1984). Persistent reactivity is a consequence of the presence of provocative visual (Stanley and Aspey, 1984; Thompson, 1989) and auditory stimuli (Tromborg, 1993).

While some species are particularly sensitive to aperiodic, punctate sounds (Gamble, 1976), others are sensitive to constant or periodic low-level noise (Stoskopf, 1983; van Rooijen, 1984). In general, the higher the amplitude of stimuli, the more effective they are in eliciting responses. Additionally, animals respond variably to sounds of different frequencies. For example, many rodents exhibit elevated arousal when subjected to ultrasonic sounds, including conspecific vocalizations. Ultrasonic noise is particularly problematic because it is imperceptible to technicians responsible for its regulation (Bell, 1974).

Heightened reactivity to various classes of noise is an especially important consideration for the managers of highly inbred animal populations (Cottereau, 1978; Belyaev, Plyusnina, and Trut, 1984). Some research suggests that the effects of inbreeding depression are compounded under stressful conditions. Inbred populations of fruit flies (*Drosophila melanogaster*) are less able to adapt to a wide range of stressful conditions (Miller, 1994). Some strains of highly inbred mice exhibit pathological startling or audiogenic seizures when confronted with intense punctate noise (Henry, 1967). Some inbred silver foxes (*Urocyon cinerebargenteus*) and thoroughbred horses (*Equus caballus*) fail to habituate to the regularly recurring punctate noise associated with sonic booms (Belyaev, Plyusnina, and Trut, 1984; Cottereau, 1978).

Variation in behavior associated with acoustically mediated arousal can provide an index of stress level (Henkin and Knigge, 1963). In several species of laboratory and zoo animals, indices of elevated stress include increases in cryptic behavior, startle responses, elimination, locomotor stereotypies, and aggression; they can also exhibit decreases in foraging and exploratory behavior (Anthony, Ackerman, and Lloyd, 1959; Carlstead, Brown, and Seidensticker, 1993; Mason, 1991; Snyder, 1975). In cats (*Felis spp.*), arousal can be assessed on the basis of piloerection (Fuchs, Edinger, and Siegel, 1985). In squirrels (*Spermophilus spp.*), it can be assessed on the basis of piloerection of the tail (Hennessy, Owings, Rowe, Coss, and Leger, 1981). Both behaviors are widely regarded as indicators of sympathetic nervous system activity (Coss, 1993; Siegel and Skog, 1970). Research on leopard cats (*Felis bengalensis*) revealed that stereotypical pacing and increased levels of urinary cortisol also can serve as indices of elevated sympathetic nervous system activity (Carlstead, Brown, and Seidensticker, 1993).

While moderate stress can be adaptive, chronically elevated stress can compromise the health of animals, diminishing their value as subjects in behavioral studies, appropriateness as models for biomedical research, or effectiveness in educational exhibits.

Physiologically, prolonged exposure to intense noise is associated with increased activity in the sympathetic division of the autonomic nervous system. Its prolonged activation is correlated with increased activity in the hypothalamic-pituitary-adrenal system, elevated metabolic rates, increased blood pressure, and tachycardia (Ames, 1978; Anthony, Ackerman, and Lloyd, 1959; Henkin and Knigge, 1963; Martin, Sacket, Gunderson, and Goodlyn-Jones, 1988; Snyder, 1975). The concomitantly elevated concentrations of epinephrine, adrenocorticotropin, and adrenal corticosteroids alter a multitude of metabolic pathways (Anthony, Ackerman, and Lloyd, 1959). In fact, urinary cortisol is a reliable measure of sympathetically mediated corticotropic activity (Carlstead, Brown, and Seidensticker, 1993).

Continuously elevated levels of these compounds compromise the efficiency of the immune system by reducing the biosynthesis of antibodies and inhibiting the activity of

B-lymphocytes (Snyder, 1975; Stoskopf, 1983). Thus, chronically stressed animals are more susceptible to disease.

Further, reproduction and development can be impaired in acoustically stressed animals (Anthony and Harclerade, 1959; Gamble, 1976). Chronically stressed female mammals frequently exhibit elevated levels of follicle-stimulating hormone, prolonged estrus, and premature parturition. Similarly stressed males can exhibit atrophied testicles and reduced rates of spermatogenesis (Snyder, 1975; van Hooff, 1986). Acoustically mediated chronic stress has been correlated with hypodevelopment, hyperdevelopment, and other congenital anomalies in fetal rats. In many pups surviving to term, low thresholds to startle were observed (Gever, 1966). These are important considerations for managers of populations of animals housed in the typically noisy surroundings of captivity.

Continuous exposure to noise can compromise the integrity of the auditory system. Minimally, it results in elevated auditory thresholds. Temporary threshold shifts provide a mechanism for accommodating a wide range of sound intensities. The underlying mechanisms of temporary shifts are not clearly understood, but probably involve changes in the membrane structure of the stereocilia, exhaustion of the intercellular mechanism, changes in the morphology of the tectorial membrane, reductions in the vascular supply to the organ of Corti, and fatigue of the afferent nerves. While subjects can recover from short-term exposure to noise, continued exposure to elevated intensities of sound can result in irreversible threshold shifts. Brown (1976) reported, in a comparison of audiograms for a variety of rodents, that virtually all wild specimens had lower sensitivity thresholds than their laboratory counterparts. The permanent shifts in laboratory animals represent a loss of auditory acuity and probably involve structural changes in the organ of Corti (Carder and Miller, 1969, 1971, 1972). This reduced sensitivity can result from cochlear damage, including injury to the basilar membrane, tectorial membrane, or stereocilia (Carder and Miller, 1972; Gamble, 1982; Stebbens, 1983). Permanent threshold shifts have been observed after laboratory primates have been exposed to noise exceeding 85 dB repeatedly (Moody, Stebbins, Johnsson, and Hawkins, 1976). Chinchillas (*Chinchilla spp.*) exhibit a demonstrable loss in auditory acuity when exposed to the sounds of machinery at intensities ranging from 65-105 dB for as few as two days (Carder and Miller, 1969, 1971, 1972). Eighty-five dB has been proposed as the absolute maximum acceptable limit for sound intensities in animal care facilities. Unfortunately, some facilities regularly approach or exceed this sound pressure level (Anthony, Ackerman, and Lloyd, 1959; Pfaff and Stecker, 1976).

Although sound intensities in zoos seldom attain this level, they are still higher than those typical of most natural habitats (Tromborg, 1993; Tromborg and Coss, 1995). Further, the structures of natural acoustic environments are considerably different from those characterizing artificial environments.

Natural Habitat Acoustics

The physical nature of acoustic environments is an important, though often overlooked, aspect of an animal's surroundings (Ames, 1978; Busnel, 1978; Kinsler, Frey, Coppens, Sanders, 1982; Shaw, 1978). The historical and contemporary physical characteristics of acoustic habitats can exert influences on the morphology of vocal signals (Bowman, 1979; Brown, Gomez, and Waser, 1995; Klump and Shalter, 1984; Morton, 1975; Conner, 1982; Richards and Wiley, 1980; Schwagmeyer and Brown, 1984; Waser and Brown, 1984, 1986; Waser and Waser, 1977; Wiley and Richards, 1978). The physical nature of acoustic habitats influences signal morphology by differentially affecting the efficiency and accuracy with which acoustic signals can be transmitted (Brown, Gomez, and Waser, 1995; Waser and Waser, 1977). While the long-distance propagation of signals can be advantageous, it makes signals more susceptible to exploitation by a variety of percipients (Dawkins and Krebs, 1978; Harper, 1984; Krebs and Davies, 1984; Markl, 1985). Limitations on the efficiency of acoustic signals are largely a function of the rates of their degradation due to any of several environmental phenomena. These factors include spherical spreading, scattering by physical barriers, absorption by the atmosphere, and reverberation produced by micrometeorological and physical heterogeneities. Acoustic signals are frequently deflected at the ground-air interface; are diffracted, refracted, and reflected within stratified propagation media; and are subject to constructive and destructive multipath interference. The combination of these factors comprises the phenomenon of environmental attenuation (Richards and Wiley, 1980; Waser and Brown, 1984, 1986; Wiley and Richards, 1978).

Environmental attenuation can increase the perceiver's difficulty in interpreting signals. Increased error rate is a reduction in the information content of signals (Attneave, 1959; Shannon and Weaver, 1962). Increased error rates in perception frequently are indicative of reduced information content in signals. In some instances, these sources of signal degradation can provide animals with information enabling them to locate the source of long-distance vocalizations (Morton, 1986; Snowdon and Hodun, 1981). However, the propagation efficiency of vocal signals is not the only measure of their effectiveness. Many important vocal signals, such as contact calls, are structured for low-intensity close-range effectiveness (Cleveland and Snowdon, 1982; Snowdon, 1986; Snowdon and Hodun, 1981). Ultimately, however, signal degradation imposes a limit on the propagation distances that can be accommodated between signaler and recipient (Morton, 1975). Even under ideal conditions, sound attenuates at a rate of 6 dB per doubling of distance, due to spherical spreading. In habitats with complex structures or temporal and spectral distributions of ambient noise, the effectiveness of acoustic signals is reduced even more over distance (Waser and Waser, 1977).

Ambient noise levels attain the highest transient peaks in rain forests. There overall averages are higher in riverine habitats compared with temperate forests and lowest in savanna habitats (Brown, 1989). In rain forest habitats, ambient noise levels typically range from 27 dB (SPL) at 06:00 to 48 dB at 16:00, depending on the level of wind activity and the rustling of leaves. In riverine habitats, ambient noise levels typically range from 27 dB at 06:00 to 37 dB at 07:00, depending on the cumulative levels of bird vocalizations, insect stridulation, and the rustling of leaves. In savanna habitats, ambient noise levels range from 20 dB at 06:00 to 36 dB at 12:00, depending on the level of wind activity (Brown, 1989; Brown, Gomez, and Waser, 1995; Waser and Brown, 1986; Wiley and Richards, 1978). Environmental noise levels recorded in alpine and oak savanna habitats in California ranged from lows of 30 dB to highs of 52 dB, depending on wind activity or the presence of noise generated by human technology (Tromborg, unpublished data, 1993).

Such variation in background noise influences which frequencies are most discernable in each type of habitat. Contemporary animal signal morphologies represent adaptations to historic acoustic conditions. Deviation from historic conditions could encourage evolutionary change of signal morphology in order to maintain signal effectiveness under altered acoustic conditions (Klump and Shalter, 1984; Waser and Brown, 1984).

Highly adapted acoustic signals possess structures to effect specific outcomes most efficiently within a specific range of environmental conditions (Bowman, 1979; Conner, 1982; Klump and Shalter, 1984; Morton, 1975; Waser and Brown, 1986; Wiley and Richards, 1978; Zahavi, 1982). For example, species dwelling in open habitats typically possess graded vocal repertoires featuring relatively low frequency, amplitude-modulated signals. Species dwelling in forested habitats typically possess more discrete, categorical vocal repertoires featuring high frequency, frequency-modulated signals (Marler, 1955, 1965, 1977, 1982; Snowdon, 1986; Wiley and Richards, 1978). Generally, low-frequency signals propagate farther than high-frequency signals of equivalent amplitude. The distance at which acoustic signals remain effective is largely a function of the intensity of environmental noise and its masking effects. Masking effects arise primarily from zoogenic sources such as bird vocalizations, frog vocalizations, and insect stridulation, and environmental sources such as wind and vegetative rustling (Gerhardt and Klump, 1988; Schwartz and Wells, 1983a, 1983b; Waser and Brown, 1986; Wiley and Richards, 1978). Waser and Waser (1977) reported that in one tropical forest, due to the stridulations of cicadas, transient background noise levels exceeded 75 dB and were uncomfortable to experience.

Environmental noise almost certainly influences the ability of perceivers to extract information effectively from acoustic sources, including the vocal signals of conspecifics

(Butler and Naunton, 1962; Carhahart, Tillman, and Greetis, 1969; Gerhardt and Klump, 1988; Pollac and Pickett, 1958; Schwartz and Wells, 1983a, 1983b). Noise also obscures the location and sources of sound generated by competitors, prey, and predators as they move about in their environments (Knudsen, 1984; Yost, 1992). The same reduction in the effectiveness of acoustic signals occurs in noisy artificial environments. Vocalizations adapted to function effectively under specific acoustic conditions do so less effectively due to masking or even jamming. In some rare instances, species demonstrating vocal lability could experience an alteration of the morphology of susceptible vocal signals in both production and perception (Snowdon, 1986). While environmental noise, along with its masking effects, pose potential acoustic problems in artificial environments, it might also provide one solution for improving their acoustics.

Acoustic Masking

The phenomenon of acoustic masking involves the reduction in the detectability of one signal, termed the probe, as a function of the simultaneous presence of another, termed the masker. Physiologically, the effect is generally agreed to arise from adaptation and suppression. Suppression is mechanical in nature and arises when two signals are simultaneously present, resulting in the inhibition of the signal's effectiveness in modulating the movement of the tympanic membrane and concomitant displacement of the stereocilia. Adaptation is physiological and is the decrease in the response of a receptor to a specific tone as a result of a previous history with that tone. The greater the intensity of the masking signal, relative to the probe, and the more similar their frequencies, the greater the degree of masking. Usually, the masker is a broad-band, lower-intensity signal which occludes variation in the probe and reduces the ratio of signal to noise (Fletcher, 1938; Moore, 1982; Vartanyan and Egorovas, 1990; Wegel and Lane, 1924). Jamming is a more intense form of interference, making a signal unintelligible through the introduction of a more intense, competing signal (Snowdon, 1986).

The masking effects produced by the interaction of noise coming from insects, birds, vegetation, and wind, as suggested above, reduce the discriminability of vocal signals (Butler and Naunton, 1962; Carhahart, Tillman, and Greetis, 1969; Gerhardt and Klump, 1988; Pollac and Pickett, 1958). Consequently, many forest-dwelling birds and primates emit most of their long-distance vocalizations in the early morning hours, when the masking effects of environmental noise or attenuating effects of stratification are at their lowest (Wiley and Richards, 1978).

In noisy environments, animals unable to discriminate acoustic phenomena such as the sounds of approaching predators may exhibit reluctance to emerge from cover. This is more likely to occur after a prolonged period of time spent within an occluded refuge—a period during which the ability to assess the state of the surroundings is reduced or altogether absent.

Enhancing Artificial Environments

The acoustics of environments can be improved by reducing intrusive exogenous noise. They might also be improved through the introduction of continuously applied, low-level environmental sounds. While additional environmental noise can mask potentially important acoustic information, it can also mask provocative noise. Naturalistic environmental sounds could, for instance, serve to disguise or attenuate the prominence of the anthropogenic noise so typical of laboratories and zoos. Acoustically enhanced environments could attain a degree of ecological authenticity through the introduction of environmentally relevant sounds into the *acoustic background* (Ogden and Lindburg, 1991; Ogden, Lindburg, and Maple, 1994; Tromborg, 1993). They could attain greater authenticity through the introduction of biologically salient sounds into the *acoustic foreground* (see Chapter 5; Markowitz, Aday, and Gavazzi, 1995; Tromborg, 1993). Juxtaposed against distal background (diffused) sounds, these proximal foreground (focused) sounds could serve as probes to modulate behavior in a way directly analogous to a classic figure and ground paradigm (Israeli, 1950; Lerea, 1961; Thurlow, 1957; Tromborg and Coss, 1995). Ultimately, future acoustic enrichment approaches could be designed to provide captive animals with interactive environments so that they could negotiate with contingent features of their surroundings and to some extent, control them (see Chapter 5).

The influence of relatively naturalistic variation in the character of artificial acoustic surroundings has been inadequately explored. The following three studies are presented as efforts to begin to rectify this oversight.

Experimental Context and Rationale

This research represents the integration of two ongoing avenues of study. The first is a continuation of an overall program of study and research focusing on the antipredator behavior of sciurids (Coss, 1993). The second is a continuation of research focusing on the influence of the acoustics of artificial environments on the behavior of captive animals (Tromborg, 1993). California ground squirrels

(*Spermophilus b. beecheyi*) were selected as subjects for the following three laboratory-based studies. All three studies focus on the emergence and environmental assessment behaviors of squirrels as they enter environments following a prolonged interruption in the opportunity to assess their environments effectively. First, refuge-related acoustic behavior is examined; second, refuge-related visual behavior is examined; and third, a combination of audio, visual, and olfactory behavior near refuge is examined.

Chapter 2 focuses on the influence of manipulations of the far-field (background) component of the acoustic environment on the expression of emergence and vigilance behaviors after an overnight disruption in environmental monitoring. The emergence and scanning behavior of two groups of ground squirrels, six captured in high-altitude environments and six captured in low-altitude environments, were compared under three acoustic conditions. The three conditions were selected to assess the influence of standard, continuous, or punctate noise on the expression of vigilance as represented by emergence patterns. Individuals from two distinct populations were included to ensure that conclusions about the effects of acoustic manipulations would have a degree of generality. Visual behavior observed during emergence from nest boxes established a context for the second study.

Chapter 3 focuses on the issue of experience and its effect on vigilance as represented by emergence and scanning behavior in two groups of ground squirrels, one wild-caught and the other laboratory-born. The acoustic setting was that of a typical animal care facility, featuring some unpredictable noise. The study was designed to assess the role of experience in influencing directional biases in scanning behavior as animals habituated to a novel experimental setting. The establishment of the typical pattern of habituation also provided the context for evaluating the effects of acoustic manipulations performed as components of the third study.

Chapter 4 focuses on the issue of experience and its effect on vigilance as represented by scanning behavior in response to sounds presented in the near-field (foreground) of the acoustic environment. The same wild-caught and laboratory-reared subjects employed in the preceding research were presented with various antipredator vocalizations to assess signal semanticity, especially as it relates to spatial and temporal patterns of predatory threat.

Finally, in Chapter 5, the influence of habituation to novel settings, experiential histories, informational continuity, and the structure of the acoustic environment on the expression of environmental assessment behaviors are integrated into a discussion of importance of the environment in facilitating the development and expression of species-typical behavior in artificial settings, especially forward-looking zoos.

CHAPTER TWO

Effects of Naturalistic Environmental Sounds on the Expression of Emergence Behavior in Captive Wild-Caught California Ground Squirrels

Animals continually assess their surroundings for the presence of biologically important information. As products of long-term relationships between individual species and specific types of habitat, each species has evolved a suite of sensory adaptations optimized to discern nutritional resources, potential mates, competitors, or predatory threats within a prescribed range of environmental conditions (Bowman, 1979; Bradbury and Vehrencamp, 1998; Brown and MacDonald, 1985; Dusenbery, 1992; Eisenberg and Kleiman, 1972; Klump and Shalter, 1984; Knudsen, 1984; Lythgo, 1979; Schwagmeyer and Brown, 1984; Stebbens, 1983; Stoddard, 1980; Waser and Brown, 1984, 1986; Wasser and Waser, 1977; Webster and Webster, 1971; Wiley and Richards, 1978; Zahavi, 1982). Each adaptation is optimized to function most effectively within a range of variation in microhabitat and climatic conditions characteristic of specific ecotypes. Climatic conditions exceeding historically predictable limits can severely impair the effectiveness of sensory systems, though sensory modalities vary in their susceptibility to interference from extraneous environmental factors (Dusenbery, 1992; Marler, 1977).

The auditory channel is particularly sensitive to interference from atmospheric factors. Even under undisturbed conditions, sound is subjected to attenuation from various sources in the environment (Chapter 1; Brown, Gomez, and Waser, 1995; Richards and Wiley, 1980; Waser and Brown, 1984, 1986; Wiley and Richards, 1978). Under conditions of meteorological disruption, sounds are even more severely disrupted. They are also susceptible to degradation from anthropogenic noise (Chapters 1 and 5).

Under severe climatic conditions, the ratio of potentially important acoustic information to irrelevant background noise is reduced. Percipients experience a reduction in the ability to auditorily discriminate sounds, including noise generated by stalking predators or alarmed conspecifics (Snowdon, 1986). Animals in noisy surroundings exhibit reduced abilities to perform on auditory discrimination tasks (Ehret, 1989).

Species differ widely in the degree to which they can adapt to disrupted acoustic environments. Many social insects, birds, and mammals are tolerant of the extreme noise associated with human activities (Busnel, 1978). Others, typically shy, retiring mammals are less tolerant of noise. The most adaptable species are frequently social, usually individually and communally noisy, and behaviorally flexible (Fletcher and Busnel, 1978; Shaw, 1978).

When environmental conditions exceed those within which normal sensory behavior operates most effectively, they can alter their behavior by: (a) restricting the use of impacted channels to periods of time when they are minimally degraded; (b) shifting the perceptual emphasis from impacted sensory channels to those less degraded; and (c) remaining under cover and avoiding sensorily unfavorable conditions altogether. Temporal shifts in behavior have been observed in some forest-dwelling primates, which restrict the emission of territorial vocalizations to times of the day when there is less competition from zoogenic noise generated by birds and insects (Waser and Brown, 1984, 1986; Wiley and Richards, 1978). Thirteen-lined ground squirrels (*Spermophilus tridecemlineatus*) also restrict some of their vocal behavior to periods of reduced atmospheric noise (Schwagmeyer and Brown, 1984).

Many fossorial species are confronted not with excessive noise, but with the intermittent absence of environmental cues. California ground squirrels experience a cyclical discontinuity in the opportunity to monitor the terrestrial environment near their burrows whenever they are underground. The intervening layer of soil between the terrestrial environment and their sensory arrays virtually eliminates visual cues and greatly attenuates most frequencies of sound. Fully immersed squirrels cannot effectively monitor the terrestrial environment, and fully exposed squirrels cannot effectively monitor the subterranean environment.

Antipredator Behavior Near the Burrow

The risk assessment behavior of ground squirrels must be considered within two contexts, the subterranean and terrestrial, each imbued with a different range, composition, and spatial distribution of predatory threats. A squirrel approaching a burrow opening from above ground is confronted by an opening possessing a gradient of threat and refuge which varies with the distance between the squirrel and the entrance. The hole limits snake detectability and represents a location for strangulation or envenomation. Simultaneously, it offers refuge from aerial and terrestrial predators (Coss, 1993; Rowe, Coss, and Owings, 1986; Rowe and Owings, 1978). A squirrel approaching the burrow opening from underground is presented with a complementary gradient of increasing uncertainty. As the distance to the opening decreases, the level of threat from aerial and terrestrial predators increases as the threat from underground snakes decreases (Rowe, Coss, and Owings, 1986; Rowe and Owings, 1978). Thus, the annulus of territory surrounding the burrow opening represents a critical region wherein there is a nearly instantaneous transition in the urgency and configuration of predatory contexts (Coss and Owings, 1985; Coss and Goldthwaite. 1995). Indeed, this transition is in many ways analogous to a real-time metamorphosis in the behavioral context (D. H. Owings, personal communication, 1998). A ground squirrel located on either side of the burrow is confronted with a deficit of information about the level of threat on the other side.

Consequently, emergence behavior is probably organized to facilitate efficient refamiliarization with the terrestrial surroundings prior to emergence from the burrow, a process susceptible to interference from environmental noise. Rapid evaluation of the environment near burrows is particularly critical during the initial daily emergence into the open, after an extended overnight lapse in environmental surveillance. The behavior of emerging squirrels can be viewed within two contexts: (a) a pre-emergent condition, in which vision is ineffective and olfaction and audition predominate in monitoring, and (b) a post-emergent condition, in which vision predominates and all modalities are employed in environmental monitoring. Pre-emergent squirrels must maneuver from locations where visual cues are absent to vantage points. Post-emergent squirrels must then look in all directions in order to detect changes which have occurred since the previous surveillance period.

Psychophysical research suggests that ground squirrels possess well developed visual acuity, both photopic (Crescitelli and Pollack, 1965), and scotopic (Meyer-Oehe, 1957). However, under low-light subterranean conditions, olfaction and audition are the predominant sensory modalities. Some vestibular, proprioceptive, kinesthetic, and tactile information is probably also available to squirrels (Etienne, Teroni, Hurni, and Portinier, 1990). Vision is ineffective; squirrels may traverse burrows with their eyes closed (R. G. Coss, personal evaluation). Near the burrow opening, vision becomes increasingly effective. For emerging and fully exposed animals, it probably becomes as important as audition in monitoring behavior (Chapters 3 and 4).

It is certainly important when elevated environmental noise interferes with the ability of squirrels to monitor their surroundings acoustically as they emerge into the open. Under these circumstances, ground squirrels are likely to engage in even more visual surveillance as they emerge. The importance of well developed vision in rodent antipredator behavior has been reported elsewhere (Ellard, 1996; Kildaw, 1995; King, 1984, 1987; Hanson, 1995; Hanson and Coss, 1997; Mateo, 1996a, 1996b; McAdam and Kramer, 1998.)

Antipredator behavior also involves audition. As with other rodents, sciurids possess comparatively sensitive high-frequency audition, though most demonstrate decreasing sensitivity at lower frequencies (Ehret, 1980, 1989, 1990; Fay, 1988; Hamill, McGinn, and Horowitz, 1989; Heffner and Masterton, 1980; Henry and Chole, 1980; Kelly and Masterton, 1977; Stebbens, 1983). Based on auditory brain stem research (Kitzes, 1990), California ground squirrels appear to possess effective hearing from 0.5 kHz to 50 kHz. Sensitivity is slightly better between 4 kHz and 32 kHz and best at 12 kHz. In an unpublished study investigating response of neurons in the inferior colliculus of ground squirrels, Willit and Owings arrived at the same conclusion about the 12 kHz peak sensitivity (D. H. Owings, personal communication, 1998). When evaluated at low elevations, the low-frequency sensitivity of squirrels from higher elevations appears to be greater than that of squirrels from lower elevations (Henry and Coss, unpublished manuscript, 1996). Augmented low-frequency sensitivity appears in other fossorial animals and may facilitate detecting ground-borne vibrations (Ehret, 1990; Gulotta, 1971; Kenagy, 1976; Narins, Lewis, Jarvis, and O'Riain, 1998; Randall, 1993; Randall and Stevens, 1987; Webster, 1962). It may also represent an adaptation to accommodate the slightly less effective high altitude propagation of sound. Conceivably, the distinctly different micrometerological conditions characterizing high and low altitude habitats impose slightly different adaptive regimes on percipients.

The underlying factors which govern the manner in which animals respond to environmental variation must be considered within the context of two time scales: (a) long-term adaptations in the anatomy and physiology of perceptual systems; and (b) short-term adaptations effected behaviorally. Animals dwelling in seasonally variable habitats may respond differently to modification of the acoustic surroundings compared with those dwelling in more invariant habitats. As a greater proportion of natural and artificial environments become increasingly noisy, it behooves psychologists and zoologists to develop a more complete understanding of the influence of environmental noise on behavior.

A considerable body of research has demonstrated that many types of intense or punctate noise exert undesirable influences on the health and behavior of animals (Chapters 1 and 5). However, there has been infrequent attention devoted to investigating the influence of relatively low intensity background noise on behavior.

Theoretical research on this topic has addressed the influence of naturalistic background sounds on perceptual behavior (Brown, 1989). Applied research has investigated introducing natural sounds into artificial environments to render them more ecologically authentic for captive animals (Ogden and Lindburg, 1991; Ogden, Lindburg, and Maple, 1994; Tromborg, 1993). In each instance, the findings suggest that sound in the perceptual background is less salient than sounds in the perceptual foreground, irrespective of its ecological relevance (Israeli, 1950; Lerea, 1961; Thurlow, 1957). Obviously, more research needs to be conducted in this area.

Experimental Rationale, Questions, and Predictions

The underlying rationale for the current study was to determine whether or not background noise affected the burrow emergence and environmental assessment behavior of a captive wild animal. It explores the manner in which sound in the perceptual background might influence sensory behavior in an animal as it attempts to assess the status of its immediate surroundings at the beginning of its daily activity period.

The abundant California ground squirrel was selected to serve in this research as an analogue for less abundant, often endangered, animals frequently housed in contemporary zoological parks. These semicolonial squirrels are nonthreatened and have demonstrated both behavioral reactivity and vocal responsiveness to a variety of acoustic treatments (Owings, Borchert, and Virginia, 1977; Owings and Virginia, 1978).

