Integrating Proximate and Ultimate Causation in the Study of Vertebrate Behavior: Methods Considerations[1]

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Synopsis. Methods issues are critical for the integration of proximate and ultimate explanations of animal behavior. Understanding that evolution of behavior may begin with changes in sensory and perceptual systems is a first step. For example, advances in neurobiology can trigger questions about social behavior. Variation in the size of particular brain areas, such as the hippocampus, can be related to variation in socio-spatial systems. Second, procedures, developed in recent years, provide new avenues to understand behavior. Hormone assay techniques, such as RIA and ELISA, can be performed on some hormones from urine and feces collected in the wild. Metabolic measurement, such as the use of doubly-labeled water, make it possible to measure energy costs under field conditions. Advances in DNA technologies provide new perspectives, particularly with regard to measuring reproductive success. Third, current theories in behavior can be tested with regard to physiological mechanisms; all that is needed is some ingenuity to design and execute appropriate studies. These include kin recognition, sex ratio variation, and foraging behavior. Fourth, cross-fertilization between laboratory and field approaches produces new insights regarding behavior. Organizational effects of hormones have now been explored in field populations of mice and in domestic swine. Testing aspects of foraging behavior in the laboratory is another example. Fifth, simulation models have been used to produce new questions about both proximate and ultimate aspects of behavior. Exploring behavioral phenomena may involve semi-natural settings. The suitability of semi-natural enclosures for the study of house mouse behavior has been tested with regard to density and home range size.

INTRODUCTION

Methods considerations are critical to the integration and synthesis of proximate and ultimate causation of behavior. We use the term "methods" here to mean several things. First, we refer to the fact that all animal behaviorists must constantly consider the perceptual world or Umwelt of their subject animal. Second, we refer to a variety of techniques developed over the past several decades that open up new avenues for research in animal behavior. Third, we refer to using these techniques with regard to exploring various hypotheses and theories in animal behavior, such as

those regarding kin selection and sex ratio variation. Fourth, we note briefly the use of simulation models as an heuristic tool for stimulating questions that can be asked about both proximate and ultimate aspects of behavior. Finally, we refer to the use of both laboratory and field settings, as well as various forms of semi-natural environments for studying animal behavior. This is not intended as an exhaustive survey, but rather a compilation of our views on some keys to the integration of approaches. Also, these "meanings" for methods are not individually exclusive; there is overlap among the various areas we wish to discuss.

In the introduction to the symposium, a view of events was given concerning why an integration of proximate and ultimate causation is now in order. In this paper we examine the contention that methods will be key to this process. We will review each of the foregoing meanings for the term

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"methods" with regard to recent and future possibilities for explaining proximate and ultimate causation of animal behavior.

SENSATION, PERCEPTION AND NEURAL PROCESSES

One of the first principles most of us teach in courses on animal behavior concerns the fact that each organism has a unique set of sensory capacities and different machinery for interpreting those sensory inputs. This guiding principle will be critical as we attempt to connect proximate and ultimate approaches to behavior. A renewed understanding of what is meant by the sensory and perceptual world of the animal will enhance work on both proximate and ultimate causation.

We base this contention on the fact that one key possibility for how evolution affects animal behavior involves these same sensory and perceptual systems. In the first edition of his textbook, *An Introduction to Animal Behaviour,* Aubrey Manning (1967) signaled the importance of the animals' sensory system by indicating his view that evolution of behavior probably proceeds first with a change in sensory and perceptual mechanisms. Thus, a change in transduction capacity results in a shift in coding for frequency or intensity of a stimulus in a sensory system. Changes in the sensory system alone would not suffice to produce an effect. In addition, there must be concomitant changes in the central nervous system that receives, processes, and stores this information. Thus, the animal is able to take in and process information not previously available to it.

As noted in the introduction to the symposium, those who approach animal behavior from a proximate viewpoint use "mechanism" primarily to connote physiological events, whereas those who have a more ultimate approach often use "mechanism" to refer to behavioral events. We believe that eventually our understanding of those behavioral events will depend on an understanding of the processes that occur within and between cells. Part of the integration now underway will entail elucidation of connections between ongoing behavioral events and underlying cellular processes.

Some of this work has already begun as other papers in the symposium demonstrate.

One key to integrating work on sensory and nervous systems with behavior of individual animals and then behavioral ecology is recent work in neurobiology. A sample of these methods will give a glimpse of what lies ahead as these procedures and results obtained from their use advance the integration process.

Techniques involving histological architectonics of the brain and neural pathways, as well as single-cell recordings from neurons have been available for some decades. Findings such as those of Hubel and Wiesel (1962, 1977) concerning the correspondence of projections from the retina and the arrangements of cells at different levels in the visual cortex, indicate the detailed knowledge that can now be obtained regarding brain structure. Studies of this type continue today, as for example in the work reviewed by Knudsen and Brainard (1995) on the representation of visual and auditory space in the brain, and studies of plasticity of receptive fields in adult mammals (Weinberger, 1995). The work of Nottebohm and colleagues (Nottebohm, 1975; DeVoogd and Nottebohm, 1981) demonstrates that it is feasible to examine relationships between changes in behavior and changes in brain structure. Patterns of interconnections between neurons due to changes in dendritic growth and changes in size of brain nuclei in canaries (*Serinus canarius*) occur on a seasonal basis. These changes are functionally related to increased singing during the breeding season.

