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# ULTRASONIC VOCALIZATIONS BY ADULT RATS (*RATTUS NORVEGICUS*)

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The animals involved in this study were procured, maintained, and used in accordance with the Animal Welfare Act and the "Guide for the Care and Use of Laboratory Animals" prepared by the Institute of Laboratory Animal Resources - National Research Council.

The Office of Public Affairs has reviewed this report, and it is releasable to the National Technical Information Service, where it will be available to the general public, including foreign nationals.

This report has been reviewed and is approved for publication.

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The literature on adult rat (*Rattus norvegicus*) ultrasonic vocalizations was reviewed. Most of these studies examined ultrasounds produced during sexual behavior and during male-male aggressive interactions. During sexual behavior, both the male and female emit a 22-30 kHz, 500-3,000 ms call (the "22-kHz" call). This call is particularly characteristic of male vocalizations immediately following ejaculation. Both sexes also produce higher frequency (40-70 kHz), shorter duration calls. The male's postejaculatory 22-kHz call has not been demonstrated to influence female behavior; however, the presence of male vocalizations prior to ejaculation is related to an increase in female proceptive behavior. During aggressive encounters, the submissive male produces a 22-kHz call similar to that seen during sexual behavior, as well as other calls of higher frequency. The communicative functions of these calls have not yet been established. The 22-kHz call is also produced by rats following shock and in response to startle-eliciting acoustic stimuli. Because the call occurs in these contexts, it has been suggested that it indicates anxiety or distress. The published literature on adult rat ultrasound has been limited to studies of pairs of unfamiliar animals in artificial testing situations. Few quantitative data on the acoustic characteristics of these calls have been published.

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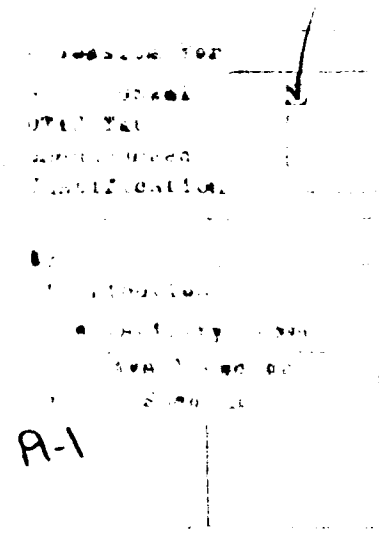

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# ULTRASONIC VOCALIZATIONS BY ADULT RATS (RATTUS NORVEGICUS)

## OVERVIEW

### Introduction

Ultrasound production by rats (Rattus norvegicus) was reported as early as 1954 by Anderson, but it was not until the work of Noirot (1968, 1972) and Sewell (1967, 1968, 1969) that systematic study of this phenomenon began. Noirot's work focused on ultrasounds produced by infant rodents. Sewell's early studies of adult rat ultrasound suggested a rich variety of vocalizations produced in many behavioral contexts. Later work focused on sounds occurring in a few restricted contexts; the most common situations examined have been male-male aggressive interactions and sexual encounters between a single male-female pair. Other studies have examined drug effects on shock-elicited ultrasound (e.g., Sales et al., 1986), ultrasound produced by pregnant females (Lewis & Schriefer, 1982), and ultrasound in isolated individuals (Francis, 1977). The focus of our report is an annotated bibliography of research on rat ultrasounds occurring in these contexts.

The literature reviewed here is concerned with ultrasonic vocalizations by adult rats (Rattus norvegicus). Studies dealing with rat auditory capabilities, anatomical and physiological mechanisms of rat ultrasound production, and audible vocalizations are not discussed, nor is the extensive literature on infant rat vocalizations. Ultrasonic communication is widespread among rodents (see Sales, 1972a; 1972b). In particular, research has focused on ultrasonic vocalizations of hamsters, laboratory mice, and deer mice (Peromyscus maniculatus). Several reference lists dealing with these topics are included in this report. One list consists of studies of infant rat ultrasound, while the others include studies of rat hearing capabilities, research on rat ultrasound production mechanisms, studies examining rat vocalizations in the audible frequency range, and studies of ultrasonic vocalizations in species other than Rattus norvegicus.

### Agonistic Behavior

Sales (1972a) presented the first detailed description of rat ultrasonic vocalizations associated with agonistic (i.e.,aggressive and submissive) behavior. She reported 2 types of calls which occurred during agonistic interactions between males - "short" pulses (3-65 ms) of 45-70 kHz and "long" pulses (800-1600 ms) of 23-30 kHz. Short pulses often showed marked frequency fluctuations; they occurred in association with overt aggressive acts, displacement behavior, or 1 rat "crawling over" another. Long pulses were of constant frequencies, or showed slow drifts in frequency. They occurred most often when one

animal was crouched in a submissive posture and the other was active. They often appeared to be correlated with the respiration pattern of the submissive animal.

While a few studies (Sewell, 1970; Sales, 1972a; Sales & Pye, 1974; Brown, 1976; Ghiselli & LaRiviere, 1977) include sample sonagrams of these calls, detailed quantitative descriptions of the structure of these calls apparently have not been published. Ghiselli & LaRiviere reported that the long pulses have energy focused primarily at an approximate frequency of 23 kHz with little frequency modulation. Takeuchi et al., (1986) reported long pulses of 22-28 kHz. Ghiselli & LaRiviere noted components of the long pulses at 71 and 121 kHz, but they apparently are the only investigators who have reported these higher frequency components. Rather than examining the structure of the calls, most researchers have simply used a heterodyne receiver tuned to a narrow frequency band to detect the rate of occurrence of the vocalizations.

Sales' early work suggested that the long pulses appeared to be submissive and the short pulses aggressive. Subsequent studies focused on determining the communicative function of these calls. These studies all examined male-male aggression, generally using the "resident-intruder" paradigm, in which a stranger (an "intruder") is introduced into the home cage of a "resident." This procedure elicits aggression on the part of the resident. Early on, it was suggested that the long pulses produced by the submissive animal (the intruder) may function to stop attack by the resident aggressor. In fact, a study by Lore et al., (1976) did seem to indicate that experienced intruders produced more long pulse vocalizations and were attacked less than naive intruders; this seemed to indicate a relationship between these calls and the cessation of aggression by the resident. Later studies, however (e.g., Takahashi et al., 1983; Thomas et al., 1983), were unable to demonstrate a relationship between vocalizations (either long or short pulses) and aggression. The question of the communicative function of ultrasound in aggressive contexts thus remains unanswered.

Early studies also suggested that the resident aggressor might be emitting the short pulse vocalizations, while the submissive intruder emitted the long pulses. Later studies in which residents or intruders were devocalized indicated that intruders were producing almost all of the short pulse sounds as well as the long pulses.

The studies of rat ultrasound during aggressive behavior have thus far been rather limited in scope. As was noted, all the studies reported here examined male-male aggression. Sales (1972a) reported short and long pulses during agonistic encounters between males and lactating females; apparently this is the only published observation of ultrasounds during male-female aggressive encounters. In addition, the contexts in which aggression was observed during these tests were very restricted.

In the wild, rats form large stable colonies of both males and females (see Barnett, 1975); an animal would thus come into frequent contact with familiar individuals with which it had established relationships. Studies of ultrasonic vocalization, however, have typically examined brief encounters between strangers in small cages. Ultrasounds might have possibly evolved in the natural setting to have some communicative functions not obvious in these restricted testing situations (e.g., recruitment of colony mates; indication of intent to flee (which would not have been possible in small testing cages)). These possibilities have not been explored thus far.

## Sexual Behavior

Both males and females produce a variety of ultrasounds during sexual behavior. One of the most frequently studied sounds is the male-produced "22 kHz" call, which primarily occurs following ejaculation (see Barfield & Geyer, 1972, 1975). Early studies concentrated on the occurrence of this call during the male's postejaculatory refractory period, but the call is also emitted prior to ejaculation, and females also emit the call on occasion (Barfield & Geyer, 1972, 1975; Thomas & Barfield, 1985). This call consists of a single component of 22-23 kHz with little frequency modulation. Typical duration of the call is approximately 1,000-3,000 ms, and intensity has been measured up to 80 dB (Barfield & Geyer, 1972, 1975).

Other calls emitted during sexual behavior were first described in detail by Sales (1972); they typically range in frequency from 40-70 kHz, with some calls having components as high as 120 kHz. Some of these calls consist of a single component with slow drifts in frequency throughout their length. Other calls are "trains" of very brief pulses (2-40 ms) with a great deal of frequency modulation (30-50 kHz). Sales reported duration of these calls to range from 2 to 500 ms. The calls apparently occur during all phases of a copulatory episode. Barfield and his colleagues, who are responsible for the majority of studies of rat ultrasound during sexual behavior, (e.g., Barfield & Geyer, 1975; Geyer et al., 1978; Thomas et al., 1981; White & Barfield, 1990) often examined the occurrence of these vocalizations by using a heterodyne receiver tuned to 50 kHz; generally no attempt was made to differentiate among calls on the basis of physical characteristics such as duration or frequency modulation patterns. Recently, White et al., (1990) divided these calls into 4 categories based on spectral and temporal characteristics; however, this classification system is essentially arbitrary and the "call types" which result do not appear to be correlated with particular behavior patterns.

Despite the fact that considerable research on rat vocalizations during sexual behavior has been conducted since 1972, surprisingly little has been clearly established concerning the structure or the functional significance of these sounds. As is

the case for ultrasounds produced during aggression, published sonagrams and acoustical analyses of the calls are rare (Sales, 1972b; Thomas & Barfield, 1985; White et al., 1990), and no studies have included complete quantitative descriptions of the calls.

Barfield & Geyer (1972, 1975) originally hypothesized that the male 22 kHz postejaculatory call functioned to keep the female away from the male during the male's postejaculatory refractory period, but later research did not indicate a clear relationship between the call and female behavior during this period (Anisko et al, 1978; Thomas et al., 1982a). The most common and consistent finding indicating a behavioral response to the sounds is that female darting (a type of proceptive behavior) is more frequent when male vocalizations (of all frequencies) are present. When males are devocalized, darts decrease relative to control conditions (e.g., Thomas et al., 1981; Thomas et al., 1982a; Thomas et al., 1982b).

The difficulty in clearly demonstrating a communicative function for these vocalizations may be due to the investigative methods used. In the wild or under "free-ranging" captive conditions, rats live in large, mixed-sex colonies, and mating generally occurs among several males and females at once, with the animals "taking turns" at copulation (see McClintock et al., 1982). Females often play a major role in the pacing of sexual behavior, actively approaching and avoiding males in order to solicit mounts. Despite the complexity of rat sexual behavior in the natural setting, sex-related ultrasounds have generally been examined in very restrictive, artificial conditions in which a single male and female are introduced to one another in a small enclosure and allowed to copulate for a brief period (often as brief as 5 min, or for only the first few ejaculations of a copulatory episode). In early studies, female behavior was often ignored, and it was assumed that the male was producing most, if not all, of the vocalizations detected. (Later studies indicated that females vocalize throughout a copulatory episode.) Given that rats live and mate in groups, it seems possible that vocalizations emitted during sexual behavior may be designed to communicate with group members other than the sexual partner. Males may be coordinating their behavior with other males; females may also coordinate their behavior among themselves. These possibilities apparently have never been examined in these studies.

In addition, the majority of these studies utilized heterodyne receivers tuned to a small frequency range (often 45-55 kHz) to detect ultrasounds. These receivers produce an audible signal whenever a sound within the selected frequency range is detected. This technique hardly seems to be a reliable method for examining the rate of occurrence of a signal which varies from approximately 30-120 kHz, as do higher frequency rat ultrasounds. Sounds which did not fall into the selected frequency range would have been missed. These undetected calls may likely be important

units in the sequence of vocal and non-vocal behavior occurring during copulation.

## Other Contexts

Despite Sales' early work indicating that rats produce ultrasound in a variety of contexts, little research has examined situations other than sexual and aggressive. Sales' observation that adult males vocalize when exploring a new cage has never been followed up with systematic research. Francis (1977) reported that rats produce 22 kHz sounds while housed alone and auditorily isolated from conspecifics. Lewis & Schriefer (1982) reported on ultrasounds produced by pregnant rats prior to the birth of pups. The possibility that rats may use ultrasound to echolocate also has been examined (Rosenzweig et al., 1955). Blinded subjects apparently used auditory cues to navigate through a maze. However, ultrasound was produced only rarely by the animals during testing, thus indicating that the animals probably were using reflections of audible sounds such as sniffing and footsteps. This early report apparently has never been followed up.

One topic which has been the subject of several reports is shock-elicited ultrasound, and drug effects on these vocalizations (Sales et al., 1986; Tonoue et al., 1986; Tonoue et al., 1987; van der Poel et al., 1989). Apparently no detailed studies of shock-elicited ultrasound per se have been published; however, these vocalizations reportedly are very similar to the "22 kHz" call emitted during agonistic and sexual behavior. Sales et al., (1986) report unpublished data on 20-30 kHz ultrasonic calls in response to aversive stimuli. Tonoue et al., (1986) present the most detailed data; they report 22-28 kHz pulses of 300-1,200 ms in response to shock. The calls were emitted "for several minutes" following delivery of shock. Several substances, including beta-endorphin, diazepam, and chlorpromazine, attenuate these vocalizations.

Recent work by Kaltwasser (1990) examined the occurrence of vocalizations in response to startle-eliciting acoustic stimuli. She reports calls slightly lower in frequency (approximately 19-21 kHz) than those reported to occur following shock, during aggression, or during the postejaculatory period. Other characteristics of the sound were similar to the "22 kHz" call reported in these contexts. Kaltwasser reasons on this basis that the startle-eliciting stimulus evokes anxiety in the rat.

## Criticisms of the Literature

Several important limitations of this literature have been discussed earlier. In particular, many of these studies tested animals in small enclosures which restricted normal activities and in highly artificial, unnatural social situations. Given

this limitation, it may not be surprising that the communicative functions of these calls remain unclear. Wild rats live in colonies, and apparently none of the research on these sounds has examined the possibility that the communicative function of these calls may not be apparent in behavioral tests between pairs of strangers.

In addition, in some studies, the use of a tuned heterodyne receiver to detect occurrences of sounds may have resulted in a seriously distorted picture of the relationship between ultrasound and behavior. Early studies reported the occurrence of vocalizations ranging from 20 kHz to over 100 kHz during sexual and agonistic encounters. The use of an instrument responsive to only a small range of these frequencies could result in an underestimation of the amount of vocalization occurring, and would not enable observers to discern relationships between the detected calls and calls outside the detected frequency range, or between non-vocal behavior and calls outside the detected range. In other words, in many cases, researchers may have been missing important behavioral sequences and relationships by ignoring much of the animals' vocal behavior.

A related criticism is that early researchers often made assumptions about which member of a pair was vocalizing, without carefully testing these assumptions. It incorrectly was assumed that resident males emitted the high frequency ultrasounds detected during aggression tests, and that the male produced most of the vocalizations during sexual behavior. Failure to carefully examine the sequence of sounds produced by both members of a pair meant that important interactions between the animals being tested were often ignored.

Another criticism noted earlier is the lack of published quantitative descriptive data on the acoustic characteristics of the vocalizations themselves. A few researchers have published sonagrams, but there are few basic data on temporal and spectral characteristics of the calls. There is also a lack of data on development of these calls across the lifespan. Noirot (1968) examined vocal behavior from 1 to 28 days, but little is known concerning the age at which adult rats begin emitting the calls discussed here. In addition, little is known concerning strain differences in vocal behavior, or on vocal behavior in wild Rattus norvegicus. Sales (1979;1972a) examined both of these topics, but they have not been investigated further by researchers. The existence of strain differences (which were reported by Sales) may be of special importance to researchers in this field who wish to compare results between studies which utilized different strains, as is often the case.

It is important to acknowledge the difficulties involved in performing studies which would address these criticisms. In tests of paired animals, it is often not possible to determine which animal is emitting ultrasonic vocalizations. It would be even more difficult to determine which animal was vocalizing in

studies involving larger groups, such as established colonies. Testing animals in larger, more complex enclosures might provide more data concerning the function of ultrasonic vocalizations in the animals' natural habitat (which is considerably larger and more complex than the typical testing apparatus used). However, this environment would be a very difficult situation in which to record ultrasounds. These vocalizations typically do not travel far due to their extremely short wavelengths, which are readily reflected and absorbed by objects in the environment. The use of appropriate acoustical recording equipment, rather than heterodyne receivers, would allow investigators to study in detail the physical characteristics of these vocalizations. However, equipment designed for accurate recording and analysis of ultrasound is considerably more expensive than heterodyne receivers.

Important questions remain concerning the functions of rat ultrasonic vocalizations. Very few conclusions can be drawn based on the studies reported in the literature. The "22 kHz" vocalization has been of particular interest to researchers, since it appears to occur in a variety of contexts. In tests of sexual behavior, it is occasionally emitted by males and females prior to ejaculation, and is emitted by males almost continuously for several minutes following ejaculation. It is also emitted by the submissive animal in male-male aggression tests, and occurs in response to shock and to other stimuli which may be considered aversive (e.g., startle-eliciting acoustic stimuli). Because it is emitted in these latter contexts, it has sometimes been referred to as a "distress" call, and the effects of various drugs on the rate and duration of 22 kHz calls have been taken as evidence of the anxiety-reducing properties of these substances. However, it is important to note that apparently there are no published reports demonstrating a relationship between rate, duration, or other acoustic characteristics of the 22 kHz call and intensity of aversive stimuli. The exact nature of the relationship between this call and aversive stimulation thus remains to be delineated.

## ANNOTATED BIBLIOGRAPHY

### Reviews and General Papers

Anderson, J.W. The production of ultrasonic sounds by laboratory rats and other mammals. Science, 119, 808-809 (1954).

This study is an early report of ultrasound in laboratory rats and 7 other species. Rats were found to produce ultrasounds of 21.5 to 26.5 kHz, with durations of 1/30 s to 2.5 s. These sounds could sometimes be correlated with respiration. In addition, audible sounds produced by the rats sometimes had ultrasonic components. "Short snuffling sounds" made by the rats as they moved around in the cage had components up to 80 kHz.

Bell, R.W. Ultrasounds in small rodents: Arousal-produced and arousal-producing. Developmental Psychobiology, 7, 39-42 (1974).

The author maintains that attempts to classify rat ultrasounds in terms of specific meanings or functions is premature (at the time of this publication) due to lack of data demonstrating correlations between calls and recipient behavior. A more parsimonious explanation is that the calls reflect states of arousal, and that they elicit arousal in conspecifics. This paper is not a research report; no new data are presented.

Brown, A.M. Ultrasound and communication in rodents. Comparative Biochemistry and Pharmacology, 53A, 313-317 (1976).

This study is a very brief review of the literature on rodent ultrasound up to 1976. Major topics covered are ultrasound production by infants, ultrasound production by adults, the communicative function of ultrasounds, and the hearing capabilities of rodents. Treatment of each topic is very brief, but informative. The author stresses the importance of understanding and testing the hearing capabilities of species used in studies of ultrasonic emissions. Many feral species apparently have more sensitive hearing than their laboratory bred counterparts, and apparently many lab strains may be susceptible to infections which cause hearing loss.

Nyby, J., and Whitney, G. Ultrasonic communication of adult myomorph rodents. Neuroscience & Biobehavioral Reviews, 2, 1-14 (1978).

This paper is a review article. Topics covered include the mechanism of production of rodent ultrasounds (evidence from Roberts, 1975a, 1975b, indicates that while these sounds are probably not produced by vibration of the vocal chords, they are

produced in the larynx), the general spectral, temporal, and intensity characteristics of the sounds produced by Rattus norvegicus and Mus musculus (sounds occur in pulses which range from 3 ms to as long as 2 or 3 s; frequencies range from about 22 kHz for rats to up to 80 kHz for some mouse calls; and sound pressure levels are generally around 70-85 dB although infant mice can produce sounds at 100 dB), and data from studies of hearing in rats and mice which indicate that these animals are capable of hearing these sounds. Ultrasound production and hearing capabilities of other species (e.g., Peromyscus, Apodemus) are only briefly discussed. Thus far, apparently all myomorph species examined have the ability to hear in the ultrasonic range.

Ultrasounds occur during courtship and sexual behavior in numerous species, including Mus musculus, Rattus norvegicus, Mesocricetus auratus (golden hamster), Dicrostonyx groenlandicus (collared lemming), Apodemus sylvaticus (wood mouse), Peromyscus maniculatus (deer mouse) and Acomys cahirinus (spiny mouse). The most detailed investigations of vocalizations during sexual behavior have been carried out on laboratory mice, laboratory rats, hamsters, and lemmings. In mice, chemical cues, especially those in female urine, appear to be especially important in eliciting ultrasounds.

Rats emit several types of ultrasounds during courtship and mating (Sales, 1972b, described these calls in detail). Short pulses between 3-50 ms at a frequency of 50-70 kHz are most frequent when the male is first placed in the female's cage, when the male is investigating the cage, or is unsuccessfully attempting to mount the female. A second type of ultrasound consists of longer pulses (100-500 ms). Frequencies show "slow drifts" between 40-50 kHz. A third type of sound is often interspersed with these; this third type consists of trains of brief pulses (2-40 ms) with rapid frequency shifts of up to 70 kHz within a single brief pulse. While these calls generally seemed to be associated with activities of the male (specifically sniffing the cage or the female), the identity of the animal producing the sounds was not specifically determined.

A fourth type of sound which occurs during rat sexual behavior was described by Barfield and Geyer (1972, 1975). This call occurs following ejaculation and consists of trains of long duration sounds (approximately 1-3 s) of almost pure tones of approximately 22-23 kHz. The period during which these sounds are emitted corresponds to the male's absolute refractory period, during which the male is physiologically incapable of mating. During this period, the male's EEG pattern shows slow-wave, sleep-like activity. The postejaculatory 22 kHz signal appears to be identical to the signal emitted by subordinate male rats in the presence of an aggressive or dominant animal. This similarity led Barfield and Geyer to hypothesize that the calls reflect similar motivational states, namely, withdrawal or contact avoidance.

Ultrasounds also occur during aggression in rats and some other myomorph species (e.g., Acomys cahirinus, Apodemus sylvaticus). Other species (e.g., Mus musculus, Mesocricetus auratus) apparently do not emit ultrasounds during agonistic encounters. Sales (1972a) described 2 types of calls emitted by rats in these situations. The first type was associated with aggressive behavior by a male or lactating female. These calls were relatively short pulses (3-65 ms) of 40-70 kHz. The second type of call consisted of trains of long pulses (800-1,600 ms) of 23-30 kHz. These calls have narrow bandwidths, and they often appear to be almost pure tones. Nyby and Whitney note that this sound "appears virtually identical to" the 22 kHz postejactulatory sound. During agonistic encounters, these sounds are associated with an irregular pattern of respiration by the subordinate male which corresponds to the emission of the sounds. During sound emission, the subordinate is often in a submissive crouch position, although the sounds are sometimes emitted while the animal is grooming or moving about. Studies subsequent to Sales' initial report have investigated the function of this sound; they suggest that the sound may be important in the establishment and maintenance of dominance relationships. (Studies published subsequent to this review have not always provided clear evidence that the call acts to regulate aggressive behavior; see Lore et al., 1976; Thomas et al., 1983; Takahashi et al., 1983; Takeuchi & Kawashima, 1986).