Free-living squirrels exhibit a persistent responsiveness to salient sounds, especially to the antipredator vocalizations of other squirrels. As with other animals, they also persist in responding to noise in the laboratory.

Anecdotal evidence suggests that ground squirrels are less likely to remain above ground during turbulent weather featuring wind or rain (R. G. Coss, personal communication, 1997; Schwagmeyer and Brown, 1984). Others have reported that a variety of species respond to disturbed meteorological conditions by avoiding exposure or increasing reliance on vision (Quenette, 1990; Underwood, 1982). Some of the apparent reluctance to remain in the open could be an artifact of the masking or jamming effects of elevated environmental noise on auditory discrimination. Conceivably, fossorial animals, when unable to discern the presence of imminent threat effectively, might alter the way they organize their emergence behavior. Reorganization is likely to be especially evident after a lengthy period during which opportunities to monitor the surroundings have been disrupted. This type of interruption in the receipt of information occurs cyclically during the nocturnal retirement into burrows. The cumulative effect of elevated environmental noise should be evident through changes in emergence and monitoring behavior as animals assess the relative uncertainty of terrestrial environments versus the security of burrows.

The structures of both natural and artificial acoustic habitats possess both background (far field) and foreground (near field) elements. In a sense, they can be considered within the perceptual construct of figure and ground (Chapter 5). Natural acoustic environments typically feature distal background elements which are comprised of a broad suite of relatively low-intensity constant environmental noise generated by various organisms, vegetation, and wind (Waser and Brown, 1986; Wiley and Richards, 1978). There can also be proximal foreground elements which might be generated by the same sources, though they are usually higher in intensity. Aperiodic—therefore novel—acoustic features in either the background or foreground can possess varying degrees of salience to perceivers. A considerable body of research reveals that most mammals, either free-living or captive, habituate to the presence of constant noise in the perceptual background (Busnel, 1978; Ogden, Lindburg, and Maple, 1994; Stoskopf, 1983).

Environmental noise in the perceptual background, either artificially or naturally occurring, could work in at least two ways. Relatively homogeneous naturalistic sounds could function as acoustic maskers. As such, they would reduce the prominence of, and attention devoted to, provocative noises generated near animal dwellings. Conversely, slightly less homogeneous sounds could simply be perceived as additional environmental noise. In this context, the addition of more acoustic energy would interfere with auditory discrimination. The first proposal would be corroborated if subjects demonstrated reduced visual attention to spurious noise and spent more time in the open. The second construct would be corroborated by increased reliance on vision and decreased time spent in the open. With respect to its applications to regulating provocative noise in captive settings, less tangible influences and outcomes could involve the cognitive benefits of providing animals with acoustic surroundings possessing some degree of ecological relevance.

Materials and Methods

Subjects

Two groups of California ground squirrels obtained from meteorologically distinct habitats served as subjects in this study. Many of the same squirrels served as subjects in corticosteroid and auditory brain stem research discussed herein. Six squirrels, three males and three females, were caught near the Coast Range foothills at Camp Ohlone, near Sunol, California. The habitat at this site has an average elevation of 366 m and consists predominantly of oak savanna. The animals were minimally one year of age at the time of capture. At the time of the study, the weights of the females ranged from 498–820 g, averaging 676 g. Males ranged in weight from 866–1000 g, averaging 915 g.

The second group of squirrels, consisting of three males and three females, was captured in the Sierra Valley, located within the Great Basin Valley on the eastern slope of the northern Sierra Nevada range in California. The habitat at the trapping site has an elevation of 1900 m and is primarily open grassland with widely scattered conifers. These animals were also assumed to be at least one year of age at the time of capture. At the time of the study, the weights of the females ranged from 618–958 g, averaging 797 g. The males ranged in weight from 802–1100 g, averaging 951 g.

All subjects were captured during the 1990 trapping season and held in quarantine until they were gradually transferred to the animal care facility of the Psychology Department at the University of California, Davis, between October 1991 and March 1992, where they remained for two years. The subjects were approximately three years old at the time of the study.

Rearing and Maintenance Conditions

All 12 subjects were maintained in wire-screened cages with horizontal dimensions of 39 x 56 cm and heights of 25 cm. Each cage featured attached nest boxes with horizontal dimensions of 22.5 x 38 cm and heights of 22 cm. These boxes, with the addition of naturalistic nesting materials, afforded dark refuges simulating natural nest chambers. The animals were regularly provided with various preparations of either Purina or PMI rodent diet (#5001 or #5014) and water on an ad libitum basis. Occasionally, the diet was supplemented with additional nuts, fruits, vegetables, and grains.

The animals were housed under conditions with temperatures varying between 68 and 70 F. The walls of the animal care facility were uniformly cream colored, evenly distributing light emanating from three banks of overhead fluorescent fixtures. The animals were regularly exposed to a 12-hour photoperiod at an intensity of 55.6 footcandles from 07:00–19:00 each day. All subjects had views of other wire mesh cages, many housing other squirrels.

Simple visual surroundings were complemented with more complex acoustic surroundings. The constant, low-level background noise had a relatively homogeneous energy distribution over a wide band of frequencies. The sound pressure levels typically ranged from an average minimum of 40 dB (SPL) during evening hours to an average maximum of 75 dB during daytime maintenance procedures. These are typical values for contemporary animal care facilities. These values do not take into consideration the aperiodic, short, intense bursts of punctate noise common in laboratories. These include impact or impulse noise produced by the transporting of metal cages, cleaning of litter pans, and the refilling of food bins. Additionally, cat vocalizations, rattlesnake rattling, and the alarmed vocalizations of other squirrels were sometimes audible.

In effect, the subjects had experienced normal environmental complexity during their first year of life, but were provided with reduced visual, acoustic, and social complexity for the two years that they were housed in the animal care facility.

Experimental Setting

The venue for the experiment consisted of two adjacent rooms in the Psychology Department's animal care facility. A monitoring room provided a location for the experimental apparatus, its operation, and the observation of the subjects. The adjacent experiment room provided a controlled setting within which the subjects were placed for exposure to treatments and unobtrusive observation. The equipment housed in the monitor room included a Panasonic VHS AG-185U video camcorder, which functioned as a low light (1 lux) color camera. Its output was fed to a FOR.A VTG-22 video field time generator, which numbered each video field. Its output, in turn, was fed to a Panasonic VTR NV-8030 time-lapse surveillance videotape recorder for step-lock recording. Its period was set at 300 msec time steps, yielding nine hours of continuous video recording.

The audio monitoring and playback equipment was comprised of two distinct systems. The playback system consisted of a SoundTech PL-150 low-noise integrated power amplifier (75 W rms per channel), which received the output from a Sony CDP-25 compact disc player, and a Teac A-20 10-band graphic equalizer for modifying the frequency balance of the treatments to conform to the room acoustics. The output of the disc player was amplified by the SoundTech PL-150 stereo amplifier, which in turn powered four wide-range loudspeakers.

The experiment room's monitoring system included a Realistic MPA-35-A integrated power amplifier (35 W rms), AudioTechnica 440 dynamic microphones (40 Hz–18 kHz), a JVC KD-V200 stereo cassette recorder, and Sony MDR-1 stereo headphones. The timing of the operation of these units was controlled with a Dayton 2E-408 repeat cycle analog electric timer.

The experiment room had floor dimensions of 2.43 x 2.90 m and a height of 2.53 m. Its walls were a uniform cream color, evenly distributing light emanating from an overhead array of three rectangular fixtures. Throughout the study, automatically timed illumination cycles began at 07:00 and continued for 12 hours until 19:00. The average intensity of illumination was 55.6 footcandles, measured at squirrel level with a Minolta LX-100 photometer.

The entrance to the room had a solid core door with tight rubber seals providing some acoustic isolation from ambient noise generated elsewhere in the animal care facility. Typically, extraneous noise with frequencies between 1 kHz and 4 kHz was attenuated by nearly 20 dB. Animals positioned within the nest box probably heard the sounds generated within the experiment room attenuated between 10 and 20 dB, depending on the their locations in the nest box. This degree of attenuation is probably similar to that heard by free-living animals while they are within their burrows at distances of from 15–20 cm from its opening (R. G. Coss, personal communication, 1997).

Acoustic events occurring within the experiment room were monitored via two dynamic microphones symmetrically suspended by flexible conduit from the wall adjoining the monitor room. The intensity of sound within the room was continuously monitored with a Realistic 332050 analog sound intensity meter mounted between them.

Treatments were administered through four Realistic Optimus 7 loudspeakers (40 Hz–18 kHz). These were suspended from the ceiling in each corner at heights of 0.6 m above the floor via heavy chains shrouded in 5 cm PVC conduit. This elaborate arrangement was designed to discourage the subjects from gnawing the cables. The suspension of the speakers from the ceiling, the insertion points of the microphone conduits into the wall, and the presence of associated cables gave the setting a slight degree of vertical complexity.

The loudspeakers were arranged in a geometric "X" pattern to eliminate the creation of a bilateral sound image in the playback room. Further, each was oriented away from the center of the room (facing into each corner) to maximize dispersion of the program material. This arrangement was conceived to reflect sound from all surfaces in the room, creating a more evenly distributed, continuous sound image. This approach was calculated to reduce the ability of the subjects to localize point sources. The subjective effect was to increase the ratio of reflected to direct sound, reminiscent of the effect of a long, indirect path on an acoustic signal (Wiley and Richards, 1978). Point sources were further obscured when animals were nestled within their acoustically opaque nest boxes.

The animals were provided with a naturalistic substrate in the form of a layer of pine shavings at a depth ranging from 10-20 cm. Two food and water trays allowed the animals access to water and rodent diet on an ad libitum basis. A 38.1 cm wide x 38.1 cm long x 12.7 cm high wooden nest box was located in the center of the room to function as a primary refuge for the subjects.

A 44 cm diameter convex mirror was mounted near the center of the ceiling, providing an overhead view of the entire floor of the experiment room. This allowed video recordings to be obtained from the adjacent monitor room via a one-way mirrored window in the wall between the two rooms.

Sound Treatments

Two naturalistic sound conditions were obtained from commercial compact discs featuring environmental ambiences. A thunderstorm ambience condition was obtained from "The Sounds of Nature Sampler" (1990, track 1) (Figure 1A). A temperate forest ambience condition was obtained from "Jungle Journey" (1990, track 1) (Figure 1B).

The treatments were administered using the disc player set to a continuous playback mode, which repeated the program material uninterruptedly between 9:00 and 16:00. They were presented in a balanced randomized order alternating with the animal quarters ambience condition (Laboratory). Two unaugmented control days (Habituation 1 and 2) always preceded the three randomized conditions (Laboratory, Thunderstorm, and Forest). On each succeeding day, one of these three conditions was presented to the subject for the duration of the observation period. Sound treatments were administered to the subjects at sound pressure levels ranging from 58–72 dB. On the control days and under the animal quarters condition, sound pressure levels ranged from a low of 40 dB to a high of 57 dB. Based on measurements made at Camp Ohlone and in the Sierra Valley, all of these values are representative of the quietest and noisiest conditions likely to have been encountered by the subjects prior to capture (Tromborg, unpublished data, 1993). Similar levels of noise have been reported in other ground squirrel habitats (Schwagmeyer and Brown, 1984).

Procedures

From April through September of 1993, the two groups of subjects were tested under the three sound treatment conditions. To begin the experiment, on every Monday of each experimental week a new subject, drawn alternatively from each population, was introduced into the experimental setting and allowed to habituate for one day. A second habituation day followed this, but it was considered part of the experimental design and treated as a control day (Habituation). The second through the fifth days comprised the actual experimental period. For each of the next three days, one treatment was continuously administered to the subjects. All treatments were presented in a randomized order so that no two subjects were presented with the same treatment on the same day of the week. Human intervention with the subjects was limited to a daily monitoring of the food and water supply. Each subject was transferred from its home cage to the experiment room using a sealed nest box. In the darkened room, the subject was allowed to exit its transfer box, which was positioned near the entrance of the primary nest box. Since transfer was conducted in the dark, squirrels emerging from the nest box the following day would be confronted by an unfamiliar setting. Time-lapse video recording commenced a day later, on the second control day (Habituation). On sound treatment days, video recording and acoustic playback equipment were activated automatically at 9:00—two hours after room illumination was begun at 7:00. Recordings were automatically terminated at 16:00 hours. The behavior of each subject was individually recorded over four successive nine-hour days.

Behavioral Analyses

Video recordings were analyzed on a Sony Trinitron 33 cm diagonal screen, high-resolution color monitor coupled to a Panasonic VTR MV-8030 time-lapse video recorder, which enabled recordings to be reviewed using 300 msec real-time steps and frame-by-frame analyses. Videotapes were viewed and decoded by trained pairs of researchers, who then recorded their measurements on data sheets (see Appendix 1). Interobserver reliability was well in excess of 95 percent (Bakeman and Gottman, 1997).

The following behaviors were subjected to statistical analyses:

1. Number of exit bouts. Exit bouts were counted for every event in which the squirrel completely left the nest box or when its body fully protruded from the nest box to the base of the tail.
2. Average exit bout duration. The duration of each episode was defined as beginning with a video field (i.e., frame) in which the squirrel's body was fully exposed to the base of the tail as it emerged from the nest box. It was concluded with the video field in which the squirrel entered the nest box, also up to the base of the tail. Bout duration was derived by converting video field numbers into seconds and then averaging them across all bouts.
3. Total bout duration. This interval was derived by summing all of the average bout durations together.

The decoded data were entered into GANOVA, an analysis of variance (ANOVA) statistical program developed by Woodward, Bonett, and Brecht (1990). The three variables were analyzed by two-factor between-groups (squirrel populations and sex), one-factor within-groups (sound conditions) repeated measures ANOVAs. These analyses were complemented by tests of simple main effects to compare the control and three sound conditions for each squirrel population, and squirrel population for each sound condition (Rosenthal and Rosnow, 1984). In addition to these tests, consistency in behavior under all sound conditions was assessed using intraclass correlations (Snedecor and Cochran, 1989).

Results

Qualitative Analysis

Although not originally considered as a component of the analysis, the visual behavior of pre-emergent and post-emergent squirrels serendipitously suggested an additional variable for this research and established the context for Chapter 3. Both outcomes were based on the observation that ground squirrels engage in a predictably higher level of vigilance behavior prior to exiting their burrows. During the decoding of the initial video tapes, squirrels were observed to engage in cautious visual scanning of their surroundings while emerging. Some squirrels turned their heads to peer over the top of the box, as if searching for something lurking behind them. In extreme instances, some squirrels perched on their nestbox after exiting and continued to visually scan their environment. One female behaved so erratically that her data were removed from the analysis and she was eaten. Because these behaviors were apparent only after the study was underway, visual scanning is described only qualitatively. For a more complete treatment, see the next chapter.

Scanning was considered to feature cyclical lateral displacements of the head from the midline axis of the body or a single horizontal tilting of the head from its horizontal plane. It was evaluated by counting numbers of side-to-side and upwards movements of the head during each episode (bout) of exiting from the opening of the nest box. These measurements were then averaged for the four Sunol and six Sierra Valley squirrels for which there were complete data. There is a clear trend for increased scanning under noisier acoustic conditions, with scanning being more frequent under thunderstorm ambience than under temperate forest ambience. Similarly, scanning was more apparent under the temperate forest ambience than under the unmodified conditions. Seven of eight squirrels performed greater numbers of side-to-side head motions during each exiting bout under the thunderstorm ambience condition than they did under the temperate forest ambience condition. Five of ten squirrels did the same under the temperate forest ambience condition than they did under the laboratory ambience condition. The relevance of this scanning behavior will become evident in its potential relationship with the number of exiting bouts when these are examined quantitatively.

Mean values of scanning while exiting, inferred from head motion, were not appreciably different under the four sound conditions (minimum and maximum values = 2.2-3.5 head motions per exiting bout). Examination of the first bout captured on video tape revealed higher mean values for the four sound conditions (minimum and maximum values = 4.2-5.7 head motions per exiting bout). Individual variation was considerable for lateral head motion (range = 1-19 cycles of head motion per exiting bout across all sound conditions).

Quantitative Analyses

Statistical comparisons of squirrel populations, sex, and sound-treatment conditions for total time spent out of the nest box and those for average exiting bout duration did not achieve statistical significance. The remaining variable, number of exiting bouts, yielded statistical significance for several comparisons. For the number of exiting bouts averaged for the sound conditions, the main effect for populations was significant $\left(F = 6.461, \text{df} = 1{,}8, p < 0.05\right)$, with Sunol squirrels exiting more frequently than the Sierra Valley squirrels (Figure 2A). Tests of simple main effects revealed that the Sunol squirrels exited significantly more frequently than the Sierra Valley squirrels under the thunderstorm ambience sound treatment condition $\left(F = 8.110, \text{df} = 1{,}8, p < 0.025\right)$. A standardized comparison of mean values yielded a large effect size for group differences: $\textit{Cohen's } d = 1.80\big)$. Here, effect size, as a measure of the relationship between two population means, can provide statistical power, yielding reliable information about the influence of treatments on subjects when the sample size is small. In fact, in this instance, it provides a more informative index of the magnitude of treatment effects than a simple interpretation of outcomes based exclusively on the significance level (Cohen, 1992; Hunter and Schmidt, 1990; Nelson, Rosenthal, and Rosnow, 1986; Rosnow and Rosenthal, 1989). Sunol squirrels also exited more frequently on the other sound-treatment days, with the first habituation day and temperate forest ambience condition yielding population differences in means values that approached significance, respectively $\left(F = 4.355 \text{ and } 4.099, \text{df} = 1{,}8, p < 0.10\right)$. The mean values for each population in frequency of exiting bouts are the least different under the laboratory ambience condition (Figure 2B).

The main effect for sound conditions, averaged for both populations, was not statistically significant for the number of exiting bouts. Although males exited more frequently than females, again averaged for both populations, these values were not significantly different. However, averaged for both populations, a significant sex difference was apparent under the laboratory ambience condition (simple effect: $F = 9.910$, df = 1,8, $p = 0.025$), with males exiting more frequently than females.

Intraclass correlations of the four sound conditions assessed the congruence in the behavior of each squirrel. This test is used to establish that, while individuals might differ from one another with regard to a specific measure, they were internally consistent in their own characteristics. In other words, a large intraclass correlation suggests that a high proportion of error variance arises from individual differences. In a repeated measures design, a large intraclass correlation facilitates treating each individual as a distinct class or group (Snedecor and Cochran, 1989).

The intraclass correlations were significant at the 95% confidence level for the number of exiting bouts ($r_I = 0.666$ and the total time spent out of the nest box ($r_I = 0.689$). They were not significant for the average exiting bout duration ($r_I = 0.247$). The significant intraclass correlations revealed that, although squirrels differed individually in their exiting behavior, each was internally consistent in its pattern of exiting under the four sound conditions.

Discussion

The primary rationale underlying this study was to investigate the effect of noise in the acoustic far-field on the emergence and assessment behavior of ground squirrels. Ground squirrel populations selected for study were obtained from distinctly different microhabitats at low and high elevations, characterized by climatic differences and acoustic conditions. Squirrels presented with low-level homogeneous noise in the perceptual background could provide insight into whether naturalistic sounds work by masking provocative noise and/or by impairing auditory discrimination. Masking provocative exogenous noise, naturalistic sounds should have promoted decreased numbers of exiting bouts, extended durations of time spent in the open, and reduced rates of visual scanning. Jamming the auditory channel, naturalistic sounds should have promoted increased numbers of exiting bouts, reduced durations of time spent in the open, and increased visual scanning.

The results suggest that, overall, the influence of naturalistic background sounds is slight. However, the lower exiting rate of Sierra Valley squirrels compared with Sunol squirrels is significant. This population difference was even more pronounced under the thunderstorm ambience condition. The thunderstorm ambience condition is characterized by low intensity, slight amplitude modulation and a wide, even distribution of energy. Its homogeneous acoustic structure might have functioned similarly to a conventional acoustic masker. Acoustic maskers can reduce signal-to-noise ratios or elevate auditory thresholds, impairing an animal's ability to discriminate ecologically relevant acoustic events from the background noise. The finding that the thunderstorm ambience condition exerted the greatest effect on behavior suggests that it could have interfered with a squirrel's ability to extract important acoustic information from its surroundings. Unable to discriminate acoustic information, a squirrel might be less likely to emerge into an uncertain environment.

Alternatively, this finding might reflect an interaction between thunder and the slightly greater auditory sensitivity of Sierra Valley animals to low frequency punctate sounds, such as those associated with the thunderstorm ambience condition. Augmented low-frequency sensitivity is observed when squirrels from the high elevation alpine environments and squirrels from low elevation coastal environments are compared at sea level, where the difference in low-frequency sensitivity is pronounced. If assessed in their native habitats, the hearing contours of the two populations would probably have been equivalent (Henry and Coss, unpublished manuscript, 1996).

The acoustic landscape of the Sierra Valley is distinctly different from that of the coastal foothills. The less efficient conductivity of sound in meteorologically variable mountain habitats compromises the reliability of the acoustic channel. Lower atmospheric density at higher elevations reduces the conductivity of sound frequencies below 4.0 kHz (Kinsler, Frey, Coppens, and Sanders, 1982). Sounds are attenuated in a frequency-dependent manner by atmospheric turbulence, stationary and dynamic heterogeneities, and stratified temperature gradients, transforming the atmosphere into an anisotropic transmission medium. This selectively attenuates frequencies below 1500 Hz and above 2500 Hz. Low frequencies are additionally attenuated by a variety of ground effects (Aylor, 1971; Marten, Quine, and Marler, 1977). Frequency-modulated sounds are selectively attenuated in edge habitats, while amplitude-modulated sounds are selectively attenuated in open grassland (Morton, 1975). Finally, the propagation efficiency of low-frequency sound is reduced at higher altitudes. Squirrels might adapt to these challenging acoustic conditions by evolving greater sensitivities to lower frequencies, thus maintaining effectively constant sensitivity thresholds across a broad spectrum of frequencies (Fletcher, 1992; Kinsler, Frey, Coppens, and Sanders, 1982;

Rudmose, Clark, Carlson, and Eisenstein, 1948). In the current context, the corrected low-frequency sensitivity in Sierra Valley squirrels is viewed as a sensory adaptation which maintains auditory competence in a difficult acoustic environment (Bradbury and Vehrencamp, 1998).

The lower exiting rates of Sierra Valley squirrels under the thunderstorm ambience condition might reflect reluctance by experienced animals to emerge into the open after detecting a sound which, in mountain environments, reliably signals cold, wet conditions. A reliable subterranean index to terrestrial conditions might possess value for squirrels from both populations, especially females. This observation is further supported by the lower overall rate of female exiting in both populations. Lower exiting rates in females could represent learned avoidance of impending cold, wet external conditions as signaled seismically by low-frequency ground-borne punctate noise. Learning the significance of this seismic signal has adaptive value for nursing females. The body temperatures of neonatal pups are partially maintained by contact with the body of the female during nursing. The temperature maintenance function could become compromised if the pelage of the mother were to become cold and wet. The probability of this occurring increases as the frequency of excursions into the open by females becomes more numerous. This danger is reduced if squirrels respond to the subterranean detection of thunderstorm related sound by exhibiting fewer excursions into the open. Thus, a selective advantage would be conferred on individuals possessing perceptual adaptations enhancing their ability to detect seismic signals that reliably indicate approaching inclement weather. The supposition that thunder is used as a cue is supported by the finding that the lowest rate of exiting occurs in Sierra Valley females. These squirrels inhabit environments that, compared with those of coastal foothills, are characterized by the greater regularity of thunderstorms. During some seasons, storms in mountain valleys are nearly a daily occurrence. The resulting reliable pairing of an unconditioned stimulus, stormy weather, with a conditioned stimulus, thunder, probably promoted the acquisition of signaling salience for both the natural and experimental thunderstorm sounds.

For this scenario to be plausible, sounds generated above ground or in the atmosphere would have to arrive at the entrances of burrow systems directly or would have to be conducted into them via intervening layers of earth. High-frequency sound energy is severely attenuated as it propagates over porous soil or through dense grasses adjacent to burrow openings (Aylor, 1971; Marten, Quine, and Marler, 1977). Consequently, only the lowest frequency components of atmospheric sounds enter the burrow. Burrows probably function as resonators for sounds arriving at their entrances or for those generated within them. They can also function as acoustic horns to direct incoming sounds or to amplify those generated internally. Finally, the inner surfaces of burrows can function as waveguides for ground-borne vibrations (Bradbury and Vehrencamp, 1998; Fletcher, 1992; Narins, Lewis, Jarvis, and O'Riain, 1998; Tromborg, unpublished observation, 1993). Research on burrow acoustics of anurids within the genus Leptodactylidae suggests that burrows augment some frequencies while attenuating others (Penna and Solis, 1996). This supports the contention of some researchers that acoustic information available below ground is qualitatively and quantitatively different from that available to percipients above ground (Mateo, 1996a, 1996b). Inside burrows, frequencies encompassing the range of squirrel vocalizations and the rustling of vegetation associated with the approach of predators would be greatly attenuated. Fully immersed squirrels, confronted with the requirement of assessing the risk associated with emerging into the open, almost certainly would have to compensate for the absence of reliable visual and high-frequency information generated above ground by concentrating on ground-conducted low-frequency information. In this context, the burrow operates as an acoustic funnel and can be considered a phenotypic extension of the ensconced percipient's external auditory meatus.

Alternately, enhanced low-frequency sensitivity in Sierra Valley squirrels could represent an adaptation to contend with adversaries, especially the American badger (*Taxidea taxis*), an important predator of ground squirrels found in the Sierra Valley (Minta, 1990; Towers and Coss, 1990). Reliable low-frequency hearing at high altitudes could enable squirrels to detect the digging of badgers as they attempt to breach burrow systems (Minta, 1989). Responsiveness to low-frequency, ground-borne vibrations has been reported in the sensory behavior of other rodents, e.g., kangaroo rats (*Dipodomys mironys*) (Kenagy, 1976; Narins, Lewis, Jarvis, and O'Riain, 1998; Randall, 1993; Randall and Stevens, 1987; Webster, 1962; Webster and Webster, 1971).

Brown (1989) has described an interesting relationship between the acoustic transmission qualities of a specific habitat and the low-frequency sensitivity of two species, the grey-cheeked mangabey (*Cercocebus albigena*) and the blue monkey (*Cercopithecus mitis*). Comparative research reveals that both species possess superior low-frequency auditory sensitivity. Both species inhabit tropical forests, in which low-frequency wavefronts are preserved as they propagate through the forest far more coherently than high-frequency wavefronts. The greater reliability of low-frequency signals has resulted in their being emphasized over higher-frequency vocalizations by both species (Brown, 1989). Both species, as with some fossorial rodents, exhibit a slightly hypertropic malleus and auditory bulla (Brown, 1989; Howell, 1932; Webster, 1962; Webster and Webster, 1971). The proposed linkage between enhanced low-frequency hearing, thunder, and reduced emergence to avoid inclement weather is speculative. However, it is not unreasonable from an ecological perspective that embraces the importance of learning in natural settings (Shettleworth, 1972, 1984; Tarpy, 1982). Maintenance of perceptual adaptations that facilitate detection of storm-signaling thunder can confer advantages on animals possessing them if they facilitate adaptive behavior. Microhabitat variation and associated noise levels could alter an animal's moment-to-moment decision processes, as suggested by altered patterns of emergence behavior. Any animal detecting ground- borne vibrations caused by thunder could more effectively manage its time by remaining underground when such vibrations are detected. In research conducted in laboratories and zoos, a variety of species remain under cover when confronted with elevated levels of environmental noise (Anthony, Ackerman, and Lloyd, 1959; Belyaev, Plyusnina, and Trut, 1984; Broom and Johnson, 1993; Cottereau, 1978; Ehret, 1980, 1989, 1990; Gamble, 1982; Snyder, 1975; Stoskopf, 1983; Tromborg, 1993; van Rooijen, 1984).