It seems to us that it should now be possible to use these and other neuroscience technologies to explore more directly other functional relationships, where the questions derive from behavioral ecology. For instance, one could examine changes in brain structure that take place in relation to seasonal events, such as dietary shifts or migration. Or perhaps, changes in the nervous system can be detected that relate to shifts in behavior that occur with fluctuations in population density. Considerable work has been done on population cycles in microtine rodents. It is now possible to examine the brains of, for instance, voles of

various species, from different stages of the population cycle to determine what changes in brain structure and neurochemistry accompany density increases or population crashes. On a different scale, it may be possible to explore variations in brain structure associated with species or sex differences in types of social systems or spatial distribution patterns. For example, Jacobs and colleagues (Jacobs *et al.*, 1990; Jacobs and Spencer, 1994; Jacobs, 1996) have found species and sex differences in the size of the hippocampus in kangaroo rats (*Dipodomys* spp.). Merriam's kangaroo rats (*D. merriami*) require more spatial ability with respect to seed caches than bannertail kangaroo rats (*D. specatbilis*). The former species has larger hippocampi (the site of spatial maps) than the latter. Males of both species have larger hippocampi than females, most likely related to differences in male-specific mating strategies. In a similar fashion, Fay and Popper (1994) edited a volume that summarizes relationships of behavior, brain structure, and function in mammalian hearing.

An elegant example of the integrated approach comes from studies of foraging behavior in honeybees (*Apis mellifera*) (summarized by Menzel and Muller, 1996). Beginning with factors influencing foraging patterns of bees, investigators have been able to work downward. Cues associated with the feeding site are learned by association. Classical conditioning studies, using proboscis extension as a dependent measure, provide insights concerning neural and neuropharmacological aspects of the association learning process. The neural pathways involved have been identified histologically. Finally, at the cellular level, the cAMP pathway and nitric oxide are implicated in processes that result in formation of memory traces. Work on the genetic and hormonal bases for the division of labor in honey bees is another example of integration across both proximate and ultimate mechanisms (Robinson and Page, 1988; Robinson *et al.*, 1989; Robinson, 1992).

Another example comes from recent work by Silverman, Silver, and colleagues (Silverman *et al.*, 1994; Silver *et al.*, 1996a, b) on ring doves, *Streptopelia risoria*. They report finding that after a brief period of courtship, mast cells from the immune system appear in the habenula of the brain; such was not the case for control birds. This result is surprising, since it was previously thought that the blood-brain barrier blocks movement of blood-borne cells into the brain. Additional work demonstrated that gonadal steroids, either occurring endogenously or administered exogenously, increase the number of mast cells in the brain and their state of activation. These findings suggest exciting new avenues of investigation to provide the bases for integrating proximate and ultimate processes involving the nervous, endocrine, and immune systems.

Finally, there has been progress regarding how memory traces are created and stored (Abrams *et al.*, 1991; Thompson and Krupa, 1994). These studies involve both the localization of memory within the brain and an understanding of the physical and biological mechanisms underlying longterm memory. Apparently, to date, more progress has been made with regard to these phenomena in invertebrates than in vertebrates. We won't review this literature here, but it is worth noting that fundamental changes, perhaps akin to the revolution that occurred with the elucidation of the structure of DNA, will occur in animal behavior and related fields when the memory trace problem has been solved.

The explosion of knowledge in neuroscience will provide fruitful reading for those who work primarily with ultimate causation and behavioral ecology. We have not, for instance, touched upon developmental processes, including cell death phenomena, or various forms of immunocytochemistry. Nor have we considered the underlying genetic mechanisms for these neural processes that can now be explored through procedures such as *in situ* hybridization. The sensory and perceptual worlds of the animals with which we work are no longer a mystery at the level of the nervous system. It should soon be possible to understand the evolution of, for example, variations in foraging strategies or mating systems, in terms of the underlying neural process and their endocrinological correlates. The final step

will then be to examine questions concerning the selection pressures that have shaped these neural processes? Only then will a true integration of proximate and ultimate causation be achieved.

NEW TECHNIQUES AND APPLICATIONS

As the foregoing material on the nervous system illustrates, one key to bringing different approaches to the study of animal behavior together is the variety of new techniques developed in recent decades. Most of these evolved in other fields, but innovative scientists have rapidly seen ways in which they can be applied to the study of behavior. We suspect the evolution of these new techniques has resulted in a greater ability to conceptualize new ideas about behavior, and so set in motion tests of these ideas. Further, ingenious investigators have been able to develop new uses for slightly older techniques, applying them to behavioral problems. Some additional examples should aid in making our point.

