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Article VI.—INSECT SOUNDS

By Frank E. Lutz

Probably the first definite sounds made by land-animals on this earth were made by insects. Before ever birds sang or even frogs croaked, insects had developed a chitinous covering, the segments of which, rubbing together, produced sound-waves. Whether these sound-waves were audible in the sense that there were organisms with nervous mechanisms attuned to them might be the subject of an interesting speculation. Today's crickets and katydids belong to the order Orthoptera, and orthopteroid insects were abundant in the Carboniferous. In the fields and forests of those days, or possibly earlier, was started "the poetry of earth" that "is never dead."

Judged by human ears, the best insect-musicians of today belong to rather primitive orders. The more advanced groups, such as ants, bees, flies, and butterflies, make no sounds that we can hear or else, at most, what seem to us to be nothing more than faint squeaks, buzzes, hums, or clicks. However, it is entirely probable, practically certain, that insect-sounds are not made for the purpose of being heard by human ears. Whether the insects themselves hear these sounds is the important question and one that has not been—possibly can not be—determined beyond all doubt.

In this connection it should be remembered that, in man's affairs at least, many sounds are made without intention and even contrary to desire—for examples, sneezing and snoring. No part of the success of a certain popular kind of automobile is due to the various and often loud noises emitted by the machine in action. Using an illustration more applicable to the present subject, the armor of the knights of old creaked and rattled as they moved. Their fellows were able to hear these sounds and reacted to them. A rough spot in a particular joint increased the sound made by the moving of that joint. Now, if the armor-maker purposely designed these joints to creak or if the wearer purposely creaked his armor, even if for no other motive than to tickle his pride (as has been the case with wearers of squeaking shoes), then the creaking of the joint had a significance analogous to that usually claimed for certain sounds made by insects—there was an adaptation of structure to sound-production. But, considering now the sounds made by insects, if they are merely incidental to friction between parts of their body, analogous to unintentional squeaks and rattles of knightly armor, then those sounds

have no biological significance, except as they may betray the insect to its enemies.

About fifty years ago A. H. Swinton published a book on 'Insect Variety; Its Propagation and Distribution.' It is a more or less popular presentation of the subject and contains rather good summaries of previous work, together with his deductions therefrom. His introduction to the discussion of insect-sounds contains a sentence of which the following is a part: "Reciprocating stimulatory friction of articulate parts to express emotion postulates adaptive acquisition, consequent on assumed integumental tendency under attrition to determine a smooth undulatory surface, and propagation by hereditary transmission, supposing the theory applicable." There are some that do not so suppose; others do. He then says: "The culminating points of musical perfection in a group are often indicated by other characters expressive of emotion: thus with beetles the Death Watches exhibit love and rivalry in music, and are most sensitive to touch; or the longhorns predominate in pugnacity. In Lepidoptera music is in direct relation to color, sound to beauty. Musical Orthoptera and Longicornia exhibit pugnacity. This evidently indicates parallel development of the sensorial organs."

Swinton's conclusion of the whole matter is as follows:

> Should any seek to know more of the capabilities of these lowest of ear-structures than is to be gleaned from crude anatomical description, resort may be made to observation and cautious experiment. And having notated a series of insect passages, and the excitation under which they were produced, we may, if our ear be fine, even venture on a rendering into sentiment, by the formule of Mersenne, an old and sage philospher and mathematician who flourished during the earlier portion of the sixteenth century; and the result, I think, will fully justify the assumption of a common sound-perception to our own, participated in by these humble instruments. To this end the vowels *a* and *o* must be interpreted physiologically to signify what is grand and full; the vowel *i*, that which is small and penetrating; *e*, subtlety and sorrow; *o*, is expressive of strong passion; *u*, belongs to things secret and hidden; *f*, *th*, *wh*, and the like, frequent with insects, denote sharpness or vanity; *s* and *x*, bitter things; *r*, the canine letter, violent and impetuous emotions; *m*, magnificence; *n*, things dark and obscure; and so on. Take now in illustration that pretty ballad of Percy's "O Nancy, wilt thou go with me?" and compare it in the fields with grasshopper stridulation, then it will at once strike you that while the flaunt of the first six lines will suggest the translation of many a rival challenge around, the refrain of the last couplet is nothing less than a rendering of the common pairing note. So our ballad, be it noticed, first speaks of colours and danger, *russet* gowns, *silk*en *sh*een, a wi*sh* behind, p*erils* keen, mi*sh*ap to rue, and such-like; and we think we hear the grasshoppers, each in their own dialect, defy their mates. After this comes the ten*der* *tear*, *regret*, *sc*enes so gay, and *wert* fairest of the fair; harsh retrospect, at least, it must be allowed, represented in the grating rhythms of these saddest of little lyres when death follows fast on the reproductive gatherings. And on such pleas is it we would claim for these insect ears analogous structure and perception with our own.

These passages are not quoted for approval since, if these be the strongest "pleas," most scientists of today would deny the claim; attributing human sentiments of love, appreciation of beauty, and so on, to insects is a dubious proceeding; and, until we know more about the sounds themselves, it seems rash to explain them by such a theory as that of the inheritance of acquired characters. It may be that such characters are inherited but we need better proof than has yet come from a study of insect-sounds. These quotations do, however, represent, perhaps in somewhat exaggerated form, the views that have been held by many students of the subject.

The "music" with which "the Death Watches exhibit love and rivalry" consists in tapping the sides of their burrows. If these taps are purely incidental to the insects' movements in their burrows, they come as little within the scope of this paper as the scratching of a beetle as it scrambles among dead leaves. On the other hand, if the movements are made for the purpose of producing sound, this sound may be just as truly music to the insects as is the beating of a drum to those humans who like drum-music. If the insects communciate with one another by means of these tappings, we have a most interesting habit to investigate; but it may not be a strict case of communication by means of sound, for the other insects are in the same piece of wood and may feel the taps instead of hearing them. The fact that we hear a sound does not enter into the question. True audition might be illustrated by a chairman communicating with the members of a convention by pounding his desk with his gavel; "false audition by touch" might be illustrated by one member shaking the chair of another.

The sound caused by the vibrations of the wings as an insect flies seems to be purely incidental to the movements necessary to flight. Many insects fly noiselessly—at least, we can not hear them flying—but mosquitoes, for example, in flight make a sound that is all too familiar to us. Now, it is probable that the mosquitoes can not fly without making this sound; in other words, the sound is not made intentionally; nevertheless, it might be considered to have a biological significance if it be true that the opposite sex can hear it and that the sexes are guided to each other by its aid.

This was the idea held by Prof. A. M. Mayer in his interesting paper, 'Experiments on the Supposed Auditory Apparatus of the Mosquito' (1874, American Naturalist, VIII, pp. 577–592). The essential part of his paper is as follows.

> I cemented a live male mosquito with shellac to a glass slide and brought to bear on various fibrils [of its antennæ] a ⅛th objective. I then sounded successively,

near the stage of the microscope, a series of tuning forks with the openings of their resonant boxes turned toward the fibrils. On my first trials with an Ut_4 fork, of 512 v. per sec., I was delighted with the results of the experiments, for I saw certain of the fibrils enter into vigorous vibration, while others remained comparatively at rest.

The table of experiments which I have given is characteristic of all of the many series which I have made. In the first column (A) I have given the notes of the forks in the French notation, which König stamps upon his forks. In the second (B) are the amplitudes of the vibrations of the end of the fibril in divisions of the micrometer scale; and in column (C) are the values of these divisions in fractions of a millimetre.

A	B	C
Ut_2	.5 div.	.0042 mm.
Ut_3	2.5	.0200
Mi_3	1.75	.0147
Sol_3	2.0	.0168
Ut_4	6.0	.0504
Mi_4	1.5	.0126
Sol_4	1.5	.0126
Bb_4	1.5	.0126
Ut_5	2.0	.0168

The superior effect of the vibrations of the Ut_4 fork on the fibril is marked, but thinking that the differences in the observed amplitudes of the vibrations might be owing to differences in the intensities of the various sounds, I repeated the experiment, but vibrated with lower intensities the forks which gave the greater amplitudes of co-vibration, and, although I observed an approach toward equality of amplitude, yet the fibre gave the maximum swings when Ut_4 was sounded, and I was persuaded that this special fibril was turned to unison with Ut_4 or to some other note within a semitone of it. The differences of amplitude given by Ut_4 and Sol_3 and Mi_4 are considerable, and the table also brings out the interesting observation that the lower (Ut_3) and the higher (Ut_5) harmonics of Ut_4 cause greater amplitudes of vibration than any intermediate notes. . . Experiments similar to those already given revealed a fibril tuned to such perfect unison with Ut_3 that it vibrated through 18 divisions of the micrometer or .15 mm., while its amplitude of vibration was only 3 div. when Ut_4 was sounded. Other fibrils responded to other notes, so that I infer from my experiments on about a dozen mosquitoes that their fibrils are tuned to sounds extending through the middle and next higher octave of the piano. . .

Some may assume from the fact of the co-vibration of these fibrils to sounds of different pitch, that the mosquito has the power of decomposing the sensation of a composite sound into its simple components, as is done by the higher vertebrates; but I do not hold this view, but believe that the range of co-vibration of the fibrils of the mosquito is to enable it to apprehend the varying pitch of the sounds of the female. In other words, the want of definite and fixed pitch to the female's song demands for the receiving apparatus of her sounds a corresponding range of co-vibration, so that instead of indicating a high order of auditory development it is really the lowest, except in its power of determining the direction of a sonorous centre, in which respect it surpasses by far our own ear.

Professor Mayer gave no data concerning the pitch of the female's sound or its variability. The intensity of such a sound, especially at a

distance great enough to make it a desirable factor in guiding the male, is so slight that the sound from a tuning fork on a resonant box placed near and turned toward the antenna would be like that of an artillery battle in comparison. I have watched under a high-power microscope a male mosquito's antenna when a number of female mosquitoes were flying in the vicinity and could see no motion of the "fibrils," but perhaps the microscope was not sufficiently powerful and, at any rate, we do not know how slight a variation the male can feel.

It would be interesting to know whether male mosquitoes are really guided to the females by sound, regardless of the way in which that sound is perceived. To test this I bred a large number of mosquitoes and separated the sexes before they had a chance to mate. After they had been kept for some time so that they were probably sexually mature, each sex was put in a wide-mouthed jar, the opening being covered with netting. The mouth of the jar containing the males was then brought close to that containing the females but there was no noticeable crowding of the males on the netting that separated the sexes, although the females were flying about. Thinking that the failure of the males to go toward the females might be due to the fact that the males were confined, and remembering that certain kinds of male moths are attracted great distances to a confined female, I put a jar of females near a breeding-place of mosquitoes and watched at night to see if any males came. Furthermore, to be certain that there were males in the vicinity, I released at the mouth of the jar of females many males that had not yet mated. Although the females were flying about in their jar and producing what sounded to me like their characteristic shrill note, no males came to the netting that confined the females.

This was disappointing, and doubly so because it proved nothing beyond the fact that the males did not come to those confined females. In the case of the moths, the males are supposed to locate the females by odor and, if male mosquitoes had been attracted to the jar containing the females, it would have been necessary for us to consider the possibility that odor was the guiding factor. As it was, the only thing left was to wonder how male mosquitoes do find their mates. Incidentally, it may be said that none of the experiments believed to have demonstrated that odor is the guiding factor in the case of moths have absolutely ruled out sound, and male moths have antennæ, quite as plumose, apparently as well fitted to receive sounds, as those of male mosquitoes.

