

(Lighthill 1952). Because of the effects of the half-muting operation on the quality of courtship song, we surmise that *G. chopardi* makes use of both of these variables to produce both hisses and whistles with the same pair of spiracles. The courtship whistles of half-muted males are consistently higher in frequency (by up to 1 kHz) than the same males' pre-operative whistles; they are also interrupted frequently by brief lapses into broad-band noise. If males have a fixed motor programme for the abdominal compression that forces air through the tracheal horn, the rate of air flow should be higher than normal through the single spiracle that is capable of opening, causing a shift toward a higher frequency in the resulting sound. If whistles are produced with the valve partly closed and hisses are produced with the valve fully open, the higher rate of flow in half muted males might well lead to an occasional 'blow-out' of the valve, resulting in abrupt lapses from whistle into hiss (as in Fig. 1, Plate I: 'R.Sp. Blocked' row 2).

Why does *G. chopardi* use both whistles and hisses? We suggest two explanations. First, the disturbance hiss, like many defensive sounds, has a broad frequency spectrum which probably is advantageous to the emitter, since a broad range of predators can detect the sound (Masters 1980). Second, preliminary studies show sound production is used in very similar ways in the courtship of *portentosa* and *chopardi*. The great difference in the frequency characteristics of their courtship sounds may thus represent a species isolation mechanism (both species have been collected from the same regions of Madagascar although direct evidence for sympatry is lacking; Chopard 1950). This unusual divergence in the sound signalling systems of two such closely related species undoubtedly owes its emergence to the nature of *Gromphadorhina's* method of sound production, in which the potential for frequency modulation is inherent in the design.

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Role of the Elephant Pinna in Sound Localization

Because of its unique size and mobility, the elephant pinna has been the subject of studies aimed at determining its functional significance (for a review, see Buss & Estes 1971). The results of these studies have suggested two possible roles for the elephant pinna. First, large differences in arterio-venous temperature in the pinna, coupled with the observation that elephants increase the rate at which they flap their pinnae as ambient temperature increases, suggest that the pinna plays a role in regulating body temperature. Second, the observation that elephants extend their pinnae rigidly from their heads in alarm or threat situations has been interpreted to mean that they use the pinnae to alert nearby elephants or to warn intruders. Thus, the elephant pinna has been implicated in both thermoregulation and communication.

Recently, we have had the opportunity to test the hearing capacities of a 7-year-old wild-born female Indian elephant (*Elephas maximus*) at the Ralph Mitchell Zoo in Independence, Kansas. The tests given the animal included the determination of absolute, sound-localization, and frequency-discrimination thresholds. During these tests it was noted that the elephant extended its pinnae when attempting to localize brief sounds, but did not extend them during the non-localization tests. The purpose of this paper, then, is to describe these observations and to suggest that the elephant's pinna may play an important role in the localization of sound.

The details of the behavioural procedure used to test the elephant have been described elsewhere (Heffner & Heffner 1980, 1981). Briefly, the elephant was brought into a room (6.7 × 5.6 × 4.6 m) and tethered in front of a response panel which contained three buttons mounted in a horizontal row. The animal was trained to make an 'observing' response by pressing the centre button with its trunk, a response which initiated a trial and was followed by the presentation of an auditory cue. In the sound-localization tests, the animal was then required to press the left or right button if a sound came from a loudspeaker located to the left or right of the animal, respectively. A correct response was rewarded by dispensing 30 ml of a fruit-flavoured sugar solution

into a small trough located below the centre button. In the absolute-threshold tests, the animal was required to press the centre button and then press the left button if a sound was presented from a loudspeaker and to press the right button if no sound was presented. Frequency-discrimination tests were conducted in a similar manner in which, after pressing the centre button, the animal was required to press the left button if a train of tone pulses emitted from a loudspeaker were all of the same frequency and to press the right button if the tone pulses alternated between two different frequencies. Test sessions were conducted during the quiet early morning hours shortly before the animal's morning feeding time.

Following initial training, the elephant's absolute thresholds for pure tones from 16 Hz to 12 kHz were determined. During these tests it was noted that the elephant's pinnae were maintained in the relaxed position back against its head and neck, with only occasional flapping movements such as to remove flies. However, when the sound-localization tests were given, a very different pattern of pinnae movements emerged. During sound-localization testing, the animal extended its pinnae nearly perpendicular to its head just before it pressed the centre button. After the centre button was pressed and a brief sound had been presented, the animal then moved its trunk to press either the left or right button, during which time it usually returned its ears to the normal relaxed position against its head. Following the localization tests, the elephant was tested on frequency discrimination and was re-tested on its absolute sensitivity to 4 kHz and 8 kHz. In both of these subsequent tests, the animal maintained its pinnae in the relaxed position. Thus, the elephant was observed to display pinna extension only during the sound-localization tests.