Radioimmunoassay (RIA) was developed several decades ago. Enzyme-linked forms of immunoassays (ELISA) were developed more recently (see Nelson, 1995). Initially, these techniques involved the use of laboratory animals, for example rodents (Berndtson and Desjardins, 1974; Broida et al., 1981) and birds (Adkins-Regan et al., 1990). This progressed to the capture of subject animals in the wild or confined in semi-natural settings to obtain blood, or possibly saliva or urine on which to perform assays (Wingfield and Moore, 1987; Wingfield, 1988). The use of hormone assays in conjunction with behavioral data has produced a wide range of significant findings (reviewed in Nelson, 1995).

Many of the models used to describe activities and choices made by animals, for example in foraging or reproduction, depend upon assessments of costs. These costs have most often been depicted in terms of either time or energy. Laboratory measurements of metabolism have been conducted for some decades, initially using various forms of gas analysis, but more recently involving doubly-labeled water. Now these procedures are being applied to free-ranging animals. Vehrencamp et al. (1989)

used doubly-labeled water to assess the energetic cost of male display in leks of sage grouse (Centrocercus urophasianus). Metabolic rates were four times higher than basal rates for vigorously displaying males and twice as high as for non-displaying males. Using the same technique, daily energy budgets constructed for golden-mantled ground squirrels (Spermophilus saturatus) during lactation reveal part of the cost of reproduction (Kenagy et al., 1989, 1990). There was a slight, but significant increase in metabolic rate with litter size. Using gas analysis techniques to measure metabolic rates, Metcalfe et al. (1995) found a significant positive relationship between metabolic rate and social status in Atlantic salmon (Salmo salar) and Bryant and Newton (1994) reported a similar positive relationship between higher social status and higher basal metabolic rate for dippers, Cinclus cinclus. More studies like these are needed in a wider variety of animals to obtain comparative data across species, seasons, locations, and with regard to any significant behavioral events. With such data it should be possible to perform more definitive tests of the various economic models that have been used in behavioral ecology (see Krebs and Davies, 1993).

During the past 10 years, a whole catalogue of new DNA techniques has been developed. Behaviorists wanting to answer questions, for example, about parentage and population genetics, previously had been limited to procedures such as allozyme analysis, with its limitations (Avise, 1994). These new techniques include various types of restriction analyses such as single copy nuclear DNA sequences (RFLPs), microsatellite analyses, and DNA fingerprinting, as well as DNA sequencing. They are well summarized in recent books by Avise (1994) and Ferraris and Palumbi (1996).

These DNA-based technologies hold great promise for studies of animal behavior and are currently being employed in many research programs. They are being used in studies of underlying genetic mechanisms, for relating behavior, reproductive success, and natural selection, and for studies of behavior as a factor in population genetics. A few examples among the many

now available include the works on birds of Burke *et al.* (1989) on parentage in dunnocks (*Prunella modularis*), Westneat (1995) on the relationship between paternity and male parental behavior in red-winged blackbirds (*Agelaius phoeniceus*), and Hahn and Fleischer (1995) on relatedness between associated female and juvenile brown-headed cowbirds (*Molothrus ater*). Herpetological examples include those of Höggren and Tegelström (1995) on multiple paternity in adders (*Vipera berus*) in a semi-natural enclosure and Scribner *et al.* (1993) on reproductive success and spatial structure of painted turtle (*Chrysemys picta*) populations. Mammalian examples include studies of variations in male-infant interactions in Barbary macaques (*Macaca sylvanus*) in an enclosed population (Paul *et al.*, 1996), migration and site fidelity in humpback whales (*Megaptera novaeangliae*) (Baker *et al.*, 1993), paternity in muskrats (*Ondatra zibethicus*) (Marinelli *et al.*, 1992), and parentage and kinship associations in African lions (*Panthera leo*) (Gilbert *et al.*, 1991).

THEORIES AND MECHANISMS

A variety of hypotheses and theories in animal behavior can perhaps be further tested by thinking in terms of both proximate and ultimate causation. Let us illustrate this with several examples. Some of these may be more testable in the immediate future while others must await further developments in terms of techniques and procedures.

Kin recognition is a key component of several current theories and hypotheses concerning animal behavior. Kin selection as an hypothesis for the evolution of altruistic behavior (Hamilton, 1963, 1964) necessitates that animals be able to discriminate kin from non-kin. That many animals can make such discriminations is no longer in question (Holmes, 1988). But, the underlying proximate bases for such discrimination are not well known. Is this process some form of phenotype matching (Buckle and Greenberg, 1981)? Does it involve cues that are learned through close social attachments? Or, are there recognition genes, possibly within the major histocompatibility

complex, as has been suggested for mice (Yamazaki *et al.*, 1976)? Blaustein and Waldman (1992) have suggested that both chemical and visual cues may be involved in kin recognition in anuran amphibians. It may be that all of these various mechanisms are operating in different species and that some species may rely on more than one such mechanism.

Different sensory mechanisms are likely involved in these recognition processes in different species. Now, if we turn our attention to what we know about physiological processes related to those sensory mechanisms within the organism, it may be possible to carry out studies that aid in discerning which mechanisms are at work in different species. It should now be possible to construct experiments in which neural and hormonal events are measured in conjunction with tests of kin recognition. Alternatively, the use of techniques such as knockout genes may supply information on the underlying genetic bases for some forms of kin recognition. Qualitative trait locus analysis would be another likely candidate technique for these sorts of studies, particularly since it is likely that such traits are generally polygenic (Takahashi *et al.*, 1994).

