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COMMUNICATION IN RED FOX DYADS:
A COMPUTER SIMULATION STUDY

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ABSTRACT

For any two animals, three major factors limit communication. These are (1) whether appropriate signal mechanisms are available to them, (2) whether the animals are motivated to communicate, and (3) whether their movements and locations are such that signal can pass between them. In this study, signal mechanisms and motivation were not considered as variables, but the role of animal movement in limiting communication was. A computer simulation study of amounts of communication which occur in red fox (Vulpes vulpes) dyads when various means of signalling are used, and when the animals move about and signal with various emission intensities and at various time intervals is reported.

Two parameters determined by the movements of any two animals affect the potential for communication by indicating optimal means of signalling and by restricting information transfer via those means. The parameters are (1) distance between the animals at points in time, and (2) times between the animals when they use corresponding areas of space. Because signals for various modes of communication differ in the way in which they are emitted and in the time over which they remain effective, the same pair of movement patterns can give more or less dyadic communication depending on the sensory mode used for signalling and, within each mode, on how the animals signal. Likewise, because of the dependence for communication on the temporal and spatial locations of the

animals, different patterns of movement will result in different levels of communication with a given means of signalling and level at which signals are emitted. Limiting conditions for dyadic communication which depended on the movements of both individuals were developed for tactile, visual, vocal, and olfactory signalling. These conditions were then employed to develop simplified models of the ways in which red fox can communicate.

Computer programs were written to control the movements of both members of red fox dyads and, on the basis of the communication models, to control the means of signalling used for communication within the dyads. Only uni-directional communication, in which one animals always acted as a signaller and the other always acted as a receiver of the signal, was simulated.

Five simulated dyads were used in the study. For each dyad, communication under a total of 154 different controls on means of signalling was simulated. Movement patterns of the animals in each dyad were different.

While the animals moved about, one of them emitted signals of a programmed kind, of a programmed emission intensity, and on a programmed schedule. Whenever the other animal moved within spatial or temporal range of these signals, communication was assumed to occur. The percent of time during which communication occurred was measured for each of the 154 different controls on means of signalling, for each of the dyads.

No tactile communication occurred between members of any of the five dyads, and close-range visual or vocal communication (from 16 m or less) occurred very rarely.

Simulation indicated that visual communication could occur frequently with reasonably short visual ranges (20 percent of the time from 306 m). However, visual communication in wild red fox is probably usually limited by darkness and terrain.

Scent path communication, where one animal crossed and reacted to the trail of scent left as the other moved about, could provide moderate levels of communication. An average of 7.6 hours of scent effect resulted in communication 20 percent of the time. Increasing scent effect times beyond about 9 hours did not result in further increases in level of communication. The primary function of scent path signalling may be to reveal the location of a signaller during the same daily activity period that scent trails are left in the wild. Ambiguity from scent persisting from one daily activity period to the next may be avoided by a signaller emitting scent which provides an optimal scent effect time of 9 hours, approximately the length of the red fox daily activity period.

For vocal signalling, changes in communication variables which increased the area covered by vocal signal, the time covered by such signal, or both, resulted in higher levels of communication. Linear increases in communication occurred with linear increases in frequency of vocalization, but the effect of increasing the vocal range on communication became less and less as the vocal range increased with a given frequency of vocalization. Vocal signalling could be an effective means for maintaining social contact in red fox dyads. Vocal signals which could be heard from 644 meters gave communication 20 percent of the time when the signaller vocalized 4.7 times per hour. However, wild red fox seldom emit loud vocalizations, and vocal communication is probably not of prime importance in maintaining dyadic social bonds.

With scent point signalling (scent marking) combinations of the three communication variables which resulted in relatively sparse, small circles of scent on the home range space gave low levels of communication. Communication was increased by changes in any combination of the three variables such that the total area of effective scent increased. When scent remained effective for 8 hours, could be smelled 96 m from the scent mark, and when the signaller marked twice per hour, communication occurred 20 percent of the time. Wild red fox scent mark more frequently, and the scent may remain effective for periods of days. Thus, high levels of dyadic communication may be achieved through scent marking, and this form of signalling may be of great importance in maintaining dyadic spacing and social bonding.

The particular movement patterns of the animals which formed each dyad had a differential effect on the level of communication, regardless of the means of signalling. The maximum levels of tactile and scent path communication which could be reached were limited by movements of the animals. Limitations placed by animal movement on visual and vocal communication could be overcome by increasing the spatial area of effect of the signal, and for scent point communication by increasing the spatial and temporal area of effect. Those means of signalling which involved the fewest communication variables were most severely limited by movements of the animals. Where more variables associated with emission of signal were available to the animal, emission could be optimized to minimize effects of movement on communication.

Likewise, because various ways of moving about differentially affected the level of communication with a particular means of signalling, levels of communication could be changed by changing the movement pattern of one or both animals. With tactile and close-range signalling, communication could be increased only by coordinating movements of dyad members such that they were seldom far apart. Some other means of communication would be necessary to establish this coordination, and to allow the animals to find each other when they became separated. Scent path communication could likewise be enhanced by coordination of movements, but not necessarily such that the animals traveled together. Rather, the coordination would require a leader-follower set of movement patterns. As shown by simulation, the initial contact or contact following separation would be enhanced by the signaller moving in a pattern in which it seldom turned and traveled at relatively high speed. For visual signalling, and for the spatial range variables of both vocal and scent point signalling, communication could be enhanced by proper choice of emission intensity and by travel by the signaller at relatively high speed. For the temporal variables of scent point signalling, communication could be made more efficient by the signaller moving at high speed and in relatively straight paths, and by choices of frequency of scent marking and scent effect time which reduce the probability that effective circles of scent overlap.

This study suggests that the animals can adjust the distance between them, the time between them, or both if prior communication has given mutual awareness of the locations and movement patterns. In these adjustments, they can increase or decrease the efficiency of signalling in one or more ways, and thus control the level of dyadic communication. These adjustments require changes in the movement patterns of one or both dyad members, and will be reflected by changes in one or both home range spaces. The degree of mutual adjustment in movement patterns which the two animals can make to change the level of dyadic communication will be limited by factors extraneous to dyadic communication, such as communication and social relations with other individuals, and dispersion of life requirements in the respective home range spaces of the dyad members.

INTRODUCTION

This paper reports a study, by computer simulation, of amounts of communication which occur in red fox dyads when the animals paired to form a dyad move about and signal in various sensory modalities and in various ways. The reader is cautioned at the outset that the situations in which wild red fox communicate were simplified in order to model movements of the animals and communication between them. In effect, I attempted to model the case in which the fewest variables affected the amount of communication which occurred. For example, communication was modeled such that the word communication, as used throughout this paper, is synonymous with reception of signal, although factors other than whether signal is received surely determine whether or not communication actually occurs (see below).

Because of this simplification, the results of simulation reported here may only approximate those which will result when more variables are added to the models and more complex situations are simulated. As more and more variables which affect communication are added, the simulation models may become a closer approximation of real situations in which communication between wild red fox occurs. The study is an attempt to establish base-line information which can give a basis for comparison as more and more variables are successively added to the models, and as the simulated situation more closely approaches the real one. This study is but a beginning of this approach to computer simulation study of communication processes among wild mammals, with red fox as an example.

In addition to establishing base-line information and in general pointing up the role of animal movement in communication, the objectives of the study were (1) to compare the various means of communication available to red fox and estimate the relative amount of communication provided by each means, (2) to determine some of the factors which limit communication with various means of signalling, and (3) to learn whether different ways of moving about have an effect on the level of communication in red fox dyads.

The role of the movements of individual mammals in limiting the amounts and kinds of communication which occur is not well understood. Of the three major factors which contribute to communication between any two free-living mammals; signal mechanisms, motivation, and location, only the first two have been subjects of major reviews (Tinbergen 1964:206-230; Andrew 1972, and others) which indicates the relative emphasis in research on the three factors. Emphasis in this paper is on the role of movement and location in communication. This emphasis does not minimize the role of signal mechanisms and motivation, but will serve to show that all three factors are necessary for effective communication among mobile, free-living mammals.

Most studies of communication begin with individuals which are at places from which they can communicate if they are motivated to do so and if they have the means for signalling and receiving signal. Yet it is clear that not all members of local species populations or even of loosely organized social groups can communicate at all times because distances between them are too great for signal to pass among them. As an example of the way in which location of the individuals has generally been ignored in studies of communication Altmann (1962a; 1965) studied communication among wild rhesus monkeys (Macaca mulatta) and computed the probabilities that certain communicative behaviors would occur in the population. These computations were made without regard for the proportion of time that the study animals were not at locations from which they could communicate. That spatial arrangements of individuals within a group could influence communication was mentioned (Altmann 1965:521), but was ignored in the exhaustive analysis.

The study of communication among free-living mammals has centered on those forms which live in groups (cf. Wickler 1967: 89-90; Rowell 1967), and the limitations which movements of individuals place on communication are less obvious when the individuals move about together. However, even where the animals under study tend to be solitary, observations on communication have been made (cf. Leyhausen 1965) only on indiviudals which were at places from which communication could occur.

The movements of individual mammals place limits on the amounts and kinds of communication which can take place among them. For communication between any two mobile, free-living mammals to occur, as defined in terms of a demonstrable behavioral reaction to receiving signal (Klopfer and Hatch 1968:32-33; Mackay 1972:3-6), locations of the individuals in time and space must of course be such that signals can pass between them. Thus, given that signal mechanisms and motivation are adequate, movements of the individuals must bring them to certain locations before communication is possible.

Given that animals can communicate if they are at appropriate locations, how much is the amount of communication which occurs influenced by how the animals move about? Two kinds of limits are placed on communication by movements of the animals and the resultant spacing between them. First, movements determine the sensory modality and within the modality the means (Scott 1968:17-19) by which communication can or cannot occur at a particular time (Theberge and Falls 1967:377). For example, movements may bring individuals to locations from which they can hear each other but cannot see each other. To quote Marler (1967:773):

> "The usefulness of certain modalities may be restricted by an animal's habits. A strictly nocturnal species has less use for visual communication than a diurnal animal has. A solitary species may have less

> use for tactile signals than does an animal
> in constant proximity with several companions."

Further, Lancaster (1968:442) and Marler (1965:583) point out that location of the animals can affect the range of choice in means of signalling which the animal can use. As distances between animals increase, there is a general tendency for less use of multimodal constellations of signal elements and greater use of less ambiguous signals sent in a single optimal modality.