Certain insects that make a buzzing, humming noise when they fly make a much shriller sound when they are caught and their wings are

held. Classic examples of this are bees and syrphid flies. Since some of these syrphid flies resemble bees in appearance (but, of course, do not sting) they are said to "mimic" bees and the shrill noise made by them when they are caught is believed to add to the deception and to persuade the captor to release them under the fear of getting stung. This implies that the enemy to be deceived can, like man, hear these sounds but, unlike most men, can not distinguish between the note of the fly and that of the bee. Probably the chief enemies of these flies are spiders and certainly the flies sound the note quite vigorously while the spiders are winding them up in silk, but just as certainly the spiders keep on winding and the flies profit nothing by the noise they make. As this shrill note is not sounded until the fly is caught, toads and the like would not hear it before the fly was inside of them and then feeling would probably give more certain information than sound as to whether the captive was a fly or a bee. Birds would be more apt to be tricked before they had swallowed, but certain fly-catchers make a specialty of catching bees and for them, at least, a fly making a noise like a bee would not be an object of terror. On the whole, if these flies do successfully mimic bees, they must do so on the strength of their looks or their flight-hum, not by the shrill sound they make when their wings are stopped from vibrating naturally.

The history of investigations concerning the production of this shrill note is very interesting. As far as we know, most insect sounds are not vocal; that is, they are not produced by lungs and larynx. Insects have no lungs such as vertebrates possess but air is conducted to various parts of the body through a system of tubes, the tracheæ. These tracheæ open to the outside through a series of holes, the spiracles. Landois, in a justly classic paper (1866, Zeitschrift für wissensch. Zoologie, XVII), described a number of experiments, including cutting off not only the wings but other parts of flies. He dissected the tracheæ and gave beautiful drawings of the spiracular membrane which he asserted was set into vibration by the insect's forced breathing, thus producing the sound. Other work confirmed this idea, and comparative anatomy showed that certain flies, such as Stratiomyidæ, that do not produce this shrill note have only feebly developed spiracular structures. No wonder, then, that Pemberton showed some timidity in announcing (1911, Psyche, XVIII, pp. 114 to 118) the results of his work. He said, in part:

> Despite the weight of testimony which seems to favor the theory of the spiracular voice, I cannot avoid the conclusion, from these observations of my own, that there has been some curious mistake about it all. My experiments with several species of Syrphidæ (*Eristalis tenax* in particular), the house fly, honey bee and the bumble bee,

show that these insects do not produce audible sounds by vibration of any portion of their spiracles or tracheæ, but that all sounds of the nature of buzzing produced by them are made solely by the wings, either by their vibration in the air or by striking the wing bases against the body wall.

In all the experiments I have kept constantly in mind Landois's theory and all my experiments have been performed in an attempt to verify it. However, not in a single instance have the results pointed in any way toward Landois's conclusions.

His experiments included pulling out, not merely cutting off, the wings; holding the wing-bases; destroying the spiracles with a needle; examining the spiracles while the sound was being made to see if there were any motions; and so on. He added:

The above experiments were carefully repeated several times with the same results in every case. They seem to prove quite conclusively that the supposed sound of the spiracles is merely a buzzing of the wing bases or a striking of them against a portion of the body-wall adjoining them. The well-adapted character of the spiracles for the production of sound if air could be very violently forced through them, combined with the confusing fact that the same pitch of sound is produced both with the wings cut off and intact, might easily lead one to conclude that the sounds were produced by some other organ than the wings.

The question may well be asked, "Why are the spiracles so modified and complex as Landois considers them?" It must be taken into consideration that the spiracles are comparatively large openings to a very delicate and vital tracheal system, which should be safely guarded at its openings against the entrance of dust particles. In most cases they are protected by a dense growth of hairs but often are not, as for example in the honey bee. The thoracic spiracles of the honey bee are poorly protected externally but within the opening this folded membranous curtain, or so-called vocal membrane, acts undoubtedly as a screen against the entrance of dust, etc.

Pemberton's conclusions received support from Aubin (1914, Journ. Royal Microscopical Society), who offers the following suggestions as to the reception and purpose of this sound.

It is evident that the organs of phonation of *Eristalis* described above are of a higher order than the stridulating organs of Coleoptera and Orthoptera and a little consideration will tend to the belief that it is not impossible that they fulfil the dual function of emitting and receiving sound. According to the laws of acoustics a stretched membrane will vibrate under the influence of external notes which are approximately in unison with the note it can itself emit; it is therefore not unreasonable to infer that the resonant areas will respond to the buzz of other individuals and thus form one of the elements of an auditory apparatus.

If it be further borne in mind that, in *Eristalis* and perhaps in other genera the note is susceptible of a somewhat syren-like modulation, it is not inconceivable that the sound produced may be the means of transmitting a variety of indications to the similarly attuned organs of other individuals.

The precise part played by buzzing in the life of the individual is somewhat obscure, but the fact that these organs are equally developed and equally efficient in both sexes of *Eristalis* would seem to indicate some function other than or in addition to a sexual one.

Such observations as I have been able to make on this point are quite insufficient to justify any conclusion, but, so far as they go they indicate that the buzz serves, *inter alia*, as a warning note to aggressors.

These observations are as follows:

(1) Several of the hover-flies, if held lightly in the fingers, will buzz for comparatively long periods and many specimens of *Eristalis*, if held by the legs, will alternate, almost without intermission, between buzzing and attempting to fly.

(2) Most Diptera, when entangled in a spider's web, will buzz at intervals. If quiescent the captive will almost invariably buzz if the spider, in order to ascertain the nature of its captive, touches it with an investigating claw.

(3) If a cage containing *Eristalis* be taken into a partially darkened room, they will cease flying and either remain stationary or crawl about slowly. Under such conditions, should one individual touch another, the one so touched will emit a short, sharp buzz which is sometimes responded to by others in the cage.

(4) A captive, under the microscope, can usually be made to buzz by touching it with a needle, more especially on the abdomen or wing shoulder.

The "resonant areas" to which reference is made are small parts of the wing-membrane and, as we know of no nervous tissue in their vicinity, it may seem to some quite "unreasonable to infer" that these nerveless areas are sound receptors. Since almost anything is conceivable, "it is not inconceivable that the sound produced may be the means of transmitting" ideas but, as Aubin said, his observations "on this point are quite insufficient to justify any conclusion." His observations as to the warning value of this sound are certainly not conclusive. About all we can say is that, when *Eristalis* vibrates its wings without flying, the bases of the wings hit against the body and make a noise.

Although the spiracular "voice" of Diptera seems to be disposed of, as far as past work is concerned, Duncan has just published a note (1924, Pan-Pacific Entomologist, pp. 42 and 43) concerning a grasshopper, *Tæniopoda picticornis*, that apparently does produce a spiracular sound, faint though it be and apparently inconsequential. He says:

> The sound is of about the intensity of that resulting when two pieces of writing paper are rubbed together and is produced by the spewing out through the second thoracic spiracles of a small quantity of watery liquid at each exhalation. Many tiny bubbles are formed each time the sound is produced. These vary a great deal in number, being at times hardly noticeable and again forming a mass a good three-sixteenths of an inch in diameter. Immediately after being formed the bubbles disappear, leaving an area around the spiracles that is wet for a second or so.
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> There are no grounds for doubt as to the mechanism by means of which the sound is produced, for in addition to the fact that it is obviously synchronous with the exhalation of air from the tracheæ and the formation of the bubbles noted, it is exactly the sort of sound that one associates with the spewing of a mixture of air and liquid through a small hole, its intensity varies according to the amount of bubbles produced, and the sound ceases entirely when the production of bubbles ceases, as it does shortly (apparently due to a using up of the supply of liquid available) if the

hoppers be continuously stimulated for a time. Moreover, the sound may be produced by nymphs as well as adults, thus eliminating the wings as stridulatory organs, and it may be produced even though the legs of the hoppers be held perfectly still. The sound is apparently under full control of the insects and, as far as I could learn, is produced only when they are disturbed.

In other words, the grasshoppers, when disturbed, contract their body, forcing a little air out of the tracheæ and, if there be any fluid present, bubbles are blown and broken, incidentally making a faint sound. Harvey (1907, Canadian Entomologist, XXXIX, p. 18) has reported that a water-bug, *Pedinocoris macronyx*, makes a "soft chirping noise" by means of its ventral spiracles as it poised just at the surface of the water.

One insect sound that long enjoyed a very interesting explanation of its purpose is the "drumming" or "trumpeting" of bumblebees. Goedart started the idea in the Seventeenth Century with his essay 'De Insectis, in Methodum Redactus; cum Notularum Additione,' in which he says that every morning about 7:00 A.M. a member of the colony goes to the top of the nest and beats his wings to rouse the others and let them know that it is time to get to work. Eight years later the great Reaumur denied the story but, as his only evidence was that he had not observed such actions, his denial carried only the weight of his authority. A French abbé, de Pluche, confirmed Goedart except to say that the rising signal is given at 7:30 instead of 7:00. Something more than a hundred years later Hoffer moved the time of the rising signal ahead to about 3:00 A.M. and said that it was kept up for about an hour. To give the remainder of this history I quote extracts from Plath's paper (1923, Psyche, XXX, pp. 146 to 154) on this subject.

Hoffer's (1882–83) confirmation again brought Goedart's "trumpeter" story into good repute among biologists for a period of more than twenty years. With apparently the single exception of Perez (1889), it was accepted—in most cases after personal verification—by Fritsch (cf. Hoffer, 1882–83, p. 25), Kristof (1883), Harter (1890), Sharp (1899), Marshall (1902), and Bengtsson (1903). Perez (p. 117), while not in the least doubting the general correctness of Hoffer's (1882–83) observations, rejected the latter's interpretation by pointing out (1) that there is little sense in having a "trumpeter" unless he be the first one to rise, and (2) that the sound produced by the "trumpeter" is of no use whatever, as far as rousing the colony is concerned, since (according to Perez) bumblebees, like honey bees and ants, are completely deaf. Perez (1889) then offers his own explanation. After expressing the opinion that the bumblebee "trumpeter" fulfills no social function, and that the "trumpeting" is probably done for his own benefit, Perez (p. 117) suggests that the "trumpeters" in bumblebee colonies, like the so-called ventilators among honeybees, are newly-hatched individuals which are training their wing muscles for the long flights which they will soon make. However, as we have already seen, Perez' (1889)

theory, although more plausible than that of Goedart (1685), seems to have made little or no impression upon contemporary biologists.

Fourteen years after the publication of this theory, a third interpretation was offered by the well-known German bee student von Buttel-Reepen (1903, 1907). Unlike Perez (1889), this author suggested that the bumblebee "trumpeter" has the same social function as the ventilators in the honeybee colony, namely, to reduce the temperature, or to expel moisture or bad odors from the nest. Similar conclusions were reached by the Norwegian biologist Lie-Pettersen (1906). This new interpretation was accepted—in some cases after extensive experimentation—by Stierlin (1906), Wagner (1907), Gundermann (1908), Lindhard (1912), and Sladen (1912).

However, within the last decade, Goedart's (1685) "trumpeter" story has found another adherent in Bachmann (1915, 1916). What is more, Bachmann (1915) has discovered that the bumblebee "trumpeter," in addition to rousing the members of the colony in the morning, also attends to the "curfew" in the evening.

Plath gives the results of his own experiments on about sixty colonies of various species of bumble-bees and concludes as follows:

1. The so-called trumpeters in bumblebee colonies are bees which are engaged in ventilating the nest.
2. This ventilation is brought about by a rapid vibration of the wings and may take place at any time during the day or night.
3. Species which nest on the surface of the ground likewise make use of this method of ventilating their nests.
4. Ventilation by fanning is also resorted to by small bumblebee colonies.
5. Perez' theory, according to which the so-called trumpeters in bumblebee colonies are newly emerged individuals which are exercising their wing muscles, is not founded upon facts.

And, so, one more insect sound for which a very definite purpose had been assigned sinks into the category of a noise that is purely incidental to a movement that was not intended to make a noise.