Facultative changes in sex ratio apparently occur in a variety of animals (Clutton-Brock *et al.*, 1984; Clutton-Brock and Iason, 1986; James, 1987; but see Williams, 1979 and Gowaty, 1991). Sex ratio at birth varies with a large number of factors, including season, age, condition of the mother, stress, etc. The presumption is that these sex ratio shifts are evolutionarily adaptive. At one level, we can explain variation in terms of factors such as those just noted. That is, what evolutionary selection pressures predispose animals to possess the capacity for facultative variation in sex ratio of their progeny? However, another level of analysis must also be considered. What internal, physiological events transpire that result in differential fertilization of eggs of one sex, differential laying or deposition of eggs of one sex, or differential implantation of embryos of one sex? The underlying mechanisms almost certainly involve neural and hormonal events.

MODULATION OF SEX RATIO VARIATION

ENVIRONMENTAL EVENTS -->

(EXTERNAL: CLIMATE/SEASONS, STRESSORS, NUTRITION)
(INTERNAL: AGE, PREVIOUS REPRODUCTION)

NEURAL PROCESSING -->

HYPOTHALAMIC-PITUITARY AXIS -->
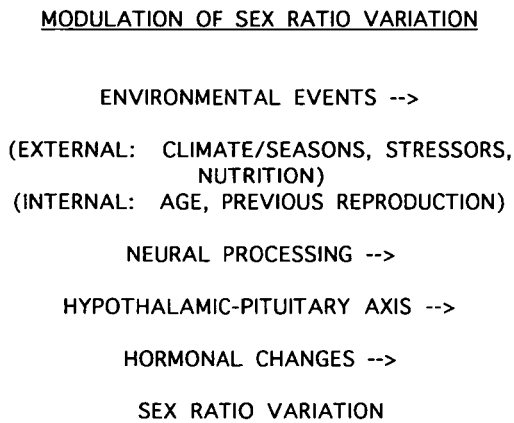
HORMONAL CHANGES -->

SEX RATIO VARIATION

FIG. 1. One model for sex ratio variation involves changes in hormone levels, resulting from sensory input, processed by the nervous system and mediated via the hypothalamic-pituitary axis.

Some progress is being made toward more proximate explanations of sex ratio variation. Clearly, even for any one species, a complex of factors is involved. James (1996) has recently provided extensive support for the hypothesis that, for humans (and by inference other mammals), hormone levels in the female and male parents at the time of conception are partially responsible for variation in birth sex ratio. If true, this finding could lead to similar studies on other vertebrates, and even invertebrates. Additional steps would be needed in such a scenario to ascertain the pathways by which hormonal variations are brought about through sensory input processes and neural pathways, presumably mediated via the hypothalamic-pituitary pathway (Fig. 1). Since even the hypothesis of hormonal modulation of sex ratio can account for only a portion of the observed variation, additional factors and physiological mechanisms must be considered. The tools and the protocols for such ventures are, it would seem, in place. We are now at a point where it is possible to dissect out the events occurring at all of the arrows in Figure 1.

Another set of examples of cross-fertilization involving proximate and ultimate causation comes from animal feeding behavior. Animals use a variety of foraging strategies to meet their daily energy and nutritional requirements. Several concepts that

have been developed to help explain the foraging patterns used by different animals may now lend themselves to further exploration at the level of physiological mechanisms. Two examples are the notion of search images and risk-sensitive foraging. The search image concept developed primarily with regard to bird feeding behavior (Pietrewicz and Kamil, 1981), but may be applicable to similar phenomena in other groups of animals as well and to situations that involve non-food stimuli. Search images involve some form of mental image that the animal forms of a particular prey item. It then appears to differentially search for that item, ignoring other palatable prey in the process. New techniques involving brain neurochemistry, tracing of neural pathways, recording from cells in various brain regions, and immunocytochemistry could be usefully applied to this phenomenon. It should be possible, with the correct procedures, to detect changes in the animals' brains as search images are formed.

Risk-sensitive foraging involves an animal being able to discriminate between patches where the total food density is about equal, but where one patch has the food distributed in clumps so the variation in food reward is large and in the other it is uniformly arrayed so the variation in food reward is minimal (a recent SICB symposium was devoted to this subject; Smallwood and Cartar, 1996). An organism that can discriminate between these two types of food distribution is said to be risk-sensitive (Stephens and Krebs, 1986). Animals may be either risk-averse, generally when they are receiving sufficient food to maintain body mass, or they can become risk-prone when the food supply is not adequate and they lose body mass (Caraco et al., 1980). One set of questions that we could ask in such a system concerns the underlying physiological changes that result in this shift in foraging strategy. How do the metabolic, hormonal, and neural pathways within the organism result in a change from being risk-prone to being risk-averse, or vice versa? We believe that the techniques and protocols are already present to commence a series of investigations to test such questions.