In the second kind of limit on communication, locations of the animals limit the amount or kind of information which can be transmitted once a communication link is possible. The information content of messages is determined to some extent by the sensory modality by which they are transmitted (Klopfer and Hatch 1968:33; Sebeok 1967:367-368; Marler 1965:547) and movements of the animals can allow choices in the modalities which the animals can use at a particular time. When, for example, both vocal and visual means of communication are possible, an animal might choose to use vocalizations, which might convey more information than visual signals. Discussion of whether or not non-human mammals do in fact choose the modality by which they communicate on the basis of attempting to maximize communication is outside the scope of this paper. Suffice it to say that movements of the individuals can provide for such choice.

Within a particular modality, different locations continue to affect the amount of communication which can occur. Marler (1968:106) points out that problems of transmission of visual signals are lessened by reduced distance between individuals. Shorter distance allows greater latitude in the visual signal mechanisms which can be successfully used, and presumably increases the amount of information which can be transmitted.

Is it important to know how often animals communicate, as well as to infer what information is communicated? Rowell (1967:284) points out that different types of social organization will result among animals which communicate the same information, but communicate that information more or less frequently. Thus one of the factors which determines the social organizational pattern in a population of mammals is the frequency with which the individuals can communicate. If the total amount of communication between any two individuals which form a dyad is important in maintaining social relations between them, it seems worthwhile to ask how often the animals are at places from which they can communicate, and how often their movements prevent communication.

When the members of a dyad do not travel together, then the opportunities for communication depend on the interaction of their patterns of movement and the range of effect of their signals. Busnel (1963:73-74) recognized this interaction, but only as it applied to the probabilities of communication among any members of a population, not between specific individuals:

> "....the probabilities of individuals meeting (male and female, for example) depend on their density per surface unit, on their total mobility and on the richness and qualities of the means of information they have at their disposal enabling them to increase their individual field of radiation and their perceptive universe. ....The range of a signal is in direct porportion to its intensity, other physical conditions of the medium and signal being equal.... if the density of the animal population is high, signals of low intensity will suffice for the information to be received, while if the density is low, the emission intensity must be greater to attain the same aim."

Communication can take place at two levels; universal and individual (Theberge and Falls 1967:335). In universal communication, some of the effects of communication may be shown through influencing other members of a population, regardless of the identities of those individuals and their social relationships with a signalling animal (Wynne-Edwards 1962:16-17; Calhoun 1963:38, 41; Altmann 1962b:280). However, many of those effects which relate directly to maintaining social relationships and social structure depend on a signaller communicating with specific individuals (individual communication), rather than with any individual which happens to be within range when he signals.

It is useful (Poirier 1968a) to analyze social communication in terms of dyads formed by pairs of animals which communicate, even when a signaller may communicate simultaneously with several individuals. In red fox, some dyads are formed by mated pairs which occupy home range space from which other red fox are excluded (Sargeant et al. in ms.; Storm 1972:73). Yet even within these dyads, red fox are generally solitary. Red fox in captivity also move and act independently of each other (Kleiman 1967:367).

Most of the communication which is assumed to occur within red fox dyads must therefore involve signalling over relatively long distances, or involve signalling by scent over relatively long time spans. Study of communication in red fox (Fox 1971: 78-79; Tembrock 1968:362-368) has concentrated on signals which function over short distances. For example, published data on the distance over which vocal signals from one red fox are heard and reacted to by other red fox are not available. The study of communication in this and other mammalian species has concentrated on the physical form of various visual and vocal signals, and on responses to signals which can be heard over relatively short distances (usually less than 10 m).

METHODS

BASES FOR SIMULATION MODELS: METHODS OF SIMULATION

Home Range Space and Individual Movement Patterns:

The movements of an individual mammal are usually confined to a limited area for at least a large portion of its lifetime. The portion of space used by an animal has been called its home range (Burt 1943). In my view, the major factor which determines where the animal goes, and thus the limits and features of the way it uses its home range space, is a set of learned responses to the local environment. This view is reflected in the way in which both home range space and individual movement patterns were simulated.

The life of an individual mammal occurs within limits of time and space, the beginning points of which are controlled by the parent(s). Suitable places where the animal could go from this initial point are, in theory, limited only by geographic and biotic barriers, by the mobility of the individual, and by its lifespan. However, most mammals confine their movements to a relatively small area for long periods of time, perhaps for their lifetime (Jewell 1966). This localization (Scott 1963:241) forms early in the lives of many mammals, but may form later after dispersal from the natal range (cf. Storm 1972:66-122; Hawkins et al. 1971; Phillips et al. 1972).

Dispersal movements generally occur in relation to sexual maturity (Blair 1953:26), a relationship confirmed for red fox (Storm 1972:71), and may be an important population regulation mechanism in some species (Krebs et al. 1973).

From a beginning point which has been determined for it, or from a point which it chooses after dispersal, an individual uses particular areas of space more often than it uses other areas, as time progresses. Many factors may influence this differential use as, for example, innately determined preference for unevenly distributed biotic and structural features of the habitat (Wecker 1963), preferences gained through influence of social associates (Terman 1963; Montgomery and Sunquist in ms.) and responses to the presence of non-associates and neighbors (Poirier 1968b:353; Hawkins and Montgomery 1969:202).

As Burt (1943) conceived the home range, this differential use of an area which is smaller than the area potentially available to the animal is a necessary feature for determining whether or not an individual has a home range. In my view, and in that of others (Scott 1963:241) those places which an animal remembers, and to which it returns more or less regularly become parts of its home range. Washburn and Hamburg (1965: 616-617) consider that familiarity with an area is the prime factor which limits use of space, rather than availability of food or method of locomotion. Jewell (1966) in his term "lifetime range" means the total area with which a mammal has become familiar. Some areas known to a mammal may change or be forgotten, and thus will no longer be included in the home range (Ewer 1968:65).

In my view, a distinction should be made between how, as observers, we conceive an individual's home range on evidence provided by movements of the animal, and the concept which the animal has of the space in which it lives. I choose to call the latter concept the animal's "home range", and the former the animal's "home range space". Places which the mammal has not visited, but which it is aware of become part of the home range (but not of the home range space) when they contribute to orientation of the individual in the space which it actually uses, its home range space.

In this view, the concept which the animal has of the space in which it lives gives rise to the differential way in which it uses space. Generally, the individual will spend time in its home range space in a non-random manner; its pattern of use of the home range space will be distinguishable from random movement. As time progresses, radio-marked mammals of several species, such as snowshoe hare (Lepus americanus), raccoon (Procyon lotor), white-tailed deer (Odocoileus virginianus) and red fox, have been shown to use a series of locations, and the spatial distribution of these locations is demonstrably different from a random distribution (Tester and Siniff 1965;

Siniff and Jessen 1969). That animals move directly between points on their home range space has been shown for white-tailed deer (Rongstad and Tester 1969:375) and for a blind raccoon (Sunquist et al. 1969).

Red Fox Movements and Home Range Space:

Considerable information is available on the characteristics of red fox home range spaces, and on the patterns of movement which occur on them. Sargeant et al. (in ms.) conducted a three-year study of radio-marked red fox on the Cedar Creek Natural History Area, near Bethel, Minnesota. Their work, supplemented with that of Ables (1959), Storm (1965; 1972), Scott (1943), Scott and Klimstra (1955) and Arnold and Schofield (1956), provided generalizations about patterns of movement, size, shape, and spacing of red fox home range spaces, and other aspects of red fox biology summarized below.

In general, each red fox home range space is surrounded by neighboring home range spaces, except at the limits of the species range and in other special situations. The total area of a typical home range space is one to three square miles (259 to 777 ha), the space being about one and one-half miles (2.4 km) across at its widest point. The space is usually shared by one adult male, one (rarely two) adult female(s), and seasonally by their young. Other red fox are excluded from this space.

Although the dyad formed by a mated pair shares the same space, the individuals are seldom together. They may use the same portions of the space, but do so at different times although they are usually active simultaneously. Most of the activity occurs at night, and the remainder during late afternoon and early morning. The animals are typically active for 8 to 10 hours of each 24.

While a fox is active, more than 80 percent of its time is spent in travel; an individual covers a major portion of the home range space during the time it moves each night. Red fox average about 8 miles (12.8 km) of travel per 24 hours, and may travel as much as 15 miles (24.1 km), all within the confines of the home range space. Borders of the space are not patrolled.

Simulation of Individual Movement Patterns:

Simulated movement patterns of 8 individual red fox were created with a Fortran IV computer program modified from the program which represents the Siniff-Jessen model of animal movement (Siniff and Jessen 1969). All simulations for this study were done with a CDC 6600 computer at the University of Minnesota.

The location, size, and shape of the area in which a simulated animal's home range space could lie were specified, and were controlled by the program. All such areas in this study corresponded to the same ellipse, which had axes of 1.0 and 1.5 miles (1,609 and 2,563 m). The movements of each animal determined where on this area its home range space actually was. Movements had a high probability of being confined to the area, because the animal was programmed so that the probability of moving to areas it had used previously was higher than movement to areas where it had never been. Before the simulation of each movement pattern, the animal was given a number of locations distributed equally over the elliptical area, and none outside it, equivalent to uniform use of all the area. Thus at the beginning, the animal could seek out any part of the area, but avoided going outside the area. As the simulation proceeded, the animal differentially used various portions of the area and tended to seek those places where it had been most often as it built up its home range space. For this study, I programmed the animals to tend to go toward places which were within 0.15 miles (241 m) of those which had been used 5 or more times previously. If they failed to find such a place, they were programmed to tend to go toward the center of the elliptical area.

The individual's movements on the area were controlled by a modified random walk procedure, as follows. With the animal at a location, initially set by me, the angle which it would turn (resulting in a direction which it would travel) and the rate of travel (resulting in the distance which it would travel during the next regular time interval) were chosen from probability distributions. Direction of travel could be biased by where the animal had previously been, as outlined above. The X-Y coordinates of the animal's next location were computed, based on the direction and distance of travel, the animal was advanced to that location, and time was incremented. Subsequent locations were computed in a like manner until a series of locations resulted. Additional features of the Siniff-Jessen model, the logic used in its development, and examples of simulated movement patterns are given in Siniff and Jessen (1969) and Siniff (1967).

In this study, all animals moved once per 5 minutes, in simulated time, until a series of 900 locations had accrued. This movement pattern, represented by the 900 serial locations, was stored on magnetic tape until needed.