The acoustic profiles of alpine and foothill environments impose different selection regimes on the two populations of squirrel. For example, when sound pressure levels were measured in both habitats over several afternoons, they ranged from 62 to 72 dB at Camp Ohlone, and from 60 to 85 dB in the Sierra Valley. Higher values were always associated with gusts of wind, a common occurrence in the mountains. Differences in selection operating on signal production or perception could drive divergence between Sierra Valley and Sunol populations. When species are geographically separated and remain so for extended periods, they can develop dialects in response to such microhabitat differences (Conner, 1982, 1985; King and West, 1980; Morton, 1975: 1986; Slobodchikoff and Coast, 1980; Sommers, 1973; Waser, 1985). The populations of squirrels represented in this study have been isolated since the late Pleistocene (Goldthwaite, 1989). An interval of this duration could have provided sufficient time for similar macrogeographic divergence to occur in the anatomy of the auditory system. Innately mediated trends in the divergence of ground squirrel perceptual and behavioral systems have been extensively discussed elsewhere (Coss and Goldthwaite, 1995; Coss and Owings, 1985).

Much of the research on evolutionary adaptations concerns the morphology of vocal signals. Vocal signals do not exist as isolated entities; they are imbedded in a constantly changing *acoustic tapestry* of background noise (Yost, 1992). Thus, it is surprising that the relationship between evolution, behavioral adaptation, background environmental noise, and foreground signal noise has been so infrequently investigated (Brown, 1989). To partially address this oversight, Brown (1989) introduced tropical forest sounds into a laboratory setting in a complex discrimination task to assess how their presence influenced the apparent prominence and discriminability of vocalizations produced by grey-cheeked mangabeys, blue monkeys, and human beings. The results revealed that, while some vocalizations were more discernable than others to human percipients, each of the nonhuman species demonstrated selective discrimination that favored vocal signals produced by its own species. Further, the performance levels did not appreciably differ in the presence of background sounds compared with their absence. These findings strongly argue for the existence of species-specific perceptual systems which have coevolved within a predictable range of environmental conditions, including the reliable presence of specific predators. Similar instances of coevolutionary relationships involving the modification of perceptual systems to accommodate sound generated by a predator have been invoked to describe the relationship between grey tits and sparrow hawks (Klump, Kretschner, and Curio, 1986).

The long-term modification of perceptual systems in response to the reliable presence of predators has been reported in Sunol squirrels (Owings and Coss, 1985). In this instance, Sunol squirrels are distinctly superior to Sierra Valley squirrels in their ability to discriminate venomous from nonvenomous species of snakes (Towers and Coss, 1990). Sunol squirrels, unlike their Sierra Valley counterparts, are more likely to encounter snake predators than squirrels dwelling at high altitudes.

Genetic evidence suggests that Sierra Valley squirrels have lived at high elevations in relative isolation from other squirrel populations since the late Pleistocene (Goldthwaite, 1989; Towers and Coss, 1990). Based on electrophoretic analysis of genetic distances calibrated to time, Sierra Valley squirrels and Sunol squirrels last shared a common ancestor approximately 228,000 +- 41,000 years ago (Goldthwaite, 1989).

The lower mean ambient temperatures at higher elevations within the Sierra Nevada mountain range are unsuitable for either rattlesnakes or gopher snakes. They are typically restricted to elevations below 1200 m. Glaciation events during the last ice age prevented snakes from recolonizing lower elevations from which they had been extirpated. Such paleoclimatic conditions and geographic isolation promoted distinctly different constellations of predators in higher and lower elevation habitats.

It is not unreasonable to suggest that prolonged associations with a specific palette of predators fostered the honing of slightly different perceptual systems in each population (Coss and Owings, 1985). Ground squirrel populations which coexist with snake predators have developed high levels of venom resistance. They also exhibit reduced latencies to differentiate venomous rattlesnakes from nonvenomous gopher snakes, possibly through modification of perceptual systems important in predator detection (cf. Coss, Gusé, Poran, and Smith, 1993; Towers and Coss, 1990).

Although visual behaviors were not quantitatively analyzed, some trends were readily apparent. The greater amount of lateral head motion per exiting bout observed under the thunderstorm ambience condition relative to the other sound conditions is suggestive of a relationship between acoustic monitoring and visual monitoring. It cannot be completely ruled out that increased side-to-side head motion represents an attempt to assess the relatively noisy environment auditorily through triangulation. It is just as probable that this pattern represents an increased emphasis on visual assessment.

Squirrels were less likely to emerge under the thunderstorm condition than any other. All but one that did emerge under this condition showed increased frequency of lateral head motion compared with other sound conditions. This behavior could have represented an attempt to overcome auditory interference from noise by increasing the frequency of visual assessment behavior. This interpretation is supported by the reliably lower numbers of side-to-side head motions per exiting bout observed under the quieter temperate forest ambience condition and the even smaller number observed under the acoustically unmodified laboratory ambience condition.

Elevated scanning does not necessarily imply a shift in perceptual emphasis away from audition toward vision. Some researchers suggest that visual scanning offers a reliable index of vigilance-related arousal (Caine, 1984; McAdam and Kramer, 1998). Scanning persists even in innocuous environments, in which animals are free from actual, though not perceived, threat (Chapters 3 and 4; Caine, 1984, 1987).

The influence of the structure of background noise on arousal is more complex than simple models suggest (e.g., Davis, 1974; Yost, 1992). As with many mammals, laboratory rodents will respond to intense punctate noise by startling (Busnel, 1978). If this punctiform noise is superimposed over homogeneous white-noise backgrounds, the intensity of startling does not decrease as it would if the punctate stimulus were masked. Instead, the startling response becomes more intense. If the presentation of the white-noise background is intermittent or variable, the intensity of the startle response decreases (Hoffman and Fleschner, 1963; Hoffman, Marsh, and Stein, 1969). This and similar findings in other sensory systems suggest that invariant perceptual backgrounds can actually increase the contrast between background and foreground. This intensifies the apparent prominence of foreground stimuli relative to the background by effectively increasing the signal-to-noise ratio (Davis, 1974). Some researchers have termed this paradoxical mechanism stochastic resonance (Henry, unpublished manuscript; Levin and Miller, 1996).

Thus, background noise does not always mask foreground noise. Its effects are variable and influenced by the signal-to-noise ratios and relative structural complexities of the two components of the contrasted sounds. Further study of the influence of environmental sound on behavior is clearly indicated before more conclusive interpretations can be drawn.

The high intraclass correlations with respect to two variables suggests that, while subjects varied widely in their response to treatments, they were internally consistent with regard to constitutional characteristics (Snedecor and Cochran, 1989). The rarity of significant results was less a consequence of random events or treatment effects and more a result of individual differences in motivation or temperament. Analyses of assays of cortical steroid mobilization after stressful handling in some of the squirrels used in this study failed to reveal reliable population or sex differences in hormone mobilization. However, large individual differences in corticosteroid mobilization were evident (Schimmel, Mendoza, Swaysgood, and Owings, unpublished data, 1993). Similar individual variability in temperament has been observed in the response of many of the same squirrels to the presentation of snake and mammalian predators (Coss and Biardi, 1997). The importance of investigating individual variation in animal behavior research has been discussed elsewhere (Hirsch, 1963; King and West, 1990).

Differences in motivation are more problematic to assess. All subjects had equal access to food, water, and shelter. All subjects were roughly equivalent in age. The most important aspect of motivational state then becomes the possibility that the animals had habituated to the treatment conditions.

Context-Specific Habituation

The absence of differential salience, which could be employed in distinguishing between treatments, offers the most parsimonious explanation for the absence of differentiation by the subjects. The homogeneous acoustic structures of the laboratory, temperate forest, and thunderstorm conditions were all structurally similar to one another, impairing the ability of subjects to reliably discriminate between them (see Figures 1A and 1B). The treatments appeared to possess little intrinsic salience to the subjects whatsoever. Although ecologically relevant, the treatments probably failed to acquire salience because of their diffused, reflected, homogeneous structure and their position in the perceptual background. This was less true for the thunderstorm condition, the only condition which yielded an effect. Its more punctate qualities probably elevated it, and incidental laboratory noise, to the perceptual foreground, where attention is focused (Guilford and Dawkins, 1991; Israeli, 1950; Lerea, 1961; Lindauer, 1989; Thurlow, 1957; Yost, 1992). The structurally homogeneous character of the acoustic treatments, the continuous presentation to the subjects in the absence of consequences, and the absence of intrinsic biological salience typifies the sort of sensory invariance likely to result in habituation (Donaho and Palmer, 1994; Marlin, 1980, 1982; Marlin and Miller, 1981; Tarpy, 1982).

The failure of the squirrels to react to punctate exogenous noise was probably also an artifact of habituation. They had all been exposed to initially provocative but eventually meaningless sounds for the two years preceding the study (Mackintosh, 1973). Even if maintenance noise regained salience through dishabituation when the squirrels were transported to the experimental setting from their holding facilities, this salience would have become meaningless after a period of repeated exposure (Mackintosh, 1973). This sort of complex interaction between homogeneous backgrounds and punctate foreground noise is discussed extensively elsewhere (Davis, 1974; Hoffman and Fleschner, 1963; Hoffman, Marsh, and Stein, 1969).

A large number of species exhibit a remarkable ability to habituate to sounds which are not biologically meaningful. Habituation probably functions as a cognitive mechanism to reduce arousal in the presence of stressors over which animals have little control. Habituation is a powerful and ubiquitous form of learning (Marlin, 1980; Marlin and Miller, 1981; Tarpy, 1982). It has even been observed in American bison (*Bison bison*), which habituate to the sounds of gunshot as animals are culled from the herd (Busnel, 1978; Shaw, 1978). Finally, the argument could be advanced that the pre-exposure of the subjects to acoustic conditions similar to the treatments for the two years preceding this research led to context-specific habituation. This pre-exposure diminished any differential salience that the treatments might have originally possessed. In invariant laboratory settings, experimental animals have been documented to habituate even to threatening, biologically important stimuli (Ellard, 1996).

Conclusions

Ultimately, the outcome of this research is consonant with other attempts to investigate the influence of the perceptual background on behavior. Research of this type has been infrequent; when it has been undertaken, the findings are characterized by small effect sizes and inconclusive results (Brown, 1989; Ogden, Lindburg, and Maple, 1994; Tromborg, 1993). Such findings could be artifacts of the manner in which most animals structure their attention. Typically, percipients focus their attention on prominent or conspicuous phenomena in the perceptual foreground and tend to ignore less meaningful features in the perceptual background (Guilford and Dawkins, 1991; Israeli, 1950; Lerea, 1961; Lindauer, 1989; Thurlow, 1957). Under this scenario, modification of the perceptual background could have been expected to exert only slight effects on behavior. From both a theoretical and a practical perspective, these observations suggest that for such experiments or acoustic enrichment procedures to yield more compelling results, treatments should feature acoustic structures markedly different from one another or from those of the background ambience.

As mentioned, when the manipulation of environmental variables focuses on the perceptual background, the magnitudes of treatment effects can be slight. Nonetheless, the underlying rationale of this avenue of research is sound and the research important. It can provide scientists with an enhanced understanding of the structure of attention. It can also foster an appreciation for the impact of both natural (zoogenic) and unnatural (anthropogenic) noise on the ability of animals to monitor their surroundings. Finally, it reveals something of the complexity of small-scale adaptations to subtle acoustic environmental features which are not always obvious to visually oriented scientists.

Summary

California ground squirrels from low and high altitude environments were compared on the basis of nest box emergence behavior under laboratory and naturalistic sound conditions.

1. Acoustics are an important aspect of the sensory and perceptual surroundings of animals.

2. Species frequently exhibit sensory and perceptual adaptations to local climatic and

physical conditions.

3. California ground squirrels exhibit only slight variation in exiting and scanning behavior when immersed in naturalistic acoustic conditions, including laboratory, temperate forest, or thunderstorm acoustic ambiences.

4. Sierra Valley squirrels possess enhanced low-frequency auditory sensitivity, possibly to compensate for the reduced effectiveness of sound propagation at high altitudes.

5. Sierra Valley squirrels emerged less frequently from cover than Sunol squirrels under the thunderstorm condition. This could be an artifact of their enhanced low-frequency sensitivity.

6. Female squirrels from both populations emerged from cover less frequently than males under the thunderstorm condition. Thunder could have become a signal about the approach of inclement weather. Females detecting this sound might emerge less frequently into the open, where their pelage could become moist and endanger the survival of pups.

7. The microclimatic and microgeographic sensory adaptations of animals are frequently overlooked in behavioral research. These adaptations can influence their responsiveness to experimental treatments.

8. Despite their subtle effects on behavior, the interaction between sound in the perceptual background and sensory behavior should be more extensively investigated. This is especially important if such sounds are to be employed in improving the acoustics of artificial habitats in laboratories and zoos.

CHAPTER THREE

Experiential Factors Mediating Vigilance Behavior of California Ground Squirrels in Novel Settings

Successful species employ a constellation of sensory and behavioral adaptations to assess the states of their surroundings (Bradbury and Vehrencamp, 1998; Brown and MacDonald, 1985; Dusenbery, 1992; Eisenberg and Kleiman, 1972; Lythgoe, 1979; Stebbens, 1983; Stoddard, 1980). Among these are the sensory systems and behaviors associated with vision. Visual behavior is exemplified by vigilance, which frequently includes scanning, orienting, and fixation. These behaviors have been observed and described in a multitude of avian and mammalian taxa (Hart and Lendrem, 1984; McAdam and Kramer, 1998; Quenette, 1990). Its functional equivalence across groups has resulted in a high degree of convergence in its behavioral properties. When variation in visual vigilance does occur, it is frequently manifested in the proportion of time devoted to scanning, variable emphases on continuous versus episodic scanning, length of scanning bouts, length of interscan intervals, and the frequency of bouts per unit time (Caraco and Lima, 1987; Hart and Lendrem, 1984; Lendrem, Stretch, Metcalfe, and Jones, 1986). Such variation originates with differences in the age, sex, social system, social status, or experience of the percipient (Bedford, 1995; Coss, 1978, 1979; Rowell and Olson, 1986; Williams and Meck, 1991).

The primary functions of visual vigilance are the detection of predators (Bertram, 1980; Caraco, 1983, 1985; Caraco and Lima, 1987; Coss and Owings, 1985; Curio, 1969;

Elcavage and Caraco, 1983; Hanson and Coss, 1997; Hart and Lendrem, 1984; Lythgoe, 1979; Quenette, 1990) and prey (Curio, 1969, 1975; Leyhausen, 1979; Schaller, 1972; Webster and Webster, 1971). In social species, vigilance provides a means for monitoring the disposition of group members and their response toward provocative sources of stimuli (Bossema and Burgler, 1980; Betts, 1976; Burger and Gothfeld, 1994; Hennessy and Owings, 1978; Roberts, 1996; Rowell and Olson, 1986; Sullivan, 1984; Underwood, 1982; Wirtz and Wawra, 1986). Vigilance almost always increases when predators are detected directly, or indirectly through the change in behavior of alerted group members (Armitage, 1982; Curio, 1975; Goldthwaite, 1989; Hanson, 1995; Harper, 1984; Hart and Lendrem, 1984; Lendrem, 1983). Vigilance is reliably instigated by the perception of either conspecific or heterospecific antipredator vocalizations (Chapters 1 and 4; Cleveland and Snowdon, 1982; Klump and Shalter, 1984; Leger and Owings, 1978; Owings and Virginia, 1978; Owings, Hennessy, Leger, and Gladney, 1986; Shriner, 1995, 1998; Tromborg, 1993). Changes in vigilance behavior convey information to prey about approaching predators or to predators about the wariness of intended prey (Endler, 1984; Leyhausen, 1979; Schaller, 1972; Sullivan, 1984; Underwood, 1982).

Different patterns of vigilance result from the requirement to balance time budgets between the demands of antipredator behavior and maintenance activities, especially foraging (Caraco, 1983, 1985; Caraco and Lima, 1987; Lima, 1986; Lima, Valon, and Caraco, 1985; Poysa, 1987).

To maximize the efficiency of environmental monitoring while exerting minimal impact on foraging efficiency, various time allocation strategies have been adopted. A general form of scanning consists of constant, essentially random glancing bouts performed by all members of social groups. Random, low-levl individual scanning yields nearly constant environmental monitoring at the group level. Individuals forage nearly constantly, only episodically assessing their surroundings (Bertram, 1980; Caraco, 1983; Caraco and Lima, 1987; Elcavage and Caraco, 1983). A variation of this strategy features longer periods of concentrated visual monitoring interspersed with intermittent bouts of foraging (Wawra, 1988; Wirtz and Wawra, 1986). This pattern of vigilance has been observed in blue tits *(Parus caeruleus)* (Lendrem, 1983), house sparrows *(Passer domesticus)* (Lima, 1986), ostriches *(Struthio camelus)* (Hart and Lendrem, 1984), teals *(Anas crecca)* (Poysa, 1987), a variety of African antelopes within the families *Antilocapridae* and *Cervicapridae* (Underwood, 1982), several East African cercopithecids, e.g., *Cercopithecus mitis* (Cords, 1990), saddleback tamarins *(Saguinus fuscicolis)* (Caine, 1984); red-bellied tamarins *(Saguinus labiatus)* (Caine, 1986), cotton-top tamarins *(Saguinus o. oedipus)* (Tromborg, 1993), and even humans *(Homo sapiens)* (Wawra, 1988).

Many species emphasize such apparently random patterns of scanning (Bertram, 1980; Hart and Lendrem, 1984; Lendrem, 1983; Lendrem, Stretch, Metcalfe, and Jones, 1986; Pulliam, 1973). Unpredictable patterns of visual scanning could operate as an antipredator strategy (Hart and Lendrem, 1984; Lendrem, 1983; Lendrem, Stretch, Metcalfe and Jones, 1986; Poysa, 1987; Pollium, Pyke, and Caraco, 1982). Confronted by unpredictable behavior, a swooping raptor or a furtively approaching mammal cannot assess which moments are most advantageous for advancing toward prey (Bertram, 1980; Lendrem, 1983a; Leyhausen, 1979). Both lions *(Panthera leo)* and domestic cats *(Felis sylvesteris catus)* have been observed to cease advancing toward targets if the intended victims interrupt foraging to elevate their heads, orient toward the stalker, or engage in scanning (Hart and Lendrem, 1984; Leyhausen, 1979; Schaller, 1972).

Other species demonstrate a pattern of vigilance characterized by regular bouts of visual monitoring. These include purple sandpipers (*Caladrus maratima*), downy woodpeckers (*Picoides pubescens*), and blue tits (*Parus caeruleus*). These strategies conform to a time-dependent model yielding maximum foraging efficiency and optimal levels of vigilance (Carico, 1982, 1983; Caraco and Lima, 1987; Caraco, Martindale, and Pulliam, 1980; Curio, 1975; Hart and Lendrem, 1984; Lendrem, 1983a; Lendrem, Stretch, Metcalfe, and Jones, 1986; Lima, 1983).

Social systems influence the amount of time individuals devote to vigilance. Members of large social groups frequently engage in lower levels of vigilance than members of smaller groups (Bertram, 1980; Caraco, 1983, 1985; Caraco and Lima, 1987; Curio, 1969; Elcavage and Caraco, 1983; Ferguson, 1987; Krebs, 1993; Lendrem, 1983b; Lima, 1986; Loughry and McDonough, 1989; Poysa, 1987; Pulliam, 1973; Quenette, 1990; Sullivan, 1982; Underwood, 1982; Wawra, 1988). The reduction in individual scanning is a function of its equal diffusion among group members (Krebs and Davies, 1993; Lipetz and Beckoff, 1982; Roberts, 1996; Wirtz and Wawra, 1986). The lower requirement for each group member's vigilance is counterbalanced by the group's constituting a clumped resource. Such an aggregation may attract predators, thus requiring additional vigilance (Ferguson, 1987).

In a few social species, there is a clear division of labor. Individuals assume sentinel duty on a sequential, alternating, or rotating basis, while other group members concentrate on foraging. This form of vigilance has been observed in a variety of species, including jungle babblers (*Turdoides squamiceps*) (Gaston, 1977), cotton-top tamarins (*Saguinus o. oedipus*) (Wolters, 1978), dwarf mongooses (*Helogale undulata*) (Rasa, 1986, 1989), and meerkats (*Suricata suricatta*) (Moran, 1984).

In many species, however, the relationship between group size and vigilance is obscured by a multitude of factors (Elcavage and Caraco, 1983; Ferguson, 1987; Lima, 1986; Lipetz and Beckoff, 1982). In some terrestrial herbivores, vigilance is higher in animals near the periphery of social groups. Males and nonlactating females tend to be more vigilant than lactating females (Burger and Gothfeld, 1994). Smaller individuals are more vigilant than larger ones (Quenette, 1990; Roberts, 1996; Underwood, 1982; Wawra, 1988).

The body condition of percipients influences short-term decisions about the primacy of vigilance over foraging. For example, Belding's ground squirrels (*Spermophilus beldingii*) with adequate body mass or fat stores are more likely to cease foraging to respond to conspecific antipredator vocalizations than animals with deficits in energy reserves. Vigilance remains secondary to foraging until percipients obtain adequate energy reserves (Bachman, 1993).

Vigilance does not always occur in an antipredator context; it can be directed at conspecifics (McDonough and Loughry, 1995; Schaller, 1972; Wawra, 1988). For example, male nine-banded armadillos (*Tatusia novemcincta*) direct elevated vigilance toward other males when females are present (McDonough and Loughry, 1995). In social species, individuals monitor the behavior of others to extract information about the environment indirectly (Burger and Gothfeld, 1994; Hennessy, Owings, Rowe, Coss, and Leger, 1981; Roberts, 1996; Underwood, 1982; Wawra, 1988).

Social factors interact with the physical environment to govern the pattern of vigilance. The presence of visually obstructive environmental features, including trees, dense vegetation, holes, obstructive rocks, detritus, or uneven terrain can influence the level of scanning (Ferguson, 1987; Leger, Owings, and Coss, 1983; Lima, 1986). Many species devote more time to vigilance in visually occluded surroundings (Ferguson, 1987; Hart and Lendrem, 1984; Lima, 1986). This pattern has been observed in thirteen-lined ground squirrels *(Spermophilus tridecemlineatus).* These effects are more noticeable in young animals, especially near burrow openings (Arenz and Leger, 1997a, 1997b). Similar effects have been observed in African antelopes *(Antilocapridae)* (Underwood, 1982) and white-browed sparrow weavers *(Plocepasser mahli)* (Ferguson, 1987). Many other small mammals, including grey squirrels *(Sciurus carolinensis),* eastern chipmunks *(Tamais striatus),* and golden-mantled ground squirrels *(Spermophilus lateralis)* also become more vigilant as they move away from cover into the open and less so as they move from the open into cover (Ellard, 1996; Kildaw, 1995; Lima, Valons, and Caraco, 1985; McAdam and Kramer, 1998; Newman and Caraco, 1987; Shriner, 1995, 1998). Other small mammals, including woodchucks *(Marmota monax),* prairie dogs *(Cynomys ludovicianus),* pikas *(Ochotona princeps),* and eastern chipmunks *(Tamais striatus)* devote more time to vigilance and less to foraging as they move away from familiar territories or refuges (Ellard, 1996; Burke Da Silva, Kramer, and Weary, 1994; Kildaw, 1995; Kramer and Bonofont, 1997; McAdam and Kramer, 1998).

Finally, one variable that can influence vigilance patterns is the location in space of percipients as they monitor their environments. Ground-based vigilance must be considered within a different vulnerability context than vigilance based on an arboreal or subterranean location (Ferguson, 1987; Hart and Lendrem, 1984; Leger, Owings, and Coss, 1983; Lima, 1986, 1995; Moran, 1984). In each context, the directions from which threats emanate and the routes of escape are differently constrained. It is within such a context of dimensional complexity featuring aerial, terrestrial, and subterranean elements that the antipredator behavior of California ground squirrels (*Spermophilus b. beecheyi*) is considered.

Recovery of Environmental Information

Visual vigilance is critical when there has been an interruption in environmental surveillance. Interruptions of extended length occur daily for ground squirrels when they retire into their burrows and in red-bellied tamarins (*Saguinus labiatus*) when they retire into their nests. Tamarins exhibit elevated vigilance prior to retirement and immediately after arising the following morning (Caine, 1984). California ground squirrels also exhibit elevated vigilance when they first emerge each morning, frequently interrupting foraging to search for predators (Owings, Borchert, and Virginia, 1977; Owings and Virginia, 1978). While squirrels are underground, the directional effectiveness of audition is reduced and the use of vision in monitoring is entirely precluded. When squirrels reemerge, it is essential for them to recover environmental information rapidly, facilitating refamiliarization with their surroundings. Increased surveillance allows them to detect changes in the presence and location of threats that have appeared while they were sheltering in their burrows. Ground squirrels refresh their knowledge of the local surroundings by maneuvering to a vantage point and looking in different directions.

Surveillance can be considered within two burrow-related contexts: (a) a before-exiting context, under which olfaction and audition predominate over vision in environmental assessment, and (b) an after-exiting context, when the effectiveness of vision equals that of olfaction and audition and all sensory modalities are employed in environmental monitoring (Webster and Webster, 1971).

Squirrels immersed within burrows almost certainly emphasize olfaction and audition as they negotiate burrow runs. Like the majority of mammals, squirrels derive considerable information from olfactory cues (Brown and McDonald, 1985; Steiner, 1974; Stoddard, 1980). They also obtain information from vestibular, proprioceptive, kinesthetic, and tactile sources as they move about in burrow systems (Etienne, Teroni, Hurni, and Portinier, 1990). Research on their auditory physiology suggests that they possess effective hearing between 0.5 kHz and 44.0 kHz, with maximum effectiveness between 4.0 kHz and 24.0 kHz (Hamill, McGinn, and Horowitz, 1989; Henry and Coss, unpublished manuscript, 1996). Ground squirrels possess well developed photopic vision and functional scotopic vision (Crescitelli and Pollack, 1965; Meyer-Oehe, 1957).

Since vision is ineffective underground, squirrels probably traverse burrow systems with their eyes closed (Coss and Owings, 1985). For emerging and fully exposed animals, vision probably becomes as important as audition, possibly assuming sensory primacy.

Visual monitoring, especially scanning behavior, has been described extensively elsewhere (Bertram, 1980; Bossema and Burgler, 1980; Caine, 1984; Caraco, 1982, 1983; Coss, 1978; Curio, 1975; Hanson and Coss, 1997; Hart and Lemdren, 1984; McAdam and Kramer, 1988; Mateo, 1996a, 1996b; Moran, 1984; Roberts, 1996; Shriner, 1998;

Underwood, 1982; Wawra, 1988).

There are at least two distinct elements to visual scanning: (a) a dynamic component, featuring turning, tilting, or rotating the head in each of three planes toward a particular spatial direction, and (b) a static component, featuring the arresting of head motion in a particular orientation to fixate a target (see McAdam and Kramer, 1998). The cumulative effects of variation in these patterns of scanning characterize the requirement to organize visual behavior to maximize the probability of detecting predators. In the evolutionary time frame, the temporal patterning and physical configuration of scanning probably reflect adaptations to the long-term stable relationships between percipients and the spatial location from which specific types of predatory threat emerged (Coss and Goldthwaite, 1995; Coss and Owings, 1985). Such an evolutionary history is likely to foster directional biases in visual scanning, especially during burrow emergence. Proximately, when a squirrel refreshes its knowledge about its surroundings, the direction of scanning should reflect the statistical probability of predators appearing in specific spatial domains. Experience in detecting predators in these domains would be predicted to strengthen preexisting scanning biases.

Ground squirrels are regularly preyed on by a variety of subterranean, terrestrial, and aerial predators, each of which comprises a threat from a specific vector in space. Subterranean predators include northern Pacific rattlesnakes *(Crotalus viridis oreganus),* Pacific gopher snakes *(Pituophis melanoleucus catenifer),* and badgers *(Taxidea taxus).* Primary terrestrial predators include coyotes *(Canis latrans),* foxes *(Vulpes vulva spp.),* and bobcats *(Lynx rufus).* Major avian predators include golden eagles *(Aquila chrysatos)* and red-tailed hawks *(Buteo jamaicensis)* (e.g., Fitch, Swenson, and Tillotson, 1946; Fitch, 1948, 1949; Linsdale, 1946; Minta, 1990).