These are just a few examples, among many that could be selected in terms of current theories and hypotheses in animal behavior, which are subject to the sort of cross-fertilization thinking that we believe is needed to provide for an integration and synthesis of ultimate and proximate causation. By examining each of these phenomena from a physiological perspective it is now possible to both begin to explore the underlying neural and hormonal processes and to enhance, by that very process, the nature of our testing at the level of the ecology and evolution of these behavior patterns. Conversely, we think it is possible to take events that we know occur in the nervous system and generate ideas that can be tested in a natural or semi-natural setting to obtain a better understanding of the evolution and functional significance of those behaviors. This has already been accomplished for example with the investigations of seasonal changes in birdsong (Nottebohm, 1981; Nottebohm *et al.*, 1986).

SIMULATION MODELING

Another useful tool for working out the integration of proximate and ultimate causation involves the use of models, coupled with simulations of events. These sorts of techniques are used to generate predictions about behavioral systems that can then be tested. Duvall and Beaupre (this symposium) have used simulation models to make predictions about the activity budgets of rattlesnakes (*Crotalus viridis* and *C. atrox*). Their models incorporate key features such as locating food and mates, avoiding predators, and locating refugia for the night. The models make explicit predictions with respect to locating food, primarily in the form of clusters of deermice (*Peromyscus* spp.), and with respect to locating mates and achieving successful copulations (Duvall *et al.*, 1992, 1993, 1997). These predictions are then tested by using radiotelemetry to track and observe individuals and groups of rattlesnakes. The value of the models in this instance lies in the predictions that can then be tested empirically using field methods. Predicted rates of snakes encountering clusters of deermice distributed in different arrays in nature can be compared directly

with the snakes' behavior. Both time and energy serve as currencies and the efficiency of the various processes can be explored with respect to natural selection. For example, patterns of foraging behavior can be tested with respect to predicted and actual energy expenditure.

Models and simulations are also used in a broader sense. By that we mean that generalizations can be attempted that incorporate data from a variety of species (Arnold and Duvall, 1994; Harvey, 1994). The general features and constraints of such models have been examined by Harvey (1994) and Krebs and Davies (1993). In behavioral ecology, models of these types have been used extensively to explore reproductive success (fitness), foraging strategies, and social systems. For example, we have learned a great deal about the factors that influence the manner in which animals seek, handle, and consume various food items (Stephens and Krebs, 1986). Factors affecting reproductive success have been studied in a wide variety of both vertebrates and invertebrates (Clutton-Brock, 1988).

With the increased knowledge we are now gaining concerning internal processes, such as those of the nervous and endocrine systems we noted earlier, it should be possible to explore the underlying physiological processes that have been selected. Whether it is feeding, mating, or some other activity that is under investigation, we should now be able to use the same sorts of models that have been employed so effectively by the behavioral ecologists to derive predictions at another level. These predictions might include, for example, changes in brain chemistry in relation to feeding behavior, or variations in brain structure depending upon the social system of the species. In this way, a true integration across several levels, ranging from the cell to populations of organisms can be achieved.

LABORATORY AND FIELD

Both laboratory and field conditions have advantages and disadvantages; we need not elaborate these here. As noted in previous sections, one example of the rapprochement between proximate and ultimate causation

is the translation of what have been primarily laboratory techniques to the field. Conversely, some types of questions that arise under field conditions have been effectively tested in more controlled laboratory settings. There is also, in between, the use of semi-natural settings. We believe that thinking in terms of the cross-over between laboratory and field settings is a strong stimulus to the processes that result in development of both new ways to test old ideas and the emergence of entirely new ideas.

One example of a phenomenon that was elucidated in a laboratory setting is that the organizational effects of hormones during development in mammals can be mediated by intrauterine position (Clemens *et al.*, 1978; vom Saal, 1979, 1989). In particular, females exposed to androgens from males are masculinzed to varying degrees with respect to morphology, physiology, and behavior. This is most pronounced for females that are positioned in utero between two males. What are the consequences of this phenomenon under field conditions? We have recently explored these effects in house mice living in outdoor enclosures and in domestic swine.

Behavioral and reproductive consequences of variation in intrauterine position, using anogenital distance in young mice as a bioassay, were tested using wild house mice, *Mus domesticus,* in eight 0.1-ha field enclosures (Drickamer, 1996). Vandenbergh and Huggett (1995) have shown that the anogenital distance is a useful index of intrauterine position in house mice. We found that male mice with larger anogenital distances were more aggressive as adults, had larger mean home range size and were more likely to disperse than males with smaller anogenital distances. Female mice with smaller anogenital distances were more likely to attain reproductive status, had a higher rate of pregnancy, and had more pregnancies on average than females with larger anogenital distances. Survival was not related to anogenital distance for either sex. In utero exposure to higher levels of testosterone apparently enhances behavior related to reproductive success for

males and decreases reproductive success for females.

An ultimate question related to the intra-uterine position effect concerns whether the positioning of fetuses of the two sexes in the horns of the uterus is random. Recent evidence suggests that in gerbils (*Meriones unguiculatus*) and rats (*Rattus norvegicus*) there are nonrandom patterns of sex distribution between the two uterine horns (Clark and Galef, 1990; Bacon and McClintock, 1994). Further data on additional species are needed before any generalizations can be made concerning potential selection pressures that might affect this phenomenon.