The computer program tested the movement patterns which it simulated against the distribution of locations which resulted from the movement patterns of radio-tracked red fox (Siniff and Jessen 1969:210-213). For this study, a grid-system of 0.10 mile-square (161 m square) grids was superimposed over the elliptical area. The number of simulated locations which fell into each square was counted. The frequency distribution of number of locations per square was tested, by a goodness of fit procedure, against the distribution of locations which resulted when radio-tracking data from red fox were summarized in a like manner. All movement patterns simulated for this study showed satisfactory fit. Moreover, visual comparisons of computer-generated plots of real and simulated movement patterns showed them to be very similar.

Characteristics of Simulated Individual Movement Patterns:

Eight movement patterns were simulated, and each pattern had individual characteristics which resulted from the random walk procedure used in the simulation. Four parameters were used to distinguish among the movement patterns (Table 1). Two parameters: mean rate of movement, and angle turned between successive locations (Siniff and Jessen 1969:189), were used to characterize the way an individual moved about its home range space. Angles turned were compared with respect to the tendency of an individual to travel straight ahead, or within 30° of straight ahead, in successive movements. An animal with a high mean rate of travel and a high tendency to travel straight ahead (for example, No. 5; Table 1), would cover its home range space relatively quickly. Siniff (1967:41) showed no apparent relationship between these parameters for a particular real movement pattern. However, animals simulated for this study tended to travel in relatively straighter paths when they moved at higher rates of travel.

Table 1. Comparison of 4 parameters of the movement patterns of the 8 simulated red fox used in the study. Two parameters: mean rate of movement and; percentage of the movements which tended toward straight ahead travel, describe the way in which an individual moved about the home range space. The other two parameters: the K value of the negative binomial distribution and; the total number of grid squares used, describe the distribution of locations on the home range space after a series of movements by the individuals.

Number of the Individual	Mean Rate of Movement (mph)	Percent of Movements Within ±30° of Straight Ahead	K	Total Number of Grid-squares Used
1	0.721	32.1	0.562	78
2	0.719	29.8	0.231	56
3	0.731	34.0	0.559	77
4	0.736	34.7	0.675	77
5	0.759	34.4	0.676	77
6	0.697	32.2	0.665	74
7	0.748	30.9	0.394	78
8	0.722	29.8	1.140	92

The remaining two parameters: the K value of the negative binomial distribution fit to the number of locations per square (Siniff 1967:38; Siniff and Jessen 1969:197-199), and the total number of squares used by the animal, were used to describe each individual's distribution of locations after a series of movements. With respect to the overall pattern with which an animal used the elliptical area, a high K value and use of a high number of squares indicate that the individual used a relatively large portion of the area, and that it used all parts of it relatively infrequently. Animal No. 8 (Table 1) provides an example of such a movement pattern. The animal used 92 squares, while animal No. 2 used only 56, both in their respective series of 900 locations.

Communication and the Location of Home Range Space:

The relative locations of the home ranges of any two individuals have a great influence on whether or not they can communicate and if so, on the constraints which movement patterns and signalling place on the amount of communication. There is no possibility for direct communication when two animals have home ranges which are far apart in time and space. A red fox which died in 1960 cannot communicate directly with one born in 1970, even when they have the same home range space. Likewise, a red fox whose home range is in Illinois cannot communicate directly with a contemporary fox in Minnesota.

Between these extremes, we might expect that an individual would move and signal in such a way as to optimize communication with certain members of the population which are within limits of time and space such that communication can occur. Calhoun (1963:41) has proposed that small mammals will have evolved signal mechanisms which insure that an animal at the center of its home range space will respond to another individual which signals from the border of that space. Hediger (1961:54) considers that individuals of a society will be apart only to some maximum distance, termed the "social distance"; red fox seem to be what he termed "distance type" animals which avoid contact and stay at a distance from each other. Maintaining such a distance implies that the animals communicate regularly. The area about an individual in which it can influence other animals has been termed a "social force field" (McBride 1964: 79-84); this field generates the individual distances among animals. That author discusses social factors which may modify the extent of such a field, including social position of the individual, size of the group in which it lives, and frequencies of agonistic contacts.

Given that any two animals have sufficient motivation and the appropriate signal mechanisms to communicate, the relationship among movement patterns, spatial relationship of the home range spaces, and range of effect of signals which determines whether or not communication can occur, other things being equal, differs for the various modes of communication. Modes of communication as listed by Scott (1968:18-19), and classified in terms of the sense organ through which information is received, are considered. Electrical and kinaesthetic modes of communication (Busnel 1963:69) are not considered. Many variables other than those considered below surely affect communication. For example, motivational states of the animals may prevent communication although the movement patterns and range of effect of signals are adequate to allow signal to pass between them. Physical barriers, darkness, and wind may interfere with signal and prevent communication even though the conditions given below are met. However, introduction of these additional variables would have deterred from the basic aim of this study, which was to simulate communication with the fewest number of variables. Additional variables, such as those above, can be programmed into the communication models at a later time.

Tactile communication can occur only when (1) the home range spaces of two individuals overlap in both time and space, and (2) the indiviudals move in such a way that they both arrive very near the same place(s) at the same time(s). Close-range communication by any means has similar restraints, except that the animals can be some short distance(s) apart.

Visual communication can occur only when (1) the home range spaces overlap or when they have proximal boundaries no farther apart than some maximum distance over which the animals can be seen, and (2) the individuals move in such a way that they are no more than this distance apart at some point(s) in time.

Vocal communication can occur only when (1) the home range spaces overlap or when they have proximal boundaries no farther apart than some maximum distance over which the animals can be heard, and (2) the individuals move in such a way that they are no more than this distance apart when one of them vocalizes.

Olfactory communication can occur only when (1) the home range spaces overlap or have proximal boundaries no farther apart than a scent substance can disperse and remain at a concentration which will elicit a response, and (2) the individuals move in such a way that one of them arrives at a point in space, or within some maximum distance of that point, within some time after the other was at the point; both the distance and time limits are determined by dispersal of scent from the point used by the first animal.

The Communication Models:

These limiting constraints which movement of the animals place on communication were used as a basis for programming simple models which describe the way in which red fox might communicate in the varius modes. Several simplifying assumptions were used to minimize the number of variables.

With respect to the location of home range space, the only case considered was that in which boundaries of the areas containing the home range spaces of both members of the each dyad corresponded in time and space. The animals of a dyad moved about independently of each other on this space. Thus, only the range of effect of signals in time and space, the frequency with which signals were emitted, and the movement patterns of the individuals affected the amount of communication which occurred.

I assumed that only one of a dyad (signaller) could emit signals while the other (receiver) could only receive those signals. Although I assumed that communication occurred each time the one animal received signal from the other, the receiver could not react to such communication by changing its movement pattern. Signal mechanisms and motivation to communicate were assumed to be always available when I programmed the signaller to emit signal, and whenever the receiver came within range of the signal. Environmental factors such as terrain, wind, or vegetation were assumed not to interfere with signal.

Five models, each describing a means of communication, were developed to simulate communication in the four modes. Tactile, visual, and vocal modes of communication may be envisioned, in their simplest form, as each fitting one model. However, two models were necessary to exhaust the simplest means of communication in the olfactory mode. Scent path communication, as discussed by Fuller and Fox (1969:472-474) is distinguished from scent point communication (scent marking) as discussed by Eibl-Eibesfeldt (1970:310-312). A schematic summary of the processes and decisions used in the compuer simulation models for all means of communication is shown as Figure 1.

In all the models except that for tactile communication, I controlled, through the appropriate parts of the computer program, one or more of the variables (communication variable(s)) which influenced the amount of communication between the animals. The uncontrolled variable in all the models was where the animals were at particular times. Descriptions of the models are grouped according to the number of communication variables which I controlled.

The Tactile Communication Model:

Tactile communication (Fig. 2) occurred each time the simulated animals were at the same location at the same time. Animals had point dimensions, thus their locations had to exactly match. No communication variables were under my control, because only the movement patterns determined when the individuals would be at a particular location. In this

Figure 1. Schematic summary of the flow of processes and the decision used in the computer simulation models of communication in red fox dyads. See text for details of the different limitations placed on communication between the animals.