Rodents may also emit ultrasounds in other contexts. In an early report, Anderson (1954) suggested that rodents might use ultrasounds for echolocation. Later experiments indicated that this was probably not the case. It has also been reported (Sewell, 1968) that Apodemus sylvaticus emit ultrasounds when placed in a new cage, indicating that in this species ultrasound emission may be associated with territorial or exploratory behavior.

This review emphasizes the literature on mice and rats (admittedly, most of studies of rodent ultrasound have involved these species) and seems to be a thorough overview of literature published up to 1978.

Sales, G., and Pye, D. Ultrasonic Communication by Animals. London: Chapman and Hall, 1974.

Chapter 7, Ultrasound in rodents, is a detailed and thorough survey of data available through 1973. Calls of numerous species, both infants and adults, are discussed, and sample sonagrams are presented for many of the calls. In most cases, the data are from incidental observations of calls from 1 or 2 individuals, rather than systematic samples of calls from large numbers of subjects. A section on aggressive behavior and ultrasound in rats includes 2 sample sonagrams. Sonagrams of calls recorded during sexual behavior in rats are also presented. The mechanism of ultrasound production in rodents and the hearing

capacities of rodents are discussed. Overall, this record is a useful survey of data available in 1974.

Smith, W.J. The study of ultrasonic communication. American Zoologist, 19, 531-538 (1979).

The author provides an overview of the evidence concerning the functions of rat ultrasounds, particularly the 22 kHz call. He points out that the call occurs in a variety of contexts (aggression, sexual behavior, isolation), and that the responses of conspecifics presumably receiving the signal cannot always be predicted reliably. The call, then, may specify only some general information such as "that the caller will act to remain in a social circumstance, but will not readily initiate active interactional behavior and will not move about while calling." The specific behavior patterns that the caller is likely to engage in subsequently will depend on many aspects of the context in which the call is given. This type of signal, in which meaning and function may differ according to context, is typical of vertebrates.

Smith makes the important point many possible functions of rat ultrasounds have not yet been explored (as of this publication) because of the artificial situations in which these calls have typically been studied (viz., brief encounters between two strangers in a small cage). He calls for increased examination of the occurrence and function of rat ultrasounds in the naturally evolved social organizations of these animals.

Sewell, G.D. Ultrasound in rodents. Nature, 217, 682-683 (1968).

This brief report is one of the earliest published descriptions of rodent ultrasound. It is largely descriptive, with little quantitative data presented. The author discusses 2 contexts in which ultrasounds are commonly produced by infant rodents - cold stress and handling. The calls occurring in these 2 situations, while similar in many respects, differ in intensity and in developmental time course. Calls which occur in response to isolation (and, presumably, cold stress) are less intense and decline at an earlier age than do calls which occur when the young are handled.

The author reports that, unlike rats, other rodent species (e.g., lab mice, Acomys cahirinus, Clethrionomys glareolus) seem to emit few or no ultrasounds during agonistic encounters. Ultrasounds have been detected during sexual behavior in these species, however. Ultrasounds were also detected when another hamster was introduced into the cage of an estrus female hamster, when the litter of a lactating female Acomys was removed from the mother's cage, and during exploratory behavior in Apodemus sylvaticus.

Sewell, G.D. Ultrasonic signals from rodents. Ultrasonics, 8, 26-30 (1970).

This report is an overview of the author's investigations of ultrasounds in 16 rodent species. Contexts in which recording occurred, recording equipment, and recording procedures are described. Amplitude patterns, frequency characteristics, and harmonic structures of the calls are described in a general way. Examples of sonagrams of calls from several species are presented. Of particular interest are sample sonagrams from a 1-day-old rat, a 50-day-old rat, and a submissive adult rat. The ultrasound from the "submissive" rat (actual behavior of the rat is not described) is at approximately 25-30 kHz with fluctuations in amplitude throughout the call. This call appears to be the "22 kHz call" frequently reported in the literature.

## Agonistic Behavior

Berg, D.S., and Baenninger, R. Hissing by laboratory rats during fighting encounters. Behavioral Biology, 8, 733-741 (1973).

Pairs of rats exposed to aversive stimulation (e.g., tailpinch, shock) will often attack one another, sometimes producing audible sounds (such as teeth chattering and squealing) as they do so. This paper examines the occurrence of hissing, another audible sound produced by rats in this situation.

Subjects in Exp 1 were 8 male Sprague-Dawley rats, each weighing approximately 350 g. They were housed in pairs. The experimental apparatus consisted of a chamber with a hole at each end for the insertion of the rat's tail into the tailpinch mechanism. Animals were tested in 2 groups. Animals in Group I were first tested singly, then as a pair, then singly; Group II animals were tested in a pair, then singly, then paired. (The authors do not specify how many Ss served in Groups I and II, and it is not clear whether animals were always tested as part of the same pair or whether this was varied.) Subjects were tested over an 11-day period. On each day, subjects received five 30-s tailpinches, each separated by 30-90 s (the authors do not give a specific time period for this interval). Animals were placed singly in the apparatus for the first 2 days to habituate to the apparatus (no tailpinch). On Days 3-5, Group I received tailpinches individually and Group II was tailpinched in pairs. On Days 6-8, Group I was tested in pairs and Group II individually, and on Days 9-11, Group I animals were tested individually and Group II in pairs. An observer recorded whether hissing occurred following each shock. Hissing occurred on 72% of the pair-test trials and only 7.7% of the single-animal trials.

Eight male Sprague-Dawley rats (wgt. 350 g) served in Exp 2. Apparatus used was the same as in Exp 1, with a piece of clear Plexiglas which could be used to divide the apparatus in half. Subjects were tested under 3 conditions: paired (as in Exp 1), singly (as in Exp 1), and paired, but with the partition in place to keep the animals separated. Subjects were divided into 2 (presumably equal) groups. Group I was tested in the following order: paired (2 trials), partition (2 trials), paired (2 trials), singly (2 trials). Group II was tested in the order: partition, paired, partition, singly. Order of testing was thus not counterbalanced, and, as in Exp 1, subjects did not receive the same number of trials in all conditions. Hissing occurred on 60% of the paired trials, 2.5% of the single trials, and 11.5% of the partition trials. Results of an analysis of variance (ANOVA) (which may not be the appropriate statistical test) indicated a significant effect of testing condition and significant differences between each of the three conditions. The authors conclude that contact between animals is important for hissing elicitation.

Subjects in Exp 3 were 20 male Sprague-Dawley rats. A session in which hissing occurred was recorded using a "portable, battery operated tape recorder." The recorder was also used for playback of the sounds. The authors state that "the frequency range of recording and playback was 20-10,000 Hz." No further specifications are given. Contact between the 2 animals during fighting was automatically recorded by a contact relay. The procedure is not presented in detail. Animals were assigned to Group H or Group NH. All animals were tested for 3 days. The sessions were divided into prepinch, tailpinch and postpinch periods. The prerecorded hissing tape was played to Group H at some point during the session (this varied but is not clearly specified). Group NH, the control group, did not hear the tape. There was no difference between the groups in number of fighting contacts. Number of fighting contacts in Group H did not differ during trials with playback and trials without playback, either. The authors acknowledge that, as their tape contains only sounds of 10 kHz or lower, the taped hissing may not contain the components of the sound necessary to influence behavior of rats.

Recordings were made of hissing by one pair of rats (presumably adult male Sprague-Dawley as used above, but not specified.) The pair was given tailpinch as in previous experiments. Sounds were recorded using a Brüel and Kjaer 1/4 in. microphone (Type 4136), held about 6 in. from the animals. "After amplification" recordings were stored on an Ampex high-speed tape deck at 60 in./s and played back at 7.5 in./s. Hisses were identified from this tape and recorded on a Sony tape deck such that frequencies in the range from 56,000 Hz down to less than 1,000 Hz could be recorded on audio tape. The hissing signal was then delivered to a Hewlett-Packard XY plotter (Type 7035B)." The results indicated that the hissing sound contains ultrasonic components, with major energy peaks at 12, 20, and 26 kHz.

There are several methodological problems with this study. Its main contribution may be to demonstrate that some audible sounds of rats may have ultrasonic components which may have a communicative function.

Corrigan, J.G., and Flannelly, K.J. Ultrasonic vocalizations of defeated male rats. Journal of Comparative and Physiological Psychology, 93, 105-115 (1979).

The purpose of this study was to examine the conditions (specifically, those related to agonistic encounters) under which rats learn to emit the 23-30 kHz ultrasounds typically emitted by a submissive rat in the presence of a dominant animal. A series of 6 experiments was performed.

Prior to Exp 1, 5 male rats (approximately 180 days old) were chosen from a large group to be "aggressors"; these rats were chosen because they readily behaved aggressively toward intruders placed in their cages. The subjects for Exp 1 were 20 male Long-Evans rats, 90-110 days old. Ten subjects served in the experimental condition. A metal cage with a wire mesh front was placed in the home cage of an aggressor, and the aggressor was confined within this smaller cage. Each subject was placed in the home cage of an aggressor, and the number and latency of ultrasounds produced by the subject were monitored for a 5-min period while the aggressor was confined. Ultrasounds were audibly monitored using an ultrasonic detector (Model TUD-2, Psyonics, Inc.) and a UM-1 microphone maximally sensitive to 20-25 kHz sounds. The microphone was manually held over the head of the subject during testing. After the initial 5-min recording period, the holding cage was removed, and the aggressor was allowed to attack the subject. After the attack, the aggressor was again confined in the holding cage and the subject's ultrasounds were monitored for another 5-min period. Ten control subjects were treated similarly, except that the aggressor was confined to the holding cage during the entire 10-min recording period. Subjects were given 4 trials per day, with 2 h intervals between trials. Testing continued for 7 days or until subjects reached criterion (emission of ultrasounds during the 5-min preaggression period on 3 successive trials of a given day).

Analysis of the results indicated that significantly more of the experimental group subjects reached criterion (90% of experimental group reached criterion by the third day of testing; one control animal (10%) reached criterion during testing). The experimental animals that reached criterion emitted a higher mean number of sounds and showed a shorter latency to call (descriptive statistics only presented) than the single control group subject that reached criterion.

In Exp 2, the 9 experimental group animals that reached criterion in Exp 1 were retested in 3 conditions: (1) with the same aggressor male the subject was exposed to in Exp 1; the

aggressor male was confined throughout the test; (2) with an unfamiliar aggressor male in an identical testing situation; (3) in an empty (i.e., no aggressor male present) clean cage identical to the aggressor males' home cages; an inverted (empty) metal home cage was also present during this condition. These tests took place 7 days after achieving criterion in Exp 1. Latency and number of ultrasounds emitted were recorded for 5 min. Results indicated a significant effect of stimulus condition on "probability of vocalization." (It isn't clear what data this analysis was done on; perhaps number of animals calling in each condition.) Inspection of the data showed very little vocalization in the clean cage; latency and numbers of ultrasounds were similar in the familiar aggressor and unfamiliar aggressor conditions. The results obtained appear to be due to differences between subjects exposed to aggressors (whether familiar or unfamiliar) and subjects exposed to clean cages. Apparently, for animals previously subjected to intraspecific aggression, familiarity with the aggressor is not necessary. This behavior would seem to suggest that subjects are responding (emitting ultrasounds) to some specific signals (maybe chemical or visual) emitted by aggressors.

In Exp 3, subjects were exposed to stimulus animals (namely, post-pubertally castrated males and anosmic males) which normally show little aggression toward intruders. This exposure was done in an attempt to determine which stimulus characteristics of the aggressor males elicited ultrasounds in Exps 1 and 2. Subjects were 12 male Long-Evans rats, 140-150 days old. They were first placed in the cage of an unconfined aggressive male for a 1-h period, during which they were repeatedly attacked. Testing took place 5-6 days later. Each subject was tested under 4 conditions: (1) a clean cage; (2) the home cage of an aggressive male; (3) the home cage of an anosmic male; (4) the home cage of a post-pubertally castrated male. In all cases, the stimulus males were unfamiliar to the subjects, and stimulus males were confined as in Exp 1. Tests lasted 5 min, and were conducted at 1-h intervals. Latency and number of ultrasounds were recorded. Analysis of the results indicated a significant effect of condition. (As in Exp 2, it is not clear which measure was used for this analysis; possibly the number of animals emitting ultrasounds in each condition). All subjects emitted ultrasounds in the presence of the aggressive male, one subject did so in response to the clean cage, and intermediate numbers did so in response to the castrated and anosmic males. Latency and number of responses showed a similar pattern. Because the response to the anosmic male was not as strong as the response to the aggressive male, the authors argue that some cues other than olfactory (which would not differ between these 2 types of stimulus animals) must be the eliciting stimulus for ultrasounds. They suggest that some overt behavior (e.g., postures, movements) of the aggressive male may elicit ultrasound responses from other males.

Exp 4 was designed to test the relative effectiveness of odor and movement cues in elicitation of ultrasounds by intrud-

ers. Subjects were 6 mature male Long-Evans rats. One day prior to testing, each subject was given a 30-min exposure to an aggressive rat. All subjects received numerous wounds during this exposure. Each subject was tested in 6 different conditions: (1) the home cage of an aggressive male, from which the male had been removed prior to testing; (2) an aggressive male immobilized with haloperidol in its home cage; (3) an aggressive male anesthetized with sodium pentobarbitol in its home cage; (4) an untreated aggressive male in its home cage; (5) a castrated adult female in the home cage of an aggressive male; and (6) an untreated aggressor male in a clean cage. Rats immobilized with haloperidol maintain a quadrupedal stance, unlike rats under standard anesthesia, which lie prone. Conditions 2 and 3 therefore presented different visual cues to the subjects. In all conditions, stimulus animals were separated from the subjects in the wire mesh cage.

Latency to emit ultrasounds and number of ultrasounds emitted were recorded as in previous experiments. There was a significant effect of stimulus condition on the probability of ultrasonic vocalization. No subjects emitted ultrasounds in the empty aggressor's cage or in the cage containing the female. Latencies were shortest and the greatest number of ultrasounds were emitted when subjects were exposed to an aggressive rat in its home cage and to an aggressive rat in a clean cage. Very few calls were emitted in response to anesthetized or immobilized rats. These results point to the importance of movement cues on the part of the aggressive rat in stimulating ultrasonic emission by the submissive animal.

Exp 5 was designed to examine whether emission of ultrasonic vocalizations by aggressive males acted to elicit ultrasounds from submissive animals. Subjects were 8 male Long-Evans rats, 90-110 days old. Subjects were first placed in the home cage of an aggressive male rat. The aggressor was confined as in the previous experiments. Ultrasounds in the 20-25 kHz range were monitored as in the previous experiments. At the same time, signals in the 45-70 kHz range were monitored visually using a Holgate ultrasonic receiver attached to an oscilloscope. The microphone picking up the 20-25 kHz signals was held above the subject as in previous experiments. The microphone for the Holgate receiver was held above the resident aggressive animal. Ultrasonic emissions were monitored for an initial 5-min period, after which the subject animal was placed in the home cage of an unconfined aggressive male for a 24-h period. A second 5-min ultrasound recording session took place after this 24-h period.

No ultrasounds were detected during the initial 5-min testing period. Half of the subjects emitted 20-25 kHz sounds during the second testing session, but no sounds in the 45-70 kHz range were detected during the experiment. The authors state that these results indicate that 45-70 kHz vocalizations from aggressive animals are not required to elicit ultrasounds from submissive animals. Studies subsequent to this one (e.g., Thomas, et

al., 1983) have indicated that submissive animals, rather than dominant ones, may produce most of the higher frequency ultrasounds which have been noted during agonistic encounters, as well as the 20-25 kHz sounds. These higher frequency ultrasounds, if produced by the submissive animals in this experiment, may not have been picked up by the high frequency microphone located above the aggressive animal.

Exp 6 was designed to examine the importance of olfactory cues in elicitation of ultrasounds by submissive males, and to examine some of the behavior patterns exhibited by aggressive males which may be important in eliciting these sounds. Subjects were 24 male Long-Evans rats, 75-80 days of age. Each subject was exposed to an aggressive male for a 24-h period, after which subjects were examined and given a wound score. Subjects were assigned in matched pairs to the experimental and control groups on the basis of wound scores. Subjects in the experimental group were made anosmic using zinc sulfate treatment 3 days after their exposure to the aggressive male. Testing took place 6-7 days after treatment. Testing was the same as in previous experiments. Subjects were placed in the cage of an aggressive male for a 5-min period, during which ultrasounds emitted by the subject were monitored. Latency to emit ultrasound and number of ultrasounds emitted were recorded. Piloerection, aggressive posturing, audible vocalizations, and tooth chattering by the aggressive animal were also recorded (these behavior patterns were not explicitly defined by the authors).

After testing, each subject was placed with a castrated female for 5-min, and the frequency of anogenital sniffing by the male was recorded. This experiment was done to test the effectiveness of the anosmia induction procedure. In addition, after anosmia testing, each subject was placed in a standard operant chamber and given a series of footshocks. Ultrasounds were recorded during this procedure and for a 5-min period after shocks were delivered, in order to determine whether the zinc sulfate treatments affected the experimental animals' tendency to produce ultrasound.

Half of the control subjects, but only one of the subjects in the anosmic group, emitted ultrasounds when placed in an aggressive male's home cage. The control group emitted significantly more ultrasounds, and their latency to emit ultrasounds was significantly shorter, than the experimental group. Several correlation measures indicated a positive relationship between number of wounds received and emission of ultrasounds. Testing with the female indicated that the zinc sulfate treatment was effective in inducing anosmia. Shock testing indicated that, while zinc-treated animals were capable of producing ultrasound, the control group emitted more ultrasounds in response to shock, and latency to emit ultrasounds was shorter than for the experimental group.

These experiments demonstrate that rats rapidly learn to emit ultrasounds in the presence of stimuli previously associated with aggressive attacks. The authors argue that this rapid learning suggests that rats are "'prepared' to emit ultrasonic calls in anticipation of pain" (p. 113).

Ghiselli, W.B., and LaRiviere, C. Characteristics of ultrasonic vocalizations emitted by rats during shock-elicited aggression. Animal Learning & Behavior, 5, 199-202 (1977).

This study sought to describe ultrasounds (if any) emitted by rats during shock-elicited aggression, and to examine the contexts of these sounds. Subjects were 6 adult (150 days old) male Sprague-Dawley rats. All had participated in a prior learning experiment (not detailed). Shock sessions took place in a standard operant chamber illuminated by a 100 W bulb. It is not stated whether tests were conducted during the light or dark phase of the animals' cycle. Three pairs of subjects were formed, and each pair was given 5-10 sessions per day in the operant chamber. Total number of sessions and number of test days are not given. A session consisted of fifty 2.0 mA shocks of 0.5 s, delivered at 6.5 s intervals. Aggressive behavior was observed during sessions, and the number of shocks which were followed by "attacks" was recorded.

Ultrasounds were recorded using a "Kuhl" type ultrasonic microphone which was constructed by the authors. The microphone output was fed into a "frequency transformation circuit which allowed signals' frequency to be stepped down by as much as a factor of 15," making the signals audible to humans. The frequency response characteristics of this system were not given. Distance from the microphone to the vocalizing animals was not specified. The "stepped-down" signal was recorded on magnetic tape and analyzed using a Kay Sonagraph Model 7029-A (5-16,000 Hz).

No quantitative measures of agonistic behavior were presented, but the authors state that "fighting occurred at relatively low levels," and that, in general, fewer than 50% of the shocks were followed by aggression. One of the 3 pairs did not show any aggression during test sessions, and no ultrasounds were detected from this pair. Ultrasounds recorded from the other 2 pairs took the form of bands of constant frequency at about 23 kHz. A second frequency band was apparent at about 71 kHz. The calls showed no onset or offset transients, and the frequency was very constant throughout the call. In addition, the calls contained wide spectrum noise throughout the call. Two AxFxT sonagrams were presented, as well as a single AxF plot indicating 3 high intensity bands - one at 22 kHz, one at 67 kHz, and a third at 108 kHz. The author states that frequency of this third band averaged 121 kHz over all calls.

The ultrasounds most commonly occurred when one animal was in the "upright submissive" posture (described as upright but with the head level or facing down, and not facing the other rat). Ultrasounds never occurred in association with attack (biting, boxing, upright aggressive posture). No quantitative data on the occurrence of agonistic behavior were presented.

This study apparently is the only study to report harmonic components of the 22 kHz call. This result may be due to the fact that in other studies, these calls are generally examined using a bat detector, which detects sounds only within a narrow frequency range. In addition, analysis of the 22 kHz call in other studies has often been limited to simple counts of its occurrence, and has not included detailed examination of the acoustic characteristics of the call. It is unusual that no short pulse, higher frequency calls, which typically are noted during studies of aggression in rats, were detected during this study. The authors state that the absence of these calls here may be due to the species used (I assume they mean strain, since these higher-frequency calls typically have been recorded from rats), the characteristics of recording equipment used, or the absence of these calls during shock-elicited aggression. They do not discuss any characteristics of their recording apparatus which might have prevented them from detecting higher-frequency calls, and they were able to detect high frequency components of the long calls using their equipment. Overall, this study does not seem to be carefully done, and this casts some doubt on their report of harmonics of the 22 kHz call.

Lehman, M. N., and Adams, D. B. A statistical and motivational analysis of the social behaviors of the male laboratory rat. Behaviour, 61, 238-275 (1977).

The study is a detailed analysis of the sequences of behavior patterns which occur during aggressive encounters between adult male rats. Subjects were adult male rats, approximately 135 days old at the beginning of testing. Rats used were hybrids of the DA agouti, Fischer albino, and WAG-Rij albino strains. All subjects had been housed with their siblings until 25 days of age. At 90 days of age, the animals to be used as "residents" were housed alone, and those to be used as "intruders" were housed together in groups of 5 animals. For each test, an intruder was introduced into the home cage of a resident for a 20-min period. Intruders were of different hybrid strains (details not specified) from the residents. Each of the 40 residents was tested once; it is not clear whether intruders were used in more than one test. Thirty behavior patterns were scored, including aggressive and submissive postures, exploration, and self-grooming. Behavior patterns, and the animal performing them, were recorded in the order in which they occurred.

A Psyonics UMAR-2 ultrasonic receiver "with a microphone sensitivity between 20.5 and 24.5 kHz" was used to monitor ultra-

sonic emissions. This system is not described in detail; however, the article states that the ultrasounds were monitored "both aurally and visually," so this receiver most likely produces some heterodyned audio output along with an oscilloscope display. The authors state that they were able to determine which animal was emitting the ultrasounds by observing respiration of the animals.