For swine, Drickamer *et al.* (1997) first determined that the anogenital distance of newborn gilts is related to the proportion of males in the litter. Gilts from litters with more males have larger anogenital distances and gilts from litters with low proportions of males have smaller anogenital distances. Drickamer *et al.* (1997) examined the possible effect of the birth litter sex ratio of sows and gilts on their reproductive performance using a 13-year database. Gilts that failed to become inseminated on the first mating most frequently came from litters with significantly higher proportions of males than gilts that successfully conceived on the first mating attempt. Overall, sows were significantly more likely to exhibit lower rates of successful mating during their first four mating attempts if they had been born in a male-biased litter.

Hormone measurements of free-ranging animals have become an important part of many behavioral studies, particularly for birds. Examples include prolactin and helping behavior in Florida scrub jays (*Aphelocoma coerulescens*) (Schoech *et al.,* 1996), testosterone and spatial activity in dark-eyed juncos (*Junco hyemalis*) (Chandler *et al.,* 1994), and the interrelationships of testosterone, secondary sexual characters, and parasites in barn swallows (*Hirundo rustica*) (Saino and Møller, 1994). Within the past 10 years, investigators have found it possible to measure hormones in feces and urine from free-ranging animals (Monfort *et al.,* 1990, 1993). Thus, it has become possible to extend the work men-

tioned earlier on relationships between hormone levels and behavior to natural and semi-natural settings. As we learn more about the neuroendocrinological mechanisms of behavior, we suspect that it will become increasingly important to obtain field measurements of hormone levels. In effect, these sorts of determinations will be an intermediate step between the ecology and social behavior of the animals and their internal neuroendocrinology.

In addition, some investigators have been able to employ field manipulations of hormone levels to ascertain the behavioral significance of seasonal shifts in behavior. One early study of this sort was carried out by Vandenbergh and colleagues on free-ranging rhesus macaques (*Macaca mulatta*) at La Parguera, Puerto Rico (Vandenbergh and Drickamer, 1974; Vandenbergh and Post, 1976). In two separate studies, conducted in different years, first adult females and later adult males were captured and given implants of estrogen and testosterone respectively. The results indicated that males may synchronize their endocrine system and behavior with females, but not vice versa. Another hormone-related manipulation involves the use of an anti-androgen to attempt to inhibit effects of testosterone on behavior. Tokarz (1995) used an anti-androgen, cyproterone acetate, to determine that treated male brown anoles (*Anolis sagrei*) were less successful than control males in acquiring territories.

It is also possible to take questions that arise in the field and conduct pertinent tests in a laboratory setting. An excellent example of this involves work on seed caching by jays of various species in western North America (Balda, 1980; Balda and Kamil, 1988, 1992; Kamil *et al.*, 1993). Memory of seed cache locations occurs for three species, but varies according to their natural history. Although all species performed at better than chance levels, Clark's nutcrackers (*Nucifraga columbiana*) and pinyon jays (*Gymnorhinus cyanocephalus*) were better at remembering cache locations than were scrub jays (*Aphelocoma coerulescens*). This agrees well with the fact that in nature, scrub jays live at lower elevations than the other two species, endure less

harsh winter conditions, and thus are not as dependent upon cached seeds for survival. Where it is not possible to design a study to test particular questions in the field, a great deal can be learned by devising appropriate apparatus and testing procedures for use in the laboratory.

SEMI-NATURAL SETTINGS

Over the past several decades, a variety of types of semi-natural settings have been used to test questions in animal behavior. These include: structural enclosures of a variety of types and sizes designed to fit the subject animals; true islands, often with introduced animals, and sometimes with provisioning; and innovative test situations such as the use of highway cloverleaf islands (Massey and Vandenbergh, 1980, 1981; Zielinski and Vandenbergh, 1991; Zielinski *et al.*, 1992). Semi-natural settings offer some advantages in terms of control, with respect to both determining which animals are used (and having all of them individually identified) and being able to capture and measure individuals or manipulate populations. Though not often done, it is advisable to ascertain whether the general social system and pattern of spatial distribution is the same for the animals in a semi-natural setting as under free-ranging field conditions. For example, rates of grooming and aggression were not the same for rhesus macaques (*Macaca mulatta*) living in 0.1 ha outdoor enclosures as for rhesus macaques free-ranging on the same island where the enclosures were located (Drickamer, 1973).

Since 1988, we have been studying wild house mice (*Mus domesticus*) in eight 0.1 ha outdoor enclosures located near Carbondale, IL. Populations are introduced each spring and removed in late fall. On one occasion we followed some populations through the winter. Do the enclosures provide a reasonably accurate substitute for feral mice in terms of their socio-spatial relationships and density? We examined whether density and home range size were the same for enclosure mice compared to data for free-ranging wild house mice.

Are mouse densities in the enclosures similar to densities in feral populations? We first computed a minimum number known

TABLE 1. *Ranges of peak population sizes and variance estimates across the populations for each year of the study.*

	Year				
	1989	1990	1991	1992	1993
Range	16–57	15–108	14–66	13–70	19–77
Variance	258.17	1388.12	402.79	453.40	394.79
Sample Size	6	8	8	8	8

alive estimate of population size for each 3-week interval during the 30-week field season. These data provided the basis for comparisons of density within and between seasons and with other values for population density in this species.