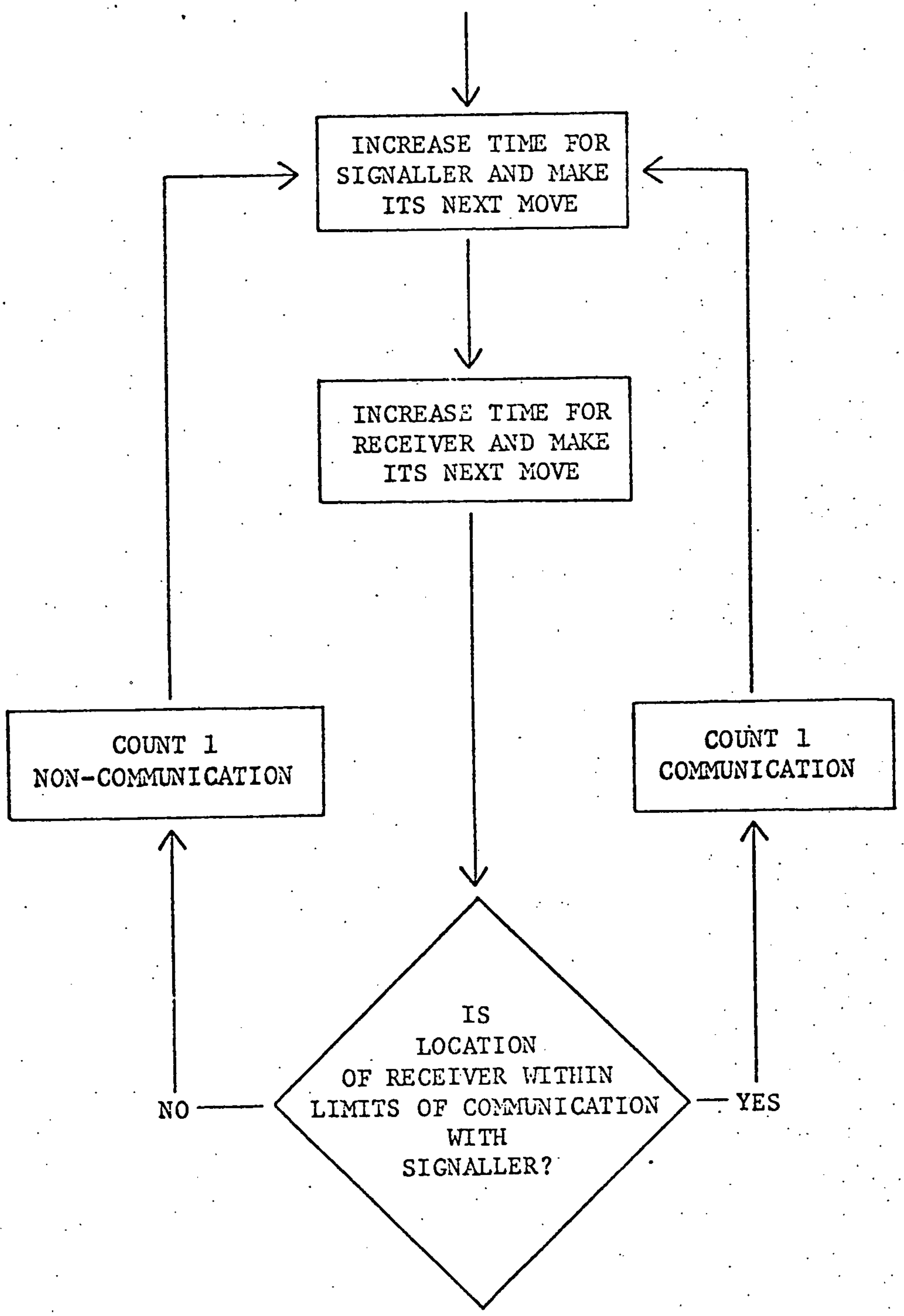
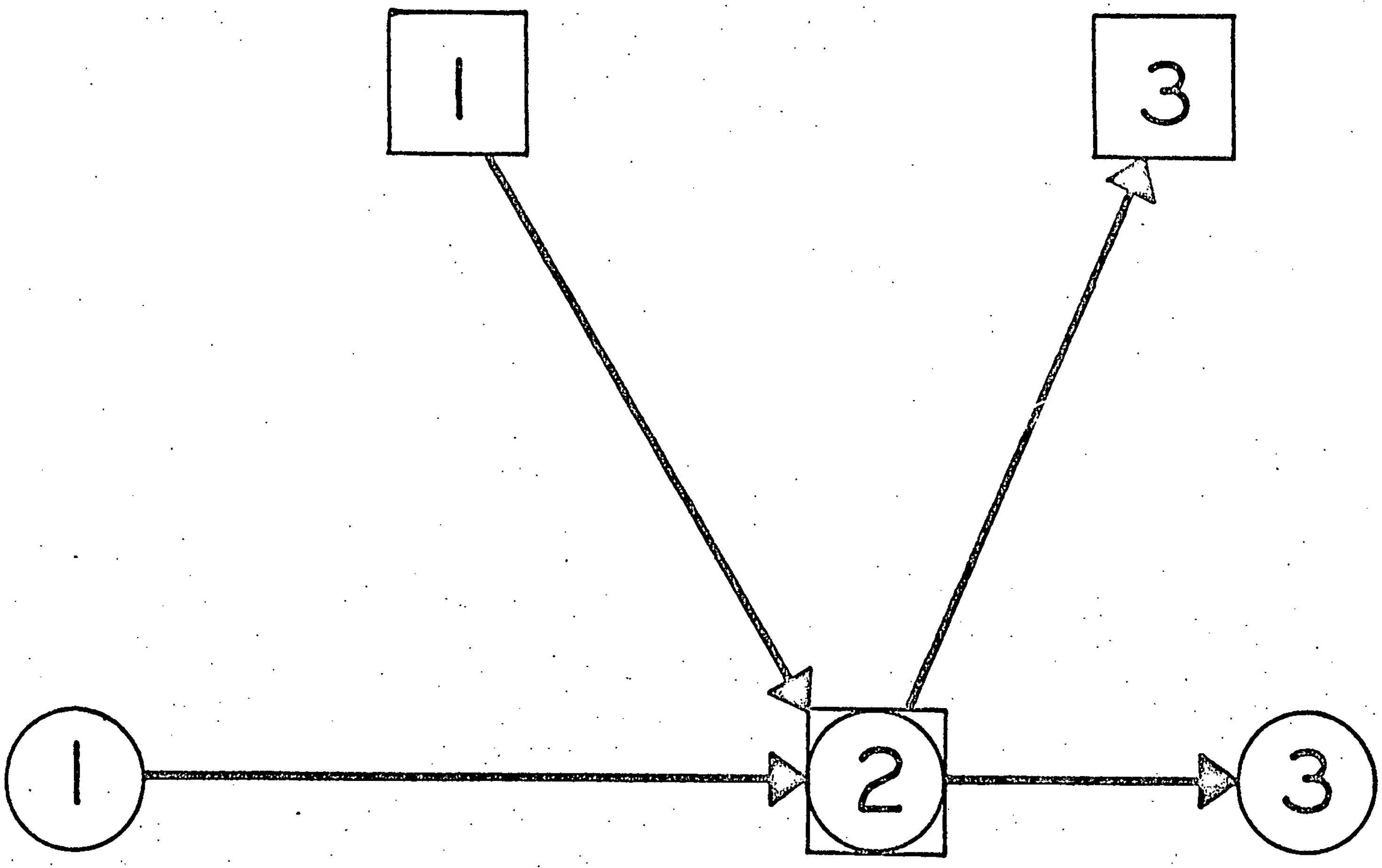

INCREASE TIME FOR SIGNALLER AND MAKE ITS NEXT MOVE
INCREASE TIME FOR RECEIVER AND MAKE ITS NEXT MOVE
COUNT 1 NON-COMMUNICATION
COUNT 1 COMMUNICATION
IS LOCATION OF RECEIVER WITHIN LIMITS OF COMMUNICATION WITH SIGNALLER?
NO
YES

Figure 2. Diagramatic illustration of the operation of the tactile communication model. Symbols indicate the locations of the members of the dyad, with circles representing the signaller and squares the receiver. Numbers inside the symbols indicate the time at which the animals were at their respective locations. Movements leading to communication at time 2 between a signaller and a receiver are shown. At time 1 the signaller is at ① and the receiver at $\boxed{1}$. At time 2, both animals move to the same location, and communication occurs. At time 3, both animals move to locations ③, $\boxed{3}$ from which tactile communication cannot occur. Communication at time 2 did not affect the movements of either animal from time 2 to time 3.



TACTILE COMMUNICATION

and all other communication models, the number of prior times communication had occurred did not affect the receiver's response to signal; communication occurred each time he and the signaller were in the same place at the same time.

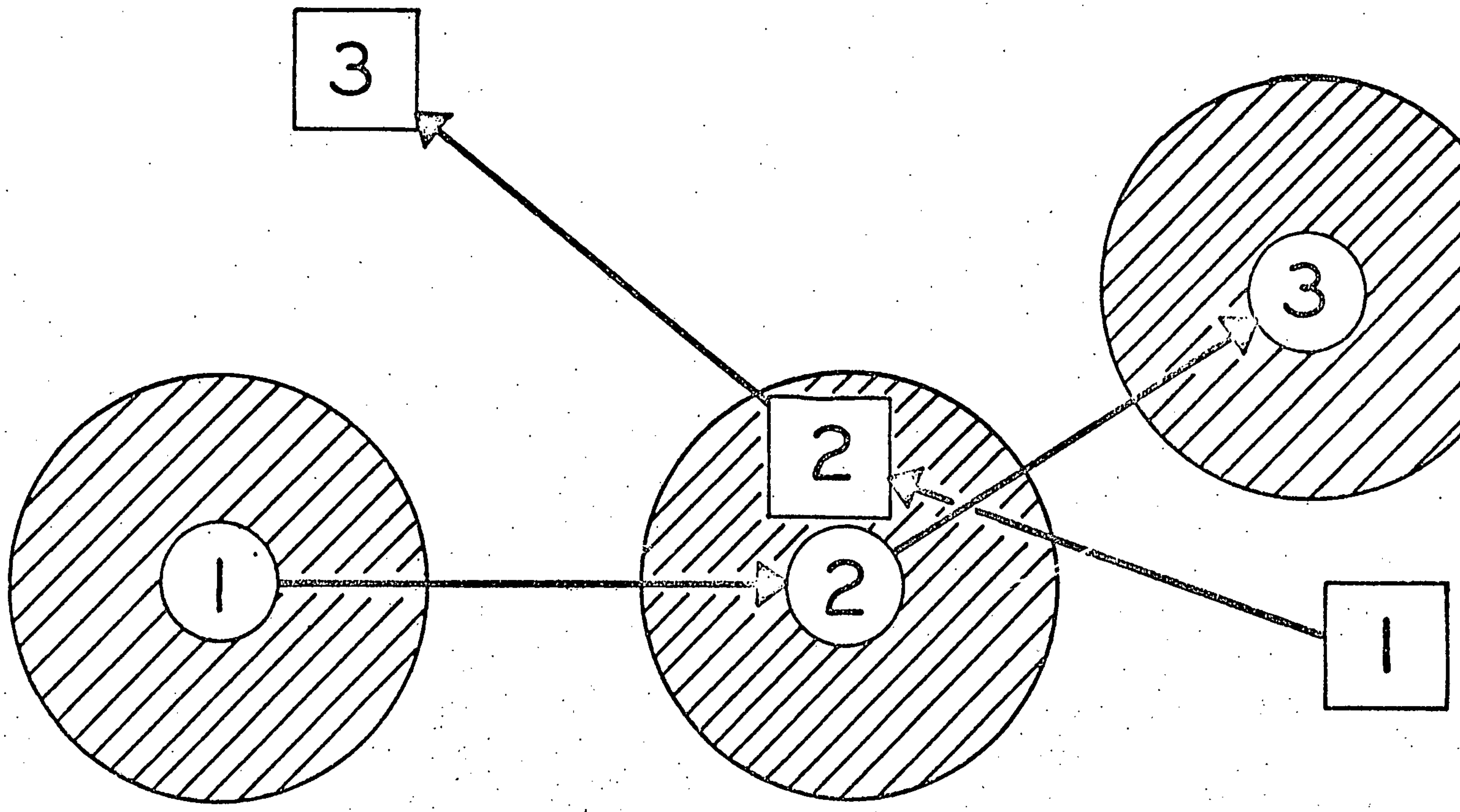
The Visual Communication Model:

Visual communication (Fig. 3) occurred each time the animals were within some distance X_i (visual range) of each other. The visual range was under my control. The signaller was equally visible to the receiver at all times from anywhere within a circle around the signaller's location; the radius of the circle was the visual range. There was no gradation of effect of the visual signal as the distance from the signaller increased, thus visual signal of strength equal to or greater than some single response threshold occurred throughout the circle of effect while signal outside the circle was below the response threshold.