The "voices" of honey-bees have long been classic. Many and various have been the descriptions and interpretations. Mrs. Comstock, in her 'How to Keep Bees,' mentioned only the queen, which she did as follows.

The belligerent attitude of the queens toward each other seems to have been so strong an emotion that a voice has been developed to express it, and is eloquent with rage and fear. This note must be heard to be understood; as nearly as I am able to spell it, it is "tse-ep, tse-e-e-ep, tse-e-ep, tsep, tsp, tsp, ts," in a sort of diminuendo. She makes the noise when she discovers another queen cell; if there is within this cell a full-fledged queen, she pipes back, but it sounds quite differently and the note is more like "quock, quock." This piping of queens is especially evident before an after-swarm is to issue. The queen will also pipe when bees gather about her and try to ball her, which is often the fate of a new queen introduced into a colony not ready to receive her. In this case the note is one of righteous anger at the indignity to her royal person. She makes this piping with some vocal instrument, not well understood. Her wings vibrate tremulously while she is piping, but she can pipe quite vociferously after her wings have been entirely cut off.

We learned from the discussion of flies that cutting off the wings is not sufficient because the bases of the wings are still there to hit against the thorax.

Cheshire in 'Bees and Bee-keeping,' discussed the bee's sense of hearing and quite properly objected to drawing sweeping conclusions from the negative results of certain experiments. He said.

> Sir J. Lubbock has commonly been regarded as asserting the total deafness of bees; but, in a correspondence of some years since, the distinguished investigator assured me his position was negative, as he merely failed to get evidence of bees hearing. Sir J. Lubbock's experiments I cannot but regard as most inconclusive, since tuning-forks, whistles, and violins, emit no sounds to which any instinct of these creatures could respond. Should some alien watch humanity during a thunderstorm, he might quite similarly decide that thunder was to us inaudible. Clap might follow clap without securing any external sign of recognition; yet let a little child with tiny voice but shriek for help, and all would at once be awakened to activity. So with the bee; sounds appealing to its instincts meet with immediate response, while others evoke no wasted emotion. In practical matters, the hearing of bees is not only often obvious, but must be taken into account—*e.g.*, when a swarm is about to be transferred to its permanent abode from its temporary one, many will stick to the sides of the latter after the bulk have been thrown out, and these, by their buzz, will distract those that are running in at the new hive door. The removal of the stragglers to a distance will end the disturbance, which will be renewed if they be returned to their former position. Some years since I was present in a tent where an expert had driven five or six stocks, and nearly a pint of lost bees had collected for mutual comfort on a piece of damp canvas, at the bottom of the tent pole, against which the last skep was made to lean, as it was stood, quite late in the evening, on a table for operation. No sooner did the bees in this skep set up the wellknown roar, than those on the canvas, so still hitherto, faced upwards, unhesitatingly ascending the pole, and setting on the outside of the roof of the receiving skep. This circumstance I remember as affording, to all who witness it, conclusive evidence of hearing.
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> In the progress of the present we moderns have, perhaps, too confidently condemned *all* the past. The conflict of the key and warming-pan of old swarming days has called forth some good-humoured but possibly not always philosophical, banter, for I confess I think, that in its day, it had its value. Piping of queens, whatever be its cause, seems to point to a sense of hearing, for it appears to be a sound made for an object, and not the result of some necessary movement.

Even Forel, that confirmed sceptic concerning the ability of insects to hear sounds as such, said in 'The Senses of Insects':

> The [strange] queen escapes but is pursued. Then in her terror, she utters "cries of fright" which disturb the whole hive. The disturbance of the hive is, indeed, not produced when the queen is caged and does not cry. Von Buttle concludes therefrom that the workers hear the queen's frightened cries.
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> I confess that the judicious remarks and the experience of an observer so excellent as von Buttel Reepen make me seriously doubt on the question of hearing in insects. Nevertheless, it fails to convert me on a fundamental point: where is its organ, if it exists as a special sense, for special energy? We know and prove without

difficulty the organs of other senses. Why not that of hearing? So long as its seat and the deafness consecutive to its extirpation have not been demonstrated there remains a possibility that even von Buttel cannot exclude, that of the "false audition by touch" of Duges. I have shown elsewhere how insects, so light and so small, are easily impressed in their tactile organs by the least vibrations of the atmosphere and of the bodies which sustain them. But precisely those of the experiments of von Buttel which peremptorily exclude sight, that is to say those which are passed in the darkness of the hive or across its contents, in no way exclude the tactile perception of vibrations. And those which seem to indicate an audition at a distance in the open air do not exclude vision. The differences of the tones emitted by bees, differences which we perceive by our hearing, might very well be perceived by them as differences of tactile vibrations, according to their amplitude, as we ourselves perceive very deep sonorous vibrations by touch, and not only by hearing. There is here a very hard question, which must be put. But whether we are dealing with hearing properly speaking or not, the fact that bees communicate their impressions and their emotions has been victoriously demonstrated by von Buttel against Bethe, and confirms what I have observed in ants.

McIndoo (1922, Journ. Comp. Neurology, XXXIV) confirmed the idea derived from recent studies of flies that the shrill "squealing" noise of bees is due to the striking of the wing-bases against the thorax. He added:

> Besides the buzzing and squealing noises made by bees, the writer often heard a crackling sound while observing these insects flying around an alighting-board. He could not detect how this sound is made, but imagined it produced by the wings striking together accidentally.
>
> All attempts, except one, trying to get bees to respond to the squealing of other bees failed. Or at least the bees exhibited no reactions which could be attributed as signs of hearing. Nevertheless, one squealing bee was held in a hidden position a few inches from an alighting-board; at once one of the many workers on this board seemed to take notice and flew to the screen behind which the squealing bee was hidden, and then it came immediately to the squealing bee, which it began to examine by running around it and smoothing its hair.
>
> A queen bee, resting on a comb with workers surrounding her, when squeezed, squealed and the near-by workers became excited. Such experiments really do not mean much, because too many interfering factors cannot be eliminated. The original plan of the writer was to carry on experiments in which he hoped to be able to classify and to record on phonograph records the various sounds heard in a hive of bees. If this were possible, he intended to reproduce these sounds and then to determine whether or not bees respond to them.

If bees have as acute a sense of smell as many students believe them to have, neither hearing nor the "false audition of touch" are necessary to explain many of the reported observations on bees. At least, the possibility of odor being concerned has usually not been excluded, although it would seem to be so in the case of a young queen, still enclosed in wax, hearing the "tse-ep" of the reigning queen and answering "quock." This dialogue needs further investigation. Sladen and others

have discussed certain scent-glands on the abdomen of bees and suggested that odors perceptible to bees are blown out from these glands by the vibration of the wings, which vibration affects human auditory organs. Even though all this be true, one would scarcely expect many different ideas to be expressed by odor. Excitement might cause excessive activity of a gland in a bee as it does of sweat glands in man and this scent might excite other bees but, if we must admit many different emotions, it becomes difficult to imagine a sufficient variety of odors and sufficient control over them to meet the needs.

Probably the emotions and the means of communicating them have been more studied in ants than in any other group of insects. Most of the essential data are given in Wheeler's 'Ants,' from which the following quotations, if not otherwise acknowledged, are taken.

Especially in the Ponerinæ and Myrmicinæ, the abdomen bears on the dorsal surface of the base of the gaster a series of fine, file-like ridges. A segment in front of this overlaps it and has a sharp edge that scrapes the file when the abdomen moves in certain ways, producing a faint sound of high pitch. "The file is, in all probability, merely a local specialization of the fine, polygonal elevations or asperities which cover the adjacent portions of the segment and are so characteristic of the chitinous investment of many parts of the body." An Australian ant has coarse ridges in one part of the file and fine ridges in another, and Sharp suggested that it may have two notes in its repertoire but apparently no one has heard it squeak. "Janet, in his studies of *Myrmica rubra*, calls attention to the fact that there are accumulations of chitinous asperities at various widely separated regions of the ant's body, especially on articulations which might, by their movements, produce sounds. But the true stridulatory organs he finds to be situated where they were seen by Landois and Sharp, i.e., at the base of the first gastric segment, and also on the corresponding part of the postpetiole."

Suggested auditory organs in ants are the "chordotonal" and the Johnstonian. The former has been considered to be the more important and the latter may be only a variety of it but apparently proof that either receives sound is lacking. A necessity of finding some auditory organ is felt and "the chordotonal organs are supposed to be auditory in function because they are most elaborately developed in the stridulating Orthoptera (crickets and katydid), and because their structure would seem to be adapted to responding like the chords of a musical instrument to delicate vibrations." "These structures, which are present in a great many insects, even in the larval stages, are typical compact, spindle-

shaped bundles of sensillæ, each consisting of a chitin-secreting gland and a nerve cell. These cells are arranged in a series at an angle to the integument and are stretched, like a tendon, across a cavity between opposite points in the cuticle, or between a point in the cuticle and some internal organ. . . Eight pairs of chordotonal organs have been seen in the ant's body, but it is not impossible, as Janet suggests, that others exist, for such minute and recondite objects are very easily overlooked even in well-prepared sections." If every insect that possesses "chordotonal organs" can hear, most insects can.

One of Lubbock's many ingenious experiments was designed "to ascertain whether ants have the power of summoning one another by sound." On a board where a colony of *Lasius flavus* was usually fed he placed some small pillars of wood about an inch and a half high and honey was placed on the top of one of them. Ants wandered all around hunting for food. Ants that had fed on the honey were captured before they descended but three were allowed to feed on top of the pillar at a time. Lubbock felt that "if they could summon their friends by sound, there ought soon to be many ants at the honey" but the other ants did not come and Lubbock concluded that "it seems obvious therefore that in these cases no communication was transmitted by sound." He might have added "or in any other way or, if there was, no attention was paid to the communication." In other words, the experiment is not crucial and, furthermore, *Lasius* belongs to the Camponotinæ, a group that is not noted for its stridulations. However, this same *Lasius flavus* has "a remarkable arrangement, which at once reminds us of that which occurs in *Gryllus* and other Orthoptera. In the femur it [a trachea] has a diameter of about $\frac{1}{3000}$ of an inch; as soon, however, as it enters the tibiæ, it swells to a diameter of about $\frac{1}{800}$ of an inch, then contracts again to $\frac{1}{5000}$. Moreover, as in *Gryllus*, so also in Formica, a small branch rises from the upper sac, runs almost straight down the tibiæ, and falls again into the main trachea just above the lower sac." The argument usually used in such a case is that this structure is probably an ear and therefore *flavus* certainly makes sounds to be heard by these ears. Lubbock continued as follows.

> Again, Professor Tyndall was good enough to arrange for me one of his sensitive flames; but I could not perceive that it responded in any way to my ants. The experiment was not, however, very satisfactory, as I was not able to try the flame with a very active nest. Professor Bell most kindly set up for me an extremely sensitive microphone; it was attached to the underside of one of my nests; and though we could distinctly hear the ants walking about, we could not distinguish any other sound.

It is, however, far from improbable that ants may produce sounds entirely beyond our range of hearing. Indeed, it is not impossible that insects may possess senses, or sensations, of which we can no more form an idea than we should have been able to conceive red or green if the human race had been blind. The human ear is sensitive to vibrations reaching at the outside to 38,000 in a second. The sensation of red is produced when 470 millions of millions of vibrations enter the eye in a similar time; but between these two numbers, vibrations produce on us only the sensation of heat; we have no special organs of sense adapted to them. There is, however, no reason in the nature of things why this should be the case with other animals; and the problematical organs possessed by many of the lower forms may have relation to sensations which we do not perceive. If any apparatus could be devised by which the number of vibrations produced by any given cause could be lowered so as to be brought within the range of our ears, it is probable that the result would be most interesting.