To accommodate the differences in the probable origins of attack typical of each guild of predator, squirrels appear to scan all spatial aspects of their surroundings. The results are directional biases in visual scanning that produce recognizable changes in head orientation. For example, squirrels scanning for aerial predators elevate the eyes. This can be accomplished by rotating the head so that one eye faces upward or by raising the head above the horizontal plane of the body. Squirrels searching for terrestrial predators obtain wider views by turning the head from side to side. Squirrels searching for subterranean or low-lying threats frequently adopt a bipedal stance, directing the eyes downward, or assume an elongate quadrupedal posture, elevating the head above the horizontal plane. Once a threat has been detected, head motion must be arrested so that the target can be fixated (McAdam and Kramer, 1998). Visual behavior consisting of intermittent head movements of short duration is termed glancing. Visual behavior involving the cessation of head motion and fixation for relatively longer periods is termed gazing (Bossema and Burgler, 1980; Coss, 1978).

The contribution of experience to the expression of vigilance has not been formally investigated. Newly emerged and inexperienced pups, unfamiliar with their surroundings, exhibit exaggerated reactivity to innocuous stimuli, including sticks and leafy substrates (Coss, 1993), and to antipredator vocalizations (Hanson, 1995; Mateo, 1996a). Free-living black-tailed prairie dog pups (*Cynomys ludovicianus*) show a tendency toward chronic arousal, even in the absence of provocative threats (Loughry, 1993). However, young squirrels exhibit increasing precision in vigilance with experience of responding in appropriate predator contexts (Mateo, 1996a, 1996b).

Ground squirrels appear to employ a combination of innate and learned mechanisms in vigilance behavior and predator recognition. This extends to the concern for the spatial domains from which major predators are likely to launch attacks. However, for complete development and expression of antipredator behavior, environments must instruct animals in ways that facilitate perceptual learning to unfold within a predictable context (Boice, 1980; Lickliter, 1991). Unfortunately, most artificial environments do not possess the complexity to foster optimal behavioral expression or development (e.g., Black and Greenough, 1986).

Experimental Rationale, Questions, and Predictions

The rationale for the following study arose from serendipitous observations during the decoding of videotapes for the preceding study (Chapter 2). Although not originally considered as a component of the behavioral analyses, the visual behavior of squirrels as they exited their nest boxes suggested an additional variable for consideration. Wild-caught ground squirrels from both Sierra Valley and Sunol engaged in predictably elevated levels of scanning prior to and shortly after exiting their nest boxes; scanning declined after they had been in the open for some time. While exiting, both groups oriented scanning upward, as if searching for aerial predators, and sideways, as if searching for terrestrial predators. This pattern of visual scanning was sufficiently compelling to suggest the current study. Consequently, the influence of development on the confirmation of scanning direction was adopted as the focus for the following research.

At the burrow opening, rapid detection of predators enhances the possibility of successful retreat into the burrow. This coupling of refuge availability and vigilance provides an impetus for the development of specific patterns of visual scanning and the context for this research. Wild-caught squirrels would have had numerous opportunities to employ scanning to observe both aerial and terrestrial predators. In contrast, squirrels born in the laboratory would not have had these perceptual or locomotive opportunities. The persistence of directional biases in visual scanning in groups with such different developmental histories might be expected if critically important antipredator behaviors are mediated by deeply canalized developmental systems resistant to disruption from inadequate experiential opportunities. Such developmental stability is likely to appear in systems arising from evolutionarily old and reliable organism-environment interactions, such as those in which prey detect predators from specific vantage points. If the attacks launched on ground squirrels by terrestrial and aerial predators have been a stable ecological property throughout phylogeny, then the differential expression of orientational biases would be subject to a consistent pattern of natural selection even in captivity (Coss and Goldthwaite, 1995). Alternatively, perceptual systems and associated behavior could be adjusted through experience.

To assess the developmental stability of orientational biases in visual scanning, subjects with different life history experiences, wild-caught and laboratory-born, can be compared in the controlled conditions of captivity. The presence of a stable perceptual system can be inferred if deprivation-reared ground squirrels display patterns of upward and sideways scanning during emergence from cover similar to those of wild-caught squirrels. Experiential adjustment can be inferred if the pattern of surveillance changes during an extended period of exploration in an environment devoid of salient sensory input. The following research investigates the hypotheses of developmental stability versus experiential adjustment. The findings are discussed in the context of other research on the influence of unresponsive habitats on neurological development and the retention of immature modes of behavior (Black and Greenough, 1986; Hanson, 1995; Markowitz, 1975; Mateo, 1996a).

Materials and Methods

Subjects

Two groups, each composed of six California ground squirrels with different ontogenetic experiences, served as the subjects for this study. The first group of squirrels, comprised of one male and five females, was captured in 1990 at approximately one year of age at Camp Ohlone, in the oak grassland habitat of the Coast Range foothills near Sunol, California. Prior to the study, this group was maintained for approximately 24 months in the animal maintenance facility of the Psychology Department, University of California, Davis.

The second group of squirrels, three males and three females, was from two litters whose mothers were trapped at the same location as the squirrels in the first group. These litters were born in the laboratory in April and May 1991 and maintained under the same conditions as the wild-caught squirrels. At the time of the study, the wild-caught squirrels were approximately 46 months of age and the laboratory-born squirrels approximately 32 months of age. Immediately preceding the inception of research, subjects ranged in weight from 494–1000 g, averaging 722 g. Because of the prevalence of multiple paternity in ground squirrels, it is unlikely that all of these littermates were full siblings (Boellstorff, 1991). Based on corticosteroid research discussed earlier and the level of reactivity toward technicians, individuals from both groups were assumed to be temperamentally equivalent (cf. Hediger, 1954; Price, 1984.

Rearing and Maintenance Conditions

All 12 subjects were maintained in wire-screened cages with horizontal dimensions of 39 x 56 cm and heights of 25 cm. Each cage featured attached nest boxes with horizontal dimensions of 22.5 x 38 cm and heights of 22 cm. These boxes, with the addition of naturalistic nesting materials, afforded a dark refuge which simulated the nest chambers of natural burrows. These detachable nest boxes also served as simulated burrows in the experimental setting. The animals were provided with various preparations of either Purina or PMI rodent diet (#5001 or #5014) and water on an ad libitum basis. Occasionally, this diet was supplemented with additional nuts, fruits, vegetables, and grains. The laboratory-born squirrels were never removed from their home cages prior to the inception of the research.

The walls of the animal maintenance rooms were uniformly cream colored, evenly distributing light emanating from three banks of overhead fluorescent fixtures. The animals were regularly exposed to a 55.6 footcandle, 12-hour photoperiod extending from 7:00 to 19:00 on a daily basis. The temperature of the maintenance and experimental rooms ranged between 68 and 70 F. All subjects had views of other wire-mesh cages, many housing other squirrels. Cages were mounted on racks with solid metal shelves, further restricting the complexity of overhead visual features and partially occluding the overhead motion of caretakers. This visual restriction was a deliberate feature of the rearing condition and was considered as a factor influencing the manner in which visual behavior developed in these squirrels.

Compared with the restricted visual surroundings, the acoustic conditions in the animal care facility were more variable, with typical sound pressure levels ranging from an average minimum of 40 dB during evening hours to an average maximum of 75 dB during daytime maintenance procedures—typical values for contemporary animal care facilities. These values do not take into consideration short, intense bursts of punctate noise, common in animal care facilities (see Chapter 2). Typically, the noise in the animal care facility was characterized by a wide energy distribution.

Thus, wild-caught squirrels experienced natural levels of sensory and behavioral environmental complexity during their first year of life. After capture, they experienced the same level of sensory and behavioral deprivation as the laboratory-born squirrels had since their births. All subjects were then maintained in sensorily unresponsive laboratory environments analogous to those associated with neonatal deprivation research. The uncomplicated maintenance conditions provided only limited stimulation from the time of capture or birth until the time of the study. During this period, all subjects experienced reduced variation in visual images and motoric opportunities. Importantly, the laboratory-born squirrels had never seen unoccluded open habitat with expansive sky-ground spatial contrasts. Additionally, all squirrels were subjected to antipredator vocalizations of conspecifics during disturbing cage maintenance procedures (Nancy Bacon, personal observation, 1996). These had never been perceived in ecologically authentic contexts by laboratory-born squirrels, and when detected by wild-caught squirrels, could not be acted on appropriately.

Experimental Setting

The venue for the experiment consisted of two adjacent rooms in the animal care facility. These rooms had a floor dimension of 2.43 x 2.90 m and a height of 2.53 m. The observation room contained video equipment, including a Panasonic VHS AG-185U video camcorder used as a 1-lux camera, a FOR.A VTG-22 video field time generator, and a Panasonic VTR NV-8030 time-lapse surveillance video tape recorder. This unilluminated room was equipped with a one-way mirrored window for video recording the interior of the experiment room housing the subjects.

The entrance to the experiment room had a solid core door with rubber seals, which provided a high degree of acoustic isolation from noise originating elsewhere in the animal care facility. A permanently mounted Radio Shack Model 33-20-50 analog sound pressure meter allowed sound intensities within the room to be monitored. Typically, sound intensities within the room ranged from 40-50 dB. Noise with frequencies between 1.0 and 4.0 kHz generated outside the room was attenuated by up to 20 dB. Animals ensconced within the nest box would experience an additional reduction in the intensity of high frequency sounds—possibly attenuated as much as those heard by immersed free-living, fully immersed animals at distances of from 15-20 cm from a natural burrow opening. Finally, the point source of the sound would be less well defined to a subject so immersed in a sound-resistant refuge.

The experiment room had the same cream color as the animal maintenance rooms and also evenly distributed light emanating from an array of three rectangular fluorescent fixtures mounted on the ceiling. The average intensity of illumination was 55.6

footcandles, measured at squirrel level with a Minolta LX-100 photometer. Light cycles were automatically timed to begin illumination at 7:00 and to terminate it at 19:00. A complex of equipment used in subsequent research (see Chapter 4), including an array of suspended microphones, speakers, and associated conduits, imparted a sense of vertical complexity to the setting. The floor was covered with a pine shaving substrate to a depth ranging from 10-20 cm. Various types of commercial rodent diet (Purina or PMI) and water were available to the subjects in trays located in the corners of the room. The nestbox (22.5 x 38 x 22 cm high, with a 7.5 x 7.5 cm entrance) was positioned with its entrance facing the video camera's focal area and the center of the room.

Procedures

During a study spanning six months in 1994, the behavior of each squirrel was videotaped over six consecutive nine-hour days. Laboratory-born squirrels were studied from January through early March, followed by the wild-caught squirrels, studied from the middle of March through early May.

To begin observations on each subject, at 07:00 on the Monday of each observation week, each squirrel was transferred in its sealed nest box from the animal maintenance room to the experiment room. The nest box was positioned with its entrance facing the center of the room at the edge of a 55.4 x 62.8 cm designated floor area comprising the video camera's field of view. After positioning the nest box, its entrance was unsealed. This arrangement permitted the videotaping of each squirrel's first bout of exiting on the first day of the experiment and subsequently at any time during the next five days. The nest box served both as the primary refuge for the subjects and as the focal point for recording the behavior of each subject as it exited from cover. Close-up video recording of the squirrel's visual behavior was accomplished by focusing the camcorder through the one-way mirrored window via a 44 cm convex mirror suspended from the center of the ceiling over the designated floor area located in front of the nest box. The camera and video recorder were automatically activated at 06:55, five minutes prior to the onset of room illumination at 7:00, to capture any occurrence of squirrel emergence when the room was illuminated. Step-lock video recordings were made at a resolution of 300 msec, yielding a nine-hour recording period. Video recording began at 07:00 and continued until 16:55, when the camcorder and video recorder were automatically deactivated.

Behavioral Measures

Direction of glancing during nest box emergence was categorized as either sideways, involving lateral displacement of the squirrel's head; or upward, involving elevation of the nose at least 10 degrees from the horizontal, with both eyes facing the camera; or rolling of the head sideways, with one eye facing the camera. Individual sideways or upward motions of the head were treated as single bouts. The duration of each glance was measured from the video frame in which head motion ceased until the video frame in which head motion resumed. These glance durations were summed to produce the total glance duration variable. Sampling of glancing bouts was initiated from the time in which the squirrel's head had protruded from the nest box up to the point where the trailing edges of the ears were visible (see Figure 7A and 7B). Sampling was terminated when the squirrel left the video field of view and its eyes were no longer visible. The conspicuous eye rings and dark irises of the squirrels provided a reliable means for assessing the direction of a squirrel's visual fixation.

Video recordings were decoded using a Sony Trinitron 33 cm high-resolution color monitor, coupled to a Panasonic NV8030 time-lapse video tape recorder. Pairs of research assistants decoded the video tapes and assessed scanning behavior from video field-by-field inspections, using video field numbers to quantify the duration of gaze bouts with a resolution of 300 ms. Interobserver agreement exceeded 95 percent (Bakeman and Gottman, 1997). All statistical analyses were conducted using GANOVA, a general linear model statistical program (Woodward, Bonett, and Brecht, 1990).

Results

Every wild-caught squirrel emerged from its nest box during the five-day study. The emergence behavior of laboratory-born squirrels was more variable: They emerged from their nest boxes only on the first and fifth days of the study. Consequently, group comparisons using repeated measures are restricted to these two days. Data were analyzed using one-factor between-groups (wild-caught and laboratory-born squirrels), two-factor within- groups (glance orientation and days) repeated measures analyses of variance (ANOVAs). Tests of simple main effects examined group differences for each day and differences between days within each group. These tests were complemented by analyses of linear and quadratic trends.

Number of Glancing Bouts

Laboratory-born and wild-caught squirrels did not differ appreciably in the number of glancing bouts (Figure 3A). The number of glancing bouts declined significantly in both groups across the five day period, and in wild-caught squirrels over three days. The main effect for glance direction, averaged for days 1 and 5, was nearly significant ($F = 4.583$, df = 1,10, $p < 0.06$). The mean value for glancing upward was substantially higher than the mean value for glancing sideways, with the standardized comparison of mean values yielding a large effect size (Cohen's $d = 0.87$) (Cohen, 1992; Hunter and Schmidt, 1990; Nelson, Rosenthal, and Rosnow, 1986; Rosnow and Rosenthal, 1989; Schmidt, 1992). This large effect size suggests that upward glancing might have a different functional property compared with sideways glancing.

Averaged for groups, the main effect comparing the difference in glancing bouts between days 1 and 5 was statistically significant ($F = 5.424$, df = 1,10, $p < 0.05$). Squirrels showed a sharp decline in the average number of glancing bouts between the first and fifth days. This mean difference in days is most apparent for the number of upwards glancing bouts (simple effect: $F = 6.248$, df = 1,10, $p < 0.05$), producing a large effect size ($d = 1.02$).

A more complete analysis of the wild-caught group employed a two-factor within groups (glance direction and days) repeated measures ANOVA. This additional analysis revealed that, averaged across days, the main effect for glancing direction was significant ($F = 10.017$, df = 1,5, $p < 0.025$). On the first day, the average number of upward glancing bouts was much greater than the average number of sideways glancing bouts ($d = 1.29$). This effect was even greater after the second day (Figure 3B). The main effect for days, averaged for glance direction, was also significant ($F = 3.135$, df

= 5,25, $p < 0.025$). Tests of simple effects revealed that both directions yielded significant differences among days (upward: $F = 2.584$, df = 5,25, $p = .05$; sideways: $F = 3.211$, df = 5,25, $p < 0.025$). A test of simple effects revealed that days 1 and 3 differed appreciably in the number of upward glances ($F = 8.855$, df = 1,5, $p < .05$, $d = 2.17$).

The above finding is corroborated by analyses of linear and quadratic trends. Trend analyses across days revealed that upward glancing was significant for both the linear trend ($F = 9.947$, df = 1,5, $p < 0.05$) and for the quadratic trend ($F = 16.371$, df = 1,5, $p = 0.01$). The linear trend for sideways glancing approached significance ($F = 6.063$, $df = 1, 5$, $p = .056$). The quadratic trend for sideways glancing was not significant. As apparent from Figure 3B, the marked quadratic trend reflects the marked decline in sideways glancing bouts and increase in the number of upward glancing bouts between the first and second days and marked decline in upward glancing bouts between the second and third days. Thereafter, the trend levels off asymptotically.

Total Glance Duration

There were no significant group differences for any aspect of total glance duration (Figure 4A). However, the main effect for glance direction, averaged for both groups, was significant ($F = 7.0898$, df = 1,10, $p < 0.025$). While exiting, squirrels averaged a 23.8 sec duration of upward glancing, compared with an average of 10.4 sec for the duration of sideways glancing. This difference generated a large effect size: $d = 1.1$. The main effect for a comparison of the first and fifth days, averaged for both glancing directions, was approximately significant ($F = 4.746$, df = 1,10, $p = 0.052$, with a moderate effect size: $d = 0.63$).

An additional analysis of presumptive habituation in the wild-caught squirrels complemented the investigation (Figure 4B). The main effect for glance direction averaged across days was significant ($F = 7.601$, df = 1,5, $p < 0.05$), with upward glancing yielding a much larger mean value than sideways glancing. Analyses of simple effects revealed that the sources for this mean difference in glancing direction were most apparent for the 3rd, 4th, and 5th days (respectively: $F = 20.505$, 11.124, and 10.939; df = 1,5, $p < 0.025$). The main effect for days, averaged for both directions, was also significant ($F = 3.027$, df 2= 5,25, $p < 0.05$). Unlike the number of glancing bouts, the linear and quadratic trends for total glance duration were not significant for either direction of gaze (Figure 4B).

Discussion

The underlying rationale of this research was to assess the influence of rearing history on the expression of directional biases in ground squirrel scanning behavior during nest box emergence. Of particular interest was the possible contribution of innate predispositions and/or experience to the expression of environmental monitoring as animals emerged from cover. The role of experience was tested through the comparison of laboratory-born and wild-caught ground squirrels after both had been housed in captivity for two years.

The results of this study suggest that early experience exerts little effect on the expression of visual assessment behavior. Wild-caught and laboratory-born squirrels behaved similarly. When introduced into a novel setting, individuals from both groups displayed initially high levels of upward and sideways scanning while exiting their nest boxes. Compared with their values on the first day, both upward and sideways glancing declined markedly by the fifth day.

Wild-caught squirrels emerged at least one time each day during the observation period. Laboratory-born squirrels failed to emerge as reliably on consecutive days. Consequently, the analyses of behavioral data are more complete for wild-caught squirrels. This restricted most of the discussion of habituation to this group. Wild-caught squirrels showed an appreciable decline in the number of sideways glancing bouts after the second day. After the third day, there was a marked decline in upward glancing bouts as well.

The similarity in the behavior of the two groups tends to suggest that a possible confound in the experimental design played little effect in influencing the results. As noted, the laboratory-born squirrels were evaluated more than a month prior to the evaluation of the wild-caught squirrels. In nature, free-living squirrels are less active at the beginning of the year, when the laboratory-born animals were tested, than they are later in the year, when the wild-caught squirrels were tested (Fitch, 1948, 1949; Linsdale, 1946; Loughry and McDonough, 1989). However, since the subjects were isolated in windowless housing under fixed photoperiods, seasonal effects probably exerted minimal impact on their overall levels of activity. In essence, laboratory-born squirrels could have been expected to exhibit torpor if seasonal effects were a factor in the expression of group differences, a result that was not observed.

The similarity in the behavioral properties of ground squirrel visual scanning, irrespective of developmental history, documents that experience in nature is unnecessary to develop directional precision in its execution. The preservation of these orientational biases in captivity suggests that their developmental expression is deeply canalized and resistant to deformation in inadequate early environments. Their immutability argues for the presence of innate perceptual expectancies arising from robust developmental processes.

Stable perceptual systems are the products of natural selection operating on ecologically old and important associations, including those between predator and prey (Coss and Goldthwaite, 1995). The reliability of perceptual and behavioral systems used in detecting predators, such as the perceptual systems of ground squirrels employed in snake recognition, are critical for survival (Coss, 1991a; Endler, 1984). As such, their expression should be resistant to deformation under developmental conditions, even those devoid of appropriate ecological features. Significant lability in such systems could result in susceptibility to deformation under environmental conditions at variance with those conforming to ontogenetic expectancies of a species.

As a case in point, when the antisnake behavior of snake-inexperienced, laboratory-reared ground squirrel pups was compared with that of snake-experienced, two-year-old adults, little evidence of developmental lability was observed. Presented with a garter snake, laboratory-born pups demonstrated essentially adult patterns of antisnake behavior. They were, however, highly excitable, exhibiting elevated levels of substrate throwing and tail flagging. Adults were less vigilant than pups in monitoring the snake, especially when they were out of its striking range (Coss and Owings, 1978; Owings and Coss, 1977). When the same squirrels were tested after two years in captivity with no intervening interactions with snakes, the groups showed similar antisnake tactics, suggesting developmental stability (Poran and Coss, 1990).

A developmentally stable orientational bias in scanning could also reflect a long-term evolutionary relationship between ground squirrels and the locations in space of their major predators. Attacks originating from each of these spatial domains could be thwarted by effective antipredator vigilance, precisely oriented toward specific spatial vectors. Rapid predator detection at the burrow entrance would also enable successfully vigilant squirrels to remain in or to retreat back into their burrows, reducing susceptibility to attack. Such critical behavioral predispositions would be expected to be emplaced early during development (Coss, 1991b, 1993).

Extensive research on neural development in rats reveals that by the time their eyes open and before they emerge from the dark, the rat visual cortex has finalized its endogenously mediated functional architecture (reviewed in Coss, 1991b). For a few days prior to emergence, rat pups demonstrate pattern recognition and the ability to avoid obstacles (Coss, 1991a). Ground squirrel pups, which first emerge from their natal burrows when they are around 45 days old, probably show similar patterns of neurological development (Coss, 1991a, 1991b, 1993). Thus, at least in rodents, it is likely that an early stabilization of reliable neural circuitry subserving vision facilitates effective antipredator behavior, including scanning, fixation, and pattern recognition (Coss and Owings, 1985; Coss and Goldthwaite, 1995).

It can thus be argued that natural selection has fostered the emergence of reliable neural circuitry resistant to the effects of developmental deprivation and aimed at reliable perception and behavior in post-emergent squirrels. This provides even laboratory-born squirrels with the ability to evince an organized pattern of antipredator surveillance. Such stable neuronal circuitry appears to await functional expression the first time the input parameters match those of the perceptual input (Coss, 1991b, 1993). Input parameters originate in all spatial domains and could include any variation in, for example, the current experimental setting.

Although clearly not as expansive as natural ground squirrel habitats, the experimental setting was larger and more complex than the cages squirrels were housed in for two years. Equipment including mounting hardware and cables used in the previous study (Chapter 2) imparted a sense of visual complexity to the aerial aspect of the room superficially resembling sparse arboreal foliage. The quality of the subdued lighting (55.6 footcandles) resembled the variegated light filtered through the canopy of a large tree. These features created a somewhat visually occluded environment that could conceivably conceal danger. They also provided features at which an animal could direct its gaze.

When squirrels initially emerged into this novel, more spacious setting, they were afforded opportunities to explore for food and water, while orienting and moving about more dynamically than they could in their home cages. It also provided laboratory-born squirrels with the first opportunity to express functional upward scanning behavior similar to the opportunities afforded the wild-caught squirrels early in life.

Thus, on the first day of the study, all subjects engaged in elevated levels of upward and sideways scanning as they emerged from nest boxes. Although visual behavior has not been examined with the same level of resolution as the current study, elevated visual scanning has nonetheless also been reported by other researchers in free-living ground squirrels as they emerge from cover (Owings, Borchert, and Virginia, 1977; Owings and Virginia, 1978). High levels of scanning in emerging squirrels facilitates the rapid assessment of the environment for the presence or absence of predators, important for emerging animals deprived of visual input while underground. Confirmation of danger results in a failure to emerge; failure to confirm the presence of danger enables squirrels to proceed with environmental exploration at a distance from refuge.

It follows that the reluctance of laboratory-born squirrels to emerge from cover could represent uncertainty about the possibility of threats in unfamiliar surroundings. Alternatively, their reluctance to emerge from cover could be simply reduced motivation to explore, given the limited possibilities for such behavior during their development (Mason, 1979; D. H. Owings, personal communication, 1998).

The effect could also be an artifact of the retention of juvenile behavioral characteristics in laboratory-born squirrels. Hanson (1995) reported that in a comparison of habitat utilization in pups, juveniles, and adult squirrels, the youngest animals spent the most time under cover. Younger squirrels also devoted more time to vigilance than older squirrels. It should be noted, however, that the literature on age class relationships and vigilance is inconclusive (Quenette, 1990).

Reluctance to emerge from cover along with heightened vigilance could also indicate elevated arousal. Elevated arousal in the absence of legitimate threat is another manifestation of juvenile behavior. The assertion that pups are more susceptible than other age classes to arousal is suggested by the higher levels of tail piloerection under provocation, a reliable indicator of autonomic activity (Hanson, 1995; Hennessy, Owings, Rowe, Coss, and Leger, 1981).

Since levels of vigilance probably correlate with activation of the autonomic nervous system, they can provide a direct index of psychological arousal and an indirect index of physiological arousal (Snyder, 1975; Stoskopf, 1983). Chronically elevated arousal has been associated with failure to adapt to novel surroundings (Chapter 1; Clark and Galef, 1980; Erwin, 1979; Meyer-Holzapfel, 1968; Snyder, 1975; Stoskopf, 1983). Its persistence in adulthood has implicated inadequate developmental conditions (Greer, Diamond, and Tang, 1982; Coss and Globus, 1979; Black and Greenough, 1986; Rosenzweig, Bennett, and Diamond, 1972). Susceptibility to arousal has been reported in inbred research animals (Henry, 1967; Miller, 1994) and in captive wild animals (Cairns, Gariepy, and Hood, 1990; Clark and Galef, 1980; Meyer-Holzapfel, 1968).

Susceptibility to arousal is also characteristic of free-living juvenile ground squirrels (Hanson, 1995; Hanson and Coss, 1997; Mateo, 1996a, 1996b). Conceivably, smaller animals exhibit higher levels of vigilance than larger animals because they are susceptible to attack from a greater number of predators (Loughry and McDonough, 1988, 1989; Underwood, 1982). Conversely, decreased vigilance in adults could be an artifact of a perceived lower vulnerability arising from a larger body size (Hennessy, 1984; Owings and Loughry, 1985). A similar trend in the relationship between body size and risk assessment has been observed in African cichlids (Coss, 1979). Perhaps elevated scanning in laboratory-born squirrels reveals the incomplete development of their ability to assess the level of risk associated with inert environmental features relative to their size and ability to escape.

An evolutionary perspective on ontogeny does not preclude the possible contribution of learning to the development of the behavioral properties of scanning. In fact, learning is the essential component in the maintenance of knowledge about constant changes in an animal's immediate surroundings (Tarpy, 1982). However, evidence that vigilance varies as a function of experience with spatially specific threats remains incomplete. Laboratory-based research on golden hamsters (*Mesocricetus auratus*) suggests that they can learn to associate extremely provocative stimuli with various spatial aspects of their surroundings (Etienne, Teroni, Hurni, and Portinier, 1990). Spatial learning and memory has been discussed in a variety of other species, including captive sciurids (Bedford, 1995; Bowe, 1984; MacDonald, 1997; Williams and Meck, 1991).

In nature, ground squirrel pups remain in close proximity to their mothers and natal burrows for at least several weeks after first emergence. Such a long-term association provides a context for observational learning and social facilitation (Galef, 1981, 1988), opportunities ordinarily available only to free-living squirrels. Clearly, for the first year of their lives, the wild-caught squirrels had very different spatial experiences from their laboratory-born counterparts. Thereafter, all squirrels lived under the same degree of spatial restriction. The aerial aspect of their visual fields was obstructed by the solid metal shelves of the rack system holding their cages. Laboratory-born squirrels had never observed a terrestrial or avian predator, been attacked by a predator, nor had they witnessed an attack by a predator on another squirrel. Conceivably, wild-caught squirrels had had these experiences. If so, they would have experienced the different levels of danger presented by mammalian and avian predators (Hanson and Coss, 1997; Leger, Owings, and Coss, 1983).