The Scent Path Communication Model:

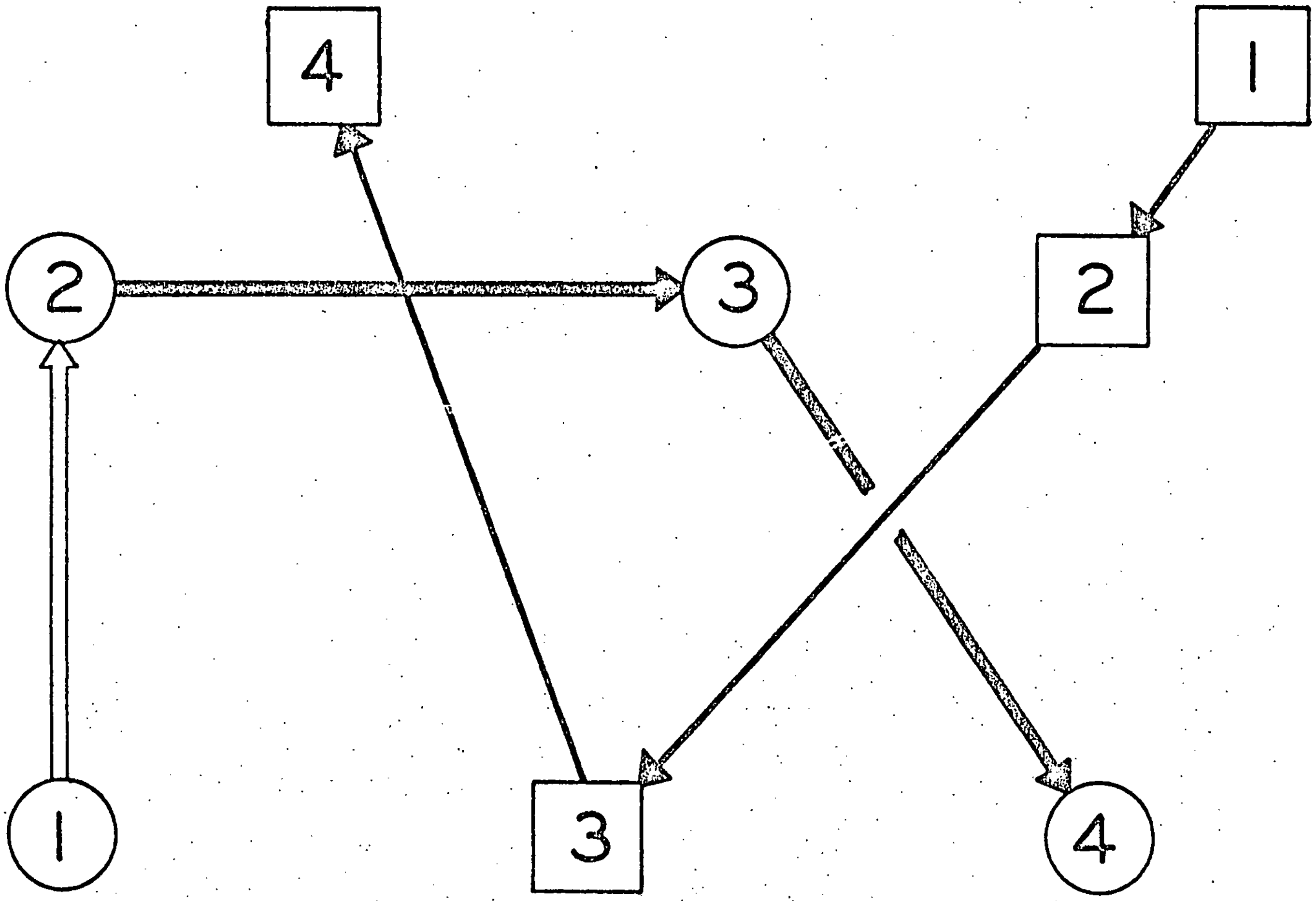
Scent path communication (Fig. 4) occurred each time the receiver crossed the travel path of the signaller within X_i minutes (scent effect time) after the signaller had used that portion of its travel path. The travel path was the line which connected successive locations used by an animal. The communication variable, scent effect time, was under my control.

Figure 3. Diagramatic illustration of the operation of the visual communication model. Symbols indicate the locations of the members of the dyad, with circles representing the signaller and squares the receiver. Numbers inside the symbols indicate the time at which the animals were at their respective locations. The shaded areas around locations of the signaller represent the simulated visual range, and the resulting areas in which visual communication could occur. Movements leading to communication at time 2 are shown. The signaller is at ① and the receiver at $\boxed{1}$ at time 1. At time 2, the animals move to ② and $\boxed{2}$ and communication occurs because the receiver is within visual range of the signaller (within the shaded area which represents the circle of radius visual range). At time 3, the animals move to locations ③, $\boxed{3}$ from which visual communication cannot occur. In this sequence of movements, there were two times when communication could not occur and one when it did. Communication thus occurred 33 percent of the time.



VISUAL COMMUNICATION

Figure 4. Diagramatic illustration of the operation of the scent path communication model. Symbols indicate the locations of the members of the dyad, with circles representing the signaller and squares the receiver. Numbers inside the symbols indicate the time at which the animals were at their respective locations. Heavy lines connecting circles indicate effective scent paths, while the open line between circles indicates a scent path which is no longer effective. Scent effect time is 10 minutes, thus the scent path left by the signaller between times 1 and 2 becomes ineffective when the signaller moves between times 3 and 4. Movements leading to communication between times 3 and 4 are shown. The receiver moves from $\boxed{1}$ to $\boxed{3}$ and no communication results because the signaller has not yet traveled from ③ to ④. When the receiver moves from $\boxed{3}$ to $\boxed{4}$ it crosses a scented travel path, the scent is still effective, and communication occurs. Had the receiver crossed the line connecting ① and ② when it moved between times 3 and 4, no communication would have resulted from its last move.



SCENT PATH COMMUNICATION

I assumed that the signaller constantly emitted a scent substance as it moved about the home range, thus leaving a path of scent. The scent was emitted such that the scent path did not increase in width with time, but had only line width at all times while scent remained effective. The scent remained equally effective during the entire scent effect time, and disappeared instantaneously, (or reached a concentration which was below response threshold), at the end of that time.

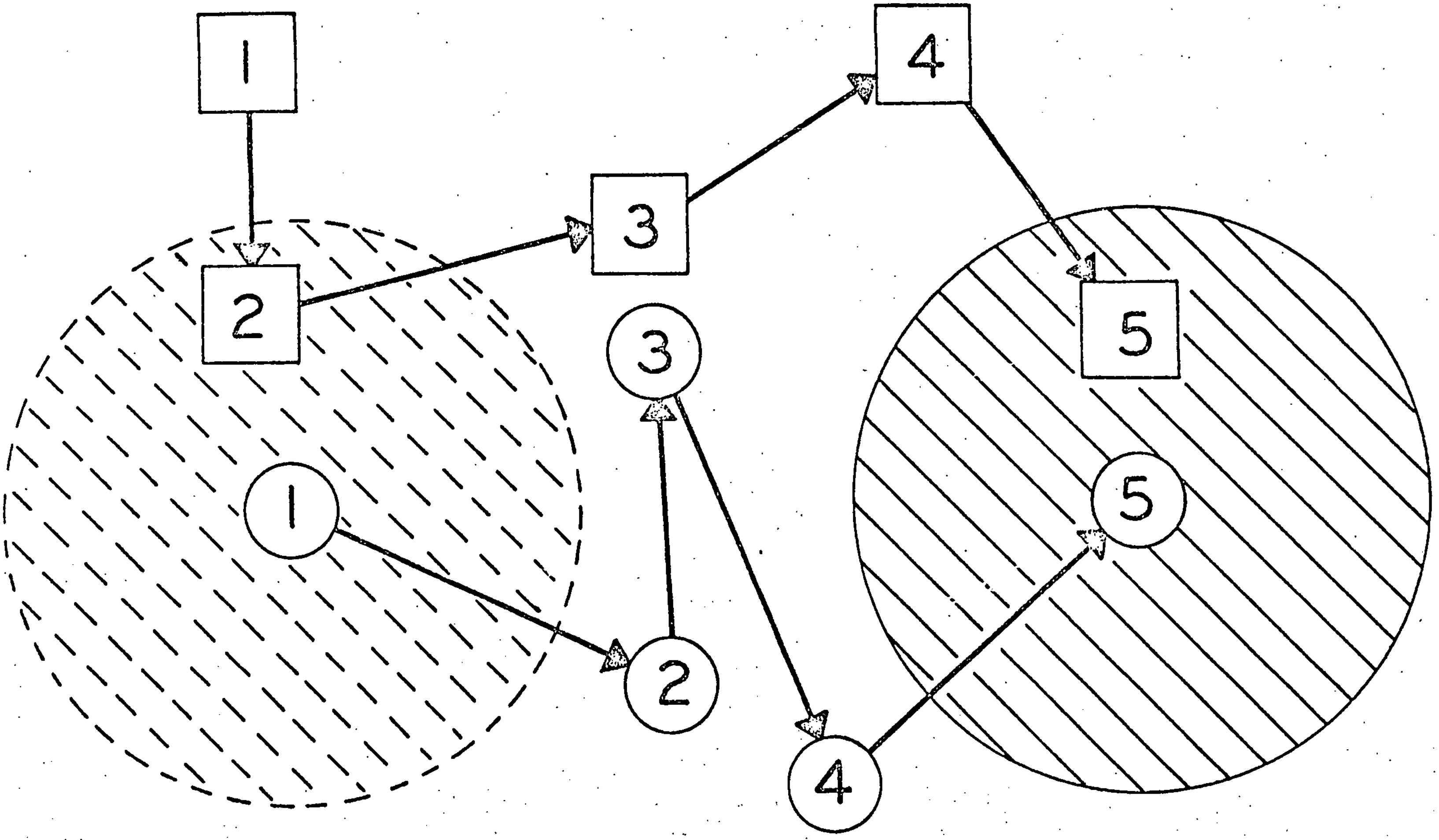
The Vocal Communication Model:

Vocal communication (Fig. 5) occurred each time the animals were within some distance X_i (vocal range) of each other at a time when the signaller vocalized; the signaller vocalized after each regular Y_ith time interval (vocalization frequency). The vocal signal could be heard equally well from anywhere within a circle of radius X_i about the location of the signaller. There was no gradation of effect of the signal as the distance from the signaller increased. Two communication variables, vocal range and vocalization frequency, were under my control.