The befuddled state of scientific opinion on the matter of sounds and sound-reception by these much-studied insects is shown by the following portion of Wheeler's concluding paragraph.

Huber (1910) and Forel (1874) deny that ants hear sounds, and the latter, while admitting that they respond easily to grosser mechanical shocks, failed to obtain any response to sounds of a very high pitch. Lubbock (1881), on the other hand, believed that they react to such sounds, but he failed to obtain any experimental evidence for his view. Parker and Miss Fielde (1904) failed to observe any reactions to "aerial sound waves from a piano, violin and Galton whistle, which collectively gave a range of from 27 to 60,000 vibrations per second." The insects reacted, however, to vibrations reaching them through the soil and other solids. These vibrations were received through the legs, as they were perceived even when the antennæ, head, abdomen and any one or two pairs of legs were removed. In contradiction to this view and that of Forel, several authors have recently maintained that ants do perceive aerial vibrations. That this is the case has been stated by Weld (1899) for *Cremastogaster lineolata, Lasius americanus* and *Aphænogaster* sp., and by Metcalf (1900) for "a small black ant." Wasmann (1891, 1899) has recorded similar, rather inconclusive observations. I have also virtually expressed myself in favor of such a view in one of my papers (1903), in a passage which has been overlooked or misunderstood by some recent students of this subject, and may therefore be repeated in this place: "Stridulation, at least among the Myrmicinæ, Ponerinæ and Dorylinæ, is an important means of communication, which Bethe has completely ignored and even Forel and other myrmecologists have failed to appreciate. It readily explains the rapid congregation of ants (Myrmicinæ) on any particle of food which one of their number may have found, for the excitement of finding food almost invariably causes an ant to stridulate and thus attract other ants in the vicinity. It also explains the rapid spread of a desire to defend the colony when the nest is disturbed. This is especially noticeable in species of *Pheidole, Myrmica* and *Pogonomyrmex*. It is the secret of being able in a short time to catch ants like *P. molefaciens* in great numbers by simply burying a wide-mouthed bottle up to its neck in the mound of the nest. An ant approaches and falls into the bottle. It endeavors to get out, and failing, begins to stridulate. This at once attracts other ants which hurry over the rim and forthwith swell the stridulatory chorus till it is audible even to the human ear. More ants are attracted and soon the

bottle is filled. [May not the real attraction have been odor or may there have been no attraction at all, the hurrying ants, distracted by the damage to their nest falling into the bottle by simple accident?] If it be corked and shaken for the purpose of still further exciting its contents, and then held over another *Pogonomyrmex* colony whose members are peacefully sauntering about on the dome of the nest, the wildest excitement will suddenly prevail, as if there had been a call to arms or to dinner. [Of course, odor was excluded here if the cork was left in, as it probably was not.] Even more remarkable is the stridulation in a colony of *Atta fervens* (=*texana*), the Texan leaf-cutting ant. Here the different ants, from the huge females through the males, large soldiers and diminishing casts of workers to the tiny minims, present a sliding scale audibility. The rasping stridulation of the queen can be heard when the insect is held a foot or more from the ear. To be audible the male and soldier must be held somewhat closer, the largest workers still closer, whereas the smallest workers and minims, though stridulating, as may be seen from the movements of the gaster on the postpetiole, are quite inaudible to the human ear. It is not at all improbable that all this differentiation in pitch [volume?], correlated as it is with a differentiation in the size and functions of the various members of the colony, is a very important factor in the cooperation of these insects and of ants in general. The contact-odor sense, important as it undoubtedly is, must obviously have its limitations in the dark, subterranean cavities in which the ants spend so much of their time, especially when the nests are very extensive like those of *Atta*. Under such conditions stridulation and hearing must be of great service in maintaining the integrity of the colony and of its excavations." If the view of Miss Fielde and Parker be accepted, we must suppose that the *Pogonomyrmex*, in the experiment above described, were thrown into agitation by vibrations passing from the bottle of stridulating ants through my body to the soil of the nest. It seems to me much more probable that the ants perceived the stridulation directly as aerial vibrations. More numerous experiments, however, have been recently performed by Turner (1907). Although he worked only with Camponotine ants (*Formica fusca* and *F. sanguinea*), which are not known to stridulate, he found that they responded to vibrations as low as 256 and as high as 4,138 per second. "The responses, in the form of zigzag movements, were usually slight for pitches higher than 3,000 vibrations per second and sometimes slight for other pitches; but, to most pitches under 3,000 vibrations per second, the ants usually responded in a pronounced manner, usually darting about as though much excited." Turner believes that he took sufficient precautions, by resting the nest on cotton and felt, to exclude the transfer to the ants of vibrations through the floor, table and walls of the nest. It is, however, extremely difficult to prove that such vibrations were excluded, and for this reason we cannot, with the data at hand, reject the statements of Miss Fielde and Parker. As these authors say: "It has long been recognized by physiologists, if not by the scientific public, that touch and hearing in the vertebrates are very closely related. The apparent separateness of these senses in us is due to the fact that the air waves by which our senses are usually stimulated are too slight to affect our organs of touch. If, however, we transfer our experiments to water, we at once meet with a medium in which, as has long been known, vibrations can be both heard and felt. In dealing with a like question among the lower animals it therefore seems to us misleading to attempt to distinguish touch from hearing, and we shall be more within the bounds of accuracy if we discuss the question from the standpoint of mechanical stimulation rather than attempt to set up questionable distinctions based upon human sensations."

I regret that no colony of *Pogonomyrmex* is available to me at the present time. The largest ant-nests in this vicinity are those of *Formica exsectoides* and, as this species not only does not make sounds audible to man but belongs to a group that is practically silent as far as unaided human ears can tell, work on it can not be set forth as comparable with Wheeler's experiments on *Pogonomyrmex*. However, I pushed a test-tube into such a nest until the open mouth of the tube was flush with the surface of the nest. Ants came rushing out and crowded around the point of disturbance; one ant fell into the tube, then another and another until there was quite a collection entrapped. Then the excitement subsided and only occasionally did an ant come to the tube and join her imprisoned comrades. Next I pushed into the nest four test-tubes differing as follows: two were covered with coarse netting, one containing ten live ants and the other empty; the remaining two were covered with thin rubber (not stretched but with the edges fastened tightly against the tube), one containing ten live ants and the other empty. The rubber certainly prevented any ant-odor from escaping. Of course, the rubber might also confine sounds inaudible to us but audible to ants, if such sounds were made. However, the rubber was thin and not under tension; also, this same arrangement did not appreciably alter either the volume or the character of faint stridulations made by other insects—for example, the longicorn beetle *Tetraopes tetraophthalmus*. A much more uncertain thing about the experiment was interpreting the actions of the ants. They came rushing out of the nest as before and ran pell-mell over the mouths of all the tubes. If the mouths of the tubes had not been covered, many would have been trapped. The difficulty was that the ants moved so rapidly and each looked so much like the others that I could not get any trustworthy statistics concerning the number of different visits made to each tube but my impression (strengthened by repetitions of the experiment) was that, if any tube received more attention than would be given to any foreign object pushed into the nest, it was the tube covered with coarse netting and containing living ants. This is what would be expected if one thinks that ants are attracted by the odor of excited imprisoned comrades and such expectation may have been the chief basis of my impression.

The stridulatory organs of beetles have been very well reviewed by Gahan (1900). Not as a conclusion to be drawn from his study but merely as a statement of fact, he said that "wherever any part of the external surface of the body is subjected to the friction of an adjoining part by the movements of the insect, there, in some species or another, these organs

are almost sure to be found. They do not remain constant in position even among the different genera of the same family, yet they sometimes appear unexpectedly having almost identically the same position and structure in one genus that they have in a genus of some totally different family." Many of these stridulations are very distinctly audible to man—for example, those of certain long-horned beetles when the beetles are held and make all sorts of motions in an effort to escape. It is also said that some beetles stridulate while mating. Then, too there is the sound made by the "June bugs" and others during flight—Shakespeare's "shard-borne beetle with his drowsey hum." It is what Riley had in mind when he said:

> The beetle booms adown the glooms
> And bumps along the dusk

but the beetle probably had no more intention of booming than it had of bumping. At least none has been proven, neither has the existence of special sound-receiving organs in any kind of beetle, unless "chordotonal organs" be such.

Although the sound-producing organs of most beetles are very simple in structure, the wood-boring larvæ of certain Passalidæ have extreme modifications for this purpose. Sharp (Cambridge Natural History, VI, p. 192) figures one of these from Borneo. He says:

> The larvæ are very interesting, from the fact that they appear to have only four legs. This arises from the posterior pair being present only as very short processes, the function of which is to scrape striated areas on the preceding pair of legs and so produce sound. In the species figured this short leg is a paw-like structure, bearing several hard digits; but in other species it is more simple, and without the digits. The perfect insect has no sound-producing organs, and it is very remarkable therefore to find the larvæ provided with highly-developed stridulatory structures. No auditory organ is known, unless the peculiar spiracles be such.

Sharp gives no explanation of the reason for the existence of this power to produce sound. As they are larvæ, it can not be a sexual call. As they are buried deep in decaying wood, it is probably not for the purpose of frightening enemies, although a sufficiently great imagination might conceive it to be so. It has even been suggested that the sound is a warning to brothers and sisters in the same mass of wood that the particular spot in which they are feeding is preempted.

The various clickings and other faint sounds made by certain butterflies and moths may be passed at present. They do not differ materially in method of production and known biological significance from those already mentioned. In some cases "ears" have been described, being situated on the abdomen, and, as was pointed out above, the

antennæ of moths seem to be structurally as well fitted to perceive sound as do the antennæ of mosquitoes. A fairly complete bibliography concerning the auditory powers of Lepidoptera is given by Turner and Schwarz (1914, Biol. Bull., XXVII, p. 291). The following quotations, the first from the paper just mentioned and the others from a paper by Turner in the same volume, p. 332, are of interest in connection with the ability of insects to hear sounds audible to us although they themselves do not make such sounds.

> We do not consider the failure of these moths to respond to certain sounds of low pitch a proof that they do not hear such sounds; indeed, we are inclined to believe that these creatures respond only to such sounds as have a life significance. Three things render this last assumption probable: (1) The fact that *C. unijuga*, which at first did not respond to whistling, did so readily after once a blast of air had been allowed to strike her body simultaneously with the sounding of the whistle; (2) that most of the natural enemies of these moths produce high pitched sounds and trains, and brass bands and other producers of low pitched or coarse sounds do not directly affect the survival of these moths; and (3) by carefully conducted field experiments, we were able to induce three specimens of *C. neogama* to respond to sounds to which the species does not usually react.
>
> It seems certain that all four of the species of giant silk-worm moths investigated can hear. Three of the species respond readily to a large range of sounds. The third, *Telea polyphemus*, normally does not respond to sounds; unless remaining as immobile as possible be considered a response. By experimentally causing the moth to associate some disagreeable experience with certain sounds, it can be induced to respond to those sounds.
>
> There is much evidence that the responses of moths to stimuli are expressions of emotion. The fact that an insect does not respond to a sound is no sign that it does not hear it. The response depends upon whether or no the sound has a life significance.

Leaving the insects having complete metamorphosis and considering the rather primitive order Orthoptera, we find among the saltatorial groups an abundance of species having highly developed organs for producing and possibly for receiving sounds. Sharp noted that the musical powers are especially characteristic of the male sex and stated that "there is evidence that these powers are of great importance to the creatures, though in what way is far from clear." He does not say what this evidence is but, since the way in which these powers are important is far from clear, the fact of their existence is probably what he had in mind as the evidence of their great importance. At any rate, this is a characteristic neo-Darwinian argument.

One of my early ventures into scientific discussion was inspired by a translation of a paper by Portchinsky (1886) and had the following to say concerning the short-horned grasshoppers.