Because the elephant was not continuously observed during testing, it is not possible to say if it extended its pinnae on each of the more than 1000 sound-localization trials it received each session. However, we observed consistent pinna extension on trials involving the following stimuli: single clicks, 100-ms bursts of white noise, 100-ms bursts of filtered noise with centre frequencies from 125 Hz to 8 kHz, and 100-ms tone pips ranging in frequency from 125 Hz to 8 kHz. In addition, pinna extension was observed for angles of separation ranging from 0 to 60°. In short, pinna extension was observed for every stimulus and angle used in the sound-localization tests. In contrast, it was never observed during the determination of absolute and frequency-discrimination thresholds which involved frequencies from 16 Hz to 12 kHz and loudspeaker locations of 10° and 30° to the left or right of the animal.

The conditions under which pinna extension could be observed were further elucidated during a special late-morning session in which the elephant's pinna movements were photographed. Normally, the animal was not tested at this time because it had just received food and fresh water and was usually too satiated to perform reliably. When the animal was allowed to perform a sound-localization test with single clicks at an angular separation of 20°, it was noted that the animal did not at first extend its pinnae. Furthermore, while the elephant performed at a level of 90% correct, it was making more errors than it normally did on this task. After 30 trials, the angle of separation was reduced to 10°, following which the elephant made two consecutive errors. At this point the elephant began to extend its pinnae on each trial and its performance rose to near perfect. During the remainder of this session, the animal showed

signs of reduced motivation by occasionally ceasing to perform and playfully pushing on the fence behind which the loudspeakers were mounted. Though it continued to extend its pinnae on most of the trials, it occasionally failed to extend them or extended only one of them. Thus, while the poorer performance observed in this situation may have been due to reduced motivation, it is of interest to note that failure to extend the pinnae was accompanied by poorer performance in localizing sound.

In summary, the elephant was observed to extend its pinnae during sound-localization tests, but not during tests of absolute sensitivity or frequency discrimination. Pinna extension was observed to occur for a variety of different sounds and at both large and small angles. However, when the animal was insufficiently motivated to work at a steady pace, it did not always extend its pinnae and its error rate increased. These observations suggest that elephants extend their pinnae in order to localize sound accurately.

Though it is widely believed that movable pinnae, such as the elephant's, play an important role in sound localization, it is not clear just how pinna extension enhances the ability to localize sound. While the function of the human pinna has been studied in detail, little is known concerning the contribution of large movable pinnae to sound localization (for reviews, see Butler 1975; Shaw 1974). One possibility is that extension of the pinnae may enhance the difference between the frequency-intensity spectra of the sounds reaching the two ears, thereby providing a more distinct localization cue. Another is that it may reduce the intensity of echoes reaching the ears which otherwise might interfere with accurate localization. However, at the present time, the effect of pinna extension on the sounds arriving at the two ears has not yet been determined.

The discovery that the elephant pinna plays a role in sound localization does not contradict previous ideas concerning its function. The elephant pinna may very well be a mechanism for cooling the blood and extension of the pinnae may serve to alert nearby animals. Indeed, since an elephant actively engaged in localizing a sound source is an aroused animal, it would seem natural for other animals to be alerted by the accompanying pinna extension. However, as it has been demonstrated that even a pinna as diminutive as that of humans plays a role in sound localization, it should come as no surprise that the elephant pinna may play an important role in enabling elephants to accurately localize the source of a sound.

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Sexual Terms in Sociobiology: Emotionally Evocative and Paradoxically, Jargon

'Rape', 'coy', 'cuckoldry', 'adultery', 'homosexual', 'harem' are some of the sexual terms used in sociobiology (Barash 1976, 1977; Abele & Gilchrist 1977; Thornhill 1980; and many others). I object to the use of these terms in studies of non-human sociobiology for three reasons: these words used in a sociobiological context are jargon with possible social repercussions; they are more emotionally evocative and less semantically adaptable than alternative, descriptive terms; and their use is often sensational and conducive of an inappropriate prurience.

My objection to such sexual terms is associated with semantic and definitional problems. These objectionable words are seldom defined and when they are defined, agreement on the definitions is hard to reach. 'Rape', for example, has social (Klemmack & Klemmack 1976), psychological, legal, ideological (Burgess & Holmstrom 1974; Brownmiller 1975), and now, sociobiological (Thornhill 1980) meanings. Precise definitions of these sexual phenomena are obviously imperative.