Data were analyzed by examining all sequences of 2 behavior patterns and determining whether these sequences occurred more often than expected by chance. Behavior patterns which were associated with intruder-emitted ultrasound at levels significantly higher than chance included upright posture by the intruder, intruder crouch, and self-grooming by the resident rat. The authors also state that ultrasound frequently occurred in conjunction with the full submissive posture by the intruder, but this apparently was not a significant association. When accompanied by ultrasound, crouching, upright posture, and full submissive posture by the intruder were never followed by resident attack. When not accompanied by ultrasound, these postures were significantly more likely to be followed by attack.

Two additional experiments examined the function of intruder ultrasound. In one experiment, 2 intruders were devocalized by bilateral resection of the recurrent and phasolaryngeal nerves. They were tested with an intact resident both preoperatively and 1 week postoperatively. In postoperative tests, each intruder was tested with the same resident it had been exposed to preoperatively. In the second experiment, 2 resident rats were deafened by rupturing the eardrum and destroying the middle ear ossicles. The auditory canal was then plugged with cement, and the ear canal was sewn shut. As in the first experiment, the animals were tested preoperatively (pre-op) and 1 week postoperatively (post-op). Each resident was tested with the same intruder in both pre-op and post-op tests. Based on their results, which showed that submissive postures accompanied by ultrasound were less likely to be followed by attack, the authors expected that the frequency of attack would be higher if no ultrasound was either emitted by intruders or detected by the residents during the tests. Detailed results are not presented, but the authors state that there were no differences in number of bite-and-kick attacks during pre-op and post-op tests in either experiment.

Results of the analyses of behavior sequences suggest that ultrasound emission by submissive rats may be associated with inhibition of aggression by resident animals. The number of tests performed in the deafening and muting experiments is extremely small (2 per experiment) and no definite conclusions can be drawn from these results. In addition, the results may have been influenced by the fact that the same dyads were tested preoperatively and postoperatively. Prior experience with the same individual may have influenced behavior in the post-op tests.

Lore, R., Flannelly, K., and Farina, P. Ultrasounds produced by rats accompany decreases in intraspecific fighting. Aggressive Behavior, 2, 175-181 (1976).

This study found diminution of aggression between adult male animals in response to apparently inhibitory effects of ultrasonic vocalizations and submissive postures of non-aggressive animals. The subjects were 27 adult male Sprague-Dawley rats 140 days of age at the beginning of the study; 18 served as residents and 9 served as intruders. The aggression-eliciting situation consisted of intrusion of 1 adult male into the home territory of a resident adult male. In a previous study, these authors found that aggressive behavior of "resident animals" toward male conspecific "intruders" is lower on the second exposure of intruders to residents. This reduction in aggressive behavior was possibly due to more effective, experienced signaling by the intruder on its second incursion such that "much less fighting" was elicited. Perhaps, if intruders were not given an opportunity to learn, aggression by residents toward naive intruders would not decrease. This interpretation is consistent with previous research which indicated that repeated incursions by naive intruders into established colonies continued to lead to aggression by residents. Resident learning apparently was not associated with any reduction in their aggression.

The present study sought to examine this more fully; resident animals were all naive while each of the intruders was exposed to 2 different residents. Although intruders were placed with residents for 24-h periods (successive exposures were separated by 7-8 days), all behavioral and acoustical records were made within the first 30 min of each exposure session. The recording apparatus (product of Psyonics, Inc.) was reported to be sensitive to 20-25 kHz sound. The microphone was said to be always oriented directly toward the intruder animal at a distance of about 29-33 cm. It is unclear whether vocalizations of the resident animal would have been detected while the 2 animals were widely separated, or whether there would have been any way of distinguishing vocal origin when the 2 animals were in close proximity. Its output was monitored as an audible (2-2.5 kHz) heterodyned signal and stored as deflections on an event recorder. Acoustical analyses were thus probably not performed; none were reported.

Statistical analyses of behavioral data indicated that latency from introduction of intruder to onset of fighting in the first session was significantly shorter than latency to fighting in the second session. Further, durations of offensive actions by resident animals were significantly shorter during exposure to second-time intruders. In fact, no intruders were attacked during second exposures. However, the number of ultrasonic vocalizations recorded during the second intrusion increased by a factor of about 3. Also, the time spent vocalizing during the second session increased by factor of about 9.

The authors noted that, whereas vocalization during the first session tended to follow several fighting bouts (as reported also by Sales, 1972), during the second session vocalizations "never" were associated with fighting. Apparently, vocalizations of "experienced" intruders preceded and suppressed expressions of aggression.

Sales, G. Ultrasound and aggressive behaviour in rats and other small mammals. Animal Behaviour, 20, 88-100 (1972a).

This report is the first published description of ultrasound emission by rodents during agonistic encounters. Aggressive behavior and associated ultrasounds were observed in laboratory rats (Wistar strain), wild Rattus norvegicus, and 14 other species of small mammals.

Laboratory rats (N=11) were tested in pairs. For these tests, one individual (the "intruder") was placed in the home cage of another rat (the "resident"), and behavior was observed for 1 h. Individual subjects served as both intruders and residents. Thirteen behavior patterns were recorded, including sniffing, sexual behavior, maintenance activities, and several measures of aggression. Ultrasounds were detected with a bat detector, which converted ultrasounds within a narrow frequency range to audible signals. The range of frequencies from 10 kHz to 100 kHz was swept at intervals during testing sessions. In addition, ultrasounds were picked up by another microphone which fed into a broad-band amplifier; these signals were then displayed on an oscilloscope. In some cases, ultrasounds were recorded using either a PI 6100 tape recorder at 37.5 in./s (which had a "reasonably" flat frequency response up to 100 kHz) or a Pemco 110 portable tape recorder (which had a "frequency response of 150 kHz at 30 in./s"). The signals recorded were first analyzed by ear by playing the tape at a reduced speed; initial classification of vocalization types was made in this way. Samples of each type of ultrasound were then analyzed using a Kay sonagraph, Type 675. The upper frequency limit of the sonagraph was 15 kHz, so the tapes were replayed at a reduced speed for analysis.

In a previous study of rat ultrasound (Sewell, 1967), 2 types of pulses were noted; both types were recorded here as well. "Short" pulses typically lasted 3-65 ms with a frequency of approximately 45-70 kHz. Short pulses sometimes showed marked frequency fluctuations. "Long" pulses (generally 800-1,600 ms, maximum duration 3,400 ms) consisted of a single frequency component between 23-30 kHz. They sometimes showed slow drifts in frequency or had frequency shifts at the beginning or end of the pulse, but many were of almost constant frequency. Sample sonagrams of both a short and a long pulse are presented.

Behavior patterns which occurred simultaneously with short and long ultrasonic pulses were examined. Long pulses were most

often observed when one animal was in a submissive, crouched posture and the other animal was active. These sounds were associated with exhalations by the submissive animal. Long pulses occurred in 12 of the 20 aggression tests; aggression (in particular, instances of "attack") was lower in these tests than in the 8 tests in which long pulses did not occur. In both types of tests (long pulses emitted and long pulses not emitted), number of attacks decreased rapidly after the first 10 min of the test, but attacks decreased by a greater amount in tests with long pulses. This pattern seems to indicate an association between emission of long pulses and cessation of aggressive behavior.

Short pulses were most highly correlated with the behavior patterns "displacement behavior" and "crawling over," and with "more obvious aggressive acts." They seldom occurred when one member of the pair was showing a submissive posture, and they were also infrequent during maintenance activities and sexual behavior. It could not be determined which animal of the pair was producing short pulses at any given time, although they sometimes appeared to be synchronous with the head movements of the aggressive animal.

Lactating female rats were also observed when unfamiliar male rats were introduced into their home cages. Short pulses were produced when the females attacked males, postured aggressively, or nosed the males. Long pulses also occurred, "apparently" produced by the male. Short and long pulses similar to those produced by the lab rats were also emitted during encounters between wild rats, although little aggression was seen during these tests. Contexts in which the sounds occurred seemed to be similar to those in which they were heard in the lab rats. Long pulses produced by the wild rats were more brief (300-600 ms) than long pulses of the lab rats.

Observations of the other 14 species studied were limited, and in many cases only one paired encounter was observed. In most cases, the species which emitted ultrasounds did so during agonistic interactions (chasing and fighting) or during genital sniffing. Species which emitted ultrasound include Apodemus sylvaticus, Acomys caharinus, and Mus musculus. Three species (Lagurus lagurus, Microtus agrestis, and Sorex araneus) did not emit ultrasounds during testing.

In rats, long pulses were generally associated with behavior by the submissive animal, in particular, irregular breathing and the crouched submissive posture. However, these sounds rarely occurred when animals were exhibiting the "full submissive posture" (animal lying on its back or side; eyes closed or half-closed), and this full submissive posture was often followed by renewed attack by the resident animal. Based on these observations, the author hypothesizes that the full submissive posture signals only a temporary submission, and that long pulses, which were followed by a decrease in the number of attacks, signal a more long-lasting state of submission. The author also states

that short pulses appear to be produced by the aggressive animal in the pair (but see later reports, e.g., Thomas et al., 1983, which seem to contradict this), although it is unclear what effect, if any, they have on the submissive animal. Sales correctly points out that the communicative function of adult rat ultrasounds, if any, is unknown at this point.

The author notes that the distribution of aggression-related ultrasound among small mammal species may be related to social organization. The species which emit ultrasounds in agonistic situations generally live in colonies or show some degree of mutual tolerance for conspecifics; in these species, ultrasonic signals indicating dominant or submissive status may function to reduce aggression in a colony. The species which did not emit ultrasounds in agonistic contexts are generally solitary or territorial. For these species, signals indicating dominance status might be less important.

Sales, G.D. Strain differences in the ultrasonic behavior of rats (Rattus norvegicus). American Zoologist, 19, 513-527 (1979).

Although strain differences in ultrasound emissions of mice pups have been examined in some studies, up to the time of this publication, strain differences in rat ultrasound had not been systematically investigated. This paper reviews existing literature which suggests strain differences in rat pup vocalizations and presents data on Wistar and Lister rat pups recorded under comparable conditions. Recordings were made from individual pups during a 15-s isolation period followed by a 15-s handling period. Pups were recorded every day from Day 1 to Day 19 after birth. In general, rate of vocalization was greater in Wistar pups than for Lister pups during both isolation and handling. Isolation calls were significantly lower in frequency for the Wistar pups than the Lister pups.

Ultrasounds produced by adult (exact age not specified) male Wistar and Lister rats during aggression were also examined for evidence of strain differences. Two types of tests were performed. In "first encounters," a naive "intruder" was placed in the home cage of a naive "resident." During "second encounters," the intruder from a first encounter served as a resident, and an experienced resident or naive animal now served as the intruder. Encounters lasted for 30 min, during which the occurrence of several agonistic behavior patterns (attack, wrestle, box, aggressive upright, aggressive sideways and aggressive/submissive postures), was recorded during each 15-s period. Ultrasounds were monitored using two QMC bat detectors, one tuned to 25 kHz and the other "used in the broadband mode." Some calls were tape recorded for later sonagraphic analysis, and in some instances Sound Pressure Level (SPL) was measured "by a calibrated microphone held 30 cm above the floor of the cage." Approximate distance of the microphone from the vocalizing animals is not speci-

fied. A total of 21 tests was run (11 Wistar (8 first encounters, 3 second encounters; 10 Lister (4 first encounters, 6 second encounters)).

Statistical tests were performed for first and second encounters separately and for all encounters together on the latency to the first aggressive act, latency to the first 50 kHz (short pulse) vocalization, latency to the first 22 kHz vocalization, total number of both types of vocalization, and total number of aggressive acts. The only significant difference among the latency scores was a significantly ($p=.057$) longer latency to emit "50 kHz" calls during second encounters between Wistar rats. Wistar rats emitted significantly more "50 kHz" calls during first encounters, second encounters, and all encounters combined. The author also states that "there were no clear strain differences in the temporal pattern of aggression and ultrasound emission throughout each encounter"; some of these data are presented graphically but apparently no statistical tests were performed. SPL of the calls also differed between strains, with that for Wistar rats generally ranging between 56 and 63.5 dB, while SPL for ultrasounds of Lister rats was generally below the 54 dB noise level of the equipment. The calls also differed in some duration and frequency characteristics. Long 22-kHz calls of Lister rats were significantly longer than those of Wistar rats, and, while the long 22-kHz calls of Lister rats showed very little frequency variation across the call, those of Wistar rats were much more variable. The short 22-kHz calls of Lister rats were significantly shorter that those of Wistar rats, and the "22-kHz" calls of Wistar rats also tended to be lower in frequency.

The results clearly indicate strain differences in some characteristics (specifically, spectral frequency and duration) of adult rat ultrasounds, at least as emitted in the testing situation examined here. As the author points out, "it is less clear whether or not these differences are related to differences in behavior." This study did not find any significant differences in aggression between the two strains; however, all measures of aggression were lumped together for analysis. In addition, the method of data collection used (apparently 1-0 sampling for 15-s periods) is often not a sensitive technique for detecting differences in frequency of occurrence of behavior patterns. A more careful study of agonistic behavior in this situation may have detected strain differences related to the observed vocalization differences.

Sewell, G.D. Ultrasound in adult rodents. Nature, 215, 512 (1967).

This report seems to be an early, descriptive report of findings presented later in Sales (1972). The author reports the detection of ultrasounds from young of several rodent species (including lab rats and mice, Clethrionomys, Mesocricetus, Acomys

caharinus, Meriones shawi, M. unguiculatus, a species of Gerbillus, Apodemus sylvaticus, Mus minutoides, and a species of Thamnomys).

Ultrasounds have also been detected from adult lab rats during handling. To elicit ultrasound, adult rats were rolled on their backs and held in a position resembling the submissive posture adopted by rats during agonistic encounters. Ultrasounds were monitored audibly using a bat detector and visually using a capacitance microphone with a broad-band amplifier attached to an oscilloscope. Samples of the sounds also were recorded. Two distinct types of sounds were noted. "Short pulses" typically lasted 30-60 ms at a frequency of approximately 50 kHz. "Long pulses" of up to 700 ms typically had frequencies of about 22 kHz.

Forty introductions, in which an adult male rat was placed in the home cage of another for a 1-h period, were also performed. Long pulses were initially associated with crouch postures by the submissive animal, but also occurred during other activities. Short pulses occurred during almost all phases of aggressive behavior as well as during other activities such as feeding and cage sniffing. Long and short pulses also occurred during similar introduction tests using wild rats. Short pulses also were recorded when male lab rats were introduced into the cages of pregnant or lactating females, and during attempted mounts by males. The author states that "so far the short pulses seem to be aggressive and the long pulses submissive."

Takahashi, L.K., Thomas, D.A., and Barfield, R.J. Analysis of ultrasonic vocalizations emitted by residents during aggressive encounters among rats (Rattus norvegicus). Journal of Comparative Psychology, 97, 207-212 (1983).

In this study, rat agonistic encounters were observed using the standard resident-intruder testing paradigm. Two experiments examined the extent to which resident males emit ultrasounds and the effect of these sounds on the behavior of intruder males.

Subjects in Exp 1 were 24 adult male Long-Evans rats. Residents (n=8) were 125-150 days old at the time of testing. Intruders (n=16) were 80-100 days old at testing. Testing and recording apparatus and procedures were the same as reported by Thomas et al., (1983). Briefly, residents and males were observed during 20-min aggression tests. Aggressive behavior patterns were recorded, and vocalizations in the 20-25 kHz and 40-70 kHz ranges were monitored using two bat detectors (which provided audible signals in response to the 50 kHz ultrasounds) and an oscilloscope (which allowed visual monitoring of the 20-25 kHz sounds). Half of the intruders in Exp 1 were deafened by injection of a silicon-based ear impression compound into the auditory meatus (see Thomas et al., 1983). Each intruder was tested twice with the same resident, and each resident was given two tests with a deafened intruder and two tests with an intact intruder.

Data were analyzed using 2 (deafened vs. intact intruder) x 2 (Test 1 vs. Test 2) ANOVAs. There were no differences between deafened and intact rats on latency to emission of the first 20-25 kHz vocalization, or in duration of these sounds. There also were no differences between deafened and intact rats on latency or number of 40-70 kHz sounds emitted. More 40-70 kHz sounds were emitted during second tests than during first tests, however. Residents showed more aggressive lateral postures during tests with intact animals, and intact intruders boxed more than deafened intruders. Deaf intruders spent more time in the "freezing" posture, and both types of intruders spent more time in the freezing posture during Test 2.

The findings for the 20-25 kHz ultrasounds differ from the findings of Lore et al. (1976) that intruders showed shorter latency to emit these calls on being exposed to a resident a second time. Residents in Lore et al.'s study also were less aggressive on the second exposure to an intruder, a finding which is not replicated here. The authors speculate that this may be due to the fact that Lore et al.'s residents were relatively inexperienced fighters, while the residents used here were highly aggressive and experienced.

Although it had been found previously (Thomas et al., 1983) that resident animals were producing very few of the 40-70 kHz calls detected during these studies, the authors reasoned that the differences in behavior between the intact and deafened residents in Exp 1 may nonetheless have been due to the inability of the deafened rats to hear whatever ultrasounds the resident might be emitting, or to a general disruption of auditory capabilities. Exp 2 was designed to examine whether the vocal capabilities of the resident had any effect on the behavior of the intruder. Seven residents were used. They were first given a "devocalization control operation" (see Thomas et al., 1983, for details) and tested with intruders. Residents were then devocalized and tested again with naive intruders. Behavior patterns and vocalizations were recorded as before.

There were no significant differences in latency or number of ultrasounds of either type in the devocalized and intact resident tests, strongly suggesting that, in both intact resident and devocalized resident conditions, intruders were emitting all the ultrasounds detected, both 20-25 kHz and 40-70 kHz. There were no differences in any aggressive behavior patterns recorded. These results suggest that the increase in freezing behavior among deafened intruders in Exp 1 was due to some general effect of the deafening procedure, and not to the specific inability to hear ultrasounds emitted by the resident.

The results of these experiments, together with those of Thomas et al. (1983), demonstrate that, in the resident-intruder testing paradigm examined here, the intruder emits almost all the

ultrasounds detected, both in the 20-25 kHz range and in the 40-70 kHz range. Further, there was no clear evidence that these ultrasounds function in the regulation of aggression. The authors point out that results indicating no effect of ultrasounds on aggression may be specific to the testing paradigm, in which unfamiliar animals are introduced to one another for brief time periods, and that ultrasound may play a role in the regulation of aggression in established social groups of rats.

Takeuchi, H., and Kawashima, S. Ultrasonic vocalizations and aggressive behavior in male rats. Physiology & Behavior, 38, 545-550 (1986).

Previous studies (Takahashi et al., 1983; Thomas et al., 1983) using Long-Evans rats apparently demonstrated that the ultrasounds emitted by male rats during agonistic encounters (both the 22 kHz sounds and the briefer, 40-70 kHz pulses) do not influence the behavior of rats in agonistic situations. Devocalization of the animals used in these studies did not result in any changes in behavior of either aggressive or submissive animals. The present study examined the role of ultrasounds in aggression in another strain (Wistar) of rats.

A series of 3 experiments was performed. Subjects in all experiments were males of the Wistar/Jcl strain. All animals were at least 71 days old. Aggression tests were carried out in an "observation box." During tests, the home cage of an adult male (the "resident") was placed in the observation box, and another adult male (the "intruder") was then introduced into the resident's home cage. Several categories of aggressive behavior (e.g., attack, wrestling, aggressive-submissive postures) were recorded during these aggression tests. Ultrasounds were recorded using a QMC mini bat detector, tuned to approximately 22-28 kHz (the authors are not specific on this point). The audible output of the bat detector was recorded on a tape recorder (type not specified) during aggression tests, and the number of ultrasound sequences and duration of the ultrasound sequences were determined by transcription of this tape. (A sequence was defined as a chain of ultrasounds separated by breaks of 2 s or less between pulses.) In addition to the bat detector, vocalizations were recorded during a few tests using a condenser microphone (Brüel and Kjaer, Type 2610) and TEAC R-210-A tape recorder. (Frequency response characteristics of this system are not given by the authors.) The microphone was positioned 60 cm above the floor of the observation box. Sounds were recorded at a tape speed of 30 in./s, and the tapes were played back at 7.5 in./s for spectrographic analysis using a Kay 7800 spectrograph. Animals were tested under red illumination during the dark phase of their light-dark cycle. An open field apparatus (90 x 90 cm) was used to examine locomotor activity.

Fifty-six rats served as subjects in Experiment 1. Pairs were observed in 30-min aggression tests (as previously de-

scribed). A total of 111 aggression tests were performed. Half of the rats served as residents and half served as intruders, with each resident being exposed to 4 different intruders. It is not clear how often individual intruders were exposed to aggressive residents. Aggressive and submissive behavior patterns and ultrasounds were recorded as previously described. In general, the 2 measures of ultrasound were positively correlated with 3 of the 6 aggressive behavior patterns recorded, negatively correlated with 2 of them, and showed no relationship to the sixth. In addition, analyses of the sequential relationship of ultrasounds and aggressive behavior patterns indicated that there was no difference between the distribution of behavior patterns occurring just prior to and immediately following ultrasounds. However, the distribution of aggressive patterns during ultrasound emission was significantly different from the distribution just prior to and following ultrasound.

Thirty-two rats (some of which had been subjects in Exp I) were utilized in Exp IIa, which examined the effect of deafening on aggressive behavior. A probe was used to destroy the eardrums and middle ear ossicles of the 16 experimental group subjects. Three separate operations were performed to ensure complete deafness. Pairs of animals were tested in aggression tests in the observation box, as in Exp I. It is not clear whether both animals of a particular test pair were deafened, although this seems to be the case. There were no significant differences between the deafened and intact groups on 4 of the 6 measures of aggression, but the deafened animals spent significantly less time in boxing and wrestling than did the control pairs.

Thirty-two rats (some had been subjects in Exp I) served as subjects in Exp IIb. Half of the subjects in Exp IIb were muted by transection of the inferior laryngeal nerve; the remaining half, the control group, received a sham operation. There were no significant differences between control and muted subjects during post-operative aggression tests.

Locomotor activity in the open field and in the home cage was examined in several intact, deafened, muted, and sham-operated rats. Deafened rats were more active than intact rats in the open field, but there were no differences in locomotor activity in the home cage. There were no differences in locomotor behavior between muted and sham-operated rats.

For the spectrographic analysis, recordings were made during aggression tests of 4 pairs of intact animals. It is not clear whether these recordings were made during Exp I, IIa, or IIb. Spectrographic analysis of the ultrasounds indicated that the most common type of sound emitted was long pulses (600-2,400 ms) of 22-28 kHz. These sounds sometimes showed small frequency drifts at the beginning or end of a pulse. The authors state that these sounds were "usually emitted by the rat displaying the submissive postures," but it is not clear how they were able to determine this unambiguously. Shorter pulses (20-90 ms) of 25-34

kHz were also emitted; these were sometimes recorded during vigorous body movement (e.g., wrestling). No actual sonagrams or descriptive statistics of the sound characteristics are presented.