Considering the Orthoptera, he [Portchinsky] calls attention to the fact that the Acrididæ—unlike their relatives, the crickets and the long-horned grasshoppers—do not stridulate with their wings, but rub the femur against the raised meshwork of veinlets upon the tegmina. Another striking difference between this family and the other families of the order is that here, alone, we get the bright coloring of the inner surface of the hind legs. These are often the only bright colors the insect possesses. It has become an axiom that insects are constantly endeavoring to show their beauty —especially if it be a secondary character, as grasshopper colors often are—and in the case of the Acrididæ this can only be done by twisting their hind legs about. Such a motion would necessarily result in friction between the femur and the tegmina, friction in irritation and increased growth, and this growth is the sound organ.

An interesting analogy which he does not mention is found in the subfamily Œdipodinæ. Lugger, in describing the Œdipodinæ, said: "The insects belonging here are mostly large and showy, often possessing bright-red, yellow or even blue wings, with black bands. Nearly all the bright-colored locusts found in the United States belong to this subfamily; most of them are very conspicuous objects in flight, when they show their color, which is at other times entirely hidden. Œdipodinæ are also very noticeable on account of the rattling noise which the males of most species produce in flight." The connection here between sound and something to be called attention to is quite marked, and while it is about as hard to tell which came first—color or sound—as it is in the proverbial case of hen or egg, doubtless Portchinsky would say that the sound was originally caused by the vigorous beating of the insect's wings in its amorous display, and is as much a secondary matter as the femoral-tegminal stridulation.

In the years that have passed since this was written I have watched many of these "amorous displays," particularly those of *Dissosteira carolina*. This species has a conspicuous yellow edge on its hind wings, seen only when the creature is in flight. It is possible for this grasshopper to sail through the air for a short distance rather noiselessly but when the wings are vibrated vigorously, as when it is hovering over a particular spot, a loud crackling sound is produced, apparently by the striking of the hind wings against the front. Whenever a male is seen thus hovering, displaying his gaudy hind wings and "sounding his castanets," one can be certain that a female is almost directly underneath him. Watching her ever so closely, I have never been able to detect that she pays the slightest attention to his serenade. Perhaps this was just my misfortune or the result of faulty observation. What I did see was that the two of them, when they came near each other worked their hind legs up and down in the way that other short-horned grasshoppers do when they make sounds by rubbing their hind legs against the front wings, but I could never hear any sounds produced.

A curious thing was noticed while experimenting on the flight of this species. I mutilated specimens in various ways and turned them loose. Almost always any individuals within a few feet of the mutilated one

turned and slowly walked toward it. Was the attraction a sound which I could not hear at the distance from which I was watching or was it odor of fluid exuding from the wounds?

As far as I know, a sound which this species makes when captured has not been noted. It quite audibly "gnashes its teeth," apparently by rubbing its mandibles against the labrum. Just what good this does the grasshopper is not clear unless it be analogous to human swearing. Possibly the mutilated specimens were "gnashing their teeth" and the sound aroused the curiosity of their neighbors.

In the United States there is no species of short-horned grasshoppers that has developed unusual structures in connection with sound-production, although many of the species make sounds in one way or another. The Acridiidæ are much given to rubbing the long hind legs against the front wings. One of these insects will sit for hours on a blade of grass fiddling monotonously and, one is tempted to say, aimlessly; but can we be certain of the reasons for all of an insect's actions? Unobserved, I have watched a small boy sitting on the bank of a stream softly playing a mouth-organ. If I had asked him why he did it, the answer would probably have been "Oh! just for fun" but we can not ask the grasshopper. It is interesting to note that even immature grasshoppers sit on grass-blades and move their long hind legs up and down in just the way that would produce sounds if only they had the wings of their adult stage. Is this movement of the legs a fundamental thing and the sound which results when wings are present merely an accident or are the young practising the motions that will in later life make sounds to help them in wooing?

Among the Acridiidæ in South Africa there is a genus, *Pneumora*, in which the males rub their hind legs against ridges on a greatly inflated abdomen, the latter doubtless acting much like a resonating chamber and increasing the sound. Another South African genus, *Methone*, although having a small abdomen, has greatly modified legs. The hind pair are scarcely longer than the other legs and so the creatures do not jump, but both sexes make sounds by rubbing these hind legs against ridges on the abdomen. There are two differently formed rubbing areas on the legs and two corresponding areas on the abdomen. I do not know whether two different sounds are produced or whether they are combined. One set of these structures is about equally developed in each sex but the other set is better developed in the male.

It is possible that female grasshoppers are following the lead of the males in sound-production. Sharp said:

The apparatus for producing sound was for long supposed to be confined to the male sex of grasshoppers: it was indeed known that females made the movements appropriate for producing music, but as they appeared to be destitute of instruments, and as no sound was known to follow from their efforts, it was concluded that these were merely imitative. Graber has, however, discovered that rudimentary musical organs do exist in the females of various species of *Stenobothrus*. It is true that in comparison with those of the male they are minute, but it would appear that they are really phonetic, though we can hear no sounds resulting from their use.

Graber considers that the musical pegs of Acridiidæ are modified hairs, and he states that in certain females the stages intermediate between hair and peg can be found. There is apparently much variety in the structure of these instruments in different species, and even in individuals of the same species. In *Stenobothrus lineatus*, instead of pegs, the instrument consists of raised folds.

The possibility that insects make and hear sounds inaudible to man should, of course, always be kept in mind but we should distinguish between inaudibility due to the low intensity and that due to the high frequency of vibration. It would appear that, if the females of *Stenobothrus* do make sounds, man's inability to hear these sounds is due to the fact that there is not enough volume. In that case, if these grasshoppers can hear the sounds they make, they must have auditory powers very much better than man's in picking up faint intensities within man's range of audible frequencies; this is different from an ability to perceive vibrations having frequencies beyond man's audible range. The presumed auditory apparatus of the Acridiidæ does not seem to have any characteristics that make it especially sensitive to sounds which, for either reason, are inaudible to man, but there does seem to be a real auditory apparatus. At least, there is in most species a thin disc-like membrane on each side of the abdomen and accessory structures which may give the insect notice of any vibrations of this "ear-drum."

The remainder of the jumping Orthoptera, the long-horned grasshoppers and the crickets, are noted musicians. They make sound by rubbing together the two front wings, the tegmina. These tegmina, fitted with a file and rasping surface, usually have a peculiar modification of the venation so as to form a tympanum or sounding board. That is, the males have these structures; the females have no modifications of the tegmina and usually do not make sounds audible to man but I have found in several cases that, if one forces the female's tegmina to rub together, a quite audible sound is produced. Furthermore, there is a structure on each front leg of each sex that looks as though it might function as an ear and that has been considered to be one. Sharp's excellent description is quoted here.

The Locustidæ resemble the Acridiidæ in the possession of specialized ears and sound-producing organs; neither of these is, however, situate in the same part of

the body as in Acridiidæ. The ears of Locustidæ are placed on the front legs, below the knee; a tympanum or a crack, giving entrance to a cavity in which the tympanum is placed, being seen on each side of each of the anterior pair of limbs. In this family, as in the Acridiidæ, three kinds of ear are recognized according to the condition of the tympanum, which is either exposed or closed by an overgrowth of the integument, or in a condition to a certain extent different from either of these. The existence of ears placed on the legs is a curious fact, but it is beyond doubt in the Locustidæ, and there is good reason for believing that analogous organs exist in this situation in other Insects that have special means of sound-production, such as the ants and the Termites.

The structure of these organs in the Locustidæ has been investigated by Graber, and their acoustic functions placed beyond doubt, though to what special kind of sounds they may be sensitive is not ascertained, this point being surrounded by even greater difficulties than those we have discussed in the case of the Acridiidæ. In the Locustidæ there is a special structure of a remarkable nature in connexion with the ears. In Acridiidæ a stigma is placed close to the ear, and supplies the internal structures of the organ with air. There are no stigmata on the legs of Insects, consequently admission of air to the acoustic apparatus in Locustidæ is effected by means of a gaping orifice at the back of the prothorax, just over the base of the front leg; this communicates with its fellow of the other side, and from them there extend processes along the femora into the tibiæ, where they undergo dilatation, so as to form vesicular cavities, one of which is in proximity to each drum of the ear. These leg-tracheæ are not connected with the ordinary tracheal system; the prothoracic stigma exists in close proximity to the acoustic orifice we have described, but is much smaller than it. It is not yet clear why the acoustic apparatus should require a supply of air apart from that which could be afforded by the ordinary tracheal system. This special arrangement—to which there is hardly a parallel in Insect anatomy—has still to be accounted for; we do not know whether the necessity for it may be connected with the respiratory system or the acoustic organ.

Although the tibial ears of Locustidæ are very perfect organs, there is great difficulty in deciding on the exact nature of their functions. They would appear to be admirably adapted to determine the precise locality from which a sound proceeds, especially in those cases—and they are the highest forms—in which the tympanum is placed in a cavity the external orifice of which is a slit; for the legs can be moved in the freest manner in every direction, so as to bring the drum into the most direct line of the vibrations. But as to what kinds of vibrations may be perceived, and the manner in which they may be transmitted to the nerves, there is but little evidence. . . .

The Gryllidæ possess a pair of tympana on each front leg, but these organs contrast with those of the Locustidæ in that the pair on each leg usually differ from one another, the one on the outer or posterior aspect being larger than that on the inner or front face of the leg.

The ears of the Gryllidæ have not been so well investigated as those of the Locustidæ, but are apparently of a much less perfect nature. No orifice for the admission of air other than that of the prothoracic stigma has been detected, except in *Gryllotalpa*. On the other hand, it is said that in addition to the tibial organs another pair of tympana exists, and is seated on the second abdominal segment in a position analogous to that occupied by the ear on the first segment of Acridiidæ.

The possession of definite structural modifications of considerable extent and clearly fitted to make sound, together with what is apparently a specialized sound-receiving apparatus, is difficult to explain on any grounds other than that the sound is "intentionally" made and that it plays a part in the lives of the insects. Since only the males can make sounds but the females have "ears," it is generally supposed that the sounds are for the purpose of calling the females to them. But the males also have the same sorts of ears and so may be supposed to hear other males. Some years ago, while breeding crickets for the purpose of studying heredity, I had hundreds of them under rather constant observation. It seemed to me that I could tell by listening to the males whether they were courting females, defying other males, or just passing the time in song. At the same time, I was impressed with the fact that neither the females nor the other males appeared to pay much attention to the songsters. Often, of course, they would wave antennæ toward each other but so would they when no sound audible to us was being produced.

If it be true that large numbers of tree-crickets chirp in unison, as they are said to do, that would seem to be proof-positive that they hear each other, although I do not recall that it has been cited as a critical proof of this, the reason probably being that writers have taken such audition for granted. What are the facts in this case? While, as Shull (1907) has pointed out, Dolbear's formula is not very exact in all cases, still the number of chirps per minute for certain species about equals four times the temperature on the Fahrenheit scale minus 160. At this rate 100 to 120 chirps per minute is a fair rate. This gives about two chirps per second and Shull estimates that the silent interval is about twice as long as the chirp. As to the insects chirping in unison, Shull said.

> I found exact synchronism to be comparatively rare, and to exist only between neighboring crickets. When accurate synchronism did occur, it affected only two individuals, sometimes three. One evening I discovered two crickets about five feet apart chirping in such accurate unison that I did not at once realize that there were two crickets. One soon stopped; the second hesitated, its chirp became weak, and it even lost a beat. After an irregular solo of several minutes, the second cricket recommenced. At the first chirp the first cricket struck a note out of time, then lost a beat, as if startled. It next voiced a half-dozen weak, uncertain chirps then the call gradually grew in intensity, until the two crickets were again chirping in exact unison.