A subtle definitional difficulty surrounds the meaning of these words in studies of adaptive significance. For instance, take Thornhill's (1980) definition of rape. He says or implies (pages 52, 55, 57) that rape is forced insemination or fertilization, and limits rape to those occurrences of apparent forced insemination or fertilization that simultaneously enhance the fitness of males and decrease the fitness of females. This definition is devoid of sociological, psychological and moralistic connotations. Rape is no longer an act of sexual assault or forced intromission: gametic union or at least the deposition of sperm is also required. Most important, the future fitness of the putatively raped female and the putative rapist must also be evaluated. This is a different concept from the one used commonly for humans to mean any act of forced intromission or sexual assault. It is more than descriptive and operational: this precise and restrictive definition allows the study of a mechanism in sexual selection which overcomes mechanisms of epigamic selection. In my opinion Thornhill's (1980) examination of aspects of forced insemination in scorpionflies goes a long way toward a credible theory of the adaptive value of forced insemination. However, this special sociobiological use of 'rape' makes the word paradoxical jargon. Jargon is the specialized or technical language of a profession. 'Rape', as used in the sociobiological sense, has a new, specialized and technical meaning which is quite restrictive, yet 'rape', as a word we all recognize, does not make the new connotation obvious. The term 'rape'

is unlike, for example, 'kleptogamy', a word which many of us do not recognize, and which is thus immediately flagged as jargon.

The compounding of social arguments with arguments of adaptive significance is the crux of my concern about paradoxical jargon. I think the following examples are illustrative. At a recent scientific meeting I was asked, 'Is it rape when a virgin is forced to intercourse?' Similarly, is it rape when a post-menopausal woman is forced to intercourse? There are two answers to both questions which illustrate my point about paradoxical jargon. Obviously, both are rape — in all of the traditional, psychological, sociological, and legal ways we think of rape. However, in the sociobiological sense of Thornhill, neither of these would be rape, because in the first example the virgin could be impregnated and her genetic fitness thereby increased, and because in the second example the fitness of the male who forces a post-menopausal female to copulate would not be increased, and in addition, the fitness of the menopausal female would not be decreased. The social danger I see is the possibility of transference of the sociobiological idea to the legal realm so that legally, victims of rape will be said not to have been raped. This is not so unlikely. A similar reversal, in which the victim's motives and behaviour are tried, has led to the further victimization of women in police precincts and courts when they report rapes (Brownmiller 1975).

One way to guard against this social danger is to clearly separate legal aspects of rape from sociobiological aspects of forced insemination. I suggest that we use a descriptive and operational term like 'forced copulation' (see e.g. Gladstone 1979; Burns et al. 1980) or 'forced insemination' in discussions of non-human sociobiology and in discussions of the adaptive significance of the phenomenon in humans. I think 'rape' should be used only in traditional psychological, sociological, and legal discussions of the phenomenon among people.

My second objection is simply that the emotions evoked by these words suggest important bias similar to those pointed out by opponents of sociobiology (e.g. Lewontin 1977). In line with their criticisms, Thornhill's hypothesis can be said to reflect current, male-centred, American attitudes as easily as it reflects the biology of scorpionflies. In general, the suggestion of bias is easily eliminated by unevocative, adaptable, operational, alternative terms such as 'forced copulation' for rape (Gladstone 1979; Burns et al. 1980), 'one-male social unit' for harem, 'kleptogamy' for cuckoldry (May & Robertson 1980; Gowaty 1981), 'unisexual' for homosexual. These terms have other advantages. 'One-male social unit' can easily become 'two-male social unit' or 'multi-male social unit', while the idea of a 'double-harem' is at best ambiguous. Cuckoldry is kleptogamy as experienced by one participant in a threesome of participants. The adulterer is one participant; the cuckold and cuckold are the others. 'Kleptogamy' is jargon, as are 'adulterer', 'cuckold', and 'cuckolder', but it is easily-identified jargon which has the advantage of clarifying how the sexual strategies of the three participants are related; and 'kleptogamy' has no emotional or moral connotations.

Even though I think 'cuckoldry' is an inferior alternative to 'kleptogamy', the interesting defence of the term 'cuckoldry' made by Power et al. (1981) is to be lauded in that they examined the etymological roots of the word. Because science is culture-bound, etymologies may give important insight into the broader meanings of words, and reveal potential sources of emotional and societal bias. A false argument in favour of the term