The direct observation of a predator by a squirrel probably facilitates learning about both the predator and its location in space (Bowe, 1984; Ellard, 1996; MacDonald, 1997). Sympathetic activity associated with the presence of provocative stimuli in a specific location and the extreme psychological and physiological arousal associated with fear can enhance retention and consolidation of memories of the event (Brown and Kulik, 1977; Cook and Mineka, 1989, 1990; Garcia and Koelling, 1966; McGaugh, 1989; Miller, 1995). After an arousing encounter with a predator, a squirrel might exhibit persistent concern for spatial domains from which attacks were launched (Armitage, 1982). This scenario possibly explains the orientational biases observed in wild-caught squirrels, which might have interacted with various classes of predator.

The maintenance of orientational biases in antipredator behavior might follow an epigenetically open program (Mayr, 1974) similar to that observed in the maturation of antipredator behavior in juvenile vervet monkeys *(Cercopithecus aethiops)* (Seyfarth, Cheney, and Marler, 1980). Ground squirrels have demonstrated a similar ability to become more selective in their vigilance behavior with experience as they mature (Hanson, 1995; Hanson and Coss, 1997; Mateo, 1996a, 1996b; Seyfarth and Cheney, 1980). Newly emerged pups are extremely excitable and respond to auditory and visual prompting by orienting indiscriminately toward all spatial vectors in their surroundings (Hanson, 1995; Mateo, 1996a, 1996b). As with vervet monkeys (Seyfarth, Cheney, and Marler, 1980), immature ground squirrels have even been observed to emit antipredator vocalizations toward items as innocuous as falling leaves, behavior seldom observed in experienced squirrels (Mateo, 1996a, 1996b).

It is conceivable that the tendency to orient toward specific environmental vectors requires the reinforcement of actually detecting a threat originating from one of them. The absence of reinforcement could explain the decline in visual scanning toward both spatial vectors across the five-day study.

Declining vigilance could indicate that behavior is being adjusted through context-specific habituation as squirrels fail to detect danger. Habituation is likely to occur if animals are placed in inert, unresponsive environments devoid of salient ecological features, especially predators. It is frequently observed when animals are repeatedly exposed to even complex sets of stimuli with no apparent relevance to their behavior (Chapter 1; Donaho and Palmer, 1994; Mackintosh, 1973; Marlin, 1980, 1982; Marlin and Miller, 1981; Tarpy, 1982).

However, specific vectors of space may hold greater salience to squirrels than others. While scanning declined significantly in both orientations, sideways glancing declined more rapidly than upward glancing; squirrels persisted in glancing upward for an additional day. This finding could be interpreted as suggesting that squirrels habituated more rapidly to the absence of terrestrial threat than to the absence of aerial threat.

Because of the speed of attack, raptors represent a more urgent predator context than terrestrial predators (Coss and Owings, 1985; Owings and Hennessy, 1984). Mongolian gerbils (*Meriones unguiculatus*) exhibit a persistent heightened responsiveness to the presentation of aerial predator models in the laboratory (Ellard, 1996). This suggests that predator detection behaviors associated with aerial threats are more resistant to habituation than those associated with terrestrial threats.

Laboratory-born squirrels had never observed legitimate ecological adversaries, and wild-caught squirrels had not observed any for two years. However, for the two years preceding this research, all subjects were regularly confronted by large, looming laboratory technicians. In the absence of natural ecological threats, technicians could have become proxies for legitimate ecological adversaries. The interactions with technicians occurred within the disruptive, frequently noisy contexts of cage maintenance. During these procedures, squirrels often emitted antipredator vocalizations. Perhaps technicians became associated as contingent predictors of these provocative acoustic and physical disturbances. The heights of the cages and the restrictions that shelves imposed on the upper visual field allowed the squirrels to view technicians primarily through lateral gazing. Thus, arousal-mediated associative learning might have been expected to promote at least the persistence of sideways scanning. Yet, sideways scanning declined prior to upwards scanning, suggesting that squirrels can adapt to threats arising near the horizon.

The persistence of upwards scanning suggests that threats originating above the horizon are more persistently provocative. This argument is supported by aerial scanning in animals never exposed to an unrestricted aerial view. Upwards scanning appears to be resistant to fading and less modifiable through learning.

The persistence of vigilance in any form attests to its importance in the life histories of animals. Vigilance is important enough that it persists in unnatural settings devoid of predatory risk, even in the innocuous environments of zoos (Caine, 1984, 1986, 1987; Carlstead, Brown, and Seidensticker, 1993; Stanley and Aspey, 1984; Thompson, 1989; Tromborg, 1993). This occurs even though it is energetically expensive and unproductive. Of course, animals in artificial surroundings are presented with a different suite of threats, including ecological adversaries and visitors, as well as disruptive technicians. Persistent vigilance is directed by zoo animals toward their keepers (Carlstead, Brown, and Seidensticker, 1993; Thompson, 1989) or toward other provocative species (Caine, 1984; Stanley and Aspey, 1984). Analogously, ground squirrels direct their vigilance toward their caretakers and other intruders. Conceivably, humans and their noises begin to acquire salience as purveyors of disruption (Carlstead, Brown, and Seidensticker, 1993).

There were no sex differences in any aspect of scanning. Under natural conditions, effective predator detection is equally important to males and females. In nature, under a variety of conditions, there is a similar absence of sex differences in vigilance behavior. When sex differences are observed, they frequently involve reproductive or parental behavior (Burger and Gothfeld, 1994; Roberts, 1996; Underwood, 1982; Wawra, 1988; Wirtz and Wawra, 1986). Male ground squirrels may exhibit higher levels of vigilance than estrous females that they are guarding (McDonough and Loughry, 1995). Females supervising pups may exhibit higher levels of vigilance compared with nearby males (Loughry and McDonough, 1988, 1989; Owings, Hennessy, Leger, and Gladney, 1986). However, in the laboratory, the animals led essentially solitary existences. There was never any opportunity for reproductive interactions or resulting parental responsibilities. Differential vigilance based on different ecological requirements for males and females were not factors in this research.

There are species-dependent differences in the susceptibility of developmental pathways to retardation, permutation, modulation, or full expression as a function of environmental parameters. Developmental stability or degeneracy may be differentially encouraged by the physical specifications of the environment and the degree to which it fosters interaction between the animal and its surroundings. Either outcome can be differentially encouraged by the history of prior interactions between individuals and their surroundings, the modulation of existing biases, the existence of temporal parameters, and the possible poverty of existing stimuli (Boice, 1980; Fentress, 1983; Lickliter, 1991).

In some species, isolation rearing or extremely simplified environments are correlated with incomplete central nervous system development and behavioral deficits in adults (Coss and Globus, 1979; Coss, 1991b). What constitutes adequate ecological requirements for growing animals changes throughout development (Coss and Globus, 1978, 1979; Coss, 1991b).

Thus, the history of contexts within which an individual's behavior is expressed, the reliable presence of ecologically appropriate features, and the degree of sensory and social interactivity of environments during ontogeny strongly influence developmental trajectories (Lickliter, 1990; Miller and Gottleib, 1981). These are important considerations when comparing animals born in the laboratory with those born in natural surroundings; they extend to the environments in which animals mature and under which they are tested (Fentress, 1983; Schneirla, 1950).

Accordingly, inadequate opportunities to interact with salient features can retard the effective expression of labile behaviors. Behavior surviving inadequate environments is probably the product of robust developmental systems. Antipredator vigilance almost certainly represents such a category of reliable behavior arising from ecologically old and stable relationships between environment, predator, and prey, (Coss and Goldthwaite, 1995). These behaviors are so stable that they are expressed by captive animals in environments devoid of contingencies similar to those experienced by free-living conspecifics. Appearing early in life, sculpted by natural selection, honed by experience, vigilance persistently defies chance unto death.

Conclusions

California ground squirrels engage in relatively constant antipredator behavior. Vigilance persists in captivity, rearing history notwithstanding. Consequently, squirrels offer a reasonable model for studying vigilance in captivity.

The behavioral similarities between laboratory-born and wild-caught squirrels suggest an innate predisposition to scan for predators. This robustness should be expected for behavioral systems that await functional expression under the stochastic conditions which characterize initial or sudden encounters with predators. Such robustness is implied by the propensity of both groups to monitor the aerial vector of the environment, especially the wild-caught squirrels, even after several days of exploring the experimental setting in the absence of confirming threat. The slightly greater frequency and duration of upward-oriented scanning suggests that swiftly flying raptors pose a more urgent threat to squirrels than slower moving mammals. The slightly more rapid rate of habituation to terrestrial threats corroborates this assertion. It also supports the presumption that learning plays a role in the adjustment of vigilance behavior. Compared with wild-caught squirrels, laboratory-born squirrels exhibited a greater reluctance to emerge from their nest boxes. This reluctance is suggestive of elevated arousal and could represent the failure of deprivation-reared squirrels, maintaining juvenile reactivity, to habituate to their novel surroundings. Unlike wild-caught squirrels, laboratory-born animals have not had the opportunity to engage in complex interactions with natural environmental contingencies. They could be manifesting the behavioral consequences of developmental retardation as expressed by the retention of more juvenile patterns of behavior.

The continued expectancy of threats, even in environments where they are not present, leads animals to search their surroundings for nonexistent danger. Especially poignant in unresponsive artificial settings, the persistence of vigilance during emergence, despite increasing familiarity with the environment, suggests the existence of memory-like processes creating expectancies in squirrels about the presence of predators with whom they have coevolved, but which are absent in captivity.

Summary

Wild-caught and laboratory-born California ground squirrels were compared on the basis of visual vigilance during their initial daily emergence from artificial nest boxes.

1. Animals treat certain spatial domains of their environments as more important than others. These vectors could represent locations from which attacks have historically originated and from which they are likely to continue.
2. Wild-caught squirrels emerged every day of the study. Laboratory-born squirrels emerged only on the first and fifth days of the study.
3. Wild-caught and laboratory-born squirrels exhibited similar patterns of both sideways and upward visual scanning. Both groups exhibited a significant reduction in scanning over the course of the study. Wild-caught squirrels showed a reduction in scanning between days one and five, with the largest decline occurring on day three.
4. Compared with wild-caught squirrels, laboratory-born squirrels exhibited sideways and upwards glancing bouts of longer duration.
5. Wild-caught squirrels demonstrated the longest and most frequent bouts of both sideways and upward glancing from the first through the third day. By the fourth day,

they exhibited a precipitous decline in both directions of glancing.

6. Patterns of sustained sideways and upward scanning, even after habituation to a novel setting, suggest that ground squirrels continue to expect encounters with aerial threats.

7. The similarities in scanning behavior in groups of squirrels with distinctly different developmental backgrounds argues for the presence of robust, stable developmental, behavioral, and perceptual systems important in antipredator behavior.

CHAPTER FOUR

Experientially Mediated Call Specificity in Naive versus Experienced California Ground Squirrels

The prevalence of antipredator behavior attests to its importance in the lives of animals (Endler, 1984). It is facilitated through a constellation of sensory arrays which can inform percipients about the state of their surroundings (Marler, 1977; Dusenbery, 1992) and can allow them to discriminate the relevant from the irrelevant (Israeli, 1950; Lerea, 1961; Lindauer, 1989; Thurlow, 1957). Vision, audition, and olfaction are differentially emphasized in diurnal, nocturnal, or crepuscular species and by those occupying subterranean, terrestrial, or aerial niches (Bradbury and Vehrencamp, 1998; Dusenbery, 1992; Webster and Webster, 1971). For a species such as the California ground squirrel (*Spermophilus b. beecheyi*), which uses both subterranean and terrestrial environments, all three sensory modalities facilitate environmental surveillance. Under conditions of reduced luminance, such as when animals are underground, audition occupies a central role in assessing the environment for danger, especially in the presence of salient acoustic phenomena.

Differential Salience of Environmental Sounds

Highly salient sounds nearly always provoke behavioral responses, even from the uninitiated. Some salient sounds possess the eliciting properties of unconditioned stimuli. Their evocative nature may be an outcome of their intensity, structure, or temporal distribution, possibly reflecting their recognizable information properties as signals and even suggesting the presence of innate recognition systems. The preceding is particularly characteristic of the extremely evocative vocal signals emitted within the predator context, termed *antipredator alarms* (Aetken and Wilson, 1979; Burnstein and Wolff, 1967; Marler, 1955, 1967, 1977; Scherer, 1985). These antipredator vocalizations are the most distinctive elements in the repertoires of most species, including ground squirrels (Hennessy and Owings, 1984).

The functional equivalence of these signals has resulted in a high degree of convergence in their acoustic structures, which are characterized by short durations, high frequencies, minimal frequency modulation, relatively pure tones, and rapid rise times (Klump and Shalter, 1984; Marler, 1955, 1967, 1977; Morton, 1977; Smith, 1977; Vencl, 1977). All of these characteristics can minimize source locatability in several ways: by minimizing phase information, reducing interaural differences, and decreasing interaural time of arrival cues (Marler, 1977; Klump and Shalter, 1984; Smith, 1977; Vencl, 1977).

Antipredator vocalizations exhibit sufficient structural similarity for them to be effective within and between taxa. Within species they can alert related conspecifics to the presence of predatory threats or confuse predators as they attempt to select a target (Brown and Schwagmeyer, 1984; Danford, 1977; Davis, 1984; Hoodland, 1996; Owings and Leger, 1980; Schwagmeyer and Brown, 1981). Their effectiveness transcends genera and even orders (Marler, 1977; Shriner, 1995, 1998; Vencl, 1977).

Antipredator vocalizations can show syntactical qualities, possess variable semanticity, and require experience to develop their pragmatic aspects. Referentiality as a construct has been viewed differently by various authors (Smith, 1977, 1981; Marler, 1977, 1985). As considered here, the referentiality of antipredator vocalizations does not necessarily imply a direct one-to-one correspondence between a signal and predator. Rather, it refers to signals which convey more general information about the possible existence of threats (see Sebeok, 1977). Associated recognition systems can semantically encode antipredator vocalizations to denote external features such as the type, location, and behavior of predators (Cheney and Seyfarth, 1985; Jurgens, 1990; Markl, 1985; Marler, 1967, 1977; Owings and Leger, 1980; Sebeok, 1977; Seyfarth and Cheney, 1980; Smith, 1977, 1981). Referentiality has been inferred in a variety of species, e.g., ringtailed lemurs (*Lemur catta*), ruffed lemurs (*Varecia variegata spp.*), cotton-top tamarins (*Saguinus oedipus spp.*) (Cleveland and Snowdon, 1982; Jolly, 1966; Macedonia and Yount, 1991; Pollock, 1986; Snowdon, 1986). Some species show high levels of signal-to-stimulus specificity and categorical variation in the predator context (Burke Da Silva, Kramer, and Weary, 1994; Cheney and Seyfarth, 1985; Cleveland and Snowdon, 1982; Hoodland, 1996; Leger and Owings, 1978; Leger, Owings, and Gelfand, 1980; Marler, 1982; Moran, 1984; Owings and Hennessy, 1984; Owings and Virginia, 1978; Robinson, 1980; Seyfarth and Cheney, 1980; Seyfarth, Cheney, and Marler, 1980). For example, superb starlings (*Sternus cyaneus*) appear to possess distinct predator alarms for airborne and earthborne threats (Seyfarth and Cheney, 1990). Vervet monkeys (*Cercopithecus aethiops*) also exhibit different antipredator vocalizations for distinct classes of predator, each posing threats from different spatial vectors (Cheney and Seyfarth, 1985; Seyfarth and Cheney, 1980).

For California ground squirrels, snakes are meaningful but manageable; approaching mammals are predictable and can be avoided in an organized manner; and avian predators allow little time for escape, eliciting the least discriminating evasive behavior (reviewed in Coss, 1991a, 1993). The locomotory and vocal behavior of squirrels varies during the differently urgent contexts associated with the detection of predators from the guilds of snakes, swift raptors, or stealthy mammals (Leger and Owings, 1978; Owings, Borchert and Virginia, 1977; Owings and Hennessy, 1984; Owings and Virginia, 1978). Their response to the extremely provocative nature of snakes is very specific and is discussed in Chapter 3 and later in this chapter (also see Coss, 1991a, 1993; Coss, Gusé, Poran, and Smith, 1993; Coss and Owings, 1985; Towers and Coss, 1990). Squirrels respond to mammalian and avian predators differentially, as if they represented distinctly different levels of urgency. Avian predators can appear suddenly and quickly swoop toward exposed squirrels, while mammalian predators execute less instantaneous attacks (Fitch, Swenson, and Tillotson, 1946).

Squirrels respond to the detection of a rapidly moving raptor by emitting whistle alarms and fleeing indiscriminately toward the nearest cover (Leger, Owings, and Boal, 1979) and to a slower moving raptor by seeking shelter in more familiar cover (Davis, 1984; Linsdale, 1946; Owings and Virginia, 1978; Robinson, 1980; Schwagmeyer and Brown, 1981; Brown and Schwagmeyer, 1984; Sherman, 1985). Squirrels detecting a stealthily approaching mammal typically assume positions near burrows or on promontories, from which they monitor the predator's movements (Owings, Borchert, and Virginia, 1977). While positioned on these vantage points, squirrels often emit chatter vocalizations and then seek the shelter of familiar burrows (Leger and Owings, 1978; Leger, Owings, and Boal, 1979; Loughry and McDonough, 1989; Owings and Leger, 1980; Owings, Hennessy, Leger, and Gladney, 1986). Although squirrel chatter and whistle antipredator vocalizations have been associated with mammals and raptors, respectively, their association with the spatial locations of these predator classes has not been clearly demonstrated.

Functional categories of antipredator vocalization vary with contextual urgency at least as much as with urgency related to predator class (or possibly spatial vector) (Macedonia and Yount, 1991; Owings, Hennessy, Leger, and Gladney, 1986; Owings and Morton, 1998). For example, ground squirrels have been reported to emit chatters (typically restricted to the mammalian predator context) at the detection of a slowly moving distant raptor. They have also been observed to emit whistles (typically emitted in the aerial raptor context) at the detection of a rapidly advancing terrestrial predator. These observations suggest that categories of antipredator vocalization may be correlated with situational urgency in addition to predator class. This reflects the different time constraints imposed on responding squirrels by various guilds of predators capable of different speeds of attack (Owings and Hennessy, 1984; Owings, Hennessy, Leger, and Gladney, 1986; Robinson, 1980). When a predator is first detected, the initial emission of provocative vocalizations (*alarms*) has a phasic function, rapidly elevating the state of vigilance of percipients, while shifting their attention toward potential danger. The repetitive emission of related, though less conspicuous, vocalizations (*warnings*) has a tonic function, maintaining an elevated state of arousal and vigilance over a longer time course (Loughry and McDonough, 1989; Owings and Hennessy, 1984; Owings, Hennessy, Leger, and Gladney, 1986).

Like most zoosemiotic communicative acts, antipredator vocalizations consist of highly ritualized natural units of behavior. For most zoosemiotic signals, their structure and emission are strongly influenced by the activity of the autonomic nervous system, rendering them primarily emotionally mediated and only partially susceptible to ontogenetic and cognitive influences (Rowell and Hinde, 1962; Scherer, 1985; Sebeok, 1977). In the predatory context, their emission reflects a sudden shift in the emotional disposition of the signaler in response to the detection of danger, influencing the signal quality and imparting information to nearby percipients about the motivational state of the signaler even as it informs them about the nature of the stimulus (Green, 1975; Loughry and McDonough, 1989; Macedonia, 1990; Macedonia and Yount, 1991; Marler, 1977; Morton, 1977, 1982; Owings and Hennessy, 1984; Owings and Loughry, 1985; Rowell and Hinde, 1962; Scherer, 1985; Sebeok, 1977; Smith, 1977, 1981; Zahavi, 1982).

If, during phylogeny, the vocalizations associated with such rapid shifts in emotional disposition were reliably coincident with the detection of danger in ways that enhanced the survival of percipients, the startling properties of antipredator vocalizations might have acquired semantic value via natural selection (Brown and Schwagmeyer, 1984; Danford, 1977; Davis, 1984; Klump and Shalter, 1984; Leger and Owings, 1978; MacWhirter, 1992; Schwagmeyer and Brown, 1981; Sherman, 1985). The affective quality of zoosemiotic signals means that secondary perceivers can assess the motivational state of vocalizers through their emissions. The actual presence of danger is not required for response, irrespective of the accuracy of the information (Dawkins and Krebs, 1978; Markl, 1985; Owings and Hennessy, 1984; Owings and Leger, 1980; Robinson, 1980; Scherer, 1985; Seyfarth and Cheney, 1980; Smith, 1981). Thus, the focus of information processing becomes a property of the percipient, either as the initial detector of potential threat or, secondarily, as the interpreter of the initial detector's vocalized state of arousal (Guilford and Dawkins, 1991; Seyfarth and Cheney, 1990). In other words, percipients become both the generators and interpreters of meaningful information (Coss, personal conclusion, 1998).

This evolutionary scenario does not preclude proximate processes. The reliable emission of antipredator vocalizations in the presence of danger frequently adjusts the referentiality of signals by means of associative learning.

Developmental Considerations

Throughout ontogeny, antipredator vocalizations are nearly universally provocative. Initially, their predictive properties with respect to the nature of danger is unrefined; they primarily incite arousal (Mateo, 1996a, 1996b). This activated physiological condition could be a requirement for an important course of directed learning to occur (Gould and Marler, 1987).

Learning involves the maturation of perceptual mechanisms important in the recognition of predators and in the execution of antipredator behavior (Cheney and Seyfarth, 1985; Hanson, 1995; Hanson and Coss, 1997; Mateo, 1996a, 1996b; Seyfarth and Cheney, 1980). In some species, where the adult forms of antipredator vocalizations possess a degree of referential specificity, this quality is not fully developed in the juvenile precursors of the adult vocalizations. For these animals, response to antipredator vocalizations becomes more precise with expression in a social context, probably through social learning, observational learning, and social reinforcement (Galef, 1988; Green, 1975; Jurgens, 1990; Maples and Haraway, 1982; Snowdon, 1986).

Such mechanisms could operate in the refinement of acoustically mediated antipredator behavior in vervet monkeys (*Cercopithecus aethiops*). Vervet monkeys possess a simple categorical repertoire of relatively specific antipredator vocalizations, one each for leopards, eagles, and snakes. Experienced adults restrict specific antipredator vocalizations to situations in which a particular type of predator has been detected. They also respond appropriately to each signal in ways that enhance evading specific predators. Those hearing eagle alarms vacate arboreal perches and seek ground cover; those hearing leopard alarms climb into trees and migrate to outer branches; those hearing snake alarms migrate from the ground into arboreal refuges.

Immature monkeys are less likely to execute the most appropriate evasive behavior during their initial exposures to alarm vocalizations. Their responses become more refined with experience, practice, and the nonreinforcement of inappropriate vocal behavior (Cheney and Seyfarth, 1985; Seyfarth and Cheney, 1980). A similar referential model has been described for ringtailed lemurs (*Lemur catta*). Taxonomic relationships are not reliable indicators of vocal development. The preceding model is less appropriate for the related ruffed lemur (*Varecia variegata*), which exhibits predominantly emotionally motivated vocal behavior (Macedonia, 1990). For further discussion of age-related factors in the development of communication, see Owings and Loughry (1989) and Owings and Morton (1998).

Some vocal development occurs in ground squirrels. Inexperienced ground squirrels respond to conspecific antipredator vocalizations with elevated arousal, even without accompanying visual provocation, suggesting that these vocalizations are innately salient (Hanson, 1995; Mateo, 1996a). In Belding's ground squirrels (*S. beldingii*), responsiveness to antipredator vocalizations is in place prior to their being perceived in an antipredator context (Mateo, 1995, 1996a, 1996b; Mateo and Holmes, 1997).

For pre-emergent squirrels, vocalizations are exclusively arousing and possess little referentiality. In a variety of ground dwelling sciurids, dams emit whistle vocalizations prior to entering burrows. Consequently, most pups have probably heard antipredator vocalizations prior to emergence, though not while seeing a predator (Loughry and McDonough, 1989; Mateo, 1996a, 1996b; Mateo and Holmes, 1997; Robinson, 1980; Sherman, 1985). They appear to acquire referentiality through associative learning after post-emergent pups observe aroused squirrels reacting to predators (Hanson, 1995; Mateo, 1996a; Scherer, 1985; Zahavi, 1982). Thus, early developmental stages provide contexts for adjusting juvenile responses to more closely resemble adult patterns, possibly through an epigenetically open program (Mayr, 1974).

While experienced adult squirrels exhibit a relatively specific pattern of evasive behavior for each antipredator vocalization, inexperienced juvenile squirrels exhibit less organized evasive behaviors. For developing squirrels, then, the referentiality of individual vocalizations is acquired as they are heard in association with specific predators and concomitant patterns of conspecific evasive behavior (Hanson, 1995; Hanson and Coss, 1997; Mateo, 1996a, 1996b).

There are several related aspects of ground squirrel antipredator behavior which appear to develop with maturation. Compared with experienced adults, immature squirrels engage in higher levels of undirected vigilance, exhibit distinctly inferior antipredator tactics related to mapping escape routes on local terrains, are less adept at distinguishing the different levels of urgency associated with different antipredator vocalizations, and are less discriminating than are adults about the differing levels of risk posed by avian versus mammalian threats (Hanson, 1995; Hanson and Coss, 1997; Loughry and McDonough, 1989; Mateo, 1996a, 1996b).

The preceding observations suggest that, though antipredator vocalizations may be innately provocative, their referential specificity is tailored through experience, and that the opportunity to observe other animals responding to their environments is critical for the acquisition of normal patterns of antipredator behavior. Such opportunities are frequently unavailable for captive animals (Markowitz, 1982).

Risk Assessment Within Two Contexts

The risk assessment behavior of ground squirrels can be considered within two contexts, the subterranean and terrestrial, each imbued with a different range, composition, and spatial distribution of predatory threats. It follows that ground squirrel antipredator behavior should be considered within two burrow-related contexts: (a) a before-exiting condition, in which olfaction and audition are more effective than vision in environmental monitoring, and (b) an after-exiting condition, in which vision is as effective as audition.

Ground squirrel antipredator behavior probably reflects a long-term association between natural environmental features, probabilistic aspects of predator encounters, and the hunting tactics of specific types of predators (Coss and Goldthwaite, 1995). Ground squirrels are regularly preyed on by a variety of subterranean, terrestrial, and aerial predators, each of which presents a threat from a specific spatial location. Subterranean predators include northern Pacific rattlesnakes (*Crotalus viridis oreganus*), Pacific gopher snakes (*Pituophis melanoleucus catenifer*) and badgers (*Taxidea taxus*).

Primary terrestrial predators include coyotes (*Canis latrans*), foxes (*Vulpes vulva spp.*), and bobcats (*Lynx rufus*). Major avian predators include golden eagles (*Aquila chrysatos*) and red-tailed hawks (*Buteo jamaicensis*) (Fitch, 1948; Linsdale, 1946; Minta, 1990).

All of these predators are capable of stealthy approaches to fully immersed, emerging, or fully exposed ground squirrels. For maximum survival value, the patterning of antipredator behavior should reflect locations from which information about the presence of danger originates most reliably. Fully immersed squirrels probably manage antipredator detection and social interactions through audition (Mateo, 1996a, 1996b; Owings, Borchert, and Virginia, 1977) and olfaction (Stoddard, 1980; Steiner, 1974). Auditory brain stem research reveals that squirrels possess effective audition between 0.5 kHz and 50 kHz, with peaks in sensitivity at 16 kHz and 24 kHz, with a best range between 4 kHz and 24 kHz (Chapter 2; Henry and Coss, unpublished manuscript, 1996). Additional information may be derived from vestibular, proprioceptive, kinesthetic, and tactile sources (Etienne, Teroni, Hurni, and Portinier, 1990).