The Scent Point Communication Model:

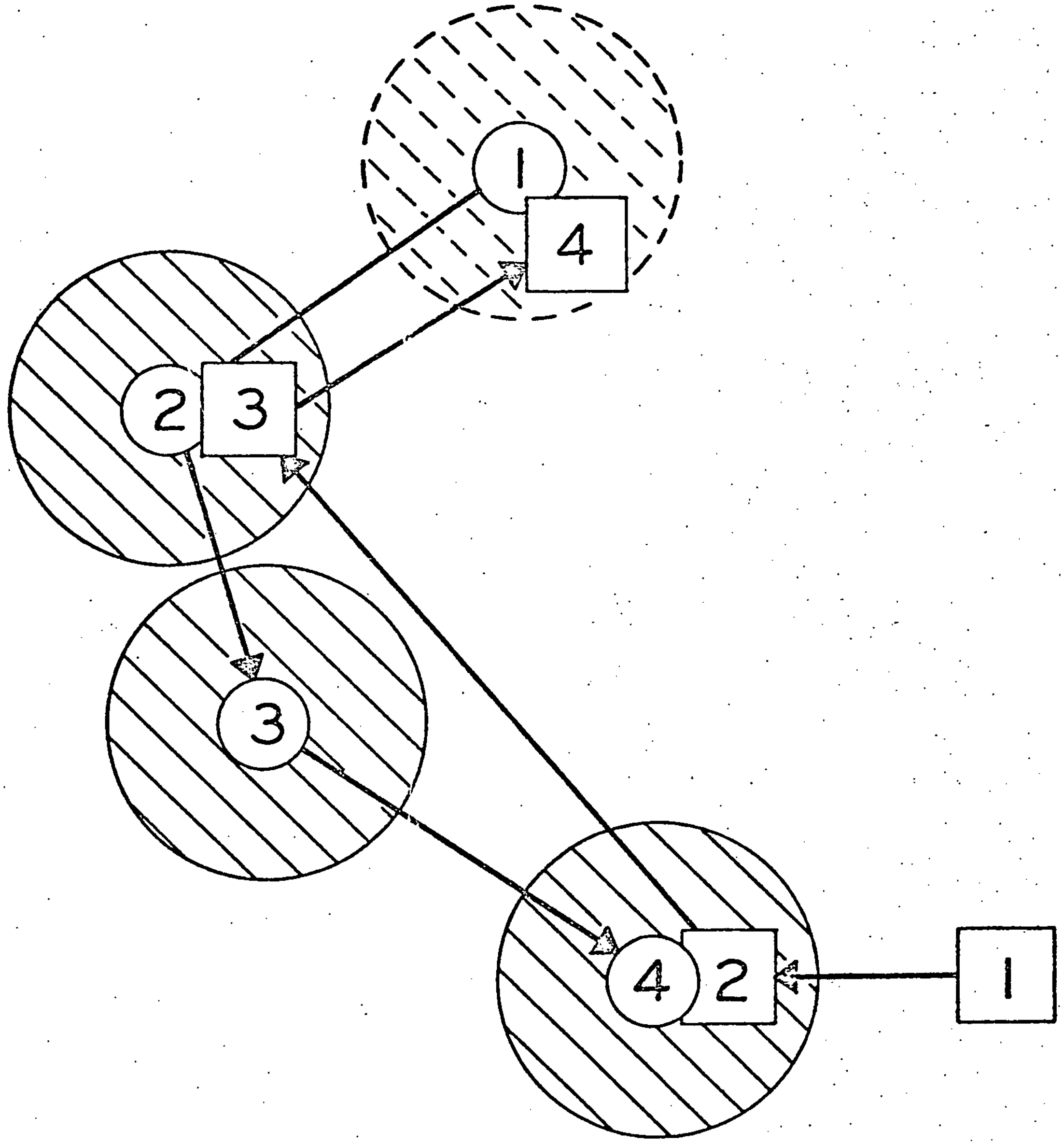
Scent point communication (Fig. 6) occurred each time the receiver was within some distance X_i (scent range) of a location scented by the signaller when not more than some time Y_i

Figure 5. Diagramatic illustration of the operation of the vocal communication model. Symbols indicate the locations of members of the dyad, with circles representing the signaller and squares the receiver. Numbers inside the symbols indicate the time at which the animals were at their respective locations. The signaller is programmed to vocalize at intervals of 25 minutes (at every fifth location), and the shaded areas around ① and ⑤ indicate the vocal range. Movements leading to communication at time 5 are shown. At time 1 the signaller vocalizes at ① but the receiver is outside the vocal range at $\boxed{1}$ and no communication occurs. No communication occurs when the receiver moves to $\boxed{2}$ because the vocal signal is no longer effective. No communication occurs at times 3 and 4 because the signaller does not vocalize at those times. At time 5 the signaller vocalizes from ⑤ and communication occurs because the receiver, at $\boxed{5}$, is within the vocal range.



VOCAL COMMUNICATION

Figure 6. Diagramatic illustration of the operation of the scent point communication model. Symbols indicate the locations of members of the dyad, with circles representing the signaller and squares the receiver. Numbers inside the symbols indicate the time at which the animals were at their respective locations. Scent effect time was programmed to be 15 minutes. Three scent points, in this case those placed at times 2, 3, and 4, are thus effective at any time. Shaded areas surrounding circles represent the areas in which scent is effective. Movements which result in communication at time 3 are shown. No communication occurs at time 2 because the signaller has not yet reached ④. Communication occurs at time 3 because the receiver at $\boxed{3}$ is within scent range of ② and the scent left there at time 2 is still effective. No communication occurs at time 4 because scent left by the signaller at ① is no longer effective.



SCENT POINT COMMUNICATION

(scent effect time) had passed after scent was deposited. The signaller deposited scent after each regular Z_ith time interval (scenting frequency), i.e. at each Z_ith location which it used. The three communication variables; scent range, scent effect time, and scenting frequency, were under my control.

I assumed that scent diffused instantaneously out to scent range X_i and that it was equally effective throughout a circle about the Z_ith location for the entire scent time Y_i. There was no gradation of effect with either distance from the scent source or the time after scent was deposited. Scent disappeared instantaneously at the end of scent time. When scent circles overlapped each other, there was no increased effect on the receiver in the area of overlap.

Use of the Models for Simulating Communication:

The movements of each of five dyads (Table 2) for each of a number of values of the communication variables were simulated using each of the five communication models.

For each of the dyads, movements with 8 visual ranges from 0 to 0.01 miles (16 m) were simultated to study tactile and close-range communication (total 40 simulations). Movements with 10 visual ranges from 0.05 miles to 0.90 miles (80 to 1,448 m) were simulated for each of the five dyads (total 50 simulations) to study visual communication. Movements with

Table 2. The combinations of movement patterns used to form the five dyads used in the study. Animal numbers refer to particular movement patterns; characteristics of the patterns are shown in Table 1. The dyads are identified by letters (A to E) throughout the paper.

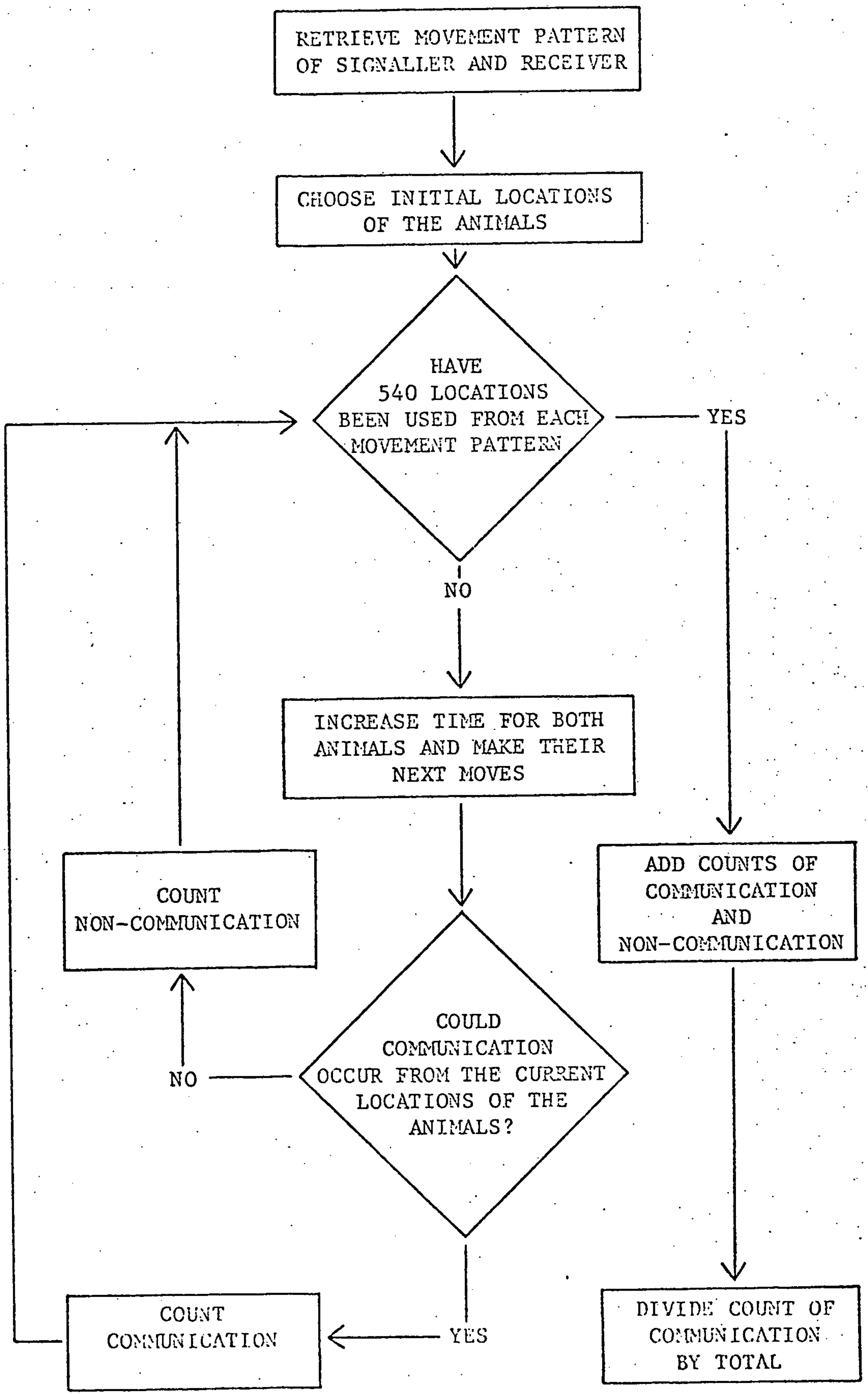
Dyad	Animal Numbers	
	Signaller	Receiver
A	1	8
B	2	7
C	3	6
D	4	5
E	5	4

8 scent effect times from 0.33 to 24 hours (total 40 simulations) were used for each of the five dyads to study scent path communication. For each dyad, movements with 48 different combinations of vocal range and vocalization frequency (total 240 simulations) were simulated to study vocal communication; vocal ranges of 0.1 to 0.8 miles (161 to 1,287 m) were combined with vocalization frequencies of 0.33 to 6.00 per hour (once per 1-1/2 hours to once per 10 minutes). Movements of each of the five dyads were simulated with 80 different combinations of scent range, scent effect time, and scenting frequency to study scent point communication (total 400 simulations); scent ranges from 0.05 to 0.50 miles (80 to 800 m), scent effect times of 1 to 8 hours, and scenting frequencies of 0.33 to 2.00 per hour (one per 1-1/2 hours to one per 30 minutes) were used in various combinations.