Peak densities in the 38 enclosure populations, measured starting at least one month after they were established, averaged (mean $\pm$ 1 SE) 36.8 $\pm$ 4.1 mice/0.1 ha (range 11–108); these values are equivalent to 368 $\pm$ 41 mice/ha. Ranges of peak density between enclosures within each year, examined across five years, were similar (Table 1), though there was considerable variation within each field season as evidenced by the large variance estimates (Table 1). The density values we obtained are in the middle of the range reported for feral house mice of 25–650 mice/ha (Anderson, 1961; DeLong, 1967; Berry, 1968; Myers, 1974; all involving free-living house mice in field settings). Our values are also within the density range (200–300 mice/ha) reported in other enclosure studies (Stueck and Barrett, 1978; Lorenz and Barrett, 1990), though they are much less than the 6,000 mice/ha obtained by Pennycuik *et al.* (1978). It could be that longer durations would result in higher densities. However, at our study site, the time period beyond 30 weeks would encompass a winter season. Data from an overwinter study using four of our populations suggests that spring population sizes are only 15–25% of those present in the fall, even with some breeding during the winter months (Drickamer, unpublished data).

Does the presence of mice that are trap-shy lead to underestimates of population density? Data from removal periods at the end of each field season revealed that only 36 unmarked mice (1% of 3,298 mice caught in the enclosures over five years)

were living in the enclosures; all were young adults. Each adult male was captured, on average ($\pm$1 SE), every 9.6 $\pm$ 0.4 (n = 265) days, and each adult female was captured, on average, every 11.6 $\pm$ 0.8 days (n = 312). We feel that our minimum number known alive estimates of population density are accurate.

Are the home range sizes for male and female house mice similar in the enclosures to what happens under free-living conditions? We recorded sex, type, and capture points for individual home-range analyses. Mice with fewer than 10 capture points were not used in home-range analyses. Juvenile captures (defined as captures of mice less than 15-g body weight and nonscrotal testes for males, and less than 13-g body weight and without perforate vaginae for females) were not included in the home-range database. Preliminary analyses revealed that home ranges were significantly larger with pre-dispersal capture points included. The number of juvenile capture points ranged from 1–5 and thus would not have provided sufficient data for obtaining a separate valid estimate of juvenile home range. With the sexes analyzed separately, preliminary analyses revealed no differences in home-range sizes of original and enclosure-born mice; mice of both types were combined for all subsequent analyses.

Home ranges were calculated using two different methods: harmonic mean home range and minimum convex polygon. We used HOME RANGE, a computer program that includes tests of assumptions and underlying distributions that must be considered in calculations of home-range estimates (Ackerman *et al.,* 1990). We examined possible outliers, autocorrelation, and underlying distributions before home ranges were analyzed further.

We examined scatter plots of capture

points and removed outliers, defined as points ≥ 15 m from the next closest point in the scatter. We removed outliers since captures were collected over time, and temporal shifts in range could give an overestimate of the area occupied by a mouse. If a mouse had <10 captures due to exclusion of outliers, we dropped it from the analysis.

Autocorrelation is a potential source of bias in radio-tracking studies when "fixes" are taken too close together in time so the points are not independent, or in spatial studies where a close spatial pattern may indicate non-independence (Swihart and Slade, 1987). We conducted live trapping two non-consecutive nights a week, and city checks were conducted weekly, giving the animals ample time to traverse their home ranges between captures. Therefore, autocorrelation was not likely a confounding factor. However, we analyzed our data to test for autocorrelation using t^2/r^2 and gamma (Schoener, 1981; Swihart and Slade, 1985) using a subsample of our dataset. Multiple captures at mouse cities were not a problem in terms of their inclusion when calculating home-range areas, since only 40% of all city checks produced any mice, and for over 90% of those checks it was a single mouse.

A key assumption is that our enclosures were large enough to avoid biasing home-range estimates. Two indices of wall use were generated to determine whether or not a significant portion of each subject's home-range perimeter included one or more walls. The first index was the ratio of total wall captures to total trap captures, and the second was the distance along walls that was incorporated in the home-range perimeter as measured by the minimum convex polygon method.

Mice were not caught frequently in wall traps even though the ratio of wall traps to total traps available was 0.48. Overall, the mean ratio ($\pm$SE) of wall captures to total captures was 0.19 $\pm$ 0.01. Male mice had a significantly higher mean proportion of wall captures (0.27 $\pm$ 0.02) than females (0.16 $\pm$ 0.02) (t = 4.65, df = 216, P < 0.0001). Mice incorporated very little of the available wall length in the perimeters of their minimum convex polygon home rang-

es. The mean distance along a wall ($\pm$SE) was 8.11 $\pm$ 0.96 m. Males had significantly more distance along walls incorporated into their home-range perimeters (14.61 $\pm$ 2.21 m) than females (4.55 $\pm$ 0.69 m) (t = 5.35, df = 216, P < 0.0001).