The results of Exp I (aggression tests in intact animals) indicated that the occurrence of 22 kHz sounds was positively correlated with some measures of aggression. The authors argue that this correlation contradicts the suggestions of previous studies (Adler & Anisko, 1979; Lore et al., 1976; Sales, 1972) that these sounds acted to inhibit aggressive behavior. They point out that these differences may be due to behavioral differences in the strains of rats tested (although Sales, 1972 also used the Wistar strain) or to differences in the testing procedures themselves. The results are consistent, however, with those of Thomas et al., (1983), which showed that neither deafening of the resident male nor devocalization of the intruder were associated with changes in aggression level during aggression tests.

The results of Exp IIa indicate that deafening the animals resulted in lower levels of aggression, suggesting that "some sonic factor" (either ultrasonic or audible) may be important in eliciting fighting in rats. The fact that deafening the animals did not result in increased levels of aggression suggests that, contrary to the hypotheses of other authors, ultrasonic emissions do not act to lower aggression. The authors argue that, if the 22 kHz sounds inhibit aggression by dominant rats, muting the animals (in Exp IIb) should have resulted in higher levels of aggression. Higher levels of aggression were not seen here, thus not supporting the hypotheses about the inhibitory effects of 22 kHz sounds.

This study has several methodological flaws which may account for some of the findings; however, at the very least, the results of the aggression tests seem to demonstrate that 22 kHz vocalizations do not function in a simple way to inhibit aggression. Further, the suggestion that strain differences in aggression and in the function of the 22 kHz vocalization may exist should be kept in mind when considering the literature on rat ultrasounds.

## Sexual Behavior

Anisko, J.J., Suer, S.F., McClintock, M.K., and Adler, N.T. Relation between 22-kHz ultrasonic signals and sociosexual behavior in rats. Journal of Comparative and Physiological Psychology, 92, 821-829 (1978).

Studies prior to this (e.g., Barfield & Geyer, 1975; Karen & Barfield, 1975) concentrated on the occurrence of the 22 kHz ultrasound following ejaculation in the male rat. This study

examined the occurrence of the call during the entire sequence of copulation in rats. In addition, because the size and complexity of the testing apparatus can affect behavior of the animals in the testing situation, the rats were observed in a larger enclosure than in previous studies.

Subjects were 7 sexually experienced male CD Sprague-Dawley rats, 150-200 days of age. The "stimulus females" (age, sexual experience, and strain not specified) were ovariectomized and brought into behavioral estrus with estrogen and progesterone injections prior to testing. The testing apparatus (overall floor area 152.4 cm x 152.4 cm) consisted of an open-field area and another area containing three smaller compartments, with a narrow passageway between them. Animals were tested during the dark phase of the light-dark cycle; the apparatus was illuminated by red light during testing. During testing, the male was placed in the apparatus for a 15-min period prior to introduction of the female. Male and female behavior patterns were scored, but these are not explicitly defined. A test continued until the occurrence of a 30-min period without an intromission by the male, or until a 60-min period without an ejaculation. Males were tested twice at intervals of at least 1 week. It is not clear how often stimulus females were used in tests.

Vocalizations were monitored using a Grason-Stadler preamplifier/microphone Model 701 (.5 in. diameter), a Grason-Stadler amplifier Model 726, and a band-pass filter. The half-power points of the filter were approximately 20 and 25 kHz. After filtering, signals were displayed on an oscilloscope. A second beam of the oscilloscope also displayed a signal whenever a vocalization was detected within the filter passband. In addition, the unfiltered original signal was displayed on a third channel of the oscilloscope. The original signal contained all frequencies picked up by the microphone. The microphone was attached to a pole assembly which could be moved by the experimenter in order to keep it in position near the subject. However, no estimate of distance from microphone to subject is given.

A 22 kHz "calling bout" was defined as a set of "bursts" (discrete waveforms) separated by less than 30 s. Forty-five percent of the ejaculatory series in this study were accompanied by 22 kHz ultrasound during the preejaculatory period. This calling bout most often took the form of single bursts of sound, rather than longer bouts, as is common during the postejaculatory period. Preejaculatory vocalization was more common during later ejaculatory series than early series. Most of this preejaculatory calling occurred during the period just prior to ejaculation, but it was present throughout the preejaculatory period. Approximately 70% of these calls occurred when the male chased the female; 26% were associated with female aggression towards the male. The authors seem to assume that the male was emitting these sounds; however, they do not address this point specifically. Presumably, the microphone would have been positioned close to both animals (who would have been in proximity to one another

during these behavior patterns) and would have picked up signals from either animal.

Twenty-two kHz ultrasounds occurred during 69% of the postejaculatory intervals (PEIs). These sounds were more common during early series; 22 kHz sounds were detected during 83% of the first 3 series (across all subjects). Percent of the PEI spent calling also declined in later series. Most calling occurred during the first three-quarters of the PEI, although some calling occurred throughout the PEI. Calling during the PEI apparently did not inhibit female solicitation behavior; there was no difference in number of solicitations during periods when males were calling and periods when they were not calling. (Once again, it is not made explicit how the experimenters determined which animal was calling.) This test and several other statistical tests indicated no relationship between male calling and inhibition of female sexual behavior or approach.

The results presented here differ somewhat from those of previous studies. In particular, the high incidence of preejaculatory 22 kHz calling, and the fact that a high percentage of PEIs were not accompanied by calling, indicate that the 22 kHz call is not as clearly associated with the PEI as previous authors (e.g., Barfield & Geyer, 1975) suggested. In addition, the fact that female solicitation apparently is not inhibited by 22 kHz calls is inconsistent with the hypothesis (Barfield & Geyer, 1972, 1975) that the call functions to inhibit female sexual behavior during the PEI. The authors suggest that the meaning of the 22 kHz signal may be more general than has previously been proposed; the male "may be informing conspecific individuals that he is unable to function optimally in a social situation." The effect of the call on the behavior of conspecifics may differ, depending on the context (postejaculatory, preejaculatory, following attack) in which it is delivered.

The authors point out that their results may differ from those of previous studies because their tests were of longer duration; previous studies terminated the observation period after only a few ejaculations had been completed. The results from the early copulatory series of this study are similar to results of previous reports. In addition, the testing apparatus used here was much larger than those used in previous studies. Although the authors point out that this may have impacted their results, they report no data on use of the enclosure by the animals during the testing sessions.

Adler, N., and Anisko, J. The behavior of communicating: An analysis of the 22 kHz call of rats (Rattus norvegicus). American Zoologist, 19, 493-508. (1979).

This paper briefly reviews the occurrence of the 22 kHz ultrasound in rats, noting that the call has been reported to occur in many different contexts. The work of Anisko et al.,

(1978) is discussed in some detail. The authors hypothesize that, in all the conditions in which the 22 kHz call is emitted (e.g., following ejaculation, following shock, following aggression by a conspecific), the rat is in a similar psychological state. Thus, although the contexts of call emission differ, the message conveyed may be essentially the same. Several experiments are reported which attempt to examine this.

In the first experiment, the authors investigated whether a 22 kHz call which had been elicited in one situation (namely, sexual behavior) would function appropriately in a different context (namely, aggression). Six male rats served as residents during this study; 36 others served as intruders. (No further information on subject characteristics is given.) An intruder was placed in a resident's home cage, and the rats were observed for 10 min. Latency to 22 kHz ultrasound and latency to a pin or bite (agonistic behaviors between the 2 males) were recorded. No information is given concerning ultrasound detection equipment.

Residents were tested 6 times with a different intruder each time. Intruders were tested twice, once under each of two conditions. In the sex condition, resident-intruder tests began immediately after the intruder had completed one ejaculatory series with a female. Sexual behavior took place in the resident's cage, with the resident separated from the copulating pair by a wooden partition. Aggression testing began after removal of the female. (It should be noted that this would not have eliminated odor or auditory cues relevant to copulation that may have been apparent to the resident male.) In the control condition, the intruder had not participated in sexual behavior, but had been placed in the resident's cage, separated by a partition, for a 15-min period prior to testing.

Latency to the onset of calling during the "aggression" phase of testing was significantly shorter when males had just copulated with a female than when they had not. (This finding is not surprising, given that 22 kHz vocalizations following ejaculation have been reported in many previous studies.) Latency to a pin or bite was significantly longer when the intruder had recently copulated with a female. The authors maintain that these findings indicate that a 22 kHz call produced in a sexual context can function in an appropriate way (namely, to inhibit aggression) in an agonistic context. Due to control problems (previously stated), however, it is not clear whether the resident rats were responding to ultrasounds or some other stimuli during the tests.

Another study by the authors (in progress at the time of this publication) examined shock-induced 22 kHz ultrasounds. Ten rats (no further information given) received shocks while in a shuttle box. Five subjects received single shocks of 0.6 ma; the remaining 5 received single shocks of 1.3 ma. Latency to begin 22 kHz ultrasound was significantly shorter in the 1.3 ma condition; however, duration of vocalizing was the same for both

groups. According to the authors, the duration of ultrasound emission following these shocks is very similar to ultrasound duration following ejaculation (but no data are presented). Adler and Anisko argue that, because 22 kHz sounds always occur following some delay period, and because duration of the calls is similar in different contexts, this suggests that these vocalizations may be due to similar "organismic states." No data are presented to support this statement, although published data concerning the latency and duration of the 22 kHz calls in various contexts certainly were available at the time of this publication.

Barfield, R.J., Auerbach, P., Geyer, L.A., and McIntosh, T.K. Ultrasonic vocalizations in rat sexual behavior. American Zoologist, 19, 469-480 (1979).

This paper is a useful review of much of the data published through 1978 on ultrasounds and rat sexual behavior. Two previously unpublished studies are briefly described. In one study, female rats were tested in a Y-maze for preference for "ultrasonic calls" (not described further) vs. silence. The females showed a "consistent preference" for the ultrasounds. The study is not described further, but it appears from the information given that adequate control stimuli (e.g., sounds other than ultrasonic, etc.) were not presented to the females. Females may show a preference for any sound over silence. In another study, which is only briefly described, females were tested with males in a tether apparatus which restricted the movement of the male. Females were tested with their hearing intact, and were tested again after being deafened. Females darted less often after being deafened, but there were no differences in measures of intromission and ejaculation latency. These results suggest that ultrasonic emissions may elicit some aspects of female behavior, but other aspects of behavior do not seem to be affected when females cannot hear.

Barfield, R.J., and Geyer, L.A. Sexual behavior: Ultrasonic postejaculatory song of the male rat. Science, 176, 1349-1350 (1972).

This study is the first published report of the occurrence of 22 kHz ultrasounds following ejaculation in the male rat. Sexual behavior of 11 male rats was observed (5 sexually experienced rats approximately 150 days old, 3 sexually experienced rats 12-18 months old, and 3 sexually inexperienced rats 70-90 days old). Each rat was observed with an estrus-induced female; it is not clear how many female rats served as subjects. Observation sessions lasted until 4 ejaculations occurred or mating activity ceased.

Ultrasounds were monitored with a Holgate ultrasonic receiver (bat detector) tuned to 22 kHz. Ultrasounds were monitored

both auditorily (using the bat detector) and visually (using an oscilloscope). Duration of the calls, as well as the occurrence of other sexual behavior patterns, was recorded during testing. Some recordings of the ultrasounds were made using a Brüel and Kjaer 0.64 cm Model 4136 microphone and Precision Instruments 6200 tape recorder (tape speed 95 cm/s). Frequency response characteristics of the recording system are not given. Sounds were played back at one-tenth recording speed and analyzed using a Kay sonagraph model 7029-A.

All subjects emitted the 22 kHz sounds during the PEI, but amount of time spent calling varied considerably among subjects. These sounds were never detected during other phases of sexual behavior. In general, ultrasound emission began shortly after ejaculation and continued during the first three-quarters of the postejaculatory interval (approximately 10 min). During ultrasound emission, the males generally were lying on the cage floor, but sometimes sounds were emitted while the males self-groomed or moved about. Females generally stayed away from the male and remained relatively inactive while the male was calling (although they sometimes approached the male and sat nearby). The authors seem to assume that the sounds are produced by the males, but they do not discuss how they were able to determine this. The calls appeared to be correlated with respiration pattern (presumably of the male). Analysis of the recordings indicated that the call consisted of 22-23 kHz pulses of 1-3 s duration, with amplitude fluctuations within and between pulses. Intensity sometimes reached 80 dB (measured 1-2 cm from the rat's head). No sonagrams are presented, but a sample oscilloscope trace of a call is.

The authors hypothesize, based on these and other observations of the 22 kHz ultrasound, that this signal reflects a state of social withdrawal. They also suggest that the emission of the call may be correlated with the male's absolute refractory period, during which male copulatory behavior apparently is not physiologically possible. They suggest that the call may function to inhibit the female's sexual behavior during this time.

Barfield, R.J., and Geyer, L.A. The ultrasonic postejaculatory vocalization and the postejaculatory refractory period of the male rat. Journal of Comparative and Physiological Psychology, 88, 723-734 (1975).

A series of 4 experiments examined 22 kHz ultrasounds emitted following copulation in rats. Experiment 1 was designed to examine the 22 kHz sound and the associated male and female behavior during rat sexual behavior. Experiment 2 examined the electroencephalograph (EEG) patterns which accompanied emission of this vocalization. Subjects were adult male Long-Evans hooded rats and Long-Evans and Sprague-Dawley females. The males had previously been determined to be reliable maters. The females were ovariectomized and brought into behavioral estrus prior to

testing with injections of estradiol and progesterone. Exact numbers and ages of subjects used are not given. Tests were carried out during the animals' dark phase. A male and female were placed in the testing apparatus (a 10-gal aquarium with cedar shavings on the floor) and mounts, intromissions, ejaculations, and 22 kHz signals were recorded. Pairs were observed until the first intromission following the third ejaculation.

Ultrasounds were monitored using a superheterodyne receiver (Holgate), which produced an audible output, and an oscilloscope, which provided visible output. Presumably, the receiver was tuned to approximately 22 kHz, but the authors are not specific on this point. In addition, ultrasounds were recorded by outputting from the receiver to the integrator channel of a polygraph (which was used for EEG recording). This recording provided an "on/off trace" which matched the audible signal from the receiver.

Some of the males tested had hippocampal and cortical electrode implants from which EEGs were recorded. Cables from these electrodes ultimately fed into a Grass Model 79 polygraph. This arrangement allowed EEG recording from moving animals during testing.

Eight males apparently were observed for Exp 1. A qualitative description is given of the 22 kHz ultrasound and the behaviors which accompany it, along with some quantitative measures. Following ejaculation, the male rat may self-groom briefly and then lie down. Emission of the 22 kHz sound generally begins within the first minute following ejaculation, and continues throughout approximately the first three-quarters of the postejaculatory interval. The postejaculatory interval itself increases in duration across successive ejaculations in the same rat, and the length of time spent emitting the 22 kHz signal increases also. After this period, the male begins to move about, and mating behavior is reinstated. During the time the 22 kHz signal is being emitted, the male shows a distinctive breathing pattern, with 1-3 s exhalations that are correlated with sound emission, and brief (0.25) pauses for inhalation. The authors state that the sound emitted is an almost pure tone of 22-23 kHz, with little frequency modulation but a great deal of amplitude variation. They present no quantitative data, sonograms, or oscilloscope tracings to substantiate this statement, and it appears to be based on their observations of the oscilloscope tracings during testing.

Females were also observed to emit the 22 kHz signal after an intromission or ejaculation. No data are presented concerning how frequently this occurred or what percentage of the females emitted the sound. The authors state that, in the females, the occurrence of the ultrasound was "usually associated with a defensive attitude and may be caused by painful stimuli resulting from the copulation." Some males also briefly emitted 22 kHz

signals during the period just prior to ejaculation, but this apparently was rare.

The results of Exp 2 indicated that the EEG patterns of the 4 male rats which were monitored were characteristic of an awake, alert animal during the beginning of the postejaculatory interval, when the animal was moving about and self-grooming. This behavior changed to a more slow-wave, sleep-like pattern when the male laid down and began vocalizing. The slow-wave pattern continued while the animal was lying down, regardless of whether vocalizations were occurring at the time. These ultrasounds therefore are not necessarily characteristic of a rat with a sleeplike EEG, but the sounds are accompanied by these slow-wave patterns most of the time.

Previous studies have indicated that shock administered to male rats during the postejaculatory interval shortens the interval to a certain extent (at most, to about 75% of its normal duration), resulting in an earlier reinstatement of mating activity. Shocks are not effective at reinstating mating activity during the first 75% of the postejaculatory interval, leading some to hypothesize that this represents an absolute refractory period, during which mating activity cannot be reinstated in the male rat. Exp 3 examined whether the ultrasound period during the postejaculatory interval corresponds to this absolute refractory period. Subjects were 8 Long-Evans males. Testing conditions were as in Exps 1 and 2. All subjects served in each of 3 conditions: (1) normal testing, no manipulation; (2)shock; (3) a new stimulus female supplied 1 min after each ejaculation. Shocks (1-3 ma., 0.5 s) for condition (2) were delivered via skin electrodes attached to the flanks. Shocks were delivered "every 30 s," presumably during the postejaculatory interval, although this is not made explicit.

Results indicate that shock did decrease the postejaculatory interval, but introduction of new stimulus females did not. The male never reinstated mating behavior while still vocalizing. The authors also "unexpectedly" found that shocks increased the time spent emitting ultrasounds, which is not surprising given that 22 kHz ultrasounds are often emitted by rats in response to aversive stimulation.

In Exp 4, the authors delivered shock only after termination of the 22 kHz signal, since in Exp 3, shock prior to this time had resulted in lengthening of the vocalization period. Long-Evans males (n=8) were used; general testing procedures were the same as previously mentioned. Subjects served in each of 3 conditions: (1) normal testing, no manipulation; (2) "preshock (to set shock level) and wires attached"; and (3) "preshock and a single shock delivered within 10 s after spontaneous cessation of vocalization." The characteristics of the preshock and when it was delivered (presumably sometime prior to the cessation of 22 kHz ultrasound) are not clear. Results indicated that, in condition 3, mating behavior was reinstated approximately 36 s after

ultrasounds ceased. This condition was much faster than when no shock was delivered during the postejaculatory interval. Both conditions 2 and 3 resulted in significantly longer vocalization time than under the no shock condition.

The authors contend that their results support their hypothesis that the vocalization period following ejaculation corresponds to the absolute refractory period. The male never reinitiates mating behavior during the vocalization period, and the 22 kHz sounds are emitted during a period of slow-wave, sleeplike EEG activity. Mating behavior could be stimulated by shock given very soon after termination of 22 kHz ultrasounds, indicating that rats are capable of sexual behavior almost immediately after they stop emitting ultrasounds. The authors argue that, given the situations in which 22 kHz ultrasounds are emitted (postejaculation, during aggression, following strong aversive stimulation), these signals may indicate a state of behavioral inhibition on the part of the rat.

Brown, R.E. The 22-kHz pre-ejaculatory vocalizations of the male rat. Physiology & Behavior, 22, 483-489 (1979).

The relationship between the preejaculatory 22 kHz call and other sexual behavior patterns was examined in 2 experiments. Eight sexually experienced male hooded rats (OLAC), at least 120 days of age, served as subjects. Ovariectomized, estrus-induced females (age and strain not specified) were also used in the mating tests. The male and female were placed in a 24 x 44 x 25 cm arena, and allowed to engage in sexual behavior until the male was satiated (30 min without an intromission or 1 h without an ejaculation). Individual males were tested 2 or 3 times; it is not clear how often females were tested. Mounts, intromissions, ejaculations, and ultrasounds were scored. Ultrasounds were monitored using a Holgate MK V ultrasonic receiver, and were recorded using a Washington Oscillograph 400 MD/2 chart recorder. During the preejaculatory period, the receiver was alternately tuned to 15-25 kHz and 40-50 kHz in an apparently random fashion. Placement of the microphone in relation to the animals is not discussed. A total of 19 mating tests were conducted.

Short bursts of 45 kHz sometimes occurred during early ejaculatory series. Twenty-two kHz preejaculatory vocalizations did not begin until late in the tests; the median ejaculatory series on which they were first detected was the fifth series. The ejaculatory series just prior to the beginning of 22 kHz sounds was compared to the series during which these calls began. Results indicated that, during series in which 22 kHz sounds began, there was a significant increase in the number of mounts, but the rate of intromission decreased, indicating that the male achieved intromission on fewer of the mounts. The author hypothesizes that these changes may be due to fatigue on the part of the male,

or to changes in the female's behavior due to fatigue or satiation.

Exp 2 examined changes in the female's behavior which were correlated with the onset of 22 kHz preejaculatory calls. Subjects were 7 sexually experienced females, which were tested in natural estrus with males from Exp 1. Mating tests were conducted as in Exp 1. The female was tested with one male until he reached the satiety criterion. He was then removed and replaced by a second male, which was allowed to copulate for 1 h. Male sexual behavior was scored as in Exp 1. In addition, female lordosis intensity and female agonistic behavior (turning away, kicking, boxing attack) were scored. Results indicated that preejaculatory 22 kHz calls were associated with lower lordosis intensity and higher levels of aggression by the female.

The results indicate that 22 kHz preejaculatory calls are associated with changes in the behavior of both the male and female as a copulatory episode progresses. However, neither the specific circumstances which elicit the vocalization (e.g., female aggression, changes in the internal state of the male), nor its communicative function, can be determined from the data presented here. It should be noted that the author apparently assumed that all 22 kHz sounds detected during the course of the study were emitted by the male, but this may not have been the case. In addition, the author was interested only in 22 kHz ultrasounds, but sounds of other frequencies also are emitted by both males and females during sexual behavior. These vocalizations may have been correlated with many of the behavior patterns examined here, making the patterns of behavior during sexual activity much more complex than is presented.

Geyer, L.A., and Barfield, R.J. Influence of gonadal hormones and sexual behavior on ultrasonic vocalization in rats: I. Treatment of females. Journal of Comparative and Physiological Psychology, 92, 438-446 (1978).

The authors examined the influence of female olfactory cues on ultrasound emission in males by presenting male rats with females of differing hormonal states, and by exposing the males to a female rat's cage litter. Subjects were 18 male Long-Evans rats, each weighing about 400 g. Fourteen ovariectomized females "obtained from the same source" (presumably they were the same strain as the males) were used as stimulus animals. The test apparatus was a rectangular cage (floor area 56 x 26 cm) divided in half by a Plexiglas divider which had a 10 x 10 cm opening covered by hardware cloth. This opening allowed the animals some contact with one another, but kept the male and female separated during testing. A second, opaque divider could be placed in the center of the cage to further reduce contact during pretest and posttest periods. The top of the cage was covered with Plexiglas on the female's side only. The cage was illuminated by red light, and testing occurred during the animals' dark phase.