The study thus involved, for each of the five dyads, simulated communication under a total of 154 different limits on communication. In all, 770 simulations were done for the study.

For each dyad, when a particular communication model and value(s) of the communication variable(s) were used, the simulation began by retrieving the movement patterns of the two animals from magnetic tape (Fig. 7). The movement patterns were then recreated simultaneously on the home range space. The initial locations of the animals were randomized, and they

Figure 7. Schematic summary of the flow of processes and decisions used in simulating communication between a particular pair of red fox which formed a dyad on the same home range space.


RETRIEVE MOVEMENT PATTERN OF SIGNALLER AND RECEIVER
CHOOSE INITIAL LOCATIONS OF THE ANIMALS
HAVE 540 LOCATIONS BEEN USED FROM EACH MOVEMENT PATTERN
YES
NO
INCREASE TIME FOR BOTH ANIMALS AND MAKE THEIR NEXT MOVES
COUNT NON-COMMUNICATION
ADD COUNTS OF COMMUNICATION AND NON-COMMUNICATION
COULD COMMUNICATION OCCUR FROM THE CURRENT LOCATIONS OF THE ANIMALS?
NO
YES
COUNT COMMUNICATION
DIVIDE COUNT OF COMMUNICATION BY TOTAL

could have been anywhere on the space. As simulated time advanced in 5-minute increments, both animals moved from location-to-location, following their previously determined movement patterns. The computer program which controlled these processes, and those described below, is shown as Appendix A. The comment cards in the printed program (lines in Appendix A with C in the left margin) provide an understanding of the logic of the program and the flow of operations which simulated communication between red fox.

While the animals moved about, the signaller emitted signals according to the schedule which I programmed for the simulation. The interaction of the movement patterns, how often the signaller emitted signals, and the range of effect of the signals, determined the level of communication which occurred.

I used 540 locations from each movement pattern (the remaining 360 were used to allow the animals to start from randomly determined locations), thus a simulation was equivalent to the movements of two red fox for 45 hours (5 days of 9 hours of fox activity each day). The program counted the number of times the movements of the animals brought them to locations from which communication could occur, and how often they were outside the limits on communication. The number of times communication was possible was divided by the total (communication plus non-communication) to give the percentage of time during each simulation when communication occurred.

The movement patterns of each of the members of a dyad remained the same, regardless of which communication model was used in a simulation, or of the values of the communication variable(s) used. Choice of the movement patterns which represented a dyad were made without regard for individual characteristics of the movement patterns; movement patterns of the animals were thus random variables in each of the simulations.

For each dyad, movement patterns of the animals were controlled variables, allowing comparison of amounts of communication which occurred with a communication model when the values of the communication variable(s) were changed between simulations. Comparisons among the dyads were also made, for the same communication model and value(s) of the communication variable(s), to indicate variation in amounts of communication attributable to characteristics of the individual movement patterns.

To compare movement patterns with levels of communication, scores for each dyad for the level of communication which resulted from each means of communication were ranked. These rank scores were then compared with rank scores for the four parameters of the movement patterns. The comparisons indicated ways in which communication was enhanced by the slight differences in the way various simulated animals moved about.

When a particular communication variable or a combination of variables was held constant for all dyads, different levels of communication resulted among the dyads (see below), because movement patterns influenced communication and each pair of movement patterns was unique. The levels of communication which resulted from each value of a communication variable (for example, a visual range of 0.40 miles of 644 m) or for each combination of communication variables (for example, a vocalization frequency of 1 per hour and a vocal range of 0.80 miles or 1,287 m) were averaged for the five dyads. Many values of the communication variable(s) were simulated for each means of communication, and the average level of communication was computed for each value or combination of values. All the average values for a particular means of communication were plotted (see for example, Figs. 8, 9 and 10) and the value(s) of the communication variable(s) which gave, on the average, 20 percent communication were interpolated from each plot. Then for each means of communication, the level of communication which resulted when the value(s) of the communication variable(s) used in simulation equalled these interpolated value(s) was ranked among the five dyads. Rank 1 was given to the dyad which showed the maximum level of communication with these value(s) of the communication variable(s).

For comparison of movement patterns with levels of communication, the five signallers and the five receivers were ranked for each of the four movement parameters. A rank of 1 for rate of travel among signallers means, for example, that the simulated animal had the highest mean rate of travel among the five signallers. Numerical bases for the rankings are shown in Table 1, while identities of signallers and receivers are shown in Table 2.

RESULTS AND DISCUSSION

LEVELS OF COMMUNICATION WITH FIVE MEANS OF SIGNALLING

Results from the simulation of each means of communication are presented as follows. The level of communication which occurred for the various values of the communication variable(s) is shown in a figure and discussed. Factors which reduced the effectiveness of attempts to increase communication are outlined and discussed. Characteristics of the movement patterns which resulted in higher or lower levels of communication for particular dyads are considered. Finally the results of the simulation are compared with available information on communication among red fox. It should be kept in mind that simulation was with deliberately simplified models. The simulation results thus may not reflect levels of communication which occur with the many variables which affect levels of communication among wild red fox.

Tactile and Close-range Communication:

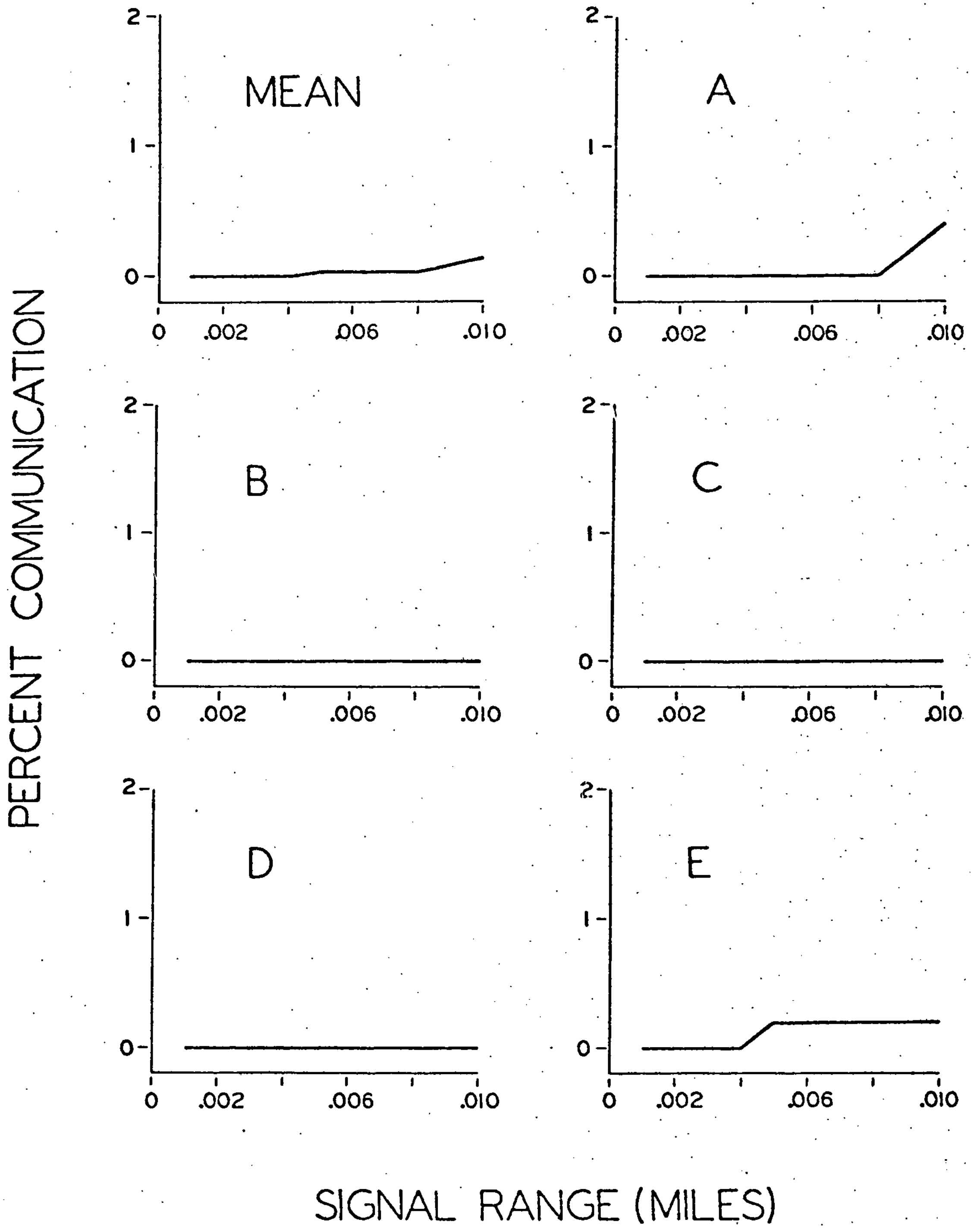
No tactile communication occurred between members of any of the five dyads (Fig. 8). Tactile communication depended on the animals being in the same place at the same time. Close-range visual and vocal communication was arbitrarily defined as occurring with visual or vocal ranges of 0.01 miles (16 m) or less and with continuous or less frequent vocalization where appropriate. Close-range communication occurred 0.15 percent of the time or less for the average of the five dyads (Fig. 8). No close-range communication occurred with signal ranges less than 0.05 miles (8 m) for any dyad, and three of the dyads showed no communication with ranges as great as 0.10 miles (16 m).