A minimum number of captures is needed before calculated home-range areas stabilize. Linear regression was used to determine the number of captures needed to achieve an asymptotic relationship between home-range size and number of captures, using values of seven or more captures as a starting point. Capture points were added in chronological order until the regression slope was not significantly different from zero, at which point home-range size had stopped increasing. Home-range size was regressed on number of captures for each sex for each of the two methods. Home-range area stopped increasing for males after 10 captures for the minimum convex polygon method and at 11 captures for the harmonic mean estimate. Home-range area stopped increasing for females after 13 captures for both methods.

We tested for a uniform distribution of capture points before calculating the minimum convex polygon estimate of home range. There are no distribution assumptions for the harmonic mean method of estimating home-range size. We next calculated home ranges for all mice using minimum convex polygon and harmonic mean methods. Variation in home-range area between sexes and methods was examined using paired and unpaired t-tests (Sokal and Rohlf, 1981). Both tests of autocorrelation produced results that indicated that this was not a significant problem with our data (Table 2).

The 38 populations, representing 3,298 different mice, yielded a sample size of 442 mice for home-range analysis, excluding subjects with nine or fewer captures, and excluding juvenile captures (Table 3). A single capture point was removed for 33 mice (7.7%) after screening for outliers; three mice were dropped from the analysis after removal of the outlier reduced their capture number below 10. Eleven percent of mice did not meet the assumptions for a

Table 2.   *Values ($\pm$ 1 S.E.) for t^2/r^2 and gamma tests of autocorrelation for capture points used for calculation of home-range areas for house mice living in enclosures.* *

Category	N	t^2/r^2	gamma
Overall	215	1.656 (0.032)	0.076 (0.016)
Original females	112	1.607 (0.044)	0.084 (0.023)
Original males	44	1.708 (0.075)	0.083 (0.033)
Enclosure-born females	26	1.732 (0.090)	0.026 (0.047)
Enclosure-born males	33	1.690 (0.081)	0.081 (0.038)

* Values of < 1.600 for the t^2/r^2 test and < 0.030 for the gamma test would indicate a significant problem with autocorrelation.

uniform distribution for calculating the minimum convex polygon estimate.

We calculated parametric unpaired t-tests to compare home-range size estimates obtained for males versus females with each method. For both the harmonic mean home range estimates (t = 5.631; df = 440; P < 0.0001) and the minimum convex polygon estimates (t = 6.691; df = 392; P < 0.0001) there were significant sex differences. Paired t-tests used to test for differences between the two methods within each sex also revealed significant effects for both females (t = 13.539; df = 244; P < 0.0001) and males (t = 11.676; df = 150; P < 0.0001). Mean home range sizes of males (minimum convex polygon = 272.7 $\pm$ 13.7 m; harmonic mean = 374.4 $\pm$ 17.5 m) were significantly larger than females' home ranges for each method (minimum convex polygon = 171.0 $\pm$ 8.3 m; harmonic mean = 257.9 $\pm$ 11.7 m). Harmonic mean estimates of home-range size were significantly larger than those using the minimum convex polygon method.

Reported home-range sizes for house mice vary greatly. For house mice in an open field, Quadagno (1968) found males' home ranges to vary between 134 m² with voles (*Microtus ochrogaster*) present and 365 m² with voles absent, using the inclusive boundary strip method. Females' home

ranges were between 118 m² with voles present and 362 m² with voles absent. Maly et al. (1985), using a grid/boundary strip index, reported home ranges of about 235 m² while Howell (1954), using a boundary strip method, reported a home range of 1,200 m² for house mice (no sex differences were reported in either study). Our values for home-range size are in the lower middle portion of this range.

Home ranges of females were smaller than males' using both estimators, possibly due to constraints imposed by energy demands of pregnancy and lactation (Bronson and Perrigo, 1987). Food supply to fuel these demands was not limiting since we provided food in excess of consumption, and females did not have to establish large home ranges to acquire the resources they needed. In addition, males are expected to have larger home ranges in a polygynous mating system, to ensure that a male's range will likely include those of several females (Gaulin and Fitzgerald, 1989). Overall, we are thus able to conclude that the 0.1 ha enclosures appear to provide a suitable approximation of the natural conditions for house mice with respect to their socio-spatial structure. The pattern of social organization we have measured in the enclosures is in fact quite similar to that reported for free-living feral house mice studied in agricultural areas with the use of radio collars (Krebs et al., 1995).

To date, we have studied various phenomena in these enclosures related to olfactory communication (Drickamer, 1995), as well as exploring the effects of urinary chemosignals on reproduction (Drickamer and Mikesic, 1990). This latter involves translating a phenomenon largely explored

Table 3.   *Sample sizes of mice that met the underlying distribution assumptions for each of the two home-range estimators.*

Sex	Total N	Harmonic mean	Minimum convex polygon
Male	167	167	150
Female	275	275	244
Total	442	442	394

in a laboratory setting to a semi-natural field environment. Our ongoing and future studies involve microsatellite-based DNA parental assignment to assess factors affecting reproductive success, measurements of hormone levels from fecal material, and explorations of the consequences of mate choice for offspring viability and reproductive success.

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