Ultrasounds were audibly monitored using a Holgate receiver tuned to 50 kHz. In addition, signals in the 15-100 kHz range were monitored visually on a Hewlett-Packard Model 130C oscilloscope. The authors state that the microphone was located "25 cm above the male"; this is best regarded as an estimate as the male would have been moving during testing. The cover over the female's half of the cage was intended to lessen the chance that female ultrasounds would be recorded.

Each male was tested in the following order: (1) two "mating experience tests" (PRE 1, PRE 2); (2) six vocalization tests; (3) two additional mating tests (POST 1, POST 2). During PRE 1 and PRE 2, males were tested with estrus-induced stimulus females until they had achieved two ejaculations (or for a maximum of 2 h). Mounts, intromissions, and ejaculations were recorded. These tests were separated by a 1-2 week interval. Vocalization tests (see below) were begun 1-2 weeks after PRE 2. POST 3 and POST 4 occurred at approximately 3 and 6 weeks after vocalization tests began. Behavioral measures were the same as in PRE 1 and PRE 2.

During vocalization tests, a female and male were placed in separate compartments of a divided cage (both opaque and Plexiglas/hardware cloth dividers in place). After a 2-min period, the opaque divider was removed; it was replaced 5 min later, and the rats remained in the cage for another 2 min (total test time 9 min). The occurrence of 22 kHz and 50 kHz ultrasounds during the time the male and female were in the cage was recorded. Each male was tested 6 times, once in each of the following conditions: (1) clean litter on the other side of the cage (CL); (2) other side of cage empty but previously occupied by an estrus female for 30 min (SOI); (3) untreated ovariectomized female on other side (OVX); (4) estrogen-treated ovariectomized female on other side (E); (5) estrogen- and progesterone-treated female on other side (EP); and (6) estrogen- and progesterone-treated female on other side; the female in this condition had been given two intromissions with another male just prior to testing (EPI). Males were tested in these conditions in a random order; tests of an individual male occurred 5-10 days apart. Stimulus females were used in up to 4 tests per day.

The authors examined several measures of vocalization. Ultrasounds of 50 kHz were detected in all conditions except CL. It was not possible to detect which animal emitted the 50 kHz sounds. When 22 kHz pulses were observed, their duration was generally less than 1 s, which is briefer than those normally observed during the postejaculatory interval. The authors attribute the 22 kHz sounds to the male, since they generally were seen to be correlated with the male's breathing pattern. In general, the results indicated the following ordering of conditions in terms of rate and maintenance of ultrasound emission (highest to lowest): EP > E > EPI = OVX > SOI > CL. In some tests, 50 kHz and 22 kHz ultrasounds were closely associated with

one another in time, and in some, an abrupt transition (less than 60 s) was seen from 50 kHz to 22 kHz vocalizations. These transitions, according to the authors "were characterized by agitated efforts of both rats to make greater contact." (No objective behavioral measures are presented on this point.) Males whose EP vocalization tests showed these transitions showed significantly shorter intromission latencies than other males during mating tests. In addition, there was a significant correlation between peak vocalization rate during the EP condition and intromission latency during PRE 2; rats that vocalized more had shorter intromission latencies.

These results demonstrate that female odor alone (SOI condition) elicited ultrasound from males, whereas simply moving them to a new cage (CL condition) did not. Ultrasound did not occur at a high rate, nor was it maintained, however, in the SOI condition, indicating that cues other than odor are important. The relationship of ultrasound pattern (transition from 50 to 22 kHz sounds) and ultrasound rate to intromission latency "suggests that specific information regarding readiness to copulate may be included in the vocalization."

The authors noted ultrasonic emission by females during the course of Exp 1; therefore they designed Exp 2 to test the effectiveness of estrous and nonestrous anesthetized females in eliciting male ultrasound. Subjects were 21 male Long-Evans rats, weighing at least 400 g. Stimulus females used in Exp 1 also were used in Exp 2. Testing apparatus and procedures were the same as for Exp 1. Each male received 2 mating experience tests. There were 4 treatment conditions: (1) male tested with estrogen- and progesterone-treated female (EP); (2) male tested with estrogen- and progesterone-treated anesthetized female (EP anes); (3) male tested with estrogen- and progesterone-treated female in the dark (no red light; EP dark); and (4) male tested with ovariectomized, untreated anesthetized female (OVX anes). The authors do not state why the male and female were tested in EP dark condition; no specific hypotheses are mentioned. Each male was tested once in each treatment condition.

The general pattern of results for ultrasound production took the form EP = EP dark > EP anes > OVX anes. Males vocalized more with estrous females than with the ovariectomized female; they also vocalized more with conscious females than unconscious females. There were no differences in the estrous female/dark and estrous female/red-light conditions. Besides not vocalizing, the anesthetized females also did not emit other behavioral cues which would be emitted by an awake female. The authors conclude that some form of interaction between the male and female is important in eliciting high rates of male ultrasound. A point that is not discussed by the authors is that, in the conditions in which the female was conscious, she may have been emitting some of the ultrasounds; this may account for the higher rate of ultrasounds in these conditions.

In general, the results of these experiments indicate that the following factors influence amount of 50 and 22 kHz ultrasound during mating tests: actual presence of the female (soiled litter presenting odor cues is not as strong a stimulus as the female herself), hormonal state of the female, and cues other than odor (such as movement) presented by the female.

Geyer, L.A., and Barfield, R.J. Regulation of social contact by the female rat during the postejaculatory interval. Animal Learning & Behavior, 8, 679-685 (1980).

The role of the male and female in regulating contact during the postejaculatory interval and the relationship between male-female proximity and 22 kHz ultrasounds were examined. Subjects were 10 ovariectomized, sexually inexperienced 4-month-old Long-Evans females. Ten sexually experienced 12-month-old males (strain not specified) were utilized in sexual behavior tests. Behavioral estrus was induced with estrogen and progesterone injections prior to testing. Mating tests were conducted in a 104 x 52 x 29 cm cage with a slate floor marked off in an 8 x 4 grid (in order to score locomotion and distance). Mounts, intromissions, ejaculations, female darting, locomotion, and separation between the male and female were scored during mating tests. Ultrasounds were monitored using a Holgate ultrasonic receiver and an oscilloscope. The receiver was tuned to 50 kHz prior to ejaculation, and to 22 kHz during the postejaculatory interval. Each female was tested twice, with a 2-week interval between tests. Females were not tested with the same male twice. A mating test lasted until the first intromission following the third ejaculation.

Behavioral measures were examined for differences across ejaculatory series (first vs. second vs. third ejaculation) and between the females' first and second mating tests. Because the experimenters felt that the 50 kHz ultrasounds were not reliably detected, these data were not analyzed. For the 22 kHz calls, vocalization termination (time from ejaculation to termination of the 22 kHz vocalization) differed between the first and second tests, with vocalization lasting longer during the second test. Duration of the 22 kHz signal was also influenced by the female's experience; in second tests, duration was significantly longer than in first tests. Females spent more time moving than did males, and, during the second test (when they were "experienced") they spent more time at a maximum distance from the males than they did during the first test.

In general, animals were farther apart during periods when 22 kHz ultrasounds were occurring than when they were not occurring. The authors use this correlation between distance and 22 kHz ultrasound to suggest that the female responds to these signals by actively staying away from the male. (Since the male is generally inactive during this period, the female is largely responsible for maintenance or avoidance of contact.) However,

demonstrating that these 2 behaviors (cessation of 22 kHz vocalization and resumption of female proximity to male) have the same time course during the postejaculatory interval is not sufficient to demonstrate any communicative function of 22 kHz sounds. This suggestion is also based on the assumption that the males (rather than the females) are emitting the 22 kHz signals. This assumption may be the case, but the authors do not state whether they were able to determine this.

Geyer, L.A., Barfield, R.J., and McIntosh, T.K. Influence of gonadal hormones and sexual behavior on ultrasonic vocalization in rats: II. Treatment of males. Journal of Comparative and Physiological Psychology, 92, 447-456 (1978).

These experiments were designed to examine the hypothesis that male rat ultrasounds reflect the male's state of "sexual readiness." Behavioral and hormonal treatments which influence the male's sexual behavior were administered, and the effects of these treatments on ultrasound production were examined.

Subjects in Exp 1 were 20 male Long-Evans rats, weighing at least 400 g. Each participated in 2 "mating experience" tests, in which the male was given a maximum of 2 h to achieve 2 ejaculations with a receptive female. The subjects had previously participated in an experiment "similar to this one." The 20 female "stimulus animals" were ovariectomized, sexually experienced, Long-Evans rats. Housing conditions and testing conditions were as described in Geyer & Barfield (1978). As in that study, incidence of both 50 kHz and 22 kHz ultrasounds was recorded during vocalization tests of male-female pairs. Each male was tested once in each of 3 conditions: (1) untreated; (2) intromission, in which the male had achieved 3 intromissions with a receptive female 1 min prior to the beginning of the vocalization test; and (3) sexual fatigue, in which the male had participated in 2.5 h of sexual activity the day prior to the test. The sexual fatigue condition was intended to "sharply reduce the sexual readiness of the male." Males were tested once per week. Females in the vocalization tests were brought into behavioral estrus with injections of estrogen and progesterone prior to being tested. Two additional mating tests were given at some point following vocalization tests.

The highest number of ultrasounds (50 kHz and 22 kHz sounds combined) occurred in the intromission condition, followed by the untreated control condition. Ultrasounds were least frequent in the sexual fatigue condition. The 22 kHz ultrasounds which occurred during the vocalization tests were generally of shorter duration than 22 kHz sounds normally noted during the postejaculatory interval. Ultrasounds of both 50 and 22 kHz occurred throughout some tests. In some tests, there was an "abrupt" transition (i.e., a pause of less than 60 s) between 50 kHz sounds and 22 kHz sounds. This transition was most likely to

occur in the intromission condition, and least likely to occur in the sexual fatigue condition. Other behavior patterns also varied with condition. The males spent the most time with their noses to the screen in the untreated condition, followed by the intromission condition, then the sexual fatigue condition. Females "darted" (a female solicitation behavior) most often in the intromission condition, followed by the control condition, and the sexual fatigue condition. In the post-vocalization test mating tests, males which had made the 50 kHz-to-22 kHz transition had a shorter latency to intromission than did the other males. Females who had just been exposed to males in the intromission condition during a vocalization test had shorter intromission latencies in mating tests.

The male's respiration pattern was often correlated with the 22 kHz pulses; the authors therefore attribute the 22 kHz ultrasounds to the males. However, high rates of vocalization often occurred when the male and female had their noses in proximity to one another at the screen; it therefore would not have been possible to determine which animal was emitting the 50 kHz sounds at any given time, and the authors point this out.

These results indicate that a male's recent sexual behavior is correlated with ultrasound emission and can influence female behavior (e.g., darting). They also indicate that the male's behavior during the vocalization test influenced the behavior of the female in subsequent mating tests. The authors hypothesize that the 50-to-22 kHz shift seen in some of the males is "a marker for facile sexual arousability."

The rats used in Exp 1 were used again in Exp 2. Data collection, testing procedures, and apparatus used were the same as in Exp 1, with the following exceptions. The cage was modified to reduce contact between the male and female, and to "eliminate a direct line between the female's head and the microphone." (The authors do not elaborate on this point.) The cage was modified by placing a wire box with a Plexiglas lid on the male's side of the wire screen. No explanation is given, but presumably this modification prevented the male and female from making nasal contact through the screen. In addition, the female was confined in a small Plexiglas box during the 1 min pre- and post-test periods. The males were matched on the basis of prior mating performance and divided into 2 groups. One group was castrated, and the other sham-operated. Vocalization tests were as in Exp 1.

The animals were tested weekly for 5 weeks following surgery. In general, castrated animals vocalized less than controls, and their latency to vocalize was longer. Nose-to-screen behavior was higher for both males and females in the intact condition than in the control condition. There were no instances of 50-to-22 kHz "transitions." It should be noted that large numbers of the subjects died (4 out of 10 in the intact group; 2

out of 10 in the castrated group), but the authors do not discuss why this might have occurred.

The authors maintain that the results of these experiments indicate that ultrasounds reflect the "sexual readiness" of the male. They occurred most often in males which had received some sexual stimulation just prior to the test, and least often in sexually fatigued males and castrated males. Darting by the female was most frequent in tests with a high rate of ultrasound, suggesting that these calls may influence female behavior. There were many other cues present in the testing situation which also may have influenced the female's behavior, however, so a definite communicative function for the calls was not established in this study.

Geyer, L.A., McIntosh, T.K., and Barfield, R.J. Effects of ultrasonic vocalizations and male's urine on female rat readiness to mate. Journal of Comparative and Physiological Psychology, 92, 457-462 (1978).

The authors examined the influence of ultrasounds and of male rat urine on female rat sexual behavior by exposing solitary females to ultrasounds and to male rat urine and observing the females' behavior during subsequent mating tests. Subjects were 16 sexually experienced, ovariectomized Long-Evans female rats; 20 sexually experienced males served in the vocalization transmission and mating test portions of the study. Urine was collected from other males not being used in the study. Cages used for testing were 52 x 26 x 29 cm, and were covered with foam and cardboard in order to sound isolate them as much as possible. "Transmitting" cages were divided down the center with a hardware cloth divider. A male and female in a transmitting cage were on either side of this divider and thus had limited contact with one another.

Vocalizations could be transmitted from the transmitting cage to the "receiving" cage using a broadcast system which consisted of a 0.64 cm Brüel & Kjaer microphone (Model 4136; flat frequency response to 100 kHz) with a Model 2619 preamplifier and a power supply, a 100X preamplifier, a Krohn-Hite band-pass filter (Model 3550) set at 20-100 kHz, another amplifier, and a condenser microphone head which functioned as a speaker. Ultrasounds produced in the receiving cage and transmitted to the receiving cage were monitored using a Holgate bat detector and an oscilloscope.

Estrus was induced in the subject females prior to testing. During testing, an individual female was placed in a receiving cage, where she was exposed to 1 of 4 treatment conditions for a 5-min period: (1) ultrasounds from a transmitting cage containing an estrous female and a male which had just delivered 3 intromissions (VOC condition); (2) sounds from a transmitting cage containing only an estrous female (C); (3) sounds as in the VCC

condition; in addition, a gauze pad containing male rat urine was placed in the receiving cage (U + VOC); and (4) male rat urine only; no sound transmission (U). Several behavior patterns (including grooming, movement, sniffing, vocalizations by the receiving female, and vocalizations being transmitted) were noted during these vocalization tests. Each female received each of these 4 treatments. It should be noted that ultrasounds being transmitted may have been emitted by the transmitting male, the transmitting female, or both. Following treatment, the female was placed in a cage with a male until 3 intromissions occurred (maximum test time 5 min). Mounts, intromissions, and female darting were scored.

During the vocalization transmission phase of the test, nose-to-screen behavior by the receiving female was higher in the U and U + VOC conditions than in VOC and C conditions, suggesting that the females were attracted to male urine. Female darting (a solicitation behavior) seldom occurred during the vocalization transmission phase. During the mating phase, females in the VOC and U + VOC conditions showed a shorter latency to dart than females in the U condition (darting was not examined in the C condition). VOC and U + VOC females also showed more darts per minute than U females. Some measures of sexual behavior (e.g., mount latency, intromission latency) did not differ across treatments. However, mounting rate was higher in the U + VOC condition than in the other conditions, and the time required to achieve 3 intromissions was briefest in the U + VOC condition, and longest in the U and C conditions (VOC was intermediate).

These results indicate that exposing the female to ultrasounds normally associated with copulation affects later behavior in the mating test. It should be noted that no data are presented concerning the ultrasounds which were actually transmitted to the females, so it isn't clear exactly what the females were exposed to. In addition, no data on the receiving female's vocal response to these transmitted signals are presented.

Karen, L.M., and Barfield, R.J. Differential rates of exhaustion and recovery of several parameters of male rat sexual behavior. Journal of Comparative and Physiological Psychology, 88, 693-703 (1975).

Rats (12 sexually experienced Long-Evans males) were tested (as in Barfield & Geyer, 1975) with estrus-induced females until they stopped achieving intromissions. Several parameters of sexual behavior were measured, such as latency to ejaculation, intromission frequency, and duration of the postejaculatory interval. The occurrence of 22 kHz ultrasounds during the postejaculatory interval was used to distinguish the absolute refractory period from the relative refractory period. The 22 kHz signals were monitored using a Holgate bat detector (presumably tuned to approximately 22 kHz, although this information is not given) and an oscilloscope. Distance from rat to receiver is not

given. The time from ejaculation to beginning of ultrasound emission was recorded, as was duration of ultrasound (presumably the entire period during which 22 kHz pulses were being emitted, although this is not specifically defined). Results involving the ultrasound measures indicate that, during early ejaculatory series, ultrasounds cease after about 65% of the postejaculatory interval has passed. The amount of time spent emitting ultrasound increased in later series, and the postejaculatory interval as a whole increased as well.

Krieger, M.S., and Barfield, R.J. Masculine sexual behavior: Pacing and ejaculatory patterns in female rats induced by electrical shock. Physiology & Behavior, 16, 671-675 (1976).

Subjects in this experiment were 8 male and 8 female Long-Evans rats. Subjects of both sexes were castrated at 5 months of age and implanted with 20 mg pellets of testosterone propionate subcutaneously. Subjects were tested in a 10-gal aquarium with an estrus-induced female for 12 min, and several sexual behavior patterns were recorded. Shocks were delivered to subjects during some tests, and changes in copulatory patterns resulting from this were examined. An unexpected finding during this testing was that 3 of the 8 females displayed the ejaculatory pattern. One of these females was tested further and found to emit 22 kHz ultrasounds during the postejaculatory interval. No quantitative data or spectrograms are presented, and no information is given concerning ultrasound monitoring procedures.

McIntosh, T.K., Barfield, R.J., and Geyer, L.A. Ultrasonic vocalizations facilitate sexual behaviour of female rats. Nature, 272, 163-164 (1978).

Subjects were 16 ovariectomized female Long-Evans rats. In addition, 7 castrated males served as stimulus animals, and 15 males and 15 females (all sexually experienced) provided the ultrasounds for transmission. Female subjects (treated with estrogen and progesterone to induce estrus) were placed in a "receiving" cage with a castrated male, and ultrasounds from a "transmitting" cage were played to the receiving cage. Transmitting cages were divided in half with hardware cloth; the male and female were placed on separate sides of the cage during transmission. The system used to transmit the ultrasounds consisted of a Brüel & Kjaer microphone (0.64 cm, Model 4136), and amplifier, and a filter. This microphone was located over the male's side of the cage (no information is given concerning the approximate distance from the microphone to the male). The sounds were relayed to a microphone head in the receiving cage which was wired to serve as a speaker.

Sexual behavior (darting and lordosis) of the receiving female was observed for a 10-min period under each of 4 condi-

tions: (1) sound transmitted from a cage containing an estrous female and a male which had previously delivered 3 intromissions (VOC); (2) sound transmitted from an empty cage (C); (3) sound transmitted from a cage containing an estrous female and a male which had just delivered 3 intromissions; also present in the receiving cage was a gauze pad impregnated with male rat urine (U + VOC); (4) sound transmitted from an empty cage; male urine present in receiving cage (U).

In the VOC and U + VOC conditions, females darted significantly more often, and latency to dart was significantly shorter, than in the C and U conditions. Lordosis frequency was also significantly higher in the conditions involving vocalization transmission (VOC and U + VOC). During some VOC and U + VOC trials, there was a shift in the frequency of these vocalizations from signals of primarily 50 kHz to 22 kHz signals. Significantly more female darting occurred in tests in which the subject female was exposed to 22 kHz signals than in tests in which no 22 kHz signals occurred.

The authors conclude that "50 kHz vocalizations elicit sexual activity in female rats." This conclusion rests on the assumption that the female subjects were affected by the transmitted ultrasound and the castrated male stimulus animals were not. This assumption may be valid; however, the authors present no data on the behavior of the stimulus males, other than to state that, while they did sniff and nudge the females, they did not mount them. The authors also apparently assume that the transmitted ultrasounds were all produced by the male in the transmitting cage; this may be likely, but there certainly is no basis for ruling out female ultrasounds. In any case, this study does present strong evidence for a communicatory function ultrasounds in rat sexual behavior.

McIntosh, T.K., and Barfield, R.J. The temporal patterning of 40-60 kHz ultrasonic vocalizations and copulation in the rat (Rattus norvegicus). Behavioral and Neural Biology, 29, 349-358 (1980).

The purpose of this study was to examine in detail the temporal relationship between 40-60 kHz ultrasounds and other behavior patterns which occur during copulation in rats. Subjects were 40 sexually experienced male Long-Evans hooded rats. They were tested with ovariectomized females which were treated with estrogen and progesterone prior to testing. Age, strain, and sexual experience of these females were not specified. A male and female were placed in an aquarium (40 x 26 x 29 cm) and the following behavior patterns were scored: mounts, intromissions, ejaculations, female darting, female hopping, 40-60 kHz vocalizations, and postcopulatory 22 kHz vocalizations. Data on 22 kHz ultrasounds was not presented here. A Holgate ultrasonic receiver tuned to 40-60 kHz and an oscilloscope were used to monitor vocalizations. The receiver microphone was mounted at the top of

the testing cage, but no estimate of distance from the microphone to the animals was given. Each male was tested once; it is not specified how often females were tested.

Males did not ejaculate in 12 of the 40 tests; in these tests, latency to emit ultrasound was longer than in tests in which ejaculation occurred. Several measures indicate that more ultrasounds were emitted in tests in which males did not ejaculate, and that vocalizations were less frequent in tests of males which mated at a faster rate. The rate of ultrasound emission was significantly higher in the 10 s preceding intromissions than in the 10 s preceding mounts. Mounts and intromissions were followed by a distinct period of silence, which was significantly longer in the case of intromissions. Ultrasound also increased in the period immediately (within 10 s) preceding ejaculation, and the amount of vocalization preceding ejaculation was significantly greater than the amount preceding intromission.

The authors hypothesize that the higher levels of vocalizing by the slower-mating males indicated a state of high arousal or frustration ("increased arousal levels in sexually excited animals in response to an uncooperative mating partner"). The results of this study, while they do not demonstrate a communicative function of 40-60 kHz ultrasounds, do indicate a clear temporal patterning of these sounds during sexual behavior. These vocalizations increase immediately preceding a mount, intromission, or ejaculation, and there is a distinct pause in vocalization immediately following a mount, intromission or ejaculation.

The authors maintain that the males (rather than the females) emitted the sounds detected during the study, based on the observation that the sounds were "directly correlated" with male behaviors. They present no data concerning this observation, however, and it seems possible that females might have emitted vocalizations correlated with male behaviors in some cases, especially if these behaviors were directed toward the female. The authors apparently counted all occurrences of 40-60 kHz ultrasounds, yet it seems questionable whether this could have been done reliably, since these pulses are often separated by very brief pauses (3-15 ms in some cases).

Parrott, R.F. Effect of castration on sexual arousal in the rat, determined from records of post-ejaculatory ultrasonic vocalizations. Physiology & Behavior, 16, 689-692 (1976).