For emerging and fully exposed squirrels, vision is an important conduit of information in assessing aerial and terrestrial surroundings for the presence of predators (Armitage, 1982; Coss and Owings, 1985; Hanson, 1995; Hanson and Coss, 1997; Leger and Owings, 1978; Loughry and McDonough, 1989; McAdam and Kramer, 1998; Owings and Virginia, 1978; Owings, Hennessy, Leger, and Gladney, 1986). Research on sciurid vision suggests that some species possess well developed photopic vision and, to a lesser extent, scotopic vision (Crescitelli and Pollack, 1965; Meyer-Oehe, 1957). As suggested above, the behavioral properties of visual scanning should reflect the spatial location from which major predators launch attacks. Squirrels searching for avian predators should rotate or elevate their heads to direct the eyes upward; those searching for mammalian predators should turn the head laterally; squirrels searching for reptilian predators should adopt a bipedal posture while directing the eyes toward the ground. If a predator is detected, head motion should be arrested and the target fixated for assessment (McAdam and Kramer, 1998; Rowell and Olson, 1986). These responses should be intensified if the presence of danger is announced acoustically.

Experimental Rationale, Questions, and Predictions

Research focusing on developmental issues in the acquisition of antipredator behavior in several species of ground squirrels suggests that some aspects of antipredator behavior are at least partially organized even prior to the instance of their first expression. Other aspects of antipredator behavior appear to acquire a more organized confirmation after they have been expressed in the appropriate social context (Coss and Owings, 1985; Hanson, 1995; Hanson and Coss, 1997; Mateo, 1996a, 1996b).

To investigate the origins of behavior within contexts devoid of many natural contingencies, California ground squirrels with different experiential histories can be compared on the basis of their responsiveness to salient environmental features in a simplified, controlled setting. The comparison of experienced wild-caught squirrels with inexperienced laboratory-born squirrels can reveal something about the contributions of innate and experiential factors to the development of the referentiality of antipredator vocalizations and the execution of directed antipredator vigilance. This is so because wild-caught squirrels have had numerous opportunities to hear antipredator vocalizations and to employ scanning to observe both aerial and terrestrial predators. Laboratory-born squirrels would not have had these perceptual opportunities. They would have heard vocalizations only within the context of disturbing laboratory maintenance procedures.

Prior research suggests that, compared with experienced adults, inexperienced pups and laboratory-born squirrels persist in higher levels of excitability when confronted with arousing stimuli. Further, it suggests that antipredator behavior associated with snakes is stabilized early in development, while that associated with mammals is modifiable through experience later in development (Coss and Owings, 1978, 1985; Owings and Coss, 1977).

Developmental stability is likely to appear in systems arising from evolutionarily old and stable organism-environment interactions, such as those in which prey must reliably detect predators occupying specific spatial vectors of their surroundings. Thus, if the attacks launched on ground squirrels by terrestrial and aerial predators have been a stable ecological property throughout phylogeny, then the differential expression of orientational biases in antipredator vigilance should be subjected to a consistent pattern of natural selection even in captivity (Coss and Goldthwaite, 1995). These biases should, then, persist in subjects irrespective of developmental history. Additionally, if during phylogeny, the emission of vocalizations were reliably coincident with specific environmental features, then certain antipredator vocalizations could possess a degree of innate referentiality. The extent to which antipredator vocalizations possess spatially-specific referentiality about the presumed historical location of predatory threats can be inferred from their impact on the behavioral properties of visual vigilance.

To assess (a) developmental stability of orientational biases in visual scanning and (b) referential specificity in antipredator vocalizations, subjects with different life-history experiences can be compared in the controlled conditions of captivity. The presence of stable perceptual systems can be inferred if deprivation-reared subjects display patterns of vigilance during emergence from cover similar to those of wild-caught subjects. Experiential adjustment can be inferred if the pattern of surveillance changes during an extended period in an environment devoid of salient environmental features. If referentiality is primarily innate, both groups should exhibit equivalent increases in vigilance behaviors in response to antipredator vocalizations. Persistence of similar orientational biases in both groups would also suggest that the referentiality of the antipredator vocalization was at least partially innate. Experiential contributions would be suggested if wild-caught squirrels exhibited more focused visual behavior compared with deprived laboratory-born squirrels, especially when presented with a provocative stimulus.

The following research compares a developmental stability hypothesis with one advocating experiential adjustment. The current findings are discussed within the context of the influence of unresponsive habitats on neurological development and the retention of immature modes of behavior (Black and Greenough, 1986; Coss, 1993; Coss and Owings, 1985; Hanson, 1995; Mateo, 1996a).

Materials and Methods

Subjects

Two groups, each composed of six California ground squirrels with different ranges of experience, served as the subjects for this study. The first group of squirrels, comprised of one male and five females, was captured in 1990 at approximately one year of age at Camp Ohlone, in the oak grassland habitat of the Coast Range foothills near Sunol, California. Prior to the study, this group was maintained for approximately 30 months in the animal care facility of the Psychology Department, University of California, Davis. The second group of squirrels comprised two litters, together yielding three males and three females, whose mothers were trapped at the same location as those in the first group. These squirrels were born in the laboratory in April and May 1991. This group was maintained in the same facility, under conditions identical to those of the wild-caught squirrels. Because of the prevalence of multiple paternity in ground squirrels, it is unlikely that all of these littermates were full siblings (see Boellstorff et al., 1994). Based on their reaction to approach by technicians, the two groups were similar in reactivity and were assumed to be temperamentally equivalent (Price, 1984). At the time of the study, the wild-caught squirrels were minimally 52 months of age and the laboratory-born squirrels minimally 38 months of age. Immediately preceding the inception of research, subjects ranged in weight from 494–1000 g, averaging 722 g.

Rearing and Maintenance Conditions

All 12 subjects were maintained in wire-screened cages with horizontal dimensions of 39 x 56 cm and heights of 25 cm. Each cage featured attached nest boxes with horizontal dimensions of 22.5 x 38 cm and heights of 22 cm. These boxes, with the addition of naturalistic nesting materials, afforded a dark refuge, which simulated the nest chambers of natural burrows. Each squirrel's detachable nest box also served as a simulated burrow in the experimental setting. In the holding facility, squirrels were maintained continuously in these cages for periods ranging from 24 to 27 months. Then, each squirrel was transferred to the experimental setting for one week to observe its vigilance and habituation in a novel setting. After this, each was returned to its home cage for an additional six to eight months (Chapter 3).

The animals were provided with various preparations of either Purina or PMI rodent diet (#5001 or #5014) and water on an ad libitum basis. Occasionally, this diet was supplemented with additional nuts, fruits, vegetables, and grains. The animals were housed under conditions having restricted visual and acoustic variability. To characterize the restricted quality of the visual environment, the walls of the animal maintenance rooms were uniformly cream colored, evenly distributing light emanating from overhead fluorescent fixtures at an intensity of 55.6 footcandles, imparting an invariant quality to the visual environment. The animals were regularly exposed to a 12-hour photoperiod extending from 07:00 to 19:00 on a daily basis. The temperature of the maintenance and experimental rooms ranged between 68 and 70 F. The subjects had views of other wire-mesh cages, many housing other squirrels. Cages were mounted on racks with solid metal shelves, restricting the complexity of the upper visual field. Shelves specifically interfered with the ability of squirrels to monitor caretakers during routine maintenance procedures. This restriction in visual experience was a deliberate feature of the rearing condition and was considered as a factor in the development of visual behavior (Chapter 3). Compared with the visual surroundings, the acoustic conditions in the animal care facility were slightly more variable. Typical sound pressure levels ranged from an average minimum of 40 dB (SPL) during evening hours to an average maximum of 75 dB during daytime maintenance procedures. These are typical values for contemporary animal care facilities. They do not, however, take into consideration short, intense bursts of punctate noise resulting from cage-cleaning procedures or the vocalizations of other laboratory animals (see Chapter 2). Many of these vocalizations were ground squirrel antipredator vocalizations elicited by the sudden appearance of animal care technicians and the noises associated with their activities. Except for animal vocalizations, most other noises in the animal care facility were characterized by a wide energy distribution.

While wild-caught squirrels had experienced natural levels of environmental complexity for their first year of life, they were deprived of environmental complexity from the time of capture until the beginning of the study. Laboratory-born squirrels received restricted sensory and behavioral interaction from a laboratory setting analogous to deprivation rearing conditions throughout their entire lives. Both groups experienced restricted variation in visual images, acoustic experiences, and motoric opportunities. Importantly, unlike wild-caught squirrels, laboratory-born squirrels had never explored an unoccluded open habitat with contrasting sky-ground spatial aspects. They had also never perceived antipredator vocalizations within an ecologically complete perceptual framework. Squirrels from both groups responded to these vocalizations with startling, refuge seeking, and counter vocalizing (Nancy Bacon, personal communication, 1996). When heard, none of the squirrels could react appropriately to these vocalizations.

Experimental Setting

The venue for the experiment consisted of two adjacent rooms in the animal care facility. These rooms had floor dimensions of 2.43 x 2.90 m and a height of 2.53 m. The observation room contained video and audio equipment, including a Sony WV-CL702 0.5 lux color videocamera coupled to a FOR.A VTG-22 video field time generator, and a Panasonic VHS AG-6730 time-lapse surveillance video cassette recorder. This room was unilluminated and equipped with a one-way mirrored window for videotaping the interior of the experiment room, where the subjects were presented with acoustic treatments. The equipment used to administer acoustic treatments and monitor acoustic events consisted of two discrete systems. Acoustic treatments were administered with a Tascam 202 MK II professional reversing dual deck cassette recorder coupled to a Teac A-20 10-band graphic equalizer and a SoundTech PL-150 low-noise integrated power amplifier (75 W/stereo channel).

The interior of the experiment room was monitored periodically by the researchers using a JVC KD-V200 stereo cassette recorder coupled to a Realistic MPA-35-A integrated power amplifier (35 W rms) via AudioTechnica ATH-M2X stereo headphones. To receive these sounds, the experiment room was equipped with two AudioTechnica 440 dynamic microphones (40 Hz-18 kHz), suspended from one wall by flexible conduit. Any movement within the nest box or vocalizations could be recorded using this monitoring system. Both systems were automatically activated with a Realistic repeat cycle electronic timer.

Treatments were administered through four Realistic Optimus 7 loudspeakers (40 Hz-18 kHz) suspended from the ceiling in each corner of the room via heavy chain, shrouded in 5-cm PVC conduit. The flexible conduit and PVC shrouds were employed to prevent damage to connecting cables resulting from gnawing by the squirrels. A centrally positioned Radio Shack Model 33-20-50 analog sound pressure meter provided a means for calibrating the intensity of the acoustic treatments. It also allowed sound intensities within the room to be constantly monitored.

A heavy, solid core door with rubber seals provided a high degree of acoustic isolation from noise originating from elsewhere in the animal care facility. Typically, midrange frequencies (1-4 kHz) of these extraneous noises were attenuated by 20 dB. In the absence of treatments, the intensity of ambient noise in the room averaged 40 dB. Animals ensconced within the nest box experienced a reduction in the intensity of sound and an obscuring of its point source similar to that experienced by fully immersed free-living squirrels at distances of 15-20 cm from a natural burrow opening.

The experiment room had the same cream color as the animal maintenance room, evenly distributing light emanating from an array of three rectangular fluorescent fixtures mounted on the ceiling. The average intensity of illumination was 55.6 footcandles, measured at squirrel level with a Minolta LX-100 photometer. Light cycles were automatically timed to begin illumination at 7:00 and to terminate illumination at 19:00. The suspension of the speakers from the ceiling, the insertion points of the microphone conduits into the wall, and the presence of associated cables imparted an internal vertical complexity to the experimental setting. The floor was covered with a pine shaving substrate to a depth ranging from 10-20 cm. Various types of commercial rodent diet and water were available to the subjects in trays located in the corners of the room.

Acoustic Treatments

The independent variables consisted of three sound conditions: (a) laboratory ambience, (b) pulsed white-noise hissing, and (c) ground squirrel antipredator vocalizations.

Chatters are one of two primary ground squirrel antipredator vocalizations. Chatters are composed of from three to seven harmonically structurally variable chat units ranging in duration from 20 ms to 1 sec (mean = 30 ms). They are frequently emitted upon the initial detection of a slowly advancing mammalian predator. Squirrels emitting chatters frequently mount promontories to observe the predator or engage in evasive activity (Owings, Borchert, and Virginia, 1977; Owings and Virginia, 1978). Squirrels presented with chatter vocalizations exhibit heightened vigilance, as suggested by elevated posture, increased locomotor activity, and decreased foraging. Chatter vocalizations appear to be somewhat iconic: Advancing predators incite vocalizations featuring more chat elements than static or retreating predators. Sudden chatters can incite rapid (phasic) shifts in physiological states. The continuous emission of individual chat units over time can maintain a slightly elevated (tonic) state of arousal (Owings, Hennessy, Leger, and Gladney, 1986; Owings and Hennessy, 1984; Loughry and McDonough, 1988).

The other primary ground squirrel antipredator vocalization is the whistle. Whistles are typically harmonically structured, low-noise, single note vocalizations with durations near 100 ms, containing little frequency modulation and with fundamental frequencies near 3.5 kHz and second and third harmonics near 7.0 and 10 kHz. Whistles are emitted in response to the perceived presence of a rapidly swooping avian predator. Respondents usually immediately begin to run toward burrows in an undiscriminating fashion while simultaneously vocalizing. When squirrels are presented with whistles, they again show vigilance, as suggested by increased locomotor activity and decreased foraging but, in this case, a quadripedal stance (Owings, Borchert, and Virginia, 1977; Owings and Virginia, 1978).

Pulsed hissing is similar to traditional white-noise control stimuli, though it also resembles some common provocative warning signals employed by a variety of species (Morton, 1977), including several species of snakes that occasionally co-opt ground squirrel burrows and prey on pups (Fitch, 1948, 1949; Morton, 1977; Rowe, Coss, and Owings, 1986; Rowe and Owings, 1978, 1990). Further, aroused rattlesnakes can produce aposematic warning rattles with their tails, which alert squirrels to the presence of a venomous, though defensive, adversary (Poran and Coss, 1990). Although recordings of ratttlesnake rattling evoke strong responses in squirrels, 10 kHz white-noise tones produce only moderate responses (Rowe, Coss, and Owings, 1986; Rowe and Owings, 1978).

Original recordings of squirrel vocalizations were obtained from a field research site near Winters, California. Virtually all recordings of squirrel vocalizations were obtained from animals while they were held in wire cage traps. Most recorded vocalizations consisted of chatters, though a few whistles were obtained from startled squirrels.

Recordings were made on a Sony model TC-D5 Pro II audio cassette recorder coupled to a Sennheiser model K3U directional microphone at distances of from 1-2 m from the subjects. The recordings were processed digitally with an Apple Macintosh II computer employing the Audio Media digital sound processing system. Recordings were digitized and then edited to filter out any background noise below 500 Hz. Any spurious sounds immediately adjacent to the exemplars were also removed. The pulsed-noise exemplars were obtained from a Marantz model 10 B high frequency analyzer. This unit produced relatively pure white-noise program material with equivalent energy distributions at all frequencies between 40 Hz and 15 kHz. Various pulse noise and antipredator vocalization exemplars were selected and a three-hour master treatment tape was produced and duplicated with a Tascam #202 MK II professional dubbing recorder onto cassettes which were used to administer treatments.

Two sets of antipredator vocalization exemplars were prepared, obtained from males and females, each consisting of one juvenile whistle, one juvenile chatter, one adult whistle, and one adult chatter (Figures 5A, 5B, 6A, and 6B).

There were 20 clusters of chatters, 10 with three chat exemplars and 10 with four chat exemplars. The three chat clusters contained chats with average durations of 330 ms and the four chat clusters had chat exemplars with average durations of 550 ms. Because these were structurally variable, they were matched for number of elements and total duration. In general, the adult chatter exemplars had higher peak frequencies and less noise than those derived from juveniles.

There were 20 1.3 sec whistle clusters consisting of three 112 ms whistles. One of the two whistle exemplars contained very little noise, though the other contained a chat-like element near its terminus. They each had a fundamental frequency near 3.5 kHz with second and third harmonics near 7.0 and 10 kHz respectively.

The pulsed white-noise *hiss* treatment consisted of 40 individual elements of a white-noise stimulus possessing essentially equal energy over a wide range of frequencies. There were four slightly different pulsed white-noise exemplars, each approximating the duration of one of the four *chatter/whistle* exemplars. Individual elements had durations ranging from 150-500 ms (mean = 300 ms).

Chatter-whistle episodes had four clusters of three or four chats alternating with clusters of three whistles administered in a quasi-random series of episodes. These three-element clusters ranged in duration from 10-30 sec (mean=24 seconds). Each phrase element within the cluster was separated by an interval ranging from 1-10 sec. The interstimulus intervals between complete chatter-whistle stimulus episodes ranged from 54-1140 sec (19 min) (mean = 414 sec). This essentially random temporal sequence was selected to mimick the variability of vocal behavior reported to occur in the field (Owings, Hennessy, Leger, and Gladney, 1986). They were presented at intensities of from 80-90 dB (SPL) measured at a distance of 1.5 m from the loudspeaker. This range is equivalent to the intensities of vocalizations emitted by trapped squirrels when measured at distances between 1 and 2 m from the cage (Dabelsteen, 1981; Kroodsma, 1989; M. T. Hanson, personal communication, 1995).

The white-noise condition was presented at an average intensity of 85 dB, measured at a distance of 1.5 m from the speaker. This intensity was selected by the experimenter because it was subjectively equivalent to the intensity of the squirrel vocalizations. The slightly lower intensity of the white-noise exemplar was further calculated to compensate for the radical difference in the structure of the two classes of sound. The energy of white-noise exemplars is distributed over a broad range of frequencies, while that of ground squirrel vocalizations is concentrated in a narrower band of frequencies. Sound pressure level meters analyze each type of sound differently. They give different readings for sounds with equal intensities simply as a consequence of their energy distributions. Usually, they underemphasize peak values for sounds with rapid rise times and those withb extremely low or high frequencies. Thus, quantative intensity information must be complemented with a subjective appraisal of loudness.

Finally, laboratory ambience characterized the typical animal care facility sound environment. Noises generated beyond the experiment room were attenuated by an average of 20 dB for critical frequencies.

Procedures

To initiate the experiment, at the beginning of each week, each subject was sealed in its nest box and transferred to the experimental room during the evening preceding the beginning of the experiment. This procedure prevented individual squirrels from associating potentially threatening technicians with the experimental setting. The subject's wooden nest box was positioned with its entrance facing the center of the room at the edge of the floor area designated as the video camera's field of view. The nest box served both as the primary refuge for the subjects and as the focal point for recording the behavior of each subject as it exited from cover into this designated area. Close-up video recording of the squirrel's behavior was accomplished by focusing the camera through the one-way mirrored window via a 44-cm diameter convex mirror suspended from the ceiling over the defined area in front of the nest box. Throughout the study, lighting, acoustic playbacks, and video recording were all automatically initiated at 07:00 and continued until 16:00, when they were automatically terminated. Step-lock video recordings were made at 433 ms time steps, providing approximately nine hours of recording time.

Each squirrel was allowed to habituate to the experiment room for 48 hours prior to the administration of treatments and the collection of data. The duration of the two-day habituation period and the subsequent two-day unaugmented intertreatment interval was determined on the basis of the results of the previous experiment, which suggested that after three days, squirrels largely habituate to novel settings (see Chapter 3).

On the third day of video recording, 40 exemplars of the antipredator vocalization or 40 exemplars of the white-noise treatment were presented in a quasi-random pattern during the first three hours of data collection. Following this, on days four and five, no treatments were administered. This intervening laboratory ambience (no sound) condition functioned similarly to the initial two-day habituation period in the experimental design. During the first three hours of the sixth day of the study, the alternate acoustic treatment was presented to the subject. The order of presentation of the antipredator vocalization or white noise was reversed for each succeeding subject. After the final treatment day, the animal was returned in its nest box to its home cage.

Behavioral Measures

The dependent variables included several measures of squirrel assessment behavior which the animals exhibited while exiting from the nest box. Two broad categories of investigative behaviors were examined during nest box exiting: (a) direction of gaze and (b) substrate sniffing. Both behaviors were assessed under two different risk-related contexts: (a) before exiting, when partially exposed squirrels were theoretically less vulnerable to predation, and (b) after exiting, when fully exposed squirrels were theoretically more vulnerable to predation.

Sampling of the duration of exiting episodes and gazing bouts in the before-exiting context was initiated with the video frame during which the squirrel's head protruded from the nest box up to the video frame in which the trailing edges of the ears were visible (Figure 7A); for the after-exiting context, sampling was initiated from that video frame in which the squirrel's head protruded past the trailing edges of the ears and was terminated when the squirrel's body had protruded from the nest box up to the base of its tail (Figure 7B). Gaze behavior after exiting was measured from the video frame in which the base of the squirrel's tail became visible up to the point in which the squirrel's eyes were no longer visible as it left the designated sampling area in front of the nest box (Figure 7B). Direction of gaze during nest box emergence was categorized as either (a) horizontal, featuring a pause in either lateral displacement or forward motion of the squirrel's head (Figure 7A), or (b) upward, featuring elevation of the nose with both eyes facing the camera or rolling the head sideways so that one eye faced the camera (Figure 7B). Each bout of pausing between head motions, either horizontal or upward, was treated as a unitary action for measuring the duration of gaze bouts. These durations were measured from the video frame in which head motion ceased until the video frame in which head motion resumed. The duration of bouts of substrate sniffing was measured from the video frame in which the head was tilted downwards until the video frame in which the head became horizontal with the substrate (Figures 7A and 7B). The dark irises and conspicuous eye-rings of the squirrels provided a reliable means for detecting head movement or assessing direction of visual fixation (Figures 7A and 7B). The precision of these measures was limited to the 433 ms video frame interval of the step-lock recorder.

Samples of gaze duration were summed to create the before-exiting and after-exiting context variables. These were then combined to yield the total gaze duration variable. Samples of sniffing duration were summed to generate the before-exiting and after-exiting context variables.

Video recordings were decoded using a Sony Trinitron 33 cm high-resolution color monitor, coupled to a Panasonic AG 6300 time-lapse video tape recorder. Pairs of research assistants decoded the tapes and assessed scanning behavior from frame-by-frame inspections, using video frame numbers to quantify the duration of gaze and sniffing bouts with a resolution of 433 ms. Interobserver agreement exceeded 95% (Bakeman and Gottman, 1997). Data derived from decoded video tapes were entered into GANOVA, a general linear model statistical program (see Woodward, Bonett, and Brecht, 1990). They were analyzed using one-factor between-groups (wild-caught and laboratory-born squirrels), one-factor within-groups (sound conditions) repeated measures analyses of variance (ANOVAs). Tests of simple main effects examined group differences for each sound condition and differences between sound conditions within each group. Planned comparisons were used to describe mean differences and standardized effect sizes.

Effect size was selected because it can provide statistical power, can add information about the relationship between two population means, and can yield reliable information about the influence of treatments on subjects when sample sizes are small. In fact, in many instances, it provides a more informative index of treatment effects than the level of significance (see Cohen, 1992; Hunter and Schmidt, 1990; Nelson, Rosenthal, and Rosnow, 1986; Rosnow and Rosenthal, 1989; Schmidt, 1992).

A planned comparison of the chatter/whistle condition as the ecologically relevant treatment (discriminative stimulus) was made with the average of both the theoretically less relevant laboratory ambience and white-noise conditions. These results are reported only when the comparisons are statistically significant.

Results

Qualitative Analyses

Some behaviors occurred so infrequently that they were not subjected to statistical analysis. A descriptive treatment of the behavior of the laboratory-born squirrels provides some insight into how time was budgeted under the various treatment conditions. For example, exiting bouts were longer for laboratory-born squirrels under the white-noise condition than under the chatter/whistle condition. Laboratory-born squirrels also tended to remain closer to the nest box opening after exiting under the chatter/whistle condition compared with other conditions. This was due, in part, to all of the laboratory-born squirrels engaging in increased cautious olfactory surveillance while exiting under this condition. Indeed, substrate sniffing was the only behavioral measure that clearly differentiated the two groups. After exiting, five of the six laboratory-born squirrels turned and investigated the opening of the nest box, treating it as a potential snake refuge. Three laboratory-born squirrels tail flagged repeatedly as they faced and investigated the nest box opening (Figures 12A and 12B). One squirrel tail flagged after approaching the entrance cautiously in an elongate posture while jumping back suddenly with a startle response. Another aroused squirrel threw substrate toward the entrance. Again, this apparent snake-directed behavior occurred only in laboratory-born squirrels under the chatter/whistle condition. Substrate sniffing was most evident under the antipredator vocalization condition, less so under the white-noise condition, and least evident under the laboratory ambience condition.

Compared with wild-caught squirrels, laboratory-born squirrels also looked upward more after exiting under the two augmented sound conditions compared with the laboratory ambience condition. Under the laboratory ambience condition, the mean bout length for looking upward after exiting was 3.75 sec, while under the chatter/whistle condition it was 9.25 sec; under the white-noise condition it was 10 seconds. Laboratory-born squirrels were significantly less vigilant when immersed in the sounds of a typical research laboratory compared with when they were presented with conspecific vocalizations.

Quantitative Analyses

Total gaze before exiting. Both groups of squirrels engaged in higher levels of scanning under the antipredator vocalization condition than under the other two conditions (Figure 8A). Although the main effect for groups, averaged for sound conditions, and the interaction between groups and sound conditions were not statistically significant, the main effect for sound conditions, averaged for both groups, was significant $\left(F = 7.369, \text{df} = 2{,}20, p < .005, power = .78\right)$. The chatter/whistle engendered significantly more gazing before exiting than the combined average of the laboratory ambience and white-noise conditions $\left(F = 8.479, \text{df} = 1{,}10, p < .025, power = .82\right)$. Tests of simple main effects revealed that both groups differentiated the three sounds $\left(\text{laboratory born: } F = 3.717, \text{df} = 2{,}20, p < .05; \text{wild-caught: } F = 3.816, \text{df} = 2{,}20, p < .05\right)$.

Planned comparisons for each group revealed that the chatter/whistle condition generated significantly higher levels of gaze than the laboratory ambience condition (laboratory born: $F = 5.915$, df = 1,10, $p < .05$; wild-caught: $F = 5.045$, df = 1,10, $p < .05$). Mean differences for both groups showed large effect sizes (respectively: Cohen's $d = 2.56$ and 1.78). Although planned comparisons for both groups indicated that behavior under the chatter/whistle and white-noise conditions did not differ significantly, the larger means for the chatter/whistle condition still produced large effect sizes (laboratory born: $d = 1.37$, wild-caught: $d = 1.61$). Similarly, for the laboratory-born and wild-caught squirrels the difference between the means for the laboratory ambience and white-noise condition was not significant, but the higher mean values for the white-noise condition produced a large effect size, respectively: $d = 1.08$ and 1.31 (Figure 8A).

Total gaze after exiting. Both groups of squirrels engaged in higher levels of scanning under the antipredator vocalization condition than under the other two conditions (Figure 8B). The main effect for groups, averaged for sound conditions, and the interaction between groups and sound conditions were not significant. As with the before-exiting context, the main effect for sound conditions, averaged for both groups, was significant ($F = 5.226$, df = 2,20, $p < .025$). The chatter/whistle engendered significantly more gazing after exiting than the combined average of the laboratory ambience and white-noise conditions ($F = 7.389$, df = 1,10, $p < .025$, *power* = .77). However, unlike the before-exiting context, tests of simple effects showed that only the laboratory-born squirrels differentiated between the sound conditions ($F = 7.308$, df = 2,20, $p < .005$). On the other hand, wild-caught squirrels engaged in much less pausing prior to leaving the designated area.

Planned comparisons revealed that, for the laboratory-born squirrels, the chatter/whistle condition yielded an appreciably higher level of total gaze than the laboratory ambience and white-noise conditions, respectively: $F = 9.349$, df = 1,10, $p < .025$; $F = 7.095$, df = 1,10, $p < .025$). As with the before-exiting context, laboratory-born squirrels gazed appreciably longer during the chatter/whistle condition than during the laboratory ambience and white-noise conditions, with mean differences producing large effect sizes, respectively: $d = 1.95$ and 1.78 (Figure 8B).