If Shull noticed only a few cases of synchronism out of the many observations which he doubtless made in preparation for writing his interesting paper, the phenomenon may not be significant after all. Let us say that the chirps are at the rate of two a second and that each chirp lasts for one-sixth of a second, with a third of a second interval between them.

As a pure matter of chance it would happen at least "rarely" that the chirps would be synchronous within the limits of perception by ear. Shull's description of the action of the pair he noticed in which a member hesitated when the other member stopped is not very impressive. These creatures do not seem to quit chirping from fatigue. Shull counted one that chirped 2640 times without stopping. When they stop, it is usually due to some external stimulus and it would be quite natural that the stimulus that made one cricket stop would make another at least hesitate. Crickets often "miss a beat" when starting or stopping and the phrase "as if startled" may not describe that particular cricket's emotion. Shull concludes his paper as follows.

> Dolbear may have gained his impression of universal synchronism[1] by observing a sporadic case of it or by actually listening to but one cricket and mistaking it for a full chorus. The intensity of sound diminishes so rapidly with increasing distance from the source, that with but one cricket chirping several feet away and the others at a greater distance an observer could easily overlook those at the greater distance. One cricket, if undisturbed, will usually perform six to eight hundred chirps without missing one, except on cool nights. Not infrequently it will perform 1500 in succession; while one "long-winded" individual which I observed continued through 2640, another 2425, a third 2228. From these figures it will be seen that breaks in the series of chirps might escape observation, and that the continuous chirping of one performer might be mistaken for a chorus in which the single crickets were not missed when they dropped out. It would thus happen that a single cricket may have been mistaken for several in unison, each performing less continuously.

Although Shull seems to have covered the ground, an illustration from my own observations may add to the evidence. Two *Œcanthus nivæus* were on one of my vines chirping in what seemed to be perfect unison. They were about six feet apart and I took a position about midway between them. Then, by careful concentration I could listen to one without paying attention to the other. One was averaging 105 chirps per minute and the other 107. Such being the case, there could not be unison, yet the chirps were so rapid and it was so difficult to keep my attention fixed on both at once that, even when I tried, I could scarcely detect the instant at which one of the insects was silent while the other was chirping. However, each was chirping quite independently of the other.

Chirping in unison, a thing that would be ideal proof that tree-crickets hear each other if it were true, does not seem to be as definitely established as one could wish it were. Of course, there might be nothing in the synchronism stories and still the crickets might hear each other. What would the crickets gain at any rate by chirping in unison? What do

[1]This impression has been gained by many observers in many localities so that Dolbear is not the sole authority for it.

they gain by chirping at all? Returning to *Gryllus*, the genus that is usually meant when we speak of crickets and the one that I personally have studied most, my observations indicate that it is almost always the male that approaches the female and not the reverse. If such be the case, the female does not locate the male by his song and by this means track him down for marriage. The male approaches the female, vibrating his wings and dancing about in front of her just as many a "voiceless" insect does in front of his prospective bride. Courtship dances are common among insects and they are usually accompanied by a vibration of wings. Among crickets and their relatives, this vibration of wings is accompanied by sounds as a result of the vibrations. Is the female impressed by these sounds and does she choose the male that makes the sound most to her liking? If so, she is a much better judge of tone, pitch, or volume than man is, for few men could distinguish between the chirps of crickets of the same species when temperature and other conditions are the same.

I spent a rather amusing hour recently watching a male *Orchelimum* (one of the long-horned grasshoppers) serenading a female *Melanoplus* (one of the short-horned grasshoppers), "caressing" her with his antennæ as he sang. How long the comedy kept up I do not know. If it had not been contrary to the canons of orthodox biology, I might have believed that the expression on the face of the female *Melanoplus* was clearly one of unsatisfied desire and sadness because the males of her genus, family, and superfamily (or suborder) could not sing so sweetly. The male *Orchelimum* seemed to be thoroughly enjoying his escapade but, of course, I do not know what either was thinking. Perhaps it was wishing that the other would get off of that particular weed-stem.

The courtship as I have observed it in *Gryllus* is rather like that recently reported by Hungerford (1924, Ann. Ent. Soc. America, XVII, p. 224) for quite a different insect, an aquatic hemipteron, *Buenoa limnocastoris*. His description is as follows.

> They sing their courting songs at all hours of the day or night—on cloudy days or clear days, in sunshine or shadow. In the aquarium containing the three pairs, there were times when all three males were chirping at once. But to appreciate the full significance of these amorous serenades, it is necessary to watch the behavior of the insects. The male singles out a female, maneuvers for a position some little distance beneath and behind her and begins a ticking sound as he slowly cruises nearer the object of his desire, his body aquiver with emotion. When within a half inch or so of the female, the ticking changes to a hum and is followed by a sudden dash to embrace her. If she eludes him, he begins all over again or transfers his affection to another. Sometimes when a female, aware of the attentions bestowed upon her, moves away from the chirping male, the latter will turn to follow another female

that may pass nearby, and resume his mating call. In a few cases one male has been observed to follow and chirp to another male. The sound produced by these insects is a ringing chick-chick-chick-chick like the ticking of a watch that can be heard fifteen or twenty feet away. This may continue for a minute or two, and then if the male has succeeded in drawing near the female, the note changes to a rapid twir-r-r made by a very rapid continuous series of chicks. The sound is made by the shuffling back and forth of the front femora and tibiæ along the beak, both legs in unison. The roughened structures near the inner base of the tibiæ and on the inner faces of the femora rub against a scraper-like device on the base of the beak. A comparison of the fore limbs and beaks of the two sexes will show the modifications developed in the male for stridulation.

The sound is an accompanyment of "courtship," not a call to bring the sexes together as the call of frogs and toads is rather well demonstrated to be and as insect calls have been supposed to be.

Distant and probably much more primitive relatives of this aquatic bug are the well-known cicadas, the "harvest-flies" or "locusts." Next to the crickets and the long-horned grasshoppers, they are the most renowned musicians among insects. Also, they rival those Orthoptera in the complication of their sound-producing organs, which are essentially a drum-head located on each side of the abdomen. This drum-head is alternately pulled by a muscle and released. A nice problem in comparative anatomy would be an investigation of possible homologies between this sound-producing organ of cicadas and what is supposed to be the sound-receiving organ of grasshoppers. Much has been written about the sound-making of these insects but probably as convenient and readable an account as any for the general reader is given by Fabre in his 'Souvenirs entomologiques,' translated by A. T. de Mattos in a volume entitled 'The Life of the Grasshopper.' The following quotation is from this translation.

In conclusion, let us ask ourselves the object of these musical orgies. What is the use of all this noise? One reply is bound to come: it is the call of the males summoning their mates; it is the lover's cantata.

I will allow myself to discuss this answer, which is certainly a very natural one. For fifteen years the Common Cicada and his shrill associate, the *Cacan*, have thrust their society upon me. Every summer for two months I have them before my eyes, I have them in my ears. Though I may not listen to them gladly, I observe them with a certain zeal. I see them ranged in rows on the smooth bark of the plane-trees, all with their heads upwards, both sexes interspersed with a few inches between them.

With their suckers driven into the tree, they drink, motionless. As the sun turns and moves the shadow, they also turn around the branch with slow lateral steps and make for the best-lighted and hottest surface. Whether they be working their suckers or moving their quarters, they never cease singing.

Are we to take the endless cantilena for a passionate call? I am not sure. In the assembly the two sexes are side by side; and you do not spend months on end in calling to some one who is at your elbow. Then again, I never see a female come

rushing into the midst of the very noisiest orchestra. Sight is enough as a prelude to marriage here, for it is excellent; the wooer has no use for an everlasting declaration: the wooed is his next-door neighbor.

Could it be a means then of charming, of touching the indifferent one? I still have my doubts. I notice no signs of satisfaction in the females; I do not see them give the least flutter nor sway from side to side, though the lovers clash their cymbals never so loudly. . . .

There is no possibility of divining or even suspecting the impression produced by the clash of the cymbals upon those who inspire it. All that I can say is that their impassive exterior seems to denote complete indifference. Let us not insist too much: the private feelings of animals are an unfathomable mystery.

Another reason for doubt is this: those who are sensitive to music always have delicate hearing; and this hearing, a watchful sentinel, should give warning of any danger at the least sound. The birds, those skilled songsters, have an exquisitely fine sense of hearing. Should a leaf stir in the branches, should two wayfarers exchange a word, they will be suddenly silent, anxious, on their guard. How far the Cicada is from such sensibility!

He has very clear sight. His large faceted eyes inform him of what happens on the right and what happens on the left; his three stemmata, like little ruby telescopes, explore the expanse above his head. The moment he sees us coming, he is silent and flies away. But place yourself behind the branch on which he is singing, arrange so that you are not within reach of the five visual organs; and then talk, whistle, clap your hands, knock two stones together. For much less than this, a bird, though it would not see you, would interrupt its singing and fly away terrified. The imperturbable Cicada goes on rattling as though nothing were afoot.

Of my experiments in this matter, I will mention only one, the most memorable. I borrow the municipal artillery, that is to say, the mortars which are made to thunder forth on the feast of the patron-saint. The gunner is delighted to lead them for the benefit of the Cicadas and to come and fire them off at my place. There are two of them, crammed as though for the most solemn rejoicings. No politician making the circuit of his constituents in search of re-election was ever honored with so much powder. We are careful to leave the windows open, to save the panes from breaking. The two thundering engines are set at the foot of the plane-trees in front of my door. No precautions are taken to mask them: the Cicadæ singing in the branches overhead cannot see what is happening below.

We are an audience of six. We wait for a moment of comparative quiet. The number of singers is checked by each of us, as are the depth and rythm of the song. We are now ready, with ears pricked up to hear what will happen in the aerial orchestra. The mortar is let off, with a noise like a genuine thunder-clap.

There is no excitement whatever up above. The number of executants is the same, the volume of sound the same. The six witnesses are unanimous: the mighty explosion has in no way affected the song of the Cicadæ. And the second mortar gives an exactly similar result.

What conclusion are we to draw from this persistence of the orchestra, which is not at all surprised or put out by the firing of a gun? Am I to infer from it that the Cicada is deaf? I will certainly not venture so far as that; but, if any one else, more daring than I, were to make the assertion, I should really not know what arguments to employ in contradicting him. I should be obliged at least to concede that the

Cicada is extremely hard of hearing and that we may apply to him the familiar saying, to bawl like a deaf man. . . .

If any one were to tell me that the Cicadas strum on their noisy instruments without giving a thought to the sound produced and for the sheer pleasure of feeling themselves alive, just as we rub our hands in a moment of satisfaction, I should not be greatly shocked. That there may be also a secondary object in their concert, an object in which the dumb sex is interested, is quite possible, quite natural, though this has not yet been proved.

Few present-day biologists would care to accept all of Fabre's conclusions in biological theory and, as to the experiment just quoted, it is quite true that the sound of an explosion is not free from criticism as a test of the ability of one cicada to hear another but it is rather curious that at least the "false audition by touch" did not come into play.

As has been previously pointed out, the only insects which have developed elaborate sound-producing structures and make sounds easily heard by man are primitive insects. For the most part, the sound-producing organs of the higher insects, at least of those which produce sounds audible to man, appear to be nothing but ordinary modifications of structure such as might be expected to arise without any particular purpose and which, having arisen, would make a noise that is purely incidental to the ordinary activities of the insect. This would not, it must be admitted, explain such elaborate modifications as are found in the wings of male crickets and their relatives or the sound-producing organs of the cicadas. If these have arisen for a "purpose" in the lives of the insects, they certainly seem to have been a magnificent experiment on the part of Nature, an experiment that did not meet with approval and was not persisted in during the evolution of higher forms. At the same time, this sound-making seems not to have been absolutely detrimental to those forms that have the structure and the habit; they are still living in spite of the fact that their music must betray their position to any enemy that has ears to hear such sounds.[1] In this connection it is to be noted that insects which make loud noises do so chiefly at night or else they are exceedingly well hidden from view, or both.