Male rat sexual behavior was examined for 2 weeks prior to and 3 weeks following castration. Subjects were 20 "sexually vigorous" Wistar rats; they were housed in pairs. They were tested with ovariectomized, estrus-induced females (age, strain, sexual experience not specified). Tests occurred in a 35 x 45 x 44 cm chamber, and lasted for 20 min. Mounts, intromissions, and ejaculations were scored. In addition, at 10 s intervals during the refractory period, the following behaviors (of the male only)

were noted: inactivity, genital grooming, non-genital grooming, exploratory activity, female-directed activity, and ultrasonic emissions. Ultrasounds were detected using an "ultrasonic microphone . . . connected to a Tektronix oscilloscope" (no further information is given). The microphone was attached to the top of the test chamber; no estimate of distance from animals to microphone is given. It is not clear whether the ultrasonic receiver was tunable to a particular frequency, and if so, what frequency was selected. The author assumes that any ultrasounds detected were emitted by the male.

Results indicated that ultrasound duration declined following castration. Significant declines were not seen until 2 and 3 weeks following castration. The number of rats vocalizing also declined significantly by the 3rd week following castration. The author does not provide enough detail concerning procedures used to allow the reader to evaluate the results of this study.

Parrott, R.F., and Barfield, R.J. Post-ejaculatory vocalization in castrated rats treated with various steroids. Physiology & Behavior, 15, 159-163 (1975).

This study investigated the effects of testosterone, 19-hydroxytestosterone, oestradiol, and dihydrotestosterone on the postejaculatory 22 kHz vocalization in castrated rats. Subjects were 29 adult male rats (Wistar, Tuck). The authors state that the rats were "sexually active"; presumably they were sexually experienced. Each subject was observed during a single 20-min test with a receptive female. The authors do not provide information concerning age, strain, or prior sexual experience of these females, nor do they state whether the females were in natural or induced estrus during testing. The testing apparatus is not described. Tests occurred during the animals' dark phase. According to the authors, "all parameters of sexual activity" (these are not specified or defined) were recorded during these tests. If a rat ejaculated prior to the end of the 20-min test period, recording continued until the end of the current postejaculatory interval. In effect, this behavior means that length of testing period may have differed for each rat. If so, this behavior may present a serious control problem, one which is not addressed by the authors.

Ultrasounds were monitored using "a specially constructed microphone and preamplifier circuit" which is not described further. No indication is given concerning the spectral sensitivity of this system or its location with respect to the animals in the apparatus. The output from this device was fed into an oscilloscope, which displayed the sounds being picked up. The investigators recorded the onset and termination of ultrasounds by monitoring their occurrence on the oscilloscope. Presumably, 22 khz sounds specifically were monitored (ultrasounds of other frequencies also occur during sexual behavior), but this is not specified.

Subjects were divided into 5 groups of 5-7 animals, and all males were castrated. Steroid injections were given daily from the time the animals were castrated until the end of the study. The 5 treatment groups were as follows: Testosterone propionate (TP) + dihydrotestosterone propionate (DHTP); 19-hydroxytestosterone propionate (19HTP) + DHTP; oestradiol dipropionate (OP) + DHTP; DHTP only; and vehicle only. Subjects were tested once each week for 3 weeks following castration.

The only behavioral measures presented are number of animals emitting ultrasounds during testing, number of animals ejaculating during testing, refractory period duration, and vocalization duration. Presumably, vocalization refers to the entire period during which 22 kHz ultrasounds were occurring, rather than to the combined durations of the individual pulses or ultrasound sequences, but this is not specified.

In general, the findings seem to indicate that rats treated with TP + DHTP, or with 19HTP + DHTP show normal refractory periods and normal levels of postejaculatory vocalization. DHTP-only animals and animals receiving the vehicle only showed increased refractory periods, but emitted ultrasounds at the same level as the TP + DHTP treated animals. OP + DHTP-treated rats seemed to show a decrease in ultrasound emission, but normal length refractory periods. The authors do not suggest why this might be the case. The results of this study should be interpreted with great caution, however, because of the extremely small sample size of some groups, because of control problems (see above), and because the information provided regarding methodology is insufficient and often cannot be interpreted.

Pollak, E.I., and Sachs, B.D. Excitatory and inhibitory effects of stimulation applied during the postejaculatory interval of the male rat. Behavioral Biology, 15, 449-461 (1975).

Two experiments examined the effects of various kinds of postejaculatory interval "stimulation" on subsequent male rat sexual behavior. Exp 1 examined the effects of presentation of a novel female at various points during a series of ejaculations; vocalizations were not examined in this experiment. In Exp 2 , shocks were delivered to the male at various points during a mating behavior test; the effects on male sexual behavior and on ultrasonic vocalization were examined. Subjects in Exp 2 were 40 sexually experienced Long Evans male rats, approximately 400 days of age. All rats had served as subjects in Exp 1. Stimulus females (age, experience, strain, not specified) were given subcutaneous estradiol benzoate implants to insure receptivity. Subjects were tested in a small aquarium (28 x 25 cm). The males received shocks via 2 safety pin electrodes inserted in the skin of their backs. Shocks were 0.5 s, 1.2-2.9 mA, delivered at 30-s intervals.

The shock level was set for an individual subject by delivering 2 to 4 shocks of various intensities just prior to testing. There were 5 treatment groups, which received shocks at various points during the sexual behavior test. Group P received 2 shocks per minutes throughout the test. Group A (absolute refractory period shock) received 5 shocks at 30-s intervals, beginning 15 s after each ejaculation. Group T received 5 shocks as above, but at 2, 3, and 4 min following the first, second, and third ejaculation, respectively. Group R received shocks at 3, 4, and 5 min following the first, second, and third ejaculations, respectively (these shocks presumably occurred during the relatively refractory period). Group S (control) did not receive shock. Mounts, intromissions, and ejaculations were scored, as were 22 kHz ultrasounds and the respiration pattern which normally accompanies 22 kHz ultrasounds.

Ultrasounds were monitored by ear using a Holgate bat detector (presumably tuned to 22 kHz, since these were the vocalizations of interest to the experimenters, but this is not specified). Because of the "unreliability of the audio signal produced by the bat detector" and because some rats produced sounds of low intensity which could not be picked up by the receiver, the authors assumed that the 22 kHz ultrasound was being emitted whenever the male breathed in irregular pattern normally correlated with the emission of 22 kHz signals. This assumption places serious limitations on the conclusions which can be drawn concerning the occurrence of ultrasounds in this study, since they may have been scored when they were not actually being emitted. In addition, the "unreliability" of the bat detector may call into question results of other studies using this instrument in similar testing situations, unless the authors are referring specifically to the unreliability of the particular detector used in this study. The use of this instrument is not made clear.

Results indicated that time from ejaculation to the termination of vocalization (or breathing pattern) in the postejaculatory interval increased with successive ejaculations; there was no relationship between this measure and when shocks were delivered during the test. In addition, vocalization (or breathing) latency (VL) increased with successive ejaculations. The A and P groups had significantly shorter VL measures than the other groups. Although this point is not discussed by the authors, this result for the A and P groups is probably due to the fact that rats emit 22 kHz sounds in response to aversive stimulation, e.g., shock, and not to any effects of the shock on sexual motivation of the male. The results reported in this study concerning the occurrence of the 22 kHz ultrasound following ejaculation and in response to shock were also reported by Barfield & Geyer (1975).

Sachs, B.D., Pollak, E.I., Krieger, M.S., and Barfield, R.J. Sexual behavior: Normal male patterning in androgenized female rats. Science, 181, 770-772 (1973).

In this study, female rats which received prenatal and postnatal testosterone treatments displayed sexual behavior patterns characteristic of male rats, including 22 kHz postejaculatory ultrasonic emissions.

Pregnant females were treated with testosterone propionate (TP) injections. Their female offspring were treated with TP postpartum, and males were injected with oil on the same schedule. Subjects (both male and female) were gonadectomized and received subcutaneous TP implants at 85 days of age. At approximately 120 days of age, subjects were tested for sexual behavior with a receptive female. Measures of sexual behavior recorded included mounts, intromissions, and ejaculations. All females treated in this way showed normal-appearing ejaculatory responses. In general, patterns of sexual behavior were similar for the males and females.

Ultrasonic vocalizations were recorded during sexual behavior tests of 5 additional females which had received TP treatment as previously described. Ultrasounds were monitored by ear using a heterodyne receiver. In 2 cases, vocalizations were also monitored visually using an oscilloscope. Presumably, the receiver was tuned to 22 kHz, although this was not specified. Twenty-two kHz ultrasounds were detected following ejaculations in all females. The authors state that the (TP-treated) females emitted the signals, but they do not state how they were able to determine this. The proportion of the postejaculatory interval during which ultrasounds were emitted was similar to that reported for males in previous studies. The authors further state that "frequency and amplitude of the vocalizations in the androgenized females were identical" to those of males, but they present no data on this point.

Sales, G.D. Ultrasound and mating behaviour in rodents with some observations on other behavioural situations. Journal of Zoology, London, 168, 149-164 (1972b).

Eleven species of rodents, including laboratory rats, were observed during sexual behavior, and ultrasounds were recorded. Ultrasounds were detected using an ultrasonic frequency converter (or "bat detector") that could be tuned to a range of 5 kHz, and another microphone and broad-band amplifier connected to an oscilloscope which provided a visual readout of the signals. Whenever possible, tape recordings were also made of the sounds, and samples of the ultrasounds were analyzed using a Kay sonograph model 675. Details of the equipment used are presented in Sales, 1972a. In some cases, a verbal description of the behavior observed was recorded on tape simultaneously with the ultrasounds.

Six male and 6 female Wistar rats were observed during 30 heterosexual encounters. Ages and prior sexual experience of the subjects are not specified. Males were introduced into females' cages, and sexual behavior was observed. Some subjects were ob-

served in only one test, while others were observed more than once. Tests lasted 10-30 min, and occurred under red illumination, apparently during the dark phase of the animals' light-dark cycle (although this is unclear).

No quantitative data are presented, which is appropriate given the lack of standardization of testing procedures. Several different types of ultrasounds were detected. When the male first entered the female's cage, during exploration of the cage by the male, and when the male nosed the female, short pulses (3-50 ms) of 50-75 kHz (range 40-116 kHz) were detected. These pulses also occasionally occurred when the male unsuccessfully attempted to mount the female, or during male or female aggressive behavior. When the male sniffed the female's genital region, prior to mounts, and during intromitted mounts, other types of ultrasound were emitted. Some of these sounds were long (100-500 ms) pulses of 40-50 kHz (range 30-55 kHz); these sounds often consisted of a single frequency component with slow drifts in frequency. Second and third harmonics were occasionally present. Sequences of very brief (2-40 ms, with interpulse intervals of 3-15 ms) pulses also occurred in these contexts. The sequences lasted up to 200 ms. Individual pulses within sequences showed one or more frequency fluctuations of up to 70 kHz. Overall frequency range of these sequences was 34-120 kHz. Sample sonograms (A x F x T graphs) are presented of these last two ultrasound types. The author states that these sounds appeared to be produced by the male, apparently since they were most closely correlated with the male's behavior.

Descriptions and sample sonograms of ultrasounds occurring during sexual behavior in the other species observed are also presented. Laboratory mice were the only species studied in detail. It is interesting that Sales does not report any instances of post-ejaculatory ultrasounds by male rats, which were first described by Barfield and Geyer (1972). It may be the case that recording and observation were terminated when a single ejaculatory series was completed; if so, the occurrence of these sounds might have been missed.

Thomas, D.A., and Barfield, R.P. Ultrasonic vocalization of the female rat (Rattus norvegicus) during mating. Animal Behavior, 33, 720-725 (1985).

This paper provides a description of the acoustic characteristics and behavioral contexts of female rat ultrasonic vocalizations during copulatory behavior. Subjects in Exp 1 were 17 Long-Evans females (5 natural estrus, 12 artificially induced estrus) and an unspecified number of sexually experienced, devocalized Long-Evans males. Behavioral testing and recordings took place in a 24 x 49.5 x 24 cm glass aquarium. Behavior of a male-female pair was observed for 5 min. Each female was tested once.

Ultrasonic vocalizations were recorded using a 0.635 cm condenser microphone (Brüel & Kjaer 135) with amplifier (Brüel & Kjaer 2610), a Krohn-Hite 3550 band-pass filter set at 20 and 100 kHz, and a Lockheed Store 4 tape recorder (tape speed 76 cm/s). Recordings were made with the microphone approximately 15 cm from the floor of the test chamber. Recordings were analyzed on a Kay 7029 Sonograph. In addition, ultrasounds were monitored using 2 heterodyne receivers (one Holgate, one QMC), both set at 50 kHz and outputting to a Textronix 5103N oscilloscope. The occurrence of ultrasounds in this frequency range was scored. The authors note that these vocalizations often occurred in bouts of rapid calls, and that there was no way of distinguishing whether a sound was produced by a single animal or by both animals calling simultaneously. Because of this mating, they suggest that the measure of calling obtained using the heterodyne receivers "probably reflects a relative index of the amount of calling rather than a precise amount of individual vocalizations."

Ultrasounds were recorded during all 17 matings. There were no apparent differences between vocalizations of natural estrus and induced estrus females (although no quantitative analyses were performed). Female vocalizations occurred in association with approaches to the male (although some approaches were not accompanied by vocalizations), with hopping and darting, with the "reflexive release" from lordosis, and when no sexual behavior was occurring. Ultrasounds were not detected during lordosis, and no 22 kHz postejaculatory calls were detected. The authors state the 22 kHz postejaculatory call "is an exclusively male-produced call"; however, Barfield & Geyer (1972; 1975) previously reported female-produced 22 kHz calls at other periods during copulatory behavior. It is not clear why these calls were not detected during this study.

The authors report that, while the physical characteristics of the calls varied widely, 2 general types of calls could be distinguished. One call was a fairly pure tone whistle of approximately 55 kHz, which had a duration of 25-200 ms. The last portion of the call often increased in intensity and showed frequency shifts. The second call type was a series of brief (approximately 10 ms), frequency-modulated pulses. Frequency varied widely, from 40 to 100 kHz. Sometimes these 2 call types occurred in succession as a long whistle followed by a series of brief pulses. Several sample sonograms are presented. The authors note that many of these calls were very similar to calls produced by male rats. No measures of the rate of occurrence of these vocalizations are presented.

In Exp 2, the role of both male and female pair members in vocalization during mating was examined by devocalizing one member of the pair. In addition, vocalization by ovariectomized females was examined in order to assess the role of ovarian hormones in female ultrasound production. Male-female pairs were tested as above. There were 4 conditions: (1) intact male, intact estrus-induced female; (2) devocalized male, intact estrus-

induced female; (3) intact male, devocalized estrus-induced female; and (4) devocalized male, ovariectomized untreated (nonestrous) female. Number of 50 kHz sounds detected (using the heterodyne receivers) was examined across groups. Apparently no recordings were made. Animals in condition (1), the control condition, produced significantly more 50 kHz sounds than did animals in conditions (2) and (3), where either the male or female was devocalized. Conditions (2) and (3) did not differ from one another, but these rates were significantly higher than condition (4). Only 1 of the 8 female subjects in condition (4) produced any 50 kHz sounds at all.

This study demonstrates that females produce ultrasonic vocalizations during mating similar to those produced by males. Male and female calls have similar frequency and duration characteristics. Female vocalizations seem to be under the control of ovarian hormones; ovariectomized females vocalized rarely. The authors note that the communicative function of female ultrasounds is not known; they suggest that the calls may draw the male's attention to the female's proceptive behavior, or that the calls may aid the male in locating the female. They also make the important point that the findings of previous studies, in which it was often assumed that only the male of a pair was vocalizing, should be reassessed in light of the findings presented here.

Thomas, D.A., Howard, S.B., and Barfield, R.J. Male-produced postejaculatory 22-kHz vocalizations and the mating behavior of estrous female rats. Behavioral and Neural Biology, 36, 402-410 (1982).

This study tested the hypothesis (Barfield & Geyer, 1972) that the male rat's 22 kHz postejaculatory vocalization functions to maintain distance between the male and female for a period following ejaculation. Subjects were 8 ovariectomized Long-Evans females; they were tested with 9 sexually experienced Long-Evans males. Six of these males were devocalized prior to testing. Animals were tested in a tether box divided by a barrier into 2 compartments; during testing, the males were tethered so that their movements were restricted to the smaller of the 2 compartments. The female could move freely throughout both compartments. A recording was made of postejaculatory vocalizations for use during testing. A male was allowed to ejaculate with an estrous female, and ultrasounds following ejaculation were recorded using a Brüel & Kjaer Model 4135 microphone and a Krohn-Hite band-pass filter set at 20 and 80 kHz. Sounds were recorded on a Lockheed Store 4 tape recorder at 15 in./s. During recording, sounds were monitored using a Holgate heterodyne receiver. Recording continued until vocalizations ceased, and then continued again with a new male. These sounds were played back through a speaker near the male during testing. An oscilloscope display was used to set amplitude of playback during testing.

Each female was tested once in each of 4 conditions: (1) with a devocalized male; (2) with a devocalized male accompanied by recorded postejaculatory vocalizations for 4.5 min beginning 30 s after the test male ejaculated; (3) with a devocalized male accompanied by recorded vocalizations for 10 min following ejaculation; and (4) with an intact male. Time spent by the female in the male's compartment, in the closest half of the large compartment, and in the farthest half of the large compartment was recorded, as well as female darts and other measures of male/female proximity.

In general, measures of female visits and male/female proximity did not differ across conditions, indicating that postcopulatory vocalizations have little influence on distance between the male and female during this period. Females directed more darts per minute to intact males than to devocalized males, and latency to solicit following ejaculation was shorter in the intact condition. Interestingly, the presence of the tape recording did not seem to influence female behavior; females treated these males the same as the devocalized male who was not accompanied by a recording. These results do not support the hypothesis that the postejaculatory vocalization functions to keep the male and female apart.

As in previous studies, the authors do not address the question of whether the female as well as the male is vocalizing during the postejaculatory interval, and they imply that the only vocalizations of interest during this period are 22 kHz sounds; this certainly may not be the case.

Thomas, D.A., Howard, S.B., and Barfield, R.J. Male-produced ultrasonic vocalizations and mating patterns in female rats. Journal of Comparative and Physiological Psychology, 96, 807-815 (1982).

In these experiments, the influence of ultrasound on female mating behavior was examined by testing females with intact and devocalized males. Subjects in all experiments were adult, sexually experienced, Long Evans rats. Females had been ovariectomized, and estrus was induced prior to testing. Seven females and 8 males were tested in Exp 1A. Four males had been devocalized by unilateral transection of the inferior laryngeal nerve; the others were intact. Testing occurred in a tether box apparatus, which consisted of a central area (1,665 $cm^2$) separated from 2 side compartments (each 915 $cm^2$) by barriers. A male was tethered in each side compartment using a 15-cm string; the female was free to cross the barriers and move throughout the apparatus. Each female was tested once, with a devocalized male in one side compartment and an intact male in the other compartment. During testing, number of female "visits" to each male, number of darts directed to each male, and amount of time the female spent in each male's compartment were scored. Ultrasounds were monitored using a Holgate heterodyne receiver. No information is given

concerning the location of the receiver or the frequency to which it was tuned. A test continued until the first postejaculatory intromission by the male which had ejaculated first during the test.

During the preejaculatory period, females directed more darts per minute to the intact male than to the devocalized male, and they spent more time in the compartment containing the intact male. Neither of these differences were significant during the postejaculatory period, however. There were no significant differences in number of visits per minute. Apparently no record was kept of ultrasounds detected during the study.

In Exp 1B, 10 females were tested once in each of 3 conditions: (1) I-I, both males in the tether apparatus were intact; (2) I-D, one intact and one devocalized male; and (3) D-D, both males devocalized. There were more darts per minute in the I-I and I-D conditions than in the D-D condition, but no difference in the number of visits per minute or amount of time spent in a male's compartment across conditions. In the I-I and D-D conditions, females directed more darts toward the male that had ejaculated first. In the I-D condition, females directed more darts toward the intact male than toward the devocalized male, regardless of whether he was the male that ejaculated first. In 50% of the I-D tests, the intact male ejaculated first, while the muted male ejaculated first on the remaining 50%. In all 3 conditions, the females spent more time with the male that had ejaculated first. In summary, females orient more darts toward intact males, but they do not preferentially spend time with them.

In Exp 2, 8 female subjects were tested in the tether apparatus as in Exp 1, this time with 2 devocalized males. In the experimental condition, a speaker located behind one of the males broadcast prerecorded rat ultrasounds, while there was no speaker behind the other male. In the control condition, the speaker broadcast amplified "tape hiss" from a blank tape. Tapes for the experimental condition were recorded using a Brüel & Kjaer .25-in. 4135 microphone with a Krohn-Hite band-pass filter set at 20 and 100 kHz. Sounds were recorded on a Lockheed Store 4 tape recorder at 30 in./s. Vocalizations were elicited by allowing a male to achieve 3 intromissions with a female, then separating the male behind a wire mesh barrier. During recording, the microphone was located 22 cm above the chamber containing the male. It is not clear whether female vocalizations could have been recorded as well, but it seems likely. Ultrasounds from 4 males were recorded to obtain a tape of sufficient length. SPL during testing was approximately 70-75 dB at 10 cm from the speaker. Tests were 10 min in duration.

The presence of either tape-recorded ultrasounds or tape hiss did not influence the number of visits by females or the amount of time a female spent in a male's compartment. However, in the experimental condition, females directed significantly more darts to the male with the ultrasound-emitting speaker. In

the control condition, there was no difference in darting directed toward the 2 males.

The results of these studies were consistent with the hypothesis that rat ultrasounds influence female solicitation (specifically, darting). The authors maintain throughout the paper that the effects of 50 kHz ultrasounds were being examined; however, this is not the case, as devocalization would have eliminated all male ultrasounds. In addition, the tape recordings used in Exp 2 would most likely have consisted of sounds of many different frequencies, from both males and females. Males and females emit a variety of sounds prior to and following ejaculation, and it cannot be determined which class of these sounds was affecting female behavior in this study.

Thomas, D.A., Takahashi, L.K., and Barfield, R. J. Analysis of ultrasonic vocalizations emitted by intruders during aggressive encounters among rats (Rattus norvegicus). Journal of Comparative Psychology, 97, 201-206 (1983).

The focus of this study was to examine the function of the ultrasonic vocalizations of intruder rats. Resident-intruder aggression tests were performed using both devocalized and sham operated intruders and deafened and intact residents. Subjects were male Long-Evans rats. In Exp 1, there were 7 resident rats. All subjects were experienced fighters approximately 1 year old. The 14 intruders were approximately 3 mos. old. Seven of the intruders were devocalized by transection of the recurrent laryngeal nerve; the remaining 7 intruders received the same operation without the nerve transection. Effectiveness of devocalization surgery was tested by holding the devocalized animals by the base of the neck and shaking them. Tests with a bat detector tuned to 22 kHz and a second test with the detector tuned to 50 kHz showed no sign of ultrasounds.