<u>Horizontal gaze before exiting</u>. Both groups of squirrels engaged in higher levels of horizontal scanning under the antipredator vocalization condition than under the other two conditions (Figure 9A). The contribution of horizontal gaze to the total gaze variable was substantial and yielded a similar pattern of mean differences. Again, the main effects for groups, averaged for sound conditions, and the interaction between groups and sound conditions were not significant. The main effect for sound conditions, averaged for both groups, was significant ($F = 8.372$, df = 2,20, $p < .005$) and yielded high statistical power (.83). The chatter/whistle engendered significantly more gazing before exiting than the combined average of the laboratory ambience and white-noise conditions ($F = 10.268$, df = 1,10, $p < .01$, *power* = .89). Tests of simple effects for both groups revealed that both groups differentiated the sound conditions (laboratory born: $F = 4.969$, df = 2,20, $p < .025$; wild-caught: $F = 3.592$, df = 2,20, $p < .05$). Planned comparisons for both groups showed that the chatter/whistle condition engendered significantly higher horizontal gazing than the laboratory ambience condition (laboratory

born: $F = 8.242$, df = 1,10, $p < .025$; wild-caught: $F = 4.903$, df = 1,10, $p < .05$) with large effect sizes, respectively: $d = 2.79$ and 1.84. The larger mean values for horizontal gaze under the chatter/whistle condition were not significantly different from the white-noise condition; these differences, however, had large effect sizes for the laboratory-born and wild-caught squirrels, respectively: $d = 1.64$ and 1.67 (Figure 9A).

Horizontal gaze after exiting. Laboratory-born squirrels engaged in significantly higher levels of horizontal scanning in response to the antipredator vocalization compared with the other two conditions (Figure 9B). Wild-caught squirrels did not exhibit significant differences in scanning under the three conditions. The main effect for groups, averaged for sound conditions, and the interaction between groups and sound conditions were not significant. Consistent with total gaze after exiting, the main effect for sound conditions, averaged for both groups, was significant ($F = 3.438$, df = 2,20, $p = .05$), with tests of simple effects indicating that only the laboratory born squirrels exhibited higher horizontal gazing that differentiated the sound conditions ($F = 5.008$, df = 2,20, $p < .025$). Planned comparisons revealed that, for the laboratory- born squirrels, only the chatter/whistle and laboratory ambience conditions yielded significant results ($F = 6.403$, df = 1,10, $p < .05$, $d = 1.63$). Despite lower levels of significance ($p = .1$), mean differences for the chatter/whistle and white-noise conditions and white noise and laboratory ambience conditions produced large effect sizes, respectively: $d = 1.24$ and 1.39. A planned comparison of only the laboratory-born squirrels, comparing the chatter/whistle and the combined average of the laboratory ambience and white-noise conditions, showed that the chatter/whistle engendered a significantly larger mean value

($F = 5.298$, df = 1,10, $p < .05$, *power* = .62) (Figure 9B).

Upward gaze before exiting. Wild-caught squirrels engaged in higher levels of scanning under the antipredator vocalization condition than under the other two conditions (Figure 10A). Laboratory-born squirrels did not exhibit significantly different levels of scanning under the three conditions. There were no significant main effects, averaged for groups or sound conditions, and there was no significant interaction between groups and sound conditions for the duration of upward gazing before exiting. Planned comparisons revealed that the wild-caught squirrels gazed upward for a longer duration than the laboratory-born squirrels under the chatter/whistle condition (Figure 10A). Wild-caught squirrels gazed upward for a longer duration under the chatter/whistle condition than under the laboratory ambience condition, although this difference disappeared in a comparison of the chatter/whistle condition and the white-noise condition (Figure 10A).

Upward gaze after exiting. Laboratory-born squirrels engaged in higher levels of scanning under the antipredator vocalization condition than under the white-noise condition and higher levels under this condition than under the laboratory ambience condition (Figure 10B). Overall, they engaged in higher levels of scanning than wild-caught squirrels. However, there were no significant main effects, averaged for groups or sound conditions. There was also no significant interaction between groups and sound conditions for the duration of upward gazing after exiting. For the laboratory-born squirrels, the three sound conditions yielded significantly different results (simple effect: $F = 4.010$, df = 2,20, $p < .05$). Planned comparisons showed that the mean value for gazing upward during the chatter/whistle condition, compared with the mean value for the laboratory ambience condition, was nearly significant ($F = 4.595$, df = 1,10, $p < .06$), and is considered relevant because of its large effect size ($d = 1.37$). Also, for the laboratory-born squirrels, a slightly smaller effect size ($d = 1.11$) was observed for the comparison of the laboratory ambience and white-noise conditions. Compared with the laboratory-born squirrels, wild-caught squirrels engaged in lower levels of upward gazing after exiting under the three sound conditions. The effect sizes for these group comparisons were substantial for the chatter/whistle and white-noise conditions, respectively: $d = .92$ and $.95$ (Figure 10B).

Substrate sniffing before exiting. Both groups of squirrels engaged in very low levels of substrate sniffing under all treatment conditions (Figure 11A). There were no significant main effects, averaged for groups or sound conditions, and there was no significant interaction between groups and sound conditions for substrate sniffing before exiting. Tests of simple effects and planned comparisons did not reveal any significant mean differences.

Substrate sniffing after exiting. Laboratory-born squirrels engaged in higher levels of substrate sniffing under the antipredator vocalization condition than under the other two conditions (Figure 11B). They engaged in significantly higher levels of this behavior compared with wild-caught squirrels. The main effect for squirrel groups, averaged for sound conditions, was significant ($F = 6.814$, df = 1,10, $p < .025$) with medium power (.73). The source of this group difference is most apparent for the chatter/whistle condition (simple effect: $F = 8.010$, df = 1,10, $p = .025$), which exhibited high power (.80) and a large effect size ($d = 1.79$). There was no significant main effect for sound conditions, averaged for both groups, and there were no significant simple effects for sound conditions for each group. The interaction of groups and sound conditions was not significant. Planned comparisons revealed that only the difference between the means for the laboratory ambience condition and chatter/whistle condition were significant ($F = 9.894$, df = 1,10, $p = < .01$). This comparison yielded high power (.87) and a large effect size ($d = 1.28$). Compared with laboratory-born squirrels, the wild-caught group engaged in very low levels of substrate sniffing after exiting (Figure 11B).

Discussion

This study investigated the influence of experiential history on the development of the referentiality of antipredator vocalizations in California ground squirrels. Referentiality would be implied by visual orientation as squirrels searched for different classes of predators as they exited from cover after hearing antipredator vocalizations in a setting initially devoid of acoustic threat. External referentiality could encompass the presence, location, and speed of attack of snakes, mammals, and raptors. Comparing the expression of antipredator vigilance in wild-caught and laboratory-born squirrels provided a context for evaluating the extent to which the referentiality of these vocalizations, their perception, and the behavior that they elicited might be mediated, either innately or experientially.

Minimally, the results suggest that squirrels from both groups differentiated the acoustic treatments. Although the comparisons did not always yield statistical significance, pairwise comparisons of mean values revealed many large standardized effect sizes. In general, all squirrels engaged in significantly more total scanning in the before-exiting context under the antipredator vocalization condition than under the white-noise condition. In both the before-exiting and after-exiting contexts, they engaged in more total scanning under the white-noise condition than under the laboratory ambience condition, albeit not at significant levels. Sound treatment differences arose from the significantly higher levels of horizontal gaze before and after exiting, with the highest levels in laboratory-born squirrels under the antipredator vocalization condition. In essence, after exiting, laboratory-born squirrels continued to discriminate between treatments and engaged in a more global assessment of their surroundings than wild-caught squirrels. They exhibited shorter excursions from cover than wild-caught squirrels, especially when the antipredator vocalization condition was compared with the white-noise condition. Once fully exposed, laboratory-born squirrels remained closer to the nest box than wild-caught squirrels, an outcome associated with their sustained scanning. Wild-caught squirrels engaged in higher levels of upward scanning before exiting than they did after exiting. This was especially apparent as they exited their nest boxes under the antipredator vocalization condition. In contrast, laboratory-born squirrels persisted in aerial scanning after exiting, reliably differentiating the antipredator vocalization condition from the building ambience condition.

Before exiting, both groups of squirrels engaged in low levels of olfactory investigation of the substrate, a behavior slightly more apparent in laboratory-born squirrels. A group difference was especially evident under the antipredator vocalization condition and slightly less so under the white-noise condition. After exiting, laboratory-born squirrels exhibited significantly higher levels of olfactory investigation of the substrate compared with wild-caught squirrels. Again, this was most evident under the antipredator vocalization condition. Because substrate sniffing required laboratory-born squirrels to shift their attention from searching for distal to proximal threats, it is reasonable to infer that this constituted snake-directed behavior (Coss, 1993). This interpretation is supported by accompanying antisnake behavior in several squirrels, as manifested by their tail flagging, jumpiness, and cautious elongate postures directed toward their nest box entrance (Figures 12A and 12B). Overall, olfactory investigation and snake-directed behavior near the nest box after exiting comprised the major distinction between the groups.

This in itself is interesting since it tends to suggest that a possible confound in the experimental design did not significantly influence its outcome. As noted, the laboratory-born squirrels were evaluated over a period of time weeks prior to the evaluation of the wild-caught squirrels. In nature, free-living squirrels exhibit seasonal variation in activity levels (Fitch, 1948, 1949; Linsdale, 1946; Loughry and McDonough, 1989). Although the animals were isolated in windowless housing under fixed photoperiods, seasonal effects still could have influenced the behavior of the subjects, contributing to group differences in behavior.

The Role of Experience

In the current experimental context, squirrels were exposed to a series of specifically evocative antipredator vocalizations. These were expected to be associated with an initially broad pattern of vigilance by both groups of subjects. The contention that antipredator vocalizations were provocative to both groups is suggested by the absence of significant group differences in gaze or olfactory behaviors during a critical information gathering context as squirrels emerged from refuge into the open. After exiting, wild-caught squirrels behaved as if their pre-emergent visual exploration was sufficient to confirm the absence of an aerial or terrestrial threat. They appeared less reluctant than laboratory-born squirrels to venture away from refuge to explore their surroundings.

Laboratory-born squirrels arguably exhibited a more sustained concern for the possible presence of an undifferentiated predatory threat. All laboratory-born squirrels exhibited perseverant searching for the distal threat that presumably incited the antipredator vocalizations. However, half of them directed most of their attention toward proximal threats associated with the formerly safe nest box, presumably attempting to discern the presence of concealed snakes. Other research has documented that both free-living and laboratory-born ground squirrels will frequently respond to a dark crevice as if it could conceal lurking snakes. Ground squirrels conduct cautious investigations of such entrances by adopting elongate postures, sniffing the substrate, and occasionally flagging their tails as they approach the opening (Coss, 1991a, 1993; Coss and Owings, 1978). In the simple surroundings of this experimental setting, primed by the antipredator vocalizations, the only salient variation affording the squirrels a potential source of threat at which to direct attention became the nest box opening. Conceivably, directed attention toward specific environmental features that historically concealed snakes comprises an important component of a ground squirrel antisnake perceptual system (Coss, 1991b).

Unlike laboratory-born squirrels, experienced wild-caught squirrels focused their vigilance on the possible presence of distal threats. Their more appropriate pattern of vigilance in the before-exiting context suggests that the antipredator vocalizations possessed a more narrow referentiality, which excluded snakes. Conversely, the broadly distributed pattern of vigilance shown by laboratory-born squirrels in the after-exiting context suggests that the referentiality of these antipredator vocalizations was less specific, encompassing potential threats from all predator guilds, including snakes.

In light of these findings, it is reasonable to argue that experience in nature is not required for the emergence of some aspects of referentiality in ground squirrel antipredator vocalizations. It is also reasonable to argue that other aspects of referentiality are refined through experience as squirrels hear antipredator vocalizations within specific predatory contexts.

It is important to examine the developmental effects of periodic exposure to vocalizations in the absence of relevant consequences. In the animal care facility, when technicians entered the squirrel room to conduct maintenance procedures, squirrels regularly emitted alarm vocalizations, sometimes inciting a cascade of vocalizations throughout the squirrel colony. All squirrels were exposed to vocalizations within the context of large, looming, provocative entities unlike most of those interacting with free-living squirrels. For laboratory-born squirrels specifically, the experience of hearing antipredator vocalizations was restricted to these circumstances. Wild-caught squirrels probably had heard these vocalizations within authentic predator contexts prior to their capture. Yet both groups exhibited continued responsivity.

Studies of latent inhibition indicate that periodic exposure to most sounds with no predictive value causes initial inhibition of the subsequent learning of a predictive association between sounds and their sequelae (Mackintosh, 1973). Since all subjects were regularly exposed to the antipredator vocalization and building ambience conditions in the absence of reliable consequences, even with provocative but inconsequential intrusions by technicians, habituation to the treatments should have been promoted. Yet squirrels continued to respond to the antipredator vocalizations, suggesting that these vocalizations had an innately provocative nature resistant to habituation.

As discussed earlier, antipredator signals are frequently provocative even to the uninitiated and resistant to habituation effects (Marler, 1977; Scherer, 1985). Mateo (1996a; 1996b) has suggested that priming might explain persistent responsivity to antipredator vocalizations. Thus, the continuous exposure of laboratory-born squirrel pups to antipredator vocalizations within the context of provocative disturbances results in adult squirrels sensitized to these sounds. Sensitization is associated with lowered response thresholds and persistent reactivity even in environments devoid of legitimately threatening features.

Thus, it could be hypothesized that the only novel sound condition was white noise and that its novelty should have promoted increased vigilance. For a multitude of species, sounds with hiss-like structures are salient and employed as warning signals (Morton, 1977), including several species of snakes which regularly co-opt ground squirrel burrows and prey on pups (Coss, 1991a; Fitch, 1948, 1949; Owings and Coss, 1977; Rowe, Coss and Owings, 1986; Rowe and Owings, 1978, 1990). For example, aroused rattlesnakes can produce aposematic warning rattles with their tails to alert squirrels to the presence of a venomous, though defensive, adversary (Poran and Coss, 1990).

However, in the current study, the squirrels did not show significantly higher levels of vigilance with white noise. Research on squirrels in the field and in the laboratory reveals that artificially generated test sounds are frequently only moderately evocative (Rowe, Coss, and Owings, 1986).

Ground squirrels, especially pups, emit snake-elicited chatter vocalizations under specific contexts (Coss, 1991a; Leger and Owings, 1980). In this study, the context within which the antipredator vocalization exemplars were recorded specifically precluded their being snake elicited (M. Hanson, personal communication, 1996). The snake-directed behavior of laboratory-born squirrels appears to have little to do with any predator-specific referentiality in the treatments. Nonetheless, the finding that the antipredator vocalization and white-noise conditions evoked reactions after years in captivity and after repeated presentation suggests that habituation was not important in modifying behavior. For a treatment of general learning models, including habituation, see Donaho and Palmer (1994), Mackintosh (1973), Marlin (1980, 1982), Marlin and Miller (1981), and Tarpy (1982).

In the current context, the relatively narrow pattern of vigilance observed in wild-caught squirrels is likely to have been a consequence of selectivity in focusing attention on the most relevant spatial aspects of the environment, as presumably signified by the antipredator vocalization. Focused attention suggests that the vocalizations possessed a narrow referentiality directed toward the types of threat that they were likely to have encountered prior to capture. The less focused pattern of vigilance evinced by laboratory-born squirrels suggested that the antipredator vocalization possessed referentiality related to general danger, not predator class, and certainly not to snakes.

This outcome characterizes the different experiences of the two squirrel groups. Laboratory-born squirrels had never heard antipredator vocalizations within the context of observing other squirrels detect or evade capture by predators or by directly detecting or evading predators themselves. The absence of the experience of responding to an antipredator vocalization in the presence of a predator conceivably resulted in the failure to form search images to serve as bases for confirmatory or disconfirmatory comparison (Langley, 1996). The constrained life histories of the laboratory-born squirrels were characterized by exiting into highly familiar, restrictive caged surroundings; they had only one prior experience of exiting into a more expansive novel setting (see Chapter 3). Wild-caught squirrels had experiences that included numerous episodes of exiting burrows within expansive settings without being confronted by imminent threats. Once they had the opportunity to respond to the environment, naive laboratory-born squirrels treated the vocalizations as generally evocative of undifferentiated threat, especially the proximal threats posed by snakes. Experienced wild-caught squirrels appeared to shift their attention from proximal threats, i.e., snakes, to distal threats, e.g., raptors and mammals. This implies that the precision of the external referentiality of antipredator vocalizations was developed as they were repeatedly emitted and detected within perceptually complete contexts early in their lives. In other words, experience provides the basic source of expectancy, while monitoring provides the process whereby expectancy is disconfirmed, or confirmed and reinforced (Coss and Owings, 1985; Marler, 1985).

Historical stability in the nature of ground-level threats might have shaped a *cognitive topography* leading to heightened vigilance in squirrels in environments where vision, or, for that matter, audition, was impaired (Chapter 2). Similarly, the predator detection and evasive behavior successfully executed by squirrels historically might promote the evolution of a cognitive topography (Coss and Owings, 1985) or *psychological landscape* (Guilford and Dawkins, 1991) that reflected rapidly unfolding predatory events and the specific tactics employed by subterranean, aerial, and terrestrial predators. There is a specific relationship between each predator guild and the location in the environment from which its members attack squirrels. Predation arising from several spatial domains could have selected a multilayered cognitive topography in accordance with historical patterns of vulnerability to predators, ability to detect predators in heterogeneous environments, and refuge availability. Thus, the cognitive system of squirrels integrates experience-based memories of predator interactions with knowledge of the spatial location of important ecological features affording refuge and expectancies of those representing threat (Coss and Owings, 1985; Gibson, 1979). Marler (1985) states: "Monkeys searching distinct aspects of their environment in response to an antipredator vocalization must have an expectation that a visual search will lead to detection of a member of a particular class of stimuli with specified properties, such as those of a soaring martial eagle."

The direction from which predatory attacks have been launched is relatively stable over evolutionary time. Selection to focus on these spatial domains results in the persistence of an orientational bias even in environments devoid of relevant threats. Natural selection pretunes perceptual systems to be maximally sensitive to the invariant properties of an environment, thus preparing perceptual systems for learning to detect appropriate information about habitat affordances (Gibson, 1979). For further discussion of cognitive interpretations of vocal, perceptual, orientational, and locomotory social communication, especially in the antipredator context, see Coss and Owings (1985), Guilford and Dawkins (1991), Owings and Morton (1998), and Marler (1985).

Effects of Developmental Retardation

One explanation for the less refined pattern of vigilance in laboratory-born squirrels is the cumulative effect of laboratory rearing on brain development (see Chapter 1). The absence of the sensory opportunity to experience environmental challenges and to act on them has been shown to affect central nervous system development in numerous species (Coss, 1991b; Rosenzweig, Bennett, and Diamond, 1972). For example, deprivation rearing in laboratory rats under conditions similar to those provided for the laboratory-born squirrels results in arrested neurological development (Black and Greenough, 1986). Animals exhibiting arrested neurological or behavioral development frequently maintain juvenile patterns of behavior throughout adulthood (Price, 1984).

For example, compared to mature adult ground squirrels, immature pups exhibit elevated physiological arousal, heightened reactivity to indeterminate provocation, and high levels of undirected vigilance when they first emerge into the open to explore their surroundings (Hanson, 1995; Mateo, 1996a). They also respond in an indiscriminate fashion to referentially specific antipredator vocalizations (Hanson, 1995; Mateo, 1996a, 1996b). In the current context, the behavior of laboratory-born squirrels is reminiscent of that shown by newly emerged pups during an initial phase of learning about the environment and its dangers (Hanson, 1995; Hanson and Coss, 1997; Mateo, 1996a, 1996b). The sensorily simplified settings within which the laboratory-born squirrels developed could have deprived them of the perceptual and locomotory interactions required for ontogeny to proceed beyond the juvenile stage. In essence, responsive environments are necessary for the perfection of adult patterns of behavior (Fentress, 1983; Lickliter, 1991). Consequently, it is reasonable to consider that the increased vigilance of laboratory-born squirrels is a manifestation of a juvenile pattern of behavior resulting from inadequate experience and arrested brain development.

The inadequate early sensory and perceptual experiences, retarded underlying neural development, and inadequate behavioral opportunities in laboratory-born squirrels probably encouraged the retention and expression of behavior associated with more stable, earlier stages of development. As squirrels develop, they are confronted with the task of distinguishing the invariant sinusoidal forms and repetitive scale patterns of snakes from the more variable visual patterns presented by birds and mammals, some dangerous and others innocuous (Armitage, 1982; Coss, 1991a; Coss and Goldthwaite, 1995; Fitch, Swenson, and Tollotson, 1946; Linsdale, 1946). The invariance of snake features facilitates their accessibility to lower-level, innately mediated systems for pattern recognition, which are functional early in development. Their early emplacement facilitates the reliable expression of snake-directed behavior, even in environments devoid of them. This stability suggests that these systems operate on stable, evolutionarily ancient ecological relationships shaped by natural selection (Goldthwaite, 1989; Coss and Goldthwaite, 1995).

The ancestors of ground squirrels have probably existed sympatrically for at least 10,000,000 years (Lundelius, et al., 1983; Miller, 1912). Snakes enter burrows for purposes of refuge and thermoregulation and to prey on young squirrels (Fitch, 1948). This long association has fostered early recognition of snakes in developing squirrels (Coss, 1991a; Coss and Owings, 1978). Laboratory-born squirrel pups recognize snakes as provocative shortly after their eyes open and before they emerge at 45 days of age (Coss, 1991a, 1993). Virtually all squirrels respond to snakes with elongate investigatory postures, piloerection, tail flagging, and substrate throwing, even during their initial introduction (Coss, 1991a, 1993; Coss, Gusé, Poran, and Smith, 1993; Hersek and Owings, 1994; Owings and Coss, 1977; Poran and Coss, 1990). The more variable configurations presented by mammals and birds probably require more complex higher-level recognition systems, which become functional later in development and which require learning. Learning is frequently constrained in captivity.

Pavlovian and Instrumental Effects

The reliable effectivness of antipredator vocalizations in effecting responses in squirrels with distinctly different developmental histories suggests that ground squirrel antipredator vocalizations function as innately provocative unconditioned stimuli which operate as reinforcers in a mixture of Pavlovian and instrumental conditioning during the development of antipredator behavior (Aetken and Wilson, 1979; Burnstein and Wolff, 1967; Owren and Rendal, 1997). Pavlovian processes confer salience on originally neutral or meaningful entities so that they acquire the predictive properties of cues through their repeated pairing with provocative stimuli. Instrumental processes involve dynamic interactions between organisms, in which percipients organize their behavior adaptively in ways that maximize reinforcement and reduce punishment. For example, immature vervet monkeys modify their vocal behavior to maximize their effect in provoking vocal responses from nearby troop members. Young monkeys acquire greater vocal effectiveness as they mature (Seyfarth and Cheney, 1980), an obvious instance of instrumental conditioning.

Squirrels must contend with aerial and terrestrial predators, each within predatory contexts representing different levels of urgency. Rapidly descending aerial predators such as eagles and hawks appear to be extremely provocative to experienced and inexperienced ground squirrels alike. Terrestrial mammals such as canids and felids appear to be moderately provocative to experienced ground squirrels but are nearly neutral to naive ground squirrels. The high levels of reactivity exhibited by naive ground squirrels to raptors strongly argues for the existence of innate recognition systems that function to detect extremely dangerous, fast-moving raptors (Coss, 1991; Hanson and Coss, 1997). In essence, raptors constitute unconditioned stimuli and evoke unconditioned responses.

Conversely, mammals become provocative to squirrels only after squirrels have witnessed or been a target of a predation event (Coss, 1993). Thus, when inexperienced laboratory-born squirrels were presented with domestic cats serving as analogues for wild felids, they failed to recognize them as potential predators (Coss, 1993; Coss and Biardi, 1997; Coss and Goldthwaite, 1995). In other words, mammals can constitute initially neutral entities to squirrels; they become provocative only after an arousing interaction. In essence, they become conditioned stimuli.

Knowledge of the strong statistical association between chatters and mammalian predators develops gradually with experience. Similarly, knowledge of the link between whistles and swooping raptors exhibits minimal developmental change. The greater rapidity of the formation of associations between whistles and rapidly swooping raptors compared with the more gradual formation of associations between chatters and the guild of stealthy mammals suggests that some aspects of predator-prey recognition and response might be primarily internally mediated, while others are primarily externally mediated (Gould and Marler, 1987). One is tempted to invoke the notion of ethological birds and psychological mammals.

Ground squirrel antipredator vocalizations possess qualities reflecting two time scales of adaptation—ultimate and proximate. Ultimately, the reliable emission of intense, high-pitched, rapid-onset vocalizations within fear-arousing contexts resulted in successful antipredator behavior, which presumably selected them to subsume a warning function. Proximately, their emission within dangerous excitatory contexts facilitates rapid acquisition of referentiality. Thus, the importance of antipredator vocalizations for percipients varies: (a) when emitted during urgent situations, they constitute unconditioned responses; (b) if perceived in the absence of unconditioned stimuli, they function as neutral stimuli; (c) for naive percipients, if they are paired with a provocative stimulus, they can function as unconditioned stimuli; and (d) for experienced percipients, if paired with a provocative stimulus, they can function as conditioned stimuli. The reliable pairing of antipredator vocalizations with the direct detection of a predator or with the antipredator behavior of conspecifics can ultimately confer on them salience, rendering them conditioned stimuli. This form of learning is probably an important mechanism in the development of predator recognition.

In the traditional Pavlovian paradigm, subjects are frequently restrained and their role in learning passive. In nature, the relationship between the organism and its surroundings is dynamic. Thus, learning in nature conforms more nearly to an instrumental model. The ability of percipients to respond actively to dangers by successfully evading them constitutes positive reinforcement. In fact, the perception of antipredator vocalizations, which effect adaptive escape behavior, can be viewed as secondary reinforcers in essentially instrumental transactions (Donaho and Palmer, 1994; Marlin, 1980, 1982; Marlin and Miller, 1981; Shettleworth, 1972, 1984; Tarpy, 1982). For various treatments of conditioning and vocal behavior see Aetken and Wilson (1997), Burnstein and Wolff (1967), and Owren and Rendal (1997).

More than likely, in nature the sequencing of stimulus and response is variable. Learning in nature probably even involves backwards conditioning. Experimentally, rats avoided the areas in a test arena where either food or predators had been presented more strongly than they did the area where they had received electric shocks. This occurred even when the shock was presented before the conditioned stimuli (Keith-Lucas and Guttman, 1975). This suggests that the cognitive appropriateness or ecological importance of the stimulus, e.g., *context*, may be more important in the acquisition of salience than the temporal sequence of detection and response (Bitterman, 1975; Bitterman, Lolordo, Overmier, and Rashott, 1979). Accordingly, predators and the location where they were detected can become extremely salient environmental features for experienced percipients (Armitage, 1982).

In nature, associative learning is frequently visually mediated. It can involve ecologically appropriate contingencies, including the behaviors of experienced adults as they interact socially, forage, and execute antipredator behavior (Hanson, 1995). The arousing context surrounding the visual detection of predators, or the observation of vocalizing conspecifics fleeing from predators might promote rapid consolidation of associations between predators and antipredator vocalizations. Perhaps such consolidation is analogous to the formation of flashbulb memories reported to occur in humans under intense arousal (Brown and Kulik, 1977; Coss and Owings, 1985).

Extended observation of experienced adults probably facilitates social learning about effective patterns of antipredator behavior. Infant vervet monkeys increase the duration of visual orientation toward their mothers following the emission of antipredator vocalizations (Seyfarth, Cheney, and Marler, 1980). Infant squirrel monkeys gradually become more responsive to adult antipredator vocalizations when these are repeatedly paired with the image of a terrestrial predator (Herzog and Hopf, 1984). Rhesus macaques (*Macaca mulatta*) appear to be able to acquire a fear response toward snake stimuli after watching a video recording of a model monkey fearfully responding to a snake stimulus (Cook and Mineka, 1989). Such experiential opportunities for learning are unavailable to captive animals, including the laboratory-born squirrels. The veracity of the concept of observational learning has been reviewed elsewhere (Galef, 1988).