It is interesting, in connection with a study of insect sounds, to consider briefly sound-production by and the auditory powers of rattlesnakes. Many snakes vibrate the tip of their tails when they are excited. This vibration may produce a rattling in dry leaves. The rattlesnakes are peculiar in that they possess at the tip of their tail a structure that rattles by itself when the tail is vibrated. This rattling expresses emo-

[1]The fact that the cicada-killing wasp, *Sphecius speciosus*, captures about as many female as she does male cicadas indicates that this insect does not hear the sounds produced by another insect in which she is clearly much interested.

tion in the sense that the tail is vibrated only or chiefly under the stress of certain emotions. In so far it is comparable with many insect sounds. Rattlesnakes have a comparatively well-developed ear-structure and, although certain features seem to be rather poorly arranged, so great an authority as Hans Gadow asserted that "snakes can hear very well." Arguing as many do when discussing insects, this would seem to be true—the rattlesnakes make a noise and they would not do so if they could not hear; furthermore, they have ear-structures. However, Manning has recently (1923, Journal Comp. Psychology, III, pp. 241–247) announced the results of his careful experiments as follows.

> Rattlesnakes (*Crotalus*) and probably *Sistrurus* and *Ankistrodon* have a very defective sense of hearing. A few rattlesnakes were proved to hear a loud sound of 43 vibrations per second and one exceptional snake (a halfgrown *Crotalus atrox*) heard a sound of 86 vibrations per second produced in air and one of 344 vibrations transmitted through the substrate. It may seem a bold statement, but I doubt if any one rattlesnake ever heard any other snake's rattle. I doubt if a snake would even hear its own rattle were it not for direct transmission through the body. In any ordinary sense of the word, rattlesnakes at least are deaf.

Although many important investigations and interesting observations have necessarily been omitted, the foregoing does, I trust, give a fair notion of the present status of the problems connected with the sounds made by insects. Considering the sounds themselves, it is to be noted that they are, for the most part shrill. That is, they are vibrations of high frequency. Furthermore, they are usually not very loud. The "piercing note" of *Brachytrypes megacephalus*, a cricket, is said to have been heard at a distance of a mile but this probably needs confirmation. Darwin recorded that he had heard cicadas when the 'Beagle' was anchored a quarter of a mile from the South American shore but he was doubtless listening to many hundreds at once, not to a single insect. The physicists have no good measure of loudness. Miller ('The Science of Musical Sounds,' p. 53) says.

> The loudness of a sound is a comparative statement of the strength of the sensation received through the ear. It is impossible to state simply the factors determining loudness. For the corresponding characteristic of light (illumination) there is a moderately definite standard, commonly called the candle power; but for sound there is no available unit of loudness, and we are dependent on the subjective comparison of our sensations. Not only are the ears of different hearers of different sensitiveness, but each individual ear has a varying sensitiveness to sounds of different pitches and, therefore, to sounds of various tone colors.
>
> In a first study of the physical characteristics of sounds we are compelled to consider the intensity not as the loudness perceived by the ear, but as determined by what the physicist calls the energy of the vibration. Fortunately, under simple conditions and within the range of pitch of the more common sounds of speech and music, there is a reasonable correspondence between loudness and energy.

The energy, or what we will call the intensity of a simple vibratory motion, varies as the square of the amplitude, the frequency remaining constant; it varies as the square of the frequency, the amplitude remaining constant; when both amplitude and frequency vary, the intensity varies as the square of the product of amplitude and frequency; or to express it by a formula, representing intensity by I, amplitude by A, and frequency by n.

$$I = n^2 A^2.$$

Now, in the case of sounds produced by insects, the amplitude is necessarily not great. The whole insect is small; the sound-producing organ is still smaller; and the insect's muscles are not strong enough to give much "push." Therefore, and this is one way of putting it, if the insect wishes to produce a loud sound, it must make the frequency of vibration great and so produce a shrill sound. Another way of putting it and one that has far more scientific safety but far less dramatic appeal is that, unless a sound made by so small and so feeble a source as an insect is shrill, it will not be loud as judged by human ears, in fact it may not be heard by men at all and so escape comment. This refers to loudness at the source of the sound. The question as to the distance to which sounds of equal energy at the source but of different frequency of vibration can be heard need not concern us here, for in most of the cases for which biological significance has been claimed the sound-producer and the sound-receiver are near to each other.

A word concerning the reception of sound may not be out of place. Thinking only of man, Miller defined sound as "the sensation resulting from the action of an external stimulus on the sensitive nerve apparatus of the ear; it is a species of reaction to this external stimulus, excitable only through the ear, and distinct from any other sensation. . . The physicist uses the word *sound* to designate the vibrations of the sounding body itself, or those which are set up by the sounding body in the air or other medium and which are capable of directly affecting the ear even though there is no ear to hear." The tuning forks ordinarily used to give "middle C" vibrate 256 times per second. If we touch such a vibrating fork, we can "feel" the vibrations. However, the vibrations of the fork can affect us without our actually touching the fork, for it sets the surrounding air to vibrating, these "sound-waves" in the air set structures in what we call our ears to vibrating and we feel these vibrations, only we call that particular sensation "hearing." Of course, all of this is very elementary and, yet, it is desirable that we understand clearly what we mean by hearing. Our ears are sensitive to only a limited range of frequencies of vibration. This range is variously stated, but sufficiently accurate and easily remembered limits are 30 and 30,000 vibrations per

second. Now, the facts that we can "hear" only with certain special structures which we call ears and that we can hear only those atmospheric vibrations which occur more frequently than 30 per second and less frequently than 30,000 per second give us no warrant for saying that creatures differently constructed can not "hear" without special ears or can not hear other rates of atmospheric vibration.

Taking up the first possibility, we note that insects possess many structures that seem well fitted for being set into vibration by impinging sound-waves. The body itself, instead of being a soft, flabby, vibrationless structure like our bodies, is a thin shell loosely filled with viscera, or rather this shell is made up of a number of thin, hard plates suspended by flexible membranes. Physically, one would expect that each of these plates and the shell as a whole would naturally vibrate when acted upon by sound waves. If this be true and if the insect can feel the vibrations thus set up, it is logomachy to say that such a sensation is not hearing. Then there are the wings that are probably more responsive to sound-waves than the most sensitive of telephone diaphragms; also the antennæ and the palpi. One would think that the insect's body is all aquiver in this noisy world but whether its nervous system is such that it can perceive these vibrations is quite another question.

And then we have the still more difficult question of "attention." I am writing this during a quiet evening in the country and have not been conscious of the fact that my auditory structures were vibrating vigorously. Now that I force myself to think about it, the typewriter is clicking, a smouldering log in the fire-place is crackling, my wife is rustling the pages of a magazine, a child upstairs dropped a shoe, two species of Orthoptera are chirping out in the yard, an automobile passed along the street, and a distant locomotive whistled. My ears have been all aquiver but I gave no response until, in the midst of it all, I felt those vibrations which meant to me that the child was saying "Good night." Perhaps, if I had not been interested in entomology, I would not have included in the above list the Orthoptera. Perhaps, if I had been more interested in automobiles than I was, I would have noticed something about the one that passed so that I would have known how many cylinders it had or that one of them was not firing properly. It is a matter of interest and of experience. We can well believe, then, that Turner, for example, was right when he said: "The fact that an insect does not respond to a sound is no sign that it does not hear it. The response depends upon whether or no the sound has a life significance."

Also, in the case of insects, it does not seem necessary to find special structures set aside as ears. If the insects feel only the vibrations of the

surface upon which they are standing, I would be willing to call that "false audition by touch" but if they consistently perceive and, when interested, react to vibrations of various parts of their body set going by sound waves, I can see no reason for not saying that they "hear" these sounds. All of this is not to say that I believe that insects do hear in this way. I do not know; but it seems possible and a number of careful experiments make it seem even probable. This probability is really not decreased by the fact that certain groups, such as the Orthoptera and the termites, have developed what appear to be special sound-receiving organs. If they have something extra, something that other insects do not have, that may be to their advantage, depending upon how this special structure functions and also upon the need for it. Since man can hear Orthoptera make sounds, man says that what seem to be specialized ears are such and have arisen for the purpose of hearing the sounds which he hears the Orthoptera make. Also, if these structures are present in a species that does not make a sound audible to us, then that creature must be making sounds that we can not hear but that it, by aid of these structures, can hear. These ideas are fairly expressed by Sharp as follows.

The forms [of Orthoptera] in which the ears are absent are usually at the same time wingless and destitute of organs of stridulation; but, on the other hand, there are species—some of them wingless—that are, so far as is known, incapable of stridulation and yet possess these ears. It is, indeed, a matter of great difficulty to decide as to the exact function of these ear-like acoustic organs, which, we may remind the reader, are peculiar to the saltatorial Orthoptera [not strictly so], and we must refer for a full discussion of the subject to Graber's masterly works, contenting ourselves with a brief outline, which we may commence by saying that the Orthoptera with ears are believed to be sensitive to sounds by means other than these organs. This suggests that the latter exist for some purpose of perception of special sound. But if so what can this be? Only the males possess, so far as we know, effective sound-producing organs, but both sexes have the special ears; moreover, these structures are present in numerous species where we do not know of the existence of phonetic organs in either sex. Thus it appears at present impossible to accept these organs as being certainly special structures for the perception of the music of the species. It is generally thought that the females are charmed by the music of the males, and that these are stimulated to rivalry by the production of the sounds; and Dufour has suggested that this process reacts on the physiological processes of the individual. There has not been a sufficient amount of observation to justify us in accepting these views, and they do not dispose of the difficulty arising from the existence of the acoustic organs in species that do not, so far as we know, produce special sounds. It is possible that the solution of the difficulty may be found in the fact that these apparently dumb species do really produce some sound, though we are quite ignorant as to their doing so. It is well known that sounds inaudible to some human ears are perfectly distinct to others. Tyndall, in his work on Sound, has illustrated this by a fact that is of special interest from our present point of view. "Crossing the Wengern Alp with a friend," he says, "the grass on each side of the path swarmed with insects which to

me rent the air with their shrill chirruping. My friend heard nothing of this, the Insect world lying beyond his limit of audition." If human ears are so different in their capacities for perceiving vibrations, it of course becomes more probable that auditory organs so differently constituted as are those of Insects from our own may hear sounds when the best human ear can detect nothing audible. On the whole, therefore, it would appear most probable that the Orthoptera provided with acoustic organs, and which we consider dumb, are not really so, but produce sounds we cannot hear, and do so in some manner unknown to us. If this be the case it is probable that these ears are special organs for hearing particular sounds.

The termites having on their legs organs similar to those of crickets and presumed to be acoustic might, according to this argument, be expected to make these inaudible-to-man sounds since they do not make very definite sounds that are audible to man. It should be remembered that these presumed sounds are inaudible to man because they have a great frequency of vibration, not because they are lacking in loudness. Recalling that, in ordinary sounds at least, loudness varies as the product of the square of the frequency times the square of the amplitude of the vibrations, it is tempting to think that insects may by microscopically small movements rub microscopically fine ridges together in such a way as to make sounds that are really loud when received by a mechanism attuned to very short wave-lengths, that is, to a large number of vibrations per second.