Aggression testing took place in wooden boxes with Plexiglas fronts. Twenty-four hours prior to testing, a resident male was placed in a testing arena. Testing took place under red illumination during the dark phase of the animals' cycle. Tests lasted for 20 min. If aggression did not occur during the first 10 min of the test, the test was terminated and the resident was excluded from the experiment. Nine behavior measures were recorded, including frequency of bites, latency of bites, duration of boxing, duration of lateral aggressive posture.

Frequency of short "50 kHz" calls, and duration of the longer "22 kHz" calls were recorded. The vocalizations were detected using 2 bat detectors (a QMC and a Holgate) positioned near the top of the testing apparatus, approximately 20 cm from each end. Approximate distance from microphones to vocalizing animals is not given. Both bat detectors were tuned to 50 kHz, in order to increase the likelihood that the sometimes faint 50 kHz calls would be detected. An audible signal was produced in response to

50 kHz calls. The output from the Holgate receiver was amplified through a Krohn-Hite band-pass filter (No. 3550) set at 20-30 kHz. This output was displayed on an oscilloscope. Thus, 22 kHz calls were monitored visually on the oscilloscope, and 50 kHz calls were monitored audibly using the bat detector output.

In Exp 1, each resident was given a 20-min test with a devocalized intruder and a 20-min test with a sham operated intruder. Order of testing was counterbalanced across residents. Results indicated no differences in agonistic behavior between tests using devocalized and sham-operated animals. The only significant differences were in duration of the 22 kHz call (these calls had been completely eliminated from the devocalized group) and in number of 50 kHz calls. In the tests with the devocalized intruders, almost no 50 kHz calls occurred, while these were fairly common in tests with a sham operated animal.

The almost complete absence of 50 kHz ultrasounds was somewhat unexpected, since it previously has been suggested (Sales, 1972; Corrigan & Flannelly, 1979) that the aggressor rat produces these sounds. Results here, however, appear to indicate that the intruder was producing almost all of the 50 kHz sounds, since they were almost completely eliminated when the intruder was devocalized. A possibility discussed by the authors is that residents may produce 50 kHz sounds chiefly in response to 22 kHz sounds; the residents here may not have produced 50 kHz sounds because the eliciting stimulus (22 kHz sounds) was not present. The results of this study also differ from those of previous studies (Sales, 1972; Lore et al., 1976) in that the aggressive behavior of the resident was not affected by the presence or absence of 22 kHz sounds. The authors state that the residents used here were experienced and highly aggressive, and may not have been responsive to the 22 kHz sounds of the intruders.

Twenty-four subjects (8 residents and 16 intruders of the same approximate ages as in Exp 1) served in Exp 2. The residents were deafened by injection of a silicone "ear impression compound" into the auditory meatus. The pinna was then sutured shut. After being used in the experiment, all deafened animals were tested for flinch responses to loud noises (hand clapping, rapping a ruler on a hard surface). None of the deafened animals flinched. Basic procedures, and behavior patterns and ultrasounds recorded, were as in Exp 1. Each resident was tested in 2 conditions, deafened and nondeafened (earplugs removed). Order of conditions was counterbalanced across residents. Intruders were used only once. Results showed no differences between the deafened and normal resident conditions on any behavioral or ultrasound measure. As in Exp 1, there was no apparent relationship between intruder ultrasound emission and aggression by the resident male. These findings are contradictory to previous reports (Lehman & Adams, 1977; Sales, 1972).

The authors conclude by stating that "to date, there have been no experimental studies that either (a) firmly established a

causal relation between intruder ultrasonic vocalizations and resident aggression or (b) provided support for the hypothesis that the function of these signals is to inhibit further aggression."

Thomas, D.A., Talalas, L., and Barfield, R.J. Effect of devocalization of the male on mating behavior in rats. Journal of Comparative and Physiological Psychology, 95, 630-637 (1981).

In this study, male rats were devocalized to assess the effect of ultrasounds on copulatory behavior of both the male and female. Subjects in Exp 1 were 15 sexually experienced male Long-Evans rats. Ten males were devocalized by bilateral or unilateral recurrent laryngeal nerve transection. The remaining males served in the control (sham-operated) condition. Each male was tested twice for sexual behavior with an ovariectomized, estrus-induced female in a 40 x 26 x 29 cm aquarium. Behavior scored included mounts, intromissions, ejaculations, female darts, and the occurrence of ultrasonic vocalizations. Tests continued until the first intromission following an ejaculation. Ultrasounds were monitored using a Holgate heterodyne receiver; the authors did not state what frequency the receiver was tuned to.

There were no differences in male copulatory behavior between the devocalized and control groups. However, the females tested with devocalized males showed fewer darts per minute than did females tested with control males. The authors state that this is due to the "effect of 50 kHz copulatory vocalizations." However, it should be noted that the devocalized males were producing no ultrasounds; the absence of darting behavior therefore cannot be attributed specifically to the absence of 50 kHz sounds. A replication of this experiment with minor methodological changes (use of females with known sexual experience; a larger control group) yielded identical results.

During these tests, faint 50 kHz vocalizations were sometimes detected. These sounds continued when the male was removed, indicating that the female was producing these sounds. Previous studies have rarely considered the possibility that females were emitting a portion of the ultrasounds detected during sexual behavior tests.

In Exp 2, males were tested in a tether apparatus which restricted their movement. This restriction allowed for a closer examination of the influence of male ultrasound on female behavior. The authors state specifically that they are interested in examining the function of the 50 kHz call, however, as previously stated, devocalization of the males does not specifically eliminate 50 kHz sounds; it eliminates all vocalizations. Subjects were 9 ovariectomized Long-Evans females approximately 4 months old. They were tested with 4 devocalized and 5 control males from Exp 1. Behavioral estrus was induced in the females prior

to testing. The test chamber (116.5 x 30 x 39 cm) was divided into 2 unequal compartments with a Plexiglas barrier; this barrier could be crossed by the untethered female. During testing, the male was tethered in the smaller compartment. The receiver microphone was placed over the smaller compartment; no estimate of distance from animal to microphone is given. Behavior patterns scored included mounts, intromissions, ejaculations, female barrier crossings to approach male, female darts, female ear wiggles, and lordosis. Tests lasted until the first intromission following ejaculation.

There were no differences in sexual behavior of the devocalized and control males. Some measures of female sexual behavior differed between the 2 conditions. When tested with the control males, females showed more darts per minute, more ear wiggles per minute, and a shorter latency to return to the male and to solicit following ejaculation. There were no significant differences in number of visits to the male, visits per minute, percentage of mounts resulting in lordosis, or time to return to the male following an intromission.

These results indicate that male vocalizations can affect some patterns of female proceptive behavior. The authors maintain that "these experiments demonstrate that the function of 50 kHz male-produced copulatory vocalizations is to facilitate the proceptive behavior of the female." As previously stated, however, some of these effects may be due to 22 kHz vocalizations, or to other male vocalizations which are known to occur during mating behavior.

White, N.R., and Barfield, R.J. Effects of male pre-ejaculatory vocalizations on female receptive behavior in the rat (Rattus norvegicus). Journal of Comparative Psychology, 104, 140-146. (1990).

In Exp 1, sexual behavior of devocalized males and intact females was observed in order to examine the role of male ultrasounds on female sexual behavior. Twenty-five pairs of Long-Evans rats were tested; all pairs were sexually experienced. Females were ovariectomized and treated with estrogen and progesterone prior to testing. The experimental group (12 pairs) was tested twice; once prior to and once following devocalization of the males. The 13 control pairs were also tested twice, at the same times, but no animals were devocalized. Testing occurred in a 138 x 42 x 34 cm apparatus. Animals were observed through 3 ejaculatory series, and the following behavior patterns were noted: approach, break off, sniff, dart, run, trail, mount, intromission, ejaculation, lordosis, female move before intromission, and ultrasounds.

A QMC heterodyne receiver on a broadband setting (20 to 100 kHz) was used to monitor ultrasounds. These calls were "easily classified as mating or preejaculatory vocalizations on the basis

of the frequency and duration of the transformed calls." The characteristics of these call types are not specified, except that "mating calls are very brief and occur in bursts," and that "preejaculatory calls are lower in frequency, longer in duration, and louder than mating calls." (These calls are described in a study published subsequent to this one; White et al., 1990.)

Female darting, intromissions, and lordoses decreased in the experimental group following male devocalization. Length of interintromission interval and frequency of female move away from male increased. These results seem to indicate an important influence of male vocalization on some aspects of female copulatory behavior.

In Exp 2, taped calls of different types were played during mating tests of female-devocalized male pairs. A stimulus tape for playback was constructed by recording vocalizations during copulatory sessions between 3 pairs of intact males and devocalized females. These sounds were recorded using a Brüel and Kjaer 4125 1/4 in. condenser microphone and preamplifier, a Brüel and Kjaer 2610 amplifier, and a Krohn-Hite 3550 filter set at 20 kHz and 100 kHz. Recordings were made on a Lockheed Store 4 tape recorder at 30 in./s. The microphone was located 22 cm above the floor of the cage. Male-female pairs to be recorded were allowed to copulate through 2 ejaculatory series. Recording began following the first intromission of a series and stopped following ejaculation. Tapes obtained in this way were examined using a Uniscan sound analyzer. Portions of tape containing clear calls of only one type, with minimal background noise, were identified and were played at one-half speed into a Kay Sonograph, which was adjusted to 32 kHz. These calls were then repeatedly played on the Kay Sonograph while being recorded by the recorder at one-half speed. These tapes were played back during testing through a speaker located in a hole in one of the cage walls. Frequency response of all equipment was flat to 100 kHz.

Nine pairs of Long-Evans rats were used as subjects; all were sexually experienced. Females were ovariectomized and hormone treated as above; males were devocalized. Pairs were observed and behavior was recorded through 3 ejaculatory series. Behavior patterns were scored as in Exp 1. Each pair was tested once in each of the following conditions: (1) control - male intact; (2) male devocalized, background noise from tape player played during test; (3) male devocalized, taped mating calls played; and (4) male devocalized, taped preejaculatory calls played. Tapes were played in the following contexts during testing: when one animal approached another, and during darting, running, trailing, mounts, intromissions, and ejaculations. This schedule for presentation of ultrasound was based on pilot observations of the occurrence of ultrasound during mating.

The results of this study are confusingly presented and difficult to interpret. One behavior pattern which clearly seems to be affected is female move before intromission, which is low

in the control condition and in the 2 playback conditions, but significantly higher in the devocalized condition. Male sniff, female sniff, and female run are lowest in the control condition, and significantly higher in the devocalized and playback conditions. This behavior indicates that the playback tapes were not equivalent to actual male vocalizations in their effects on female behavior. Unlike Exp 1, intromission, mount, and lordosis frequency were not affected by devocalization of the male, or by playback of male vocalizations. Female darting, which has been shown to be influenced by male vocalizations in previous experiments (e.g., Thomas et al., 1981; Thomas et al., 1982), did not differ across conditions here.

The authors apparently misstate their results in several places. They stated that "approaches by either sex were not affected by devocalization and playback," while a table indicated that the results for female approach were significant. In addition, they stated that "female running, female walking, and male trailing were also affected by devocalization." The table clearly shows that the only significant result among these 3 behaviors was for female running.

The authors close by suggesting that females may gain information from preejaculatory calls concerning a male's sexual state (e.g., readiness to ejaculate); the females may then optimize their reproductive success by mating or not mating with a particular male. The results of this study were not at all clear-cut, particularly since results of Exps 1 and 2 differed from one another in several important respects. The authors did not make much of an attempt to explain the differences. These experiments suggest some role of male vocalizations in facilitating female mating behavior, but the role was not clear, and the authors were not successful in demonstrating any functional differences between "mating" and "preejaculatory" calls.

White, N.R., and Barfield, R.J. Playback of female rat ultrasonic vocalizations during sexual behavior. Physiology & Behavior, 45, 229-233 (1989).

This study is very similar to a previous study by the same authors (White & Barfield, 1987). The effects of devocalizing the female and playing back her vocalizations during sexual behavior were observed, in order to examine the role of female ultrasounds in mating. Eleven Long-Evans male-female pairs were used as subjects. All pairs were sexually experienced. Females were ovariectomized, and were brought into behavioral estrus prior to testing.

Prior to testing, a stimulus tape was constructed by recording ultrasounds from three mating pairs (which were not used as subjects here). In each pair, the male had been devocalized, ensuring that any ultrasounds recorded were from the female. Recordings were made using a Brüel & Kjaer Model 4125 microphone

and preamplifier located 22 cm above the floor of the mating cage. Signals were amplified (Brüel & Kjaer Model 2610 amplifier), filtered (Krohn-Hite band-pass filter, set at 20 and 100 kHz), and then recorded using a Lockheed Store 4 tape recorder (tape speed 30 in./s). Frequency response characteristics of this system are not discussed. A stimulus tape was constructed by locating a portion of the recording which contained a clear ultrasound with little background noise. (Spectral, temporal, and amplitude characteristics of this sound are not described.) This portion of the tape was recorded at one-eighth speed on a Kay Sonograph and then rerecorded (at one-eighth speed) by repeatedly playing it on the sonograph. This rerecording resulted in a stimulus tape consisting of the same call repeated numerous times. Sonograms of stimulus tape were compared to sonograms of the original tape to ensure that there were no distortions in the playback tape.

Male-female pairs were observed under 3 conditions: (1) male and female intact; (2) female devocalized, tape recorded female ultrasounds played back; and (3) female devocalized, tape hiss played as a control. The same male-female pairs were tested in each condition. Testing occurred in a 138 x 34 x 42 cm cage; ultrasounds or tape hiss sounds were played through a speaker. Peak intensity of the ultrasound tape was set at 70-75 dB at 15 cm from the speaker. Several behavior patterns were recorded during tests, including approach, sniff, female dart, run, mount, intromission, ejaculation, lordosis, and vocalizations. Vocalizations were monitored using a Holgate or QMC heterodyne receiver, which was either set at 50 kHz or on a broadband setting (inconsistent information is given in the paper). Tests continued through 3 ejaculatory series.

Results were similar to those of White and Barfield (1987). Several behavior patterns increased in the devocalized (tape hiss) condition relative to the intact and playback conditions. These patterns included female dart, female approach male, male approach female, and female break off (orient away from male). Postejaculatory vocalizations also followed this pattern; however, as the authors state, "individual mating calls could not always be distinguished," and this, therefore, may not be a reliable finding. Some other behavior patterns were affected, but many of these showed order effects, and the results are therefore difficult to interpret. These findings replicate those of an earlier study which indicated that female proceptive behavior (e.g., darting) increases when females are devocalized. This behavior increase suggests that female ultrasounds may have a proceptive function, and that when the female is unable to vocalize, she increases other proceptive behaviors. This study also provides the "first direct evidence" that female vocalizations affect male mating behavior (approaches).

White, N.R., and Barfield, R.J. Role of the ultrasonic vocalization of the female rat (Rattus norvegicus) in sexual behavior. Journal of Comparative Psychology, 101, 73-81 (1987).

Three experiments were performed in order to examine the influence of the female's ultrasonic vocalizations on sexual behavior. Female (Long-Evans) subjects were ovariectomized and brought into behavioral estrus prior to testing. All males (also Long-Evans) were sexually experienced. Sexual behavior was observed with the animals in a tether apparatus; the female was tethered during some conditions, so that her movement was somewhat restricted. In Exp 1, ten male-female pairs were tested once in each of the following conditions: (1) intact, tethered female; (2) intact, nontethered female; and (3) devocalized, tethered female. (Condition 3 obviously occurred last for all pairs.) During testing, sexual behavior of the pair was observed through 3 ejaculatory series. Behavior patterns scored included approach, sniff, dart, run, trail (male closely follows female), mount, intromission, ejaculation, lordosis, and 50 kHz calling. Ultrasounds were monitored using a Holgate or QMC heterodyne receiver tuned to 50 kHz. The authors point out that "because the bat detector may not be able to distinguish between individual calls, calling scores should be interpreted as a relative measure of vocalization."

Results indicated, not surprisingly, that tethering the female resulted in a decrease in some of her behavior patterns. Female approaches and runs were significantly lower in frequency when females were tethered. Rates of darting and running were significantly higher in the devocalized (tethered) condition than in the intact (tethered) condition, indicating that devocalization primarily affects female solicitation behaviors. Male sniffing and mount rates were also increased when females were devocalized.

In Exp 2, males were temporarily deafened by injection of a removable plastic ear mold. Ten male-female pairs were tested as in Exp 1. It is not clear whether females were tethered or untethered during the experiment. Female darting and running, male mount rate, and rate of 50 kHz calling were all significantly higher when in the deafened male condition as in comparison with the intact male condition. Several male behaviors (male approach, male sniff) decreased when the males were deafened. However, these differences were not seen in the devocalized female condition in Exp 1. The behavioral effects of eliminating female vocalizations thus seem to differ somewhat depending on which member of the pair receives the treatment (female devocalization, male deafening).

In Exp 3, tape recorded ultrasounds were presented to male-female pairs. For recording purposes, a male and receptive female were placed in an aquarium, and the male was allowed 3 intromissions. The male and female were then recorded while sepa-

rated by a wire mesh screen. Recordings were made using a Brüel & Kjaer 4125 microphone, Brüel & Kjaer 2610 measuring amplifier, and Krohn-Hite band-pass filter set at 20 and 100 kHz. A Lockheed Score 4 tape recorder was used to record at a tape speed of 30 in. per second. The microphone was located at 22 cm above the floor of the cage during recording. Recording continued from one pair until calling ceased; the animals were then replaced by a new pair. Three pairs were used to create the tape.

Ten male-female pairs were tested in Exp 3, once in each of three conditions: (1) intact female; (2) female devocalized, recorded ultrasound presented; and (3) female devocalized, tape hiss played as a control. Ultrasounds were played back at 75-80 dB (peak intensity at 15 cm from the speaker). Females were tethered near the speaker. Testing continued through 1 ejaculatory series. Results indicated that dart rate was lowest in the intact condition, and greatest in the condition where tape hiss was presented. The rate when ultrasounds were presented was intermediate. Differences between all these conditions were significant. Other variables also differed significantly.

Overall, the results of these experiments are often inconsistent with one another and do not allow for any clear conclusions concerning the influence of female ultrasounds on mating behavior. The only consistent finding involves female darting behavior, which increased in all cases where female ultrasounds were not present or detectable by the animals. It cannot be determined from these results, however, whether this is due to the call's effect on the female's or the male's behavior.

White, N.R., Cagiano, R., and Barfield, R.J. Receptivity of the female rat (Rattus norvegicus) after male devocalization: A ventral perspective. Journal of Comparative Psychology, 104, 147-151 (1990).

Previous research indicated that females mating with devocalized males tended to move away from the male during a mount, before intromission could occur (White and Barfield, 1990). In this study, the authors examined rat copulatory behavior in detail by placing an angled mirror under the copulating pair. This arrangement gave the investigators a view of the rats' ventral surfaces and enabled them to observe copulatory events in detail, and to correlate these events with male vocal behavior.

Subjects were 24 pairs of sexually experienced Long-Evans rats. All females were ovariectomized and treated with estrogen and progesterone prior to testing. Testing occurred in a 48 x 30 x 25 cm aquarium with a mirror positioned below it at a 45 degree angle. This arrangement allowed a view of the animals' ventral surfaces. Tests were videotaped and examined later. Ultrasounds were monitored during testing using a QMC heterodyne receiver on the broad-band setting (20 to 100 kHz). The output from the receiver was channeled to the audio mechanism of the

videotape recorder. The investigators were interested in the pattern of occurrence of male and female movements during copulation, such as initial flank contact by the male, female becoming stationary, female begins to elevate rump, female rump fully elevated, and female move away from male. Tests lasted through 3 ejaculatory series. Experimental group pairs (N=12) were tested twice; once prior to and once following devocalization of the males. The control group was also tested twice, but received no surgery.

The authors examined in detail the time course of events which occurred during mounts. One finding of interest is that there were no differences in the "time course" of mounts between pairs in which the male was intact and pairs in which the male was devocalized. The authors also examined whether devocalization of the male affected the proportion of intromissions, male-terminated mounts, and female-terminated mounts. They found that pairs in which the male was devocalized had significantly fewer intromissions and a smaller ratio of intromissions to mounts. The proportion of female-terminated mounts was higher in the devocalized condition, as was the amount of female movement prior to intromission.

These results suggest that male vocalization affects female receptive behavior, since females paired with devocalized males were more likely to terminate mounts, and to move before intromission was achieved. The results shed no light on which type of vocalizations are effective, since the males were incapable of any vocalization. In addition, the effect of surgery itself was not controlled for, since the control group was not sham-operated.

White, N.R., Cagiano, R., Moises, A.U., and Barfield, R.J. Changes in mating vocalizations over the ejaculatory series in rats (Rattus norvegicus). Journal of Comparative Psychology, 104, 255-262 (1990).

The authors examined spectral, duration, and intensity characteristics of ultrasounds occurring during mating in rats. Changes in calls across 3 ejaculatory series were examined. In Exp 1, subjects were 11 sexually experienced male-female pairs of Long-Evans rats. Females were ovariectomized and treated with estrogen and progesterone prior to testing. Testing occurred in a 48 x 30 x 25 cm aquarium. Pairs were observed across 3 ejaculatory series, and the following behavior patterns were scored: approach, sniff partner, female dart, female run, male mount, female lordosis, break off contact with partner, intromission, and ejaculation.

In addition, vocalizations were recorded using a Bruel and Kjaer 4135 condenser microphone, a Bruel and Kjaer 2160 amplifier, and a Krone-Hite 3550 band-pass filter set at 20 and 100 kHz. The microphone was positioned 30 cm from the floor of the aquari-

um (no estimate of distance from microphone to animals is given). Sounds were recorded on a Lockheed Store 4 tape recorder at 30 in./s. All recording equipment had a flat frequency response to 100 kHz. Vocalizations were also monitored using a Tektronix 3105 N oscilloscope hooked to the tape recorder and a QMC heterodyne receiver. Recording began following the first intromission of a series and was terminated at ejaculation. Tapes were analyzed spectrographically using a Uniscan II sound spectrograph and a Kay Sonograph.

The authors detected only five 22-kHz calls during the study; these were not subjected to analysis. The remaining vocalizations were divided into 4 groups, based on frequency and duration characteristics. High frequency calls had frequencies of 40 kHz or greater; low frequency calls were below 40 kHz. Calls lasting 60 ms or longer were "long" calls; those 50 ms or shorter were "short" calls. (Apparently calls from 51-59 ms were disregarded.) This choice resulted in a classification of 4 call types: (1) high-short, (2) high-long, (3) low-short, and (4) low-long. It is not clear why these frequencies and durations are chosen as "dividing points," and the authors make no real attempt to justify this classification. As they point out in the discussion, this choice is "somewhat arbitrary." The authors refer to high-short calls as "mating calls"; high-long, low-short, and low-long calls are referred to as "preejaculatory calls." It is not clear why this distinction is made. One sample sonogram of each of the 4 call types was presented. The sonograms indicate obvious structural differences between the calls (e.g., frequency modulation, repeated pulses) which are not discussed by the authors.