Mode of learning notwithstanding, the formation of an association between a signal and danger should be effected rapidly. For a small, vulnerable rodent, repeated exposure to the predatory situations that facilitate learning might not be adaptive. Important associations must be formed rapidly. Perhaps sympathetically mediated, focused attention enhances the acquisition of associations among antipredator vocalizations, provocative environmental features, and adaptive evasive behavior, while memories of the association are consolidated through sympathetic hormonal activity

(Brown and Kulik, 1977; McGaugh, 1989). This form of arousal learning could account for the persistent reactivity of the laboratory-born squirrels when presented with antipredator vocalizations. For a discussion of one-trial learning and cue-to-consequence specificity and its relationship to the acquisition of associations, see Garcia and Koelling (1966).

Learning and the Acquisition of Referential Specificity

The information afforded by antipredator vocalizations is augmented over time as they are perceived in the context of predators or of aroused, responding conspecifics. Not only does the semantic value of these signals become more referentially precise, but the behavioral organization of percipients becomes more coherent as antipredator behavior is repeatedly executed in a perceptually complete context. These perceptual and behavioral opportunities were unavailable to the laboratory-born squirrels.

Nonetheless, species vary in the degree to which their responsiveness to antipredator vocalizations is subject to modification through experience (cf. Cheney and Seyfarth, 1985; Macedonia, 1990; Miller and Gottleib, 1981; Robinson, 1980; Seyfarth and Cheney, 1980). Improvements in referential specificity have been observed in a variety of mammals, including vervet monkeys (Cheney and Seyfarth, 1985), ringtailed lemurs (Macedonia, 1990), squirrel monkeys (Herzog and Hopf, 1984), and ground squirrels (Hanson, 1995). Species also differ in the relative contribution of external referentiality and internal motivation in the expression of and response to antipredator vocalizations. For example, experienced ringtailed lemurs reliably emit antipredator vocalizations and exhibit orientational biases in aerial scanning in response to the presentation of a raptor alarm vocalization, behavior similar to that observed in adult vervet monkeys and experienced ground squirrels. However, when adult ruffed lemurs, a related species, are presented with a raptor alarm vocalization, they do not orient toward the presumptive source of threat; instead, they exhibit an overall more reactive, less discriminating pattern of behavior. This more disorganized, less focused pattern of antipredator behavior is reminiscent of immature vervet monkeys and inexperienced ground squirrels (Cheney and Seyfarth, 1985; Hanson, 1995; Hanson and Coss, 1997; Leger and Owings, 1978; Leger, Owings, and Boal, 1979; Macedonia, 1990; Macedonia and Yount, 1991; Mateo, 1996a, 1996b; Pereira, Seeligson, and Macedonia, 1988). In nature, what is refined through experience is not the referential specificity of antipredator vocalizations per se, but rather the organization of behavior in response to urgent situations as presumptively signified by antipredator vocalizations (Cheney and Seyfarth, 1985; Seyfarth and Cheney, 1980).

The preceding discussion suggests that antipredator vocalizations possess naturally meaningful properties featuring innate, categorical, semantic boundaries within which graded perception is open to modification through experience (Marler, 1985). Repeated pairing of provocative stimuli with the detection or production of vocalizations eventually enhances their signaling effectiveness. The provocative nature of vocal alarms might both engender refinement of predator recognition for extremely dangerous species, while simultaneously broadening perceptual categories to encompass even those entities which were formerly innocuous (Scherer, 1985).

Conclusions

Antipredator vocalizations provide general information about the imminence of danger. When presented with antipredator vocalizations, experienced squirrels ceased aerial and terrestrial visual scanning and substrate investigations after failing to confirm the presence of danger. Presented with the same vocalizations, inexperienced squirrels responded to the failure to disconfirm the presence of danger by engaging in inefficient, undirected, perseverant search routines.

The current work provides evidence that, although the antipredator vocalizations of California ground squirrels are innately provocative, their semanticity becomes more specific as vocalizations are perceived in ecologically appropriate, perceptually complete frameworks.

The emission of antipredator vocalizations congruent with predator detection confers on them predictive properties as signals of imminent danger. To secondary percipients, the associative linkage of stimulus and signal provides reliable information about the probable source and nature of the threat. Percipients, in turn, can adjust the orientation and duration of visual, auditory, and olfactory search routines that enhance the probability of detecting predators from specific guilds.

For vocalizations to acquire such adaptive effectiveness, experience in environments with a complete complement of contingencies is critical; these are the sorts of environments ordinarily unavailable to captive animals.

Summary

Visual vigilance in wild-caught and laboratory-born California ground squirrels was compared as they emerged from nest boxes under three conditions: laboratory ambience, white noise, and antipredator vocalizations.

1. Generally, semanticity arises from a composite of innate, primarily affective components that may be augmented through experience, imbuing signals with more complex attributional functions. Semanticity can extend to the provision of inferences about the specific shapes, locations, and modes of movement of dangerous adversaries.
2. Both wild-caught and laboratory-born squirrels differentiated laboratory ambience, white noise, and antipredator vocalization sound conditions from one another.
3. Before exiting their nest boxes, wild-caught and laboratory-born squirrels confined their visual searching to spatial vectors from which raptors and cursorial mammals launch attacks.
4. After exiting, wild-caught squirrels rapidly reduced the intensity of environmental monitoring. Laboratory-born squirrels continued to search their surroundings for danger. They extended their searching for snakes, as suggested by elevated levels of substrate sniffing. Three squirrels turned to investigate the dark nest box opening, exhibited startling, assumed an elongate posture, and tail flagged. All of these behaviors typically occur in the context of squirrel interactions with snakes.
5. Snake-directed behavior appears at an early stage in the development of squirrels. Its appearance in the laboratory-born squirrels is suggestive of arrested behavioral development.
6. These findings support the contention that antipredator vocalizations can be innately evocative without possessing intrinsic, specific external referentiality.
7. Behavioral adjustment involves both ultimate and proximate mechanisms. Some important aspects of antipredator behavior are the products of robust developmental

systems that allow behavioral development to proceed in a variety of environments. Other, higher level components of antipredator behavior are modifiable through adjustment, allowing animals to adapt to variable environments.

8. Artificial environments should be designed to encourage the maintenance of robust neural structures and the preservation of species-typical behaviors.

CHAPTER FIVE

Dins and Decibels, Denizens and Dens

A primary biological rationale for the preceding series of studies was to improve the understanding of the interaction between some elements of acoustic environments and the development and expression of antipredator behavior in California ground squirrels. The information obtained through this research might be generalizable to other species housed in inadequate artificial environments, where there is a desire to foster the development and expression of species-typical behavior.

In zoos and laboratories, the structure of the acoustic environment is relatively simple. They do not possess the complexity arising from natural sources characterizing the acoustic environments typical of most natural habitats. What complexity there is comes from unnatural sources. Under simple acoustic conditions, noise becomes prominent; the irrelevant may become relevant, and even worse, falsely salient (Fentress, 1983).

Relevance and salience can become equally important qualities of an individual's perceptual surroundings. For example, relevance notwithstanding, perceptual backgrounds are typically less prominent than perceptual foregrounds. Perceptual foregrounds, again, relevance notwithstanding, are typically more salient than perceptual backgrounds. As stated in Chapter 1, the differential level of attention directed at the focused foreground and diffuse background can provide a context for viewing relevance and salience within the perceptual construct of figure and ground (Israeli, 1950; Lerea, 1961; Lindauer, 1989; Thurlow, 1957; Vecera and O'Reilly, 1989). The structure and composition of acoustic environments can possess varying degrees of both relevance and salience to percipients. Acoustic relevance is, minimally, a quality associated with ecological authenticity. The sensory appropriateness of environments arises from the long-term association of species with particular types of habitat acoustics (Bowman, 1979; Morton, 1975; Owings and Morton, 1998; Richards and Wiley, 1980; Waser and Brown, 1984, 1986; Wiley and Richards, 1978). In many natural systems, salience follows from relevance. Unfortunately, in artificial environments, it may not.

Acoustic relevance is rare or absent in the environments typical of zoos and laboratories. Acoustic salience, on the other hand, is a quality characterized by conspicuousness. Salient acoustic features are not necessarily relevant. Their prominence can arise from their intensity, abruptness, unpredictability, uniqueness, or provocative referentiality (Davis, 1974).

The relationship between the constructs is complex. Both important biological sounds and many unnatural noises are equally salient. Sensorily appropriate environments possess relevant features, some of which are also salient. Irrelevant salience is exemplified by anthropogenic noise; relevant salience is exemplified by zoogenic sound.

The acoustic structures of natural and artificial environments possess both distal (background or far field) and proximal (foreground or near field) elements (Israeli, 1950; Lerea, 1961; Lindauer, 1989; Thurlow, 1957; Vecera and O'Reilly, 1989). In natural environments, the acoustic background is usually comprised of relatively low-intensity constant noise generated by the interaction between myriad vocalizations, vegetative rustling, and atmospheric perturbation (Chapter 1; Waser and Brown, 1986; Wiley and Richards, 1978). The acoustic foreground might possess some of these elements, but may include aperiodic noise generated by the locomotor activity or vocalizations of conspecifics, competitors, or predators.

Novel, aperiodic sounds present in the perceptual landscape (Guilford and Dawkins, 1991) can occupy the attention of percipients, though those in the foreground typically possess greater salience than those in the background. In nature, most mammals rapidly habituate to low-level, continuous, periodic noise in the acoustic background and slightly less rapidly to similar noise in the acoustic foreground (Anthony, Ackerman, and Lloyd, 1959; Busnel, 1978; Cottereau, 1978; Davis, 1974; Gamble, 1982; Shaw, 1978; Stoskopf, 1983).

In artificial environments, captive mammals habituate to ecologically authentic sounds in the perceptual background (Ogden and Lindburg, 1991; Ogden, Lindburg, and Maple, 1994; Tromborg, 1993). For such ecologically relevant sounds, the absence of measurable responsiveness could be interpreted as a positive factor in that, even in the attentive background, they may be contributing to the animals' level of comfort and well-being (Rosemary Babcock, personal communication, 1998).

In contrast, in both nature and captivity, most, though not all, mammals exhibit a persistent responsiveness to high-amplitude, punctate sounds (Busnel, 1978; Guilford and Dawkins, 1991; Stoskopf, 1978). These sounds exert influences from anywhere in the perceptual landscape, though they are maximally effective when present in the acoustic foreground (Israeli, 1950; Lerea, 1961; Lindauer, 1989; Thurlow, 1957; Yost, 1992). In nature, some of these sounds appear to possess varying degrees of emotive effect. Some sounds, particularly those with rapid rise times, are simply naturally startling; other provocative sounds appear to possess some degree of innate or learned referentiality (Guilford and Dawkins, 1991; Salzinger, 1973; Smith, 1977).

Frequently, the most provocative sounds convey information about a percipient's detection of potential danger or its heightened internal emotional disposition in response to the perception of danger (Macedonia, 1990; Macedonia and Yount, 1991; Owings and Virginia, 1978; Leger and Owings, 1978; Seyfarth and Cheney, 1980).

The effects of sound on behavior are frequently subtle and paradoxical, especially for sounds in the perceptual background. The differential effectiveness of foreground compared with background sounds is partially an outcome of attention structure and its focus on the foreground (Guilford and Dawkins, 1991; Yost, 1992).

Attentional focus can be directed toward acoustic objects through the cognitive process of *object entity formation* (Yost, 1992). This mode of sound source determination involves detecting individual sound sources corresponding to auditory images and constructing an acoustic scene by juxtaposing auditory entities over a generalized acoustic background (Yost, 1992). Acoustic phenomena important for survival are thus preferentially located, identified, and reacted to. However, in simple invariant environments, inconspicuous sounds might become disproportionately conspicuous (Fentress, 1983). Invariant perceptual backgrounds can actually increase the prominence of foreground features by enhancing contrast effects, a process termed *stochastic resonance* (Davis, 1974; Henry, unpublished manuscript; Levin and Miller, 1996).

In the wild and in captivity, some sounds are perceived as generalized anxietyprovoking stimuli, not as referentially specific signals. Other sounds elicit virtually no observable response. Compared to functionally specialized antipredator systems, reactivity to some sounds appears to be more generalized. Conceivably, this is a result of the nonspecific quality of many features of the acoustic domain within which animals operate. Adaptively organized acoustic behavior must allow animals to focus attention on salient sounds, while simultaneously allowing them to habituate to less relevant sound originating outside the attentional focus (Guilford and Dawkins, 1991; Israeli, 1950; Lerea, 1961; Lindauer, 1989; Thurlow, 1957; Yost, 1992).

The impact on behavior of such background sound has not been sufficiently investigated (Ogden and Lindburg, 1991). Consequently, the efficacy of employing naturalistic background sounds as vehicles to modify and control noise, increase ecological relevance, and enhance the sensory richness for animals housed in artificial settings is not well understood and should be further explored (Tromborg, 1994; Tromborg and Coss, 1995).

The notion that artificial environments can be improved by enhancing their sensory appropriateness is a relatively recent innovation in the contemporary behavioral enrichment paradigm. Creating ecologically authentic environments is becoming particularly important as increasing numbers of species are relegated to discontinuous remnants of natural habitats and to artificial environments in zoological parks and laboratories. The small, isolated populations of endangered individuals commonly housed in zoos are susceptible to inbreeding, artificial selection, and relaxed selection, all of which can accelerate the genetic drift of captive zootype genomes from wild type genomes (Beck, 1991; Boice, 1980; Carpenter, 1983; Conway, 1974; Frankham et al., 1986). Evolutionary changes can occur more rapidly than previously believed (Weiner, 1994). Research on artificial selection in rodents reveals that permanent shifts in behavioral, temperamental, and genetic dispositions can occur in a single generation. For example, different urination rates have been correlated with elevated aggression and improved reproductive success (Cairns, Gariepy, and Hood, 1990).

Consequently, efforts should be undertaken to counteract the unintentional artificial selection almost certainly occurring in animal care facilities. Zoos and laboratories should adopt the suggestion of Schneirla (1950) and employ comparative research in a multitude of natural and artificial settings to illuminate the effects of various environmental factors on behavior. Findings from this research should be incorporated in the design of improved artificial environments. Improved environments should have as much ecological authenticity and interactivity as technology allows (Markowitz, 1982; 1997; Tromborg, 1993, 1994).

The theoretical structure of animal-environment mutualism, concepts regarding direct perception, and the role of memory and cognition in perception must all be considered during the design of appropriate environments. The *evolutionary persistence* construct (Coss, 1991b) coincides with the *behavioral enrichment* paradigm (Markowitz, 1973, 1975) and considers the possibility that animals retain perceptual biases and behavioral relics from former historic regimes of natural selection. Animals probably behave most normally in environments reminiscent of those of their ancestors and for which they are best adapted.

Thus, captive animals should experience ecologically relevant situations that offer perceptual experiences and behavioral challenges parallel to those of their wild counterparts to foster the development and expression of species-typical behavior (Markowitz, 1997). Unfortunately, an inspection of the environmental enrichment literature reveals a dearth of information about enhancing the sensory experiences of captive animals.

Traditional habitat improvement paradigms embrace a pseudo-naturalistic aesthetic that mimics some aspects of natural environments. Typically, this is done as much for its visual effect on humans as for the welfare of the nonhuman inmates (Hutchins, Hancocks, and Crockett, 1984). These passive approaches have been termed *naturalistic* to imply that in some respects they resemble natural landscapes. Such environments are usually devoid of dynamic environmental contingencies. Animals housed in passive naturalistic environments are able to exert only minimal control over their surroundings. Again, the focus is on displaying animals, not their behavior. This shortcoming is particularly pervasive in the areas of sensory and predatory behavior.

Artificial environments are not only devoid of important features, they possess other attributes in an unfortunate abundance. Because of their public charters, many animal facilities are intrinsically noisy. The acoustics in animal research facilities, zoological parks, aquaria, and disturbed natural habitats are frequently characterized by the presence of relatively intense, continuous noise or aperiodic, punctate noise. Much of this noise originates from communication devices, machinery used in maintenance, and the vocalizations of animals, including humans. The nature of the materials employed in the construction of artificial enclosures exacerbates the noise problem. Materials most desirable for hygienic reasons are also the most acoustically reflective.

The most provocative noise originates from the interaction between human activity and reflective surfaces. When the sound pressure levels were measured at the animal care facility used in this study, the values ranged from 40–85 dB (SPL). When sound pressure levels were measured at three northern California zoological parks (San Francisco, Sacramento, and Happy Hollow), they ranged from 62–78 dB, averaging 70 dB (SPL). The intensities were a function of the reflectivity of the nearby surfaces and, most importantly, the number and activity level of visitors. In general, the intensity of sounds in zoos is lower than the absolute recommended maximum value of 85 dB (SPL) (Anthony, Ackerman, and Lloyd, 1959). However, it exceeds the noise levels typical of rain forests, usually considered the noisiest natural environments.

Anecdotal evidence suggests that some noise can incite responses from vocally active zoo animals. Correlational research on red-ruffed lemurs suggests that their level of reactivity, as gauged by vocal activity, varies reliably with the number of visitors. They emit 5 percent of their vocalizations in the morning, when there are the fewest visitors; 20 percent at midday, when the number of visitors is intermediate; and 75 percent in the late afternoon, when the number of visitors is highest (Tromborg, unpublished data, 1991, 1992). This responsiveness to extraneous acoustic phenomena presents both a potential problem and an opportunity for counteracting the less desirable aspects of captivity.

Many captive animals, especially members of social species, appear to acclimate to anthropogenic noise. Noise-tolerant species include a variety of insects, fish, birds, mice, rats, cattle, monkeys, and several other domesticated species. Some species, including mosquitos, crows, and dogs, are actually attracted to anthropogenic noise, a reliable indicator of nourishment (Busnel, 1978). However, some species, such as guinea pigs (*Cavia spp.*), are extremely intolerant of noise (Fletcher and Busnel, 1978; Shaw, 1978). Virtually all recently captured and first-generation animals, even after years in captivity, appear to be reactive to intense punctate noise (Meyer-Holzapfel, 1968; Stoskopf, 1983). In response to such noise, many animals attempt to retreat from the source—not always an option for animals in restrictive surroundings (Busnel, 1978). Species differences in reactivity to noise should be considered when acoustic enrichment procedures are contemplated.

Even animals living in unaltered natural conditions must contend with elevated noise, including that associated with windy or rainy weather (and, occasionally, anthropogenic sounds such as airplanes). Any elevation in environmental noise can interfere with sensory behavior (Ehret, 1989). Since noise is an integral component of normal habitats, animals can often habituate to a variety of sounds, even those with which they are unfamiliar.

Unfortunately, there are provocative sounds that continue to elicit reactions from many animals. When possible, the intensity of this noise should be attenuated. When this approach is impractical, the quality of the acoustic environment should be altered, either through the *immersion* of animals into relevant *acoustic landscapes* or through the introduction of salient environmental sounds.

Based on research on free-living animals, conspecific vocalizations are demonstrably effective eliciting stimuli (Byrne, 1982; Cheney and Seyfarth, 1985; Kroodsma, 1989; Leger and Owings, 1978; Leger, Owings, and Boal, 1979; Loughry and McDonough, 1989; Seyfarth and Cheney, 1980; Seyfarth, Cheney, and Marler, 1980; Schwagmeyer and Brown, 1981). In zoological parks, salient sounds have been presented in the perceptual foreground to animals to incite behavior directly (Haraway, Maples, and Tolson, 1985; Maples and Haraway, 1982; Markowitz, Aday, and Gavazzi, 1995; Raemaekers and Raemaekers, 1985; Shepherdson, Bemment, Carmen, and Reynolds, 1989; Tromborg, 1993). In other instances, low-intensity environmental sounds have been introduced into the perceptual background to impart a sense of naturalism to environments (Chapter 1; Tromborg, 1994).

For example, naturalistic soundscapes were introduced into the holding facilities of a group of western lowland gorillas (*Gorilla g. gorilla*) at the San Diego Zoo. The authors were interested in determining if this approach lessened the reactivity of the animals to other provocative noises originating near their enclosures (Ogden and Lindburg, 1991). Adult animals exhibited only minor differences in behavior under naturalistic and night quarters ambience conditions. These small effects could reflect similarities in the acoustic structures of the two conditions, making interpretation of the data difficult (Ogden, Lindburg, and Maple, 1994). Importantly, the authors did not report any symptoms of acoustically mediated stress as a consequence of added environmental sounds.

Whether or not the appropriateness of the acoustic environment is enhanced through the provision of naturalistic acoustic backgrounds remains unclear. It is not entirely evident that animals immersed in naturalistic sounds react less frequently to the unnatural sounds emanating from typical animal care procedures. If they did so, it could be a result of elevated auditory thresholds, decreased information content in their surroundings, or habituation to noise devoid of consequences.

In a study of captive siamangs, presentation of recorded conspecific vocalizations increased vocal responsiveness and appeared to exert a positive effect on behavior (Shepherdson, Bemment, and Carmen, 1989). In a more extensive study, involving a pair of cotton-top tamarins at the San Francisco Zoo, animals were presented with naturalistic sounds derived from conspecifics, congeners, and prey. In response, the levels of scanning, allogrooming, and display decreased, while levels of autogrooming, vocalizing, and cryptic behavior increased (Tromborg, 1993). The results are similar to those obtained in other zoo and laboratory research and represent desirable behavioral outcomes (Cleveland and Snowdon, 1982; Haraway, Maples, and Tolson, 1981; Shepherdson, Bemment, Carmen, and Reynolds, 1989).

An even more interactive approach employed electronic generated sounds of prey to incite hunting behavior in an African leopard *(Panthera pardus).* The procedure appeared to encourage more natural sequences of locomotive predatory behavior (Markowitz, Aday, and Gavazzi, 1995).

In addition to maintaining species-typical behaviors by encouraging their expression, ecologically relevant sounds are implicated in the ontogeny of normal adult behaviors (Ehret, 1980, 1990; Snowdon, 1986). The ability to interact with acoustic elements during development is also important in the acquisition of adequate sensory motor coordination. Many species of raptors must perceive ecologically important sounds as juveniles in order to develop the ability to locate prey acoustically as adults (Knudsen, 1984). Consequently, in order to encourage normal behavioral development, artificial environments should be enhanced by providing captive animals with interactive acoustic elements, perhaps in ways that facilitate antipredator or predatory behavior.

Each species has evolved a specific *psychological landscape* (Guilford and Dawkins, 1991) or *cognitive topography* (Coss and Owings, 1985) to counteract the behavioral tactics of their major predators. However, for a variety of ethical, political, social, and practical reasons, artificial environments seldom, if ever, offer captive animals the opportunity to engage in behaviors associated with interactions between predator and prey. Wild animals brought into captivity, or those born into it, are virtually never provided with situations in which they can experience important perceptual contexts associated with antipredator vigilance or defense—or with the detection and capture of prey. In nature, the interactions between predator and prey, including vigilance, have been extensively studied (Chapter 3; cf. Owings and Virginia, 1978; Seyfarth and Cheney, 1980). Conversely, research into the development and expression of antipredator behavior in captivity has been extremely rare. It has usually taken the form of describing the vigilance behavior of animals as they respond to various forms of provocation within or near their enclosures (Caine, 1984; Carlstead, Brown, and Seidensticker, 1993; Stanley and Aspey, 1984; Thompson, 1989; Wolters, 1978). The sources of sensory stimulation eliciting these behaviors have not always been ecologically authentic. In fact, allopatric species, herbivores, and human beings have comprised the majority of the eliciting stimuli. Ungulates (Stanley and Aspey, 1984; Thompson, 1989), carnivores (Carlstead, Brown, and Seidensticker, 1993), and primates (Caine, 1984) continue to exhibit vigilance in captivity. Apparently, even human beings can be viewed as provocative, possibly as predators (Stanley and Aspey, 1984; Thompson, 1989).

Although sporadic predation events do occur in zoos, e.g., tigers *(Panthera tigris)* capturing gulls *(Larus spp.)*, almost none of them are regular components of traditional maintenance routines (Tromborg, personal observation, 1990). Virtually no zoo exhibits house mammalian predators with their normal prey. Except for insects, live prey has seldom been continuously provided to carnivores. However, in a few innovative instances, live fish have been provided to polar bears (*Ursus maritimus*) and river otters (*Lutra spp.*). Similarly creative approaches have featured automated mechanical or acoustic prey to motivate hunting (Markowitz, 1982; Markowitz, Aday, and Gavazzi, 1995).

Contemporary paradigms of environmental enrichment must include adequate contingencies for animals to express their full range of normal behaviors. Animals must be provided with the opportunity to control at least some of these contingencies (Markowitz, 1982; Markowitz and Gavazzi, 1995). In fact, in order for an animal to become a competent representative of its species, both in captivity and in the wild, some of these contingencies must be as stimulating, arousing, or even threatening. In some instances, animals should be confronted with even potentially injurious environmental challenges from which they must successfully extricate themselves (Beck, 1991). Only through the provision of such challenging environments can animals be maintained in a physically and neurologically robust condition.

Behavioral enrichment approaches which involve the provision of acoustically provocative sounds might be criticized for engendering slight increases in stress. However, prior research suggests that this is not a problem with acoustic enrichment procedures (Ogden, Lindburg, and Maple, 1994). In any case, it can be argued that the occasional elevation of arousal fosters the performance of vigilance behaviors, which themselves might be important for animals to express. Conceivably, captive animals require being confronted with environmentally challenging situations in order to promote normal behavioral and nervous system development (Black and Greenough, 1986; Coss, 1991). Animals not provided with the opportunity to interact with ecologically authentic surroundings experience incomplete neurological development, a phenomenon often observed in environmentally deprived animals (Black and Greenough, 1986). Experiential opportunities are as important in the realm of acoustics as they are in the expression of locomotor behavior (Cheney and Seyfarth, 1985; Knudsen, 1984; Seyfarth, Cheney, and Marler, 1980; Snowdon, 1986; Tromborg and Coss, 1995).

Consequently, the concept of environmental enrichment should be extended to encompass the acoustic realm. Sounds reminiscent of or derived from nature could be used to encourage cautious environmental surveillance (Tromborg, 1993). Particularly salient sounds could be employed to challenge animals with emotionally arousing situations. Periodic episodes of elevated arousal could confer beneficial cognitive effects on animals by fostering the expression of a range of behavior often rare in artificial settings.

Promoting the maintenance of robust patterns of species-typical behavior, especially in immature animals, could encourage normal nervous system development and function (Black and Greenough, 1986; Coss, 1991a). It could also maintain animals in a neurologically robust condition throughout the extended lifetimes common in captive animals (Connor, Beban, Melone, Yuen, and Diamond, 1982; Connor and Diamond, 1982; Greer, Diamond, and Tang, 1982; Soule, Gilpin, Conway, and Foose, 1986). Such genetically sound, neurologically robust, and behaviorally adept populations of captive animals would taste better and could someday successfully recolonize a restored nature.

Even if the influence of the acoustic landscape on the behavior of animals remains unclear, the increased ecological authenticity of acoustically enhanced exhibits improves their educational effectiveness. More effective conservation and natural history education enables zoos to achieve their goals as purveyors of biodiversity.

Conclusions

The enhancement of the acoustic dimension of artificial environments is the least explored of the various approaches to environmental enrichment. Minimally, the acoustics of laboratories, aquaria, and zoos can be improved through the reduction in excessively intense noise. Acoustic environments can be further modified through the application of low-level natural backgrounds. Finally, artificial settings can attain a level of salience and interactiveness through the introduction of ecologically authentic sounds, such as the vocalizations of conspecifics, predators, or prey.

Ultimately, it is imperative that environments provide animals with the opportunity to engage in the behaviors that enabled their ancestors to survive. This means that natural environments should be preserved and that artificial environments should be imbued with the sort of provocative contingencies that fostered the maintenance of survival-enhancing vigilance in the ancestors of contemporary animals. Otherwise, there will come a time indeed when the captive and free-living squirrels of tomorrow might search and search for the predators with whom they co-evolved, only to find the ghosts of predators past.

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