Now, the straight-forward method of determining this would be to stop theorizing and construct an instrument that can detect such sounds if they are made. This will doubtless be done in the not-distant future but the task is not so easy as one might wish it to be. Consider first the biological difficulty. Suppose that we could not hear the note of the katydid and could not see the wings making motions which would indicate the possible production of sound but that we had an instrument capable of detecting the katydid's note. We might keep this instrument going from dawn to dark day after day and get no indication that the katydid makes a sound, because it makes it only at night. Even if we ran the instrument at night, the chances would be great that the insect would not be singing at the time and under the conditions in which we kept it. Those who have had much experience with keeping living insects will appreciate this difficulty. Then, the physics of the problem presents difficulties. Ordinary microphones can not be used, for they depend upon diaphragms which have a definite resonance or natural periodicities of vibration. The human ear has a much greater range than most artificial diaphragms. Furthermore, since we can not hear these sounds, no matter how much we amplify them, we require either some visible evidence of their existence or a method of heterodyning that will prove to

our ears their presence. Through the very great courtesy of the Research Department of the Westinghouse Electric and Manufacturing Company, I have had at my disposal during the past summer what is probably the best apparatus yet designed for this purpose and I have also had the benefit of the interested cooperation of Dr. Phillips Thomas of that company. We did not secure any demonstration of such sounds but, considering the difficulties and the many possible sources of error, we feel that the attempt should not be abandoned. The knowledge as to whether insects do or do not make and receive sounds that are inaudible to us will be interesting. Whether such sounds, if made, are biologically important will then be a further question. Are the insect-sounds that we can hear biologically important?

In our review of the past work on this subject we have noted the following as the most important advantages claimed for the ability of insects to make sounds: (1) to frighten enemies; (2) to warn other members of the same species that a given part of the feeding ground is preempted; (3) in the case of social insects, to call members of the colony to the defense of the nest or to a supply of food; (4) to call and to charm a prospective mate; and (5) to express the "joy of living."

The matter of frightening enemies has already been discussed as fully as seems profitable. No good proof of the importance of this effect is known to me. The second point seems to me to be too far-fetched to need discussion.

The possibility that social insects "talk" to one another is fascinating. It is difficult to believe that the many activities of a large colony are the result of mere tropisms of the individuals, although a great deal of recent work points in that direction. It still seems that there may be some real means of communication between the various members of the colony, although this involves not only definite signals but intelligence enough to give, receive, and properly act upon the signals. If all of this be granted, it still remains to discover the nature of the signals. So far as we know, insects excell man only in their olfactory sense and in their ability to perceive ultraviolet light. I am not aware of a single experiment that has furnished indisputable evidence of communication between insects by means of sound. The most common defect of such experiments, apart from the frequent doubt concerning there having been any real communication, is that the possibility of reaction to odors has not been excluded and we have many reasons for believing that insects possess a well-developed olfactory sense. The fact that faint sounds within our range of audible frequencies are made at these times has been

used as proof that communication has been by means of sounds but, in addition to this being no proof, it implies that insects have a more acute hearing for faint sounds within man's range of auditory frequency than has man, and this is not even indicated by any work known to me. If social insects communicate with each other by means of sound, it seems probable that the sounds employed have a pitch above that of man's auditory range and of this we have no proof.

The belief that sounds form an important sexual attraction in the case of a few insects, although, so far as we know, they play no part in the mating of the great majority of species, rests largely upon interpretation and the doctrine of sexual selection. After watching and listening hours upon hours in broiling sun and pitch darkness to the sounds made by male Orthoptera without getting any evidence that these sounds have a sex appeal or that the males are even thinking of mating, I confess that my feelings are best expressed by the saying "I am from Missouri and want to be shown." Experiments concerning sexual selection in the case of flies (*Drosophila*) have been carried out and sexual selection seems to have been demonstrated, but the basis upon which the selection was made still remains obscure. If male crickets, say, could be muted without injuring them in any other way, we might test their ability to get a mate in competition with musical brethren but the experiment is not one to be lightly taken up. On the other hand, if the profound modifications noted on previous pages have been brought about for the specific purpose of sound-production and by sexual selection, the experiment ought to give very definite results since, under these conditions, sound might well be expected to be very important. Since I am not convinced that sound is important in the mating even of crickets, I do not believe that these structures have arisen for this purpose and in this way. However, if the "sex calls" of Orthoptera are important, it may be that other insects make love in the same way but employ sounds of such high pitches that man can not hear them. This should be investigated but it does not necessarily follow, for crickets may have one way of getting mates and beetles, for example, another. This is brought out by Prof. T. D. A. Cockerell in a personal letter concerning my recent paper on 'Some Apparently Nonselective Characters.' He says:

> As to Natural Selection, I think it is like this. Suppose you make a collection of love-letters. They would be all different. As they were (let us assume) all successful in their purpose, you would infer that the differences were not adaptive. But, in fact, each letter would represent the attempt of the organism to adapt itself to its environment. They would differ because the total result was due to the nature of the organism and the nature of the necessary adaptation. The nature of the organism is a

product of past ages. So, A, B, C, D, would each make an effort in appreciably different terms. The effort would be directed toward adaptation, but its precise form conditioned by the nature of the creature. Why should it be so, and why should results be diverse? Well, because during the past, in each particular line, certain tendencies have prevailed for reasons of the most diverse kinds and now past our finding out.

Even though it may now be past finding out why it is important that one species chirps one song while a closely related one chirps an appreciably different song, it may not be too late to discover whether or not the chirp is important at all. As to "adaptation," there has been considerable confusion. This, it seems to me, was evident in a symposium on 'Adaptation' conducted by the Entomological Society of America. Nearly every speaker mentioned some use to which an insect put a structure and then concluded that the structure arose for the purpose of being used in that way. I fear that I was quite heterodox, for I spoke in part as follows.

"Before one can either interpret or discuss an interpretation of adaptation he should have clearly in his own mind what he means by 'adaptation' and each speaker must in some way make clear to his patient audience his definition of the term.

"The human mouth can do many different things in addition to chewing and making a noise. Not infrequently we see a man putting the stem of what he calls a pipe between his jaws. Leaves of alfalfa and various other plants sold under the trade-name of 'tobacco' are put in the bowl of the pipe and ignited. This man then sucks the smoke through the stem of the pipe into his mouth, subsequently expelling the smoke either between his lips or by the way of internal passages through his nostrils. He seems to get a certain amount of pleasure and some even say profit from these actions, actions which involve a rather intricate series of anatomical—shall we say adaptations?

"The pipe was fashioned for this particular purpose and its structure may, I think, be said to be adapted to smoking in the sense in which the word adaptation should be used in this discussion but the man's teeth that hold the pipe, his mouth's connection with a pump-like arrangement in this thorax, and the internal passages between his mouth and his nostrils are merely subsequently made use of in the curious practice which he has recently and perhaps only temporarily taken up.

"Observing one of these men, I saw him fastening a notice on a bulletin board. He used his pipe like a hammer in order to drive in the pin. For this purpose the pipe functioned rather well but I do not think it could be said to be 'adapted' to driving pins even though it did drive a pin then and probably is often used in this way.

"I am told that the stem of a pipe wears a man's teeth away. Surely neither the man who uses a pipe nor the man who made it intended that this should happen. In the sense in which the word adaptation should be used in discussions concerning evolution the pipe is not adapted to wearing away human teeth even though it does do it."

Applied to the problem of insect-sounds, this line of reasoning would lead us to think that at least many of the structures by means of which insects make sounds are really not adaptations for sound-making. To have been developed by natural selection, the sounds made by these structures must have been of material advantage to the insect and proof or even fair evidence that such is the case seems to be lacking in the majority of cases. Leaving out of account for the present the Orthoptera and the cicadas, there are few or none of the sound-making insects that have well-authenticated organs of hearing or whose sound-producing organs may not quite conceivably produce the sounds by pure accident and without any purpose or profit. Until we have proof that insects in general purposely make sounds, audible to them even though inaudible to us, or that they profit by sounds which they make without intention, there is nothing in our present knowledge of the biology of insects that furnishes good ground for believing that the exceptional cases in which we hear insect-sounds are really exceptions to a rule that flies, bees, beetles and similar insects do not communicate by means of sounds. If, however, we obtain proof that insects in general do make sounds that are audible to them, even though inaudible to us, then we will have some basis for believing that insects communicate with each other in this way. As the case stands now, it seems to me that the sound-making structures of these insects were no more designed by selection (or otherwise) for that purpose than a tobacco pipe was designed to drive tacks and I even doubt the so-far published evidence that they are intentionally so used.

In the cases of Orthoptera and cicadas the presence of extreme specializations, wonderfully efficient in producing sound and apparently not used for any other purpose, gives us a reason for thinking that there is a purpose. The presence of what seems to be a definite ear in the stridulating Orthoptera is an additional reason. However, when we see that the termites, which are not known to stridulate, have the same sort of an ear as crickets and long-horned grasshoppers and that the cicadas, which produce a loud (to us) sound, probably have no ear (unless it be connected in a deafening way with the sound-producing structure), this latter reason loses some of its force. Also, the highly specialized sound-

producing mechanism of deaf rattle-snakes is, as was pointed out above, worthy of consideration in this connection. The suggested purpose of the well-developed insect sounds, a "sex call," is only imagined; it has not been proved and the chief evidence is that usually the females do not make a sound that we can hear.

If these structures have not arisen for the purpose of making sounds, why have they arisen and how? There is at present no certain answer to this question. Rugosities on the veins of insects where there is no apparent use for them are known and these are very like the "file" of a cricket's wing. There are also, among the Orthoptera, intergrades between "unmodified" venation and that of a male cricket so seemingly intended to help in producing sound. These two facts furnish material for a brief in favor of the idea that the wings of a male cricket have been developed by natural selection because it was to the advantage of the insect to chirp; but this advantage is uncertain and, even if it were certain, there would still remain the possibility that it is a secondary and accidental thing. In a former paper[1] an attempt was made to show that complicated and definite structures, including details of wing-venation, had arisen by mutation or through the action of developmental factors without any "purpose" or favoring action of natural selection. I would not be so bold as to say that this is true of the cricket's wing and the cicada's drum but I would not deny such a possibility.

At any rate, Nature has not seen fit to give the higher insects sound-producing organs that, judged by man's standards and present knowledge, can be compared in efficiency with those obtained by a few low in the phylogenetic scale. The limiting or destructive action of Nature Selection seems beyond question. It may be that sound-production, by friction and otherwise, developed among insects without any favoring or constructive action of Natural Selection, if such there be. Whether the limiting action of Selection has prevented its further development is, of course, quite uncertain but it is clear that, as far as man's unaided ears can determine, either (*a*) such development has not been greatly favored and so, presumably, is not of value to the insects or else (*b*) there is little force in the favoring action of Natural Selection. It is, of course, possible to suppose that, as insects became more "advanced," they acquired the power of communicating with each other by means of sounds of such

[1]Lutz, Frank E., 1924, 'Apparently non-selective characters and combinations of characters,' Annals N. Y. Academy of Sciences, XXIX, pp. 181–282.

short wave-length as to be inaudible to their vertebrate enemies.[1] If this were true it would, indeed, be dramatic and of great biological interest, but we have yet to discover even the production by insects of such sounds, to say nothing of proving that insects can receive and intelligently react to them.

[1]Cockerell, Miller, and Printz (1914, Zoologischen Anzeiger, XLIV, p. 434), discussing the auditory ossicles of rodents, said: "Thus there appears to be a definite relation between the size and shape of the ossicles and the voice of the animals, although this can at present only be stated in general terms. The ossicles, then, exhibit a certain parallelism with recognition marks, probably tending to make the rodents especially sensitive to the voice of their species. Perhaps some day an energetic student will collect phonographic records of the voices of mammals, and it will be possible to determine more exactly how these are related to the structure of the ears. It may be also noted that the chirping Orthoptera, much preyed on by mice, often have very high pitched 'voices,' so much so that they are sometimes inaudible to some human beings. It may be advantageous to the Orthoptera to be able to call one another in notes so shrill that to some animals they are inaudible, but it may also be advantageous to the mice to be well fitted for hearing those high sounds."