The authors present data showing significant differences in peak intensity for the different call types; however, given that the position of the microphone from the animal could not be controlled and probably was not constant, these data may not be meaningful.

Each of the 3 ejaculatory series is divided into segments, and the segments are then compared in order to determine if the occurrence of different call types differs across the series. In general, high-short calls ("mating calls") seem to be emitted at a high and constant level across the series. The remaining 3 call types (the "preejaculatory" calls) seem to increase as ejaculation approaches. The authors examined the correlations between each of the 4 call types and the sexual behavior patterns scored. They report that "high-short calling was associated with running and intromissions. Preejaculatory calls were positively correlated with approaches, darts, runs, mounts, and ejaculation." This statement is misleading, since each of the 3 "preejaculatory calls" is associated with a different set of behavior patterns, and one of the so-called "preejaculatory" calls (the low-short call) is not even positively correlated with ejaculation. Several behavior patterns were associated with more than one call type. In other words, there does not appear to be

a clear association between call type (as defined by these authors) and behavior.

The objective of Exp 2 was to determine which of the vocalizations detected in Exp 1 were produced by the male. Five pairs consisting of a male and a devocalized female were tested and recorded as before. Pairs were tested only through one ejaculatory series. The authors report that "high calls are significantly different from low calls in frequency. Short calls are different in length from long calls." This determination is a completely expected result, since high calls, by the authors' definition, are higher in frequency than low calls, and since short calls were defined to be shorter than long calls. No further results concerning patterning or rate of calling are reported. This study sheds no light on the question of whether the male, the female, or both were vocalizing in Exp 1.

Few clear conclusions can be drawn from these experiments. It is not clear at all whether the call types identified here have any functional significance. The authors conclude by raising many of the same questions which have been left unanswered by this and many previous studies of rat ultrasound. This study sheds no real light on the functional significance or motivational basis of rat ultrasound during copulation.

White, N.R., Colona, L.C., and Barfield, R.J. Sensory cues that elicit ultrasonic vocalizations in female rats (Rattus norvegicus). Behavioral and Neural Biology, 55, 154-165 (1991).

This series of 4 experiments examined the role of male odor cues in eliciting female ultrasounds. Long-Evans rats were used in all experiments, and all females were ovariectomized and sexually experienced. Estrus was induced prior to testing. Except for Exp 4, testing occurred in a 48 x 25 x 30 cm aquarium. In Exp 1, 10 female subjects were tested in each of 3 conditions: (1) with bedding material from a sexually mature male, (2) with bedding from an estrous female, and (3) with clean bedding. Bedding material was placed in a plastic container in a corner of the aquarium during testing. Females were placed in the aquarium, and sniffs and ultrasounds were scored for a 5-min period. Ultrasounds were monitored using a QMC heterodyne receiver on the broad-band (20-150 kHz) setting. Females vocalized significantly more when exposed to bedding from a male than when exposed to a female's bedding or to clean bedding. There was no difference in response to female's or clean bedding. The same pattern of results was obtained for sniff duration, with bedding from the male being sniffed longer.

In Exp 2, 10 female subjects were tested once in each of 3 conditions: (1) with a devocalized intact adult male in a holding cage in the testing apparatus; (2) with a devocalized estrous female in a holding cage in the testing apparatus; and (3) with

an empty holding cage. Vocalization and sniffing were scored as in Exp 1. Females vocalized most frequently in the presence of the male, and least in the presence of the empty holding cage. Differences across all 3 conditions were significant. Sniffing duration did not differ between conditions (1) and (2), but was significantly longer in these conditions than in (3).

Eleven females were subjects in Exp 3. Procedures were as in Exp 2, except that females were tested once with each of the following stimulus animals in a holding cage: (1) a devocalized, intact adult male; (2) a devocalized, castrated adult male; (3) a devocalized juvenile male (30-50 days old), and (4) an empty holding cage. Tests were 10-min long. Amount of vocalization among the 4 conditions showed the following pattern: intact male > castrated male = juvenile > empty cage. Female sniffing did not differ between intact and castrated adult males: number of sniffs: intact male = castrated male > juvenile > empty cage; duration of sniffing: intact male = castrated male = juvenile > empty cage.

The experimenters hypothesized, based on the previous results, that females were responding to odor cues emitted by the stimulus animals. Exp 4 was designed to examine this possibility as well as the influence of vocalizations on female behavior. Testing occurred in a specially designed apparatus which allowed olfactory contact, but no tactile or gustatory, and only limited visual contact between the subject and the stimulus animal. A stimulus tape consisting of male vocalizations recorded during mating behavior was constructed using the procedure described in White and Barfield (1989). This tape was played during testing. Females were exposed to either a devocalized, intact, sexually experienced, adult male or a devocalized, castrated adult male. Subjects (10 females) were tested in a 2 (intact vs. castrated male) x 2 (vocalization playback vs. no playback) repeated measures factorial design. There was a significant main effect of male hormonal condition on vocalization rate and duration of sniffing; vocalization occurred more often, and sniffing duration was longer, in the presence of the intact male. There was no main effect of tape presentation, and there were no interactions.

The results of these experiments indicate that females vocalize at high rates in the presence of sensory cues associated with intact adult males. The females may be responding to odor cues, as the elimination of most other cues (Exp 4) does not change this pattern of responses. Female vocalizing and sniffing were not affected by playback of recorded male ultrasounds.

## Other Contexts

Francis, R.L. 22-kHz calls by isolated rodents. Nature, 265, 236-238 (1977).

Ultrasonic sounds of approximately 22 kHz are sometimes emitted by adult male rats in sexual and agonistic contexts. This paper reports the occurrence of 22 kHz sounds by rats housed alone, in their cages, not receiving any social stimulation. Subjects were 6 adult Wistar rats (5 females, 1 male). Each animal was kept in an unused, quiet room. Food and water were checked daily, and female estrus cycles were monitored by daily vaginal smears. Ultrasounds were monitored continuously for a period of several days (number of days varied among subjects), using a bat detector tuned to 22 kHz. During some periods (not specified by the author), sounds were also monitored using a second bat detector tuned to 25 kHz. Output from the bat detectors was recorded on magnetic tape at a slow speed, which was screened later at a higher speed to detect the occurrence of ultrasounds. All ultrasounds which were separated by .1 h or less were considered to be a "bout." It is not clear from the article whether the dependent variable examined here is the duration of these bouts or the actual duration of the ultrasonic emissions.

In general, the pattern of ultrasonic emissions during the dark phase of the light-dark cycle seems to be similar across all subjects. Distribution of ultrasounds was low during the early part of the dark phase, then rose to a peak during the middle of the dark phase, after which it dropped again toward the end of the dark phase. Distribution of ultrasounds apparently did not show any pattern during the light phase. No statistics are presented, and the individual subject data presented in the form of bar graphs appears to be highly variable. The author does not make this point, but the data as presented indicate a very low rate of sound emission under these conditions. The author suggests that "spontaneous" ultrasonic emissions may be associated with periods of rest and inactivity during the dark phase, and that emission of these sounds may act to synchronize the activity of the group in colony-living rats.

Kaltwasser, M.T. Startle-inducing acoustic stimuli evoke ultrasonic vocalization in the rat. Physiology & Behavior, 48, 13-17 (1990).

This article is the first published report of ultrasonic vocalization by rats in response to acoustic stimulation. Subjects (15 male Wistar rats weighing 220-240 g at testing) were exposed to startle-inducing acoustic stimulation, and vocalizations were recorded during testing. The startle stimulus used was a 10 kHz, 20-ms signal, with rise and decay times of 0.4 ms. Intensity of the signal was 110 dB SPL. Startle stimuli were generated and controlled using a Wavetec 136 generator, a pulse generator, and a Hewlett-Packard 350D attenuator. These stimuli and a 40 dB background noise (produced by a noise generator) were presented via a Motorola Piezohorn KSN 1025 speaker located 30 cm from the testing cage. The testing cage measured 6 x 12 x 10 cm.

It is not described further. The test cage, speaker, and microphone (see below) were located in a sound proof chamber.

Vocalizations were recorded using a Brüel & Kjaer 4135 microphone, a Brüel & Kjaer 2608 measuring amplifier, and a Racal 4 DS high-speed recorder. The microphone was mounted 10 cm from the test cage. Vocalizations were also monitored using a Tektronix 5112 dual-beam oscilloscope. Recordings were analyzed with a Mosip real-time spectrum analyzer. Measurements of duration were obtained by playing back the tape at reduced speed.

On Days 1-3, individual rats were placed in the apparatus for a 2-min adaptation period. The adaptation period was followed by a series of 20 startle-eliciting stimuli presented at 20-s intervals. Recordings were made throughout the session. On Day 4, the adaptation period was followed by a series of 5 startle stimuli, and recording continued for a 3-min period following presentation of stimuli.

Percent of animals vocalizing on Days 1-3 of testing ranged from 40-70%. Within each test day, percentage of animals vocalizing increased across the session and then declined slightly. Kaltwasser reports that the vocalizations "showed the general characteristics of the so-called 22 kHz call." Vocalizations consisted of "bouts" of 12 to 20 individual pulses. Pulse duration ranged from 500 to 1,200 ms. Pauses between bouts were 1,000 ms to 5-min long. Sample sonograms are presented. Frequency of the calls appears to average 19-20 kHz, with brief upward sweeps at the beginning or end of pulses. The first pulse of a bout tended to be longer than subsequent pulses, and to have a more gradual downward frequency shift. The presentation of startle stimuli generally resulted in a pause in vocalization; this was the most notable effect of startle stimuli on call structure. Frequency composition of the calls was not affected by the presence of acoustic startle stimuli. Pulse duration was shorter and interpulse interval was longer on Days 1-3, when startle stimuli were present, in comparison with Day 4, when startle stimuli were not present. These findings should be interpreted with caution, since presentation of conditions was not counterbalanced.

Since the startle-induced ultrasonic vocalizations analyzed in this study are similar to those emitted following shock or during aggressive behavior, Kaltwasser reasoned that they may reflect fear or anxiety produced in the startle testing situation.

Lewis, P.R., and Schriefer, J.A. Ultrasound production by pregnant rats. Behavioral and Neural Biology, 35, 422-425 (1982).

Six adult female Sprague-Dawley rats (4 pregnant, 2 nonpregnant virgins) served as subjects. Observation of pregnant

females began on Day 21 of gestation. Females were observed in a sound-attenuated chamber which was fitted with a video camera and Holgate heterodyne receiver. Animals were continuously monitored during light periods via the video camera until delivery occurred (on Day 23). The heterodyne receiver was used on a broadband setting, with the lower filter at 10 kHz. A Gilson polygraph was used to obtain a continuous record of the receiver output. Ultrasound monitoring was terminated when the first pup was born. Nonpregnant subjects were observed for 3 consecutive days using the same procedure.

All subjects emitted ultrasound throughout the day, with peak emissions occurring during dark hours. Pregnant rats vocalized more than nonpregnant rats, but the difference was not significant. Ultrasound rate of pregnant females was significantly higher during the light period when birth occurred than during the previous light period. Tuning the receiver resulted in an estimate of 40 kHz for the major component of the calls. Ultrasound emission was sometimes correlated with chest or abdominal contractions, with drinking, or with scratching the cage (no quantitative data presented).

The authors noted that there was a great deal of variability in rate of ultrasound emission. They also reported that many sounds were of low intensity and were barely detectable using their equipment; they may therefore have not detected some sounds. Given these facts and the very small sample size used, it is difficult to draw many conclusions from this study. This report does describe another context in which ultrasounds are emitted by rats, however, and the rate of calling seems to be much higher than that reported by Francis (1977) for 22 kHz calls from isolated rats.

Rosenzweig, M.R., Riley, D.A., and Krech, D. Evidence for echolocation in the rat. Science, 121, 600 (1955).

Maze performance of 10 blinded rats (age, sex, strain not specified) was examined. Subjects were required to choose the left or right arm of the maze when they left the start box; on any given trial, one of the arms was blocked by a metal barrier. All rats learned to select the correct arm; some attained a level of 90% correct performance. The authors attempted to eliminate cues other than those associated with audition, although the use of odor cues may not have been completely prevented. When the angle of the barriers was changed so that sound would not have been reflected directly back to the rat, performance levels dropped to chance. Rats whose ears were "occluded" also performed at chance levels.

During some trials, ultrasound was monitored. No details are given concerning the sensitivity of the equipment used, so it is unclear whether extremely high frequency sounds could have been detected. Ultrasound was produced by the rats in the maze,

but only rarely, and ultrasound production apparently was not related to maze performance. The rats also produced audible sounds (teeth clicking, footsteps, sniffing) while in the maze. The authors hypothesize that the rats echolocated using the reflections of these audible sounds.

Sales, G.D., Cagiano, R., DeSalvia, A.M., Colonna, M., Racagni, G., and Cuomo, V. Ultrasonic vocalization in rodents: Biological aspects and effects of benzodiazepines in some experimental situations. In: GABA and Endocrine Function, eds. G. Racagni and A.O. Donoso. New York: Raven Press, 1986.

This study is a very brief review of the literature on rodent ultrasounds in a variety of contexts. The results of several unpublished studies by the authors on the effects of benzodiazepines on rat ultrasound also are presented. (The studies are not described in detail.) Decreases in duration of 20-30 kHz ultrasounds emitted in response to unavoidable footshock were found when rats were administered either diazepam or alprazolam, both benzodiazepines. The effect of diazepam was counteracted by administration of the benzodiazepine-antagonist Ro 15-1788. The authors suggest that these effects are due to the anxiolytic properties of benzodiazepines, rather than to any muscle relaxant actions of the drugs.

The authors also have noted (data not presented) that rats emit 20-30 kHz ultrasounds during avoidance learning (particularly during intertrial intervals and presentation of the conditioned stimulus), and that the ultrasounds decrease as training sessions progress and the animal learns the avoidance response. Administration of diazepam during avoidance conditioning reduced the rate of calling. The authors also report that this was accompanied by a "significant facilitation of avoidance responding." The authors suggest that "the emission of ultrasounds during an active avoidance task could represent an index of the emotional state of the animal."

Tonoue, T., Ashida, Y., Makino, H., and Hata, H. Inhibition of shock-elicited ultrasonic vocalization by opioid peptides in the rat: A psychotropic effect. Psychoneuroendocrinology, 11, 177-184 (1986).

The effects of various opioid peptides on shock-elicited ultrasound were examined. Subjects were adult male Wistar rats weighing at least 200 g (no specific information is given concerning age or weight of subjects at time of testing). Subjects were housed in groups of 3. Prior to testing, subjects were removed from home cages and placed in individual cages with metal grid floors through which electrical shock could be delivered. During testing, these cages were placed inside a sound-attenuat-

ed, darkened chamber (although, during the animals' diurnal phase).

Ultrasonic vocalizations were received by a Kunitachi Acoustic Lab condenser microphone (ACM-20F) with frequency response flat to 100 kHz. The microphone was located 10 cm above the test cage (no estimate of distance from microphone to rat was given). Following amplification, the signal was examined in 3 forms: (a) the original waveform, (b) after band-pass filtering with center frequencies of 10, 20, 30, 40, 50, 70, and 90 kHz, and (c) integrals of each filtered component (integration time of 200 ms) continuously traced by a multichannel pen recorder. From the pen deflections for each channel, measures of average relative amplitude, duration, and rate of sound pulses were derived. Additional analyses were carried out on the original waveform after A/D conversion by a Kawasaki Electronica (KE-8301), sampling time of 5 μs. Power spectra of vocalizations were computed from the digitized signal with a resolution of 1 kHz and a maximum frequency of 100 kHz. Power spectra were computed at successive moments throughout vocalizations (up to 100-ms long) and displayed consecutively.

Each shock consisted of a series of two 900 ms 1.0 mA shocks separated by 100 ms intervals. Apparently, only rats which emitted ultrasounds in response to single shocks were tested further. These rats were tested in the apparatus for 3 days. Each day's session consisted of 10 shocks separated by one minute intervals. By day 3 of testing, about one-third of the rats were emitting ultrasounds in response to shock. Only these rats were utilized in subsequent drug testing procedures. The actual number of subjects used is not given, although (from examination of tables in the article) the total number of subjects in all conditions appears to have been 110.

About one-half of the subjects were lateral-cerebroventricularly cannulated; these rats were allowed to recover and were tested for emission of ultrasound before subsequent drug treatment. Drugs examined were beta-endorphin, dynorphin, leucine-enkephalin, methionine-enkephalin, substance P (all of which were administered via the cannula), diazepam, chlorpromazine hydrochloride, and imipramine hydrochloride (which were injected subcutaneously). The measure of vocalizations used was total number, and lengths, of pen deflections during the 3-min period following a single shock. This measurement was "expressed in arbitrary units." Pen deflections, as stated above, indicated both duration and amplitude of sounds.

Ultrasounds emitted following shock generally consisted of narrow-band signals ranging in frequency between 22-28 kHz. Durations of individual pulses within vocalizations ranged between 300 and 1,200 ms. Some subjects emitted ultrasounds immediately on being placed in the apparatus (i.e., before being shocked), and ultrasonic vocalizations following shock often continued for "several minutes." Beta-endorphin attenuated or eliminated

shock-elicited ultrasonic vocalizations for a period of at least 20 min following administration (subjects were not tested beyond this). Dynorphin, M-enkephalin, and L-enkephalin attenuated ultrasounds immediately after administration, but this effect was not as long-lasting as that of beta-endorphin. Substance P caused an increase in ultrasound, although this effect was not significant 20 min after administration. Diazepam and chlorpromazine (at higher doses) attenuated ultrasound emission up to 30-60 min after injection. Imipramine had no significant effects on vocalization.

The authors argue that the drug doses used in this study were too low to produce catalepsy or immobility; therefore it seems likely that the obtained effects on ultrasonic emissions were due to anxiety and/or pain-reducing properties of the drugs. It should be noted that, although the author's summary quantifications of their acoustical records ("pen deflection amount") may be an adequate overall indication of "amount" of vocalization, the use of this measurement as the only quantitative measurement of ultrasonic vocalization ignores potentially relevant information on duration and amplitude of vocal pulses available in the author's records.

Tonoue, T., Iwasawa, H., and Naito, H. Diazepam and endorphin independently inhibit ultrasonic distress calls in rats. European Journal of Pharmacology, 142, 133-136 (1987).

Subjects in this study were male Wistar rats, 250-300 g (exact age or weight at time of testing is not given). Procedures for administering shock and for recording ultrasound were the same as those used by Tonoue et al. (1986). Only rats which reliably emitted ultrasound in response to shock were used in the study. About one-half of these rats were laterocerebroventricularly cannulated for i.c.v. injection. One group of control animals received i.c.v. saline, while another control group received subcutaneous saline. The remaining animals received either i.c.v.-administered beta-endorphin or diazepam administered subcutaneously. Animals in both of these treatment conditions (beta-endorphin or diazepam) received either no pretreatment, pretreatment with Ro15-1788 or CGS8216 (both benzodiazepine receptor antagonists), or pretreatment with naloxone (an opiate antagonist). Thirty minutes following pretreatment (if given), rats were placed in the experimental chamber and 3 footshocks were delivered at 1-min intervals. Ultrasounds were recorded for a 3-min period, which apparently began immediately after the animal was placed in the apparatus. The rat was then removed and given the treatment drug. Post-treatment shocks were given 1 min after beta-endorphin injection or 30 min following diazepam injection.

In general, ultrasounds emitted in response to shock were long pulses of greater than 500 ms, with a constant frequency between 22 and 28 kHz. A graph indicating frequency, duration,

and amplitude characteristics of a sample ultrasound is presented. Both beta-endorphin and diazepam attenuated ultrasound emission. (Ultrasound emission was expressed quantitatively as "total length of pen deflections of recordings of combined activities, including both duration and amplitude of sounds around either 20 or 30 kHz, over a 3-min period of 3 footshocks given at 1-min intervals, and was expressed in arbitrary units." See Tonoue et al., 1986, for further details.) Pretreatment with either Ro15-1788 or CGS8216 largely blocked the effects of diazepam, but had no effect on beta-endorphin treated rats. Pretreatment with naloxone blocked the effects of beta-endorphin, but failed to mitigate the effects of diazepam.

In the discussion, the authors state that the doses of diazepam and beta-endorphin which attenuate ultrasounds in this study are lower than doses which produce analgesia, sedation, or catalepsy. The drugs, therefore, seem to be exerting their effects by reducing fear or anxiety. In addition, although ultrasonic vocalizations were attenuated by these substances, audible vocalizations normally given by the rats at the time of the shock were not affected. (No data are presented on this point, however.) According to the authors, the audible vocalizations indicate that the rats were experiencing pain, therefore suggesting that the substances used in this study did not reduce ultrasounds by affecting pain perception.

van der Poel, A.M., Noach, E.J.K., and Miczek, K.A. Temporal patterning of ultrasonic distress calls in the adult rat: Effects of morphine and benzodiazepines. Psychopharmacology, 97, 147-148 (1989).

Rats (strain, sex, and age not specified) were exposed once a day to tailshock (seven 0.7 mA, 0.2 ms shocks; total duration of shock was 10 s). Sounds were recorded for a 5-min period prior to shock administration and for 1-min following shock, "using the direct mode of an instrumentation recorder." The authors provide no further information regarding recording equipment or procedures. Duration of the sounds recorded (presumably rat ultrasounds of approximately 20-30 kHz, but this is not specified) was determined by examining the tape at a reduced speed "using a customized computer system" (again not detailed). After "1 week" (5 days? 7 days?) of exposure to tailshock, drug testing was begun. Diazepam, chlordiazepoxide, morphine, or naloxone was administered I.P. prior to placing the rat in the tailshock apparatus. Four different dosages (exact dosages not specified) of each drug were used, and the effects on ultrasounds were examined. Rats apparently served in more than one condition, and adequate counterbalancing does not appear to have been done. There was no control group.

In the results section of the paper, the authors present a qualitative description of the spectral characteristics and contexts of the "distress call" of the adult rat. The information

appears to be drawn from other sources, although no other studies are cited and some information is incorrect. An undescribed method was used to determine the beginning and end of ultrasound "bouts;" the authors concluded that chlordiazepoxide and morphine affected the temporal structure of ultrasound emission, while diazepam and naloxone had no effect on ultrasound. These results are inconsistent with those of other authors (e.g., Sales, 1986; Tonoue et al., 1986, 1987) but van der Poel et al. do not discuss why this might be the case.

This study has several apparently serious methodological problems (e.g., no control group, no counterbalancing of drug treatments). In addition, essential information regarding subjects, drug dosages, and ultrasound recording procedures (e.g., age, strain, and sex of subjects; exact drug dosages; equipment used to record sound) is not provided. The results therefore cannot be clearly interpreted.

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