Tactile and other close-range means of communication were severely limited by movements of the simulated animals. These results suggest that communication by close-range means would occur very rarely between red fox, unless some other means of communication was first employed to allow the members of a dyad to move closer together. In the absence of such communication and coordination of movements, it is doubtful that close range communication would occur often enough to account for social bonding in red fox dyads.

Visual Communication:

Increasing the visual range, which increased the area in which the signaller could be seen by the receiver, increased

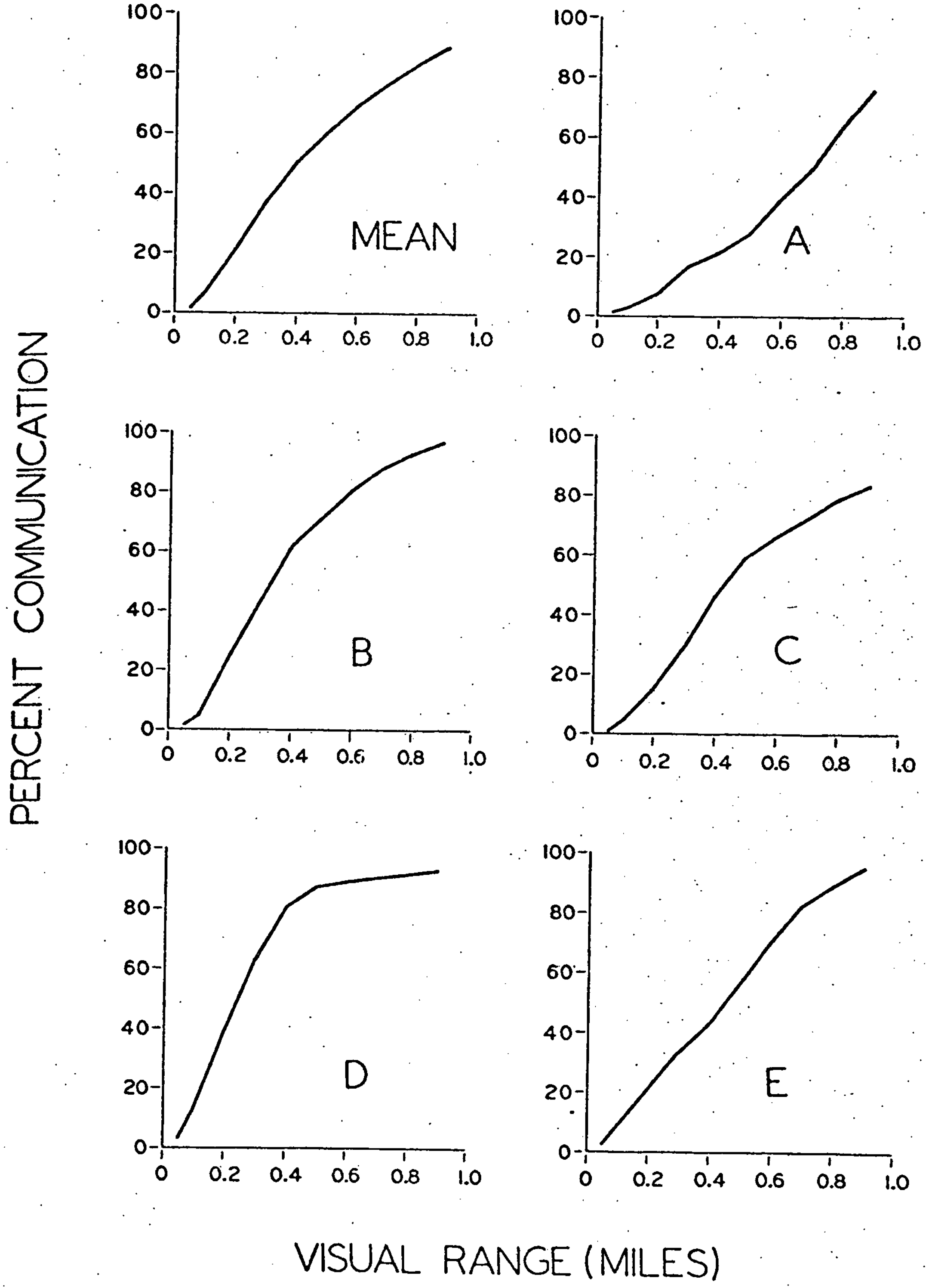
Figure 8. Levels of tactile, close-range visual, and close-range vocal communication which occurred in five simulated red fox dyads (A-E) with signal ranges of 0.01 miles (16 m) and less, and the mean levels of communication for the five dyads. Note that none of the dyads communicated more than 00.5 percent of the time of these means, and dyads B, C, and D did not communicate at all.


MEAN
A
B
C
D
E
2
1
0
0
.002
.006
.010
PERCENT COMMUNICATION
SIGNAL RANGE (MILES)

the level of communication for all dyads (Fig. 9). Because of the specified dimensions of the elliptical area which included the home range spaces, visual communication would have occurred 100 percent of the time for all dyads with a visual range of 1.50 miles (2,413 m). With that visual range a signal from anywhere on the home range space would have covered the entire space. The maximum visual range which I simulated was 0.90 miles (1,448 m), and with this range four of the five dyads communicated more than 80 percent of the time. The maximum rate of communication was 96 percent for dyad B and the minimum was 75 percent for dyad A.

With linear increases in visual range, increases in level of communication were non-linear (Fig. 9). On the average, a greater increase in communication resulted from a unit increase in visual range when the range was less than 0.40 miles (644 m). For visual ranges of 0.10 to 0.40 miles (161 to 644 m) each increase of 0.10 miles (161 m) in range gave an additional 15 percent communication. However, for ranges of 0.40 to 0.70 miles (644 to 1,126 m), an increase in visual range of 0.10 miles (161 m) resulted in only 8 percent more communication. This result may indicate that attempts by a red fox to increase visual communication by becoming more conspicuous will be more efficient if the visual signal travels less than 0.40 miles (644 m) to reach a potential receiver of the signal.

Figure 9. Levels of visual communication which occurred in five simulated red fox dyads (A-E) with visual ranges of 0.05 to 0.90 miles (80 to 1,448 m), and the mean levels of visual communication for the five dyads. On the average, the animals communicated 20 percent of the time when the receiver could see the signaller from 0.19 miles (306 m).


PERCENT COMMUNICATION
100
80
60
40
20
0
0
0.2
0.4
0.6
0.8
1.0
MEAN
A
B
C
D
E
VISUAL RANGE (MILES)

With increased visual ranges the curves (Fig. 9) showing the relationship between visual range and level of communication were inflected. This inflection suggests that some limit on an increase in level of communication was approached as the visual range increased. Wastage of visual signal emitted beyond the boundary of the home range space accounts for the limit on effectiveness of increasing visual range. For communication within any dyad by any means, signal is wasted when it goes into space not used by the receiving animal. However, such signal may not in fact be wasted when it is used for communication outside the particular dyad under consideration. Visual signal emitted to places on the home range space other than that place occupied by the receiving animal was wasted as well, but more visual signal on the home range space increased the chances that the receiver would be in a location from which it could see the signaller.

Signal was not wasted beyond the boundary of the receiver's home range space when the signaller was the same distance as the visual range from the nearest boundary of that space, or more than the visual range from any of its boundaries. For a given visual range, there was thus a set of locations which formed a threshold for such wastage of signal. Beyond these threshold locations, the amount of wasted signal increased for a given visual range whenever the signaller moved toward the boundary of the receiver's home range space or, from a given location, as the visual range increased. In general, such a set of threshold locations exist for all means of communication for each signaller using a given emission intensity in dyadic communication. Given that the signaller is aware of the extent of the receiver's home range space, the locations outline an area from which the signaller could most efficiently signal the other member of the dyad.

For a particular visual range, only differences in movement patterns could account for the different levels of communication which were shown among the dyads (Fig. 9), since all other variables were held constant. On the average, the dyads communicated 20 percent of the time when the visual range was 0.19 miles (306 m). There was considerable variation among the dyads in the amount of communication which occurred with that visual range, from 7 percent for dyad A to 36 percent for dyad D. For this and a wide variety of visual ranges, the dyads consistently ranked as follows with respect to levels of communication with a particular visual range: D = 1; B = 2; E = 3; C = 4; A = 5.

It is thus shown by variation in level of communication among the dyads that the way in which one or both members of each dyad moved about influenced their ability to communicate visually. There was no apparent rank correlation between the level of visual communication in a dyad and any of the four parameters of movement of signallers (Table 3), and the manner

Table 3. A comparison of the level of visual communication provided by the pairs of movement patterns which formed each of the five dyads with 4 parameters of the movement patterns of signallers and receivers within each dyad. Criteria for ranking the levels of communication among the dyads, and for ranking the movement patterns among signallers and among receivers are given in the text.

		Rate of Movement (mean)		Straight Ahead Travel ±30°		Contagion of Locations (K)		Total Number Grid-squares	
Dyad	Communication Rank	Signaller	Receiver	Signaller	Receiver	Signaller	Receiver	Signaller	Receiver
D	1	2	1	1	2	2	2	3	2.5
B	2	5	2	5	4	5	5	1	4
E	3	1	3	2	1	1	3	3	2.5
C	4	3	5	3	3	4	4	3	1
A	5	4	4	4	5	3	1	5	5

in which signallers moved about apparently did not greatly influence visual communication. However, there was a good rank correlation between rate of movement of receivers and level of visual communication. This result may indicate that the way in which receivers moved about had a great influence on the level of visual communication, regardless of the movement pattern of signallers. If this were true, the signaller could do little to enhance communication except change the visual range, unless it exerted some control over the receiver's movement pattern, and in so doing increased the rate at which the receiver moved about its home range space.

Although simulation shows that movements of the animals alone does not prevent significant levels of visual communication (Fig. 9), red fox are primarily nocturnal, which precludes use of visual signalling in long-range dyadic communication. Even for short-range location of prey (from 30 m or less), vision was shown to be important only during daylight hours (Osterholm 1966:54), and senses of hearing and particularly smell became more important in twilight and darkness. As stated by Osterholm (1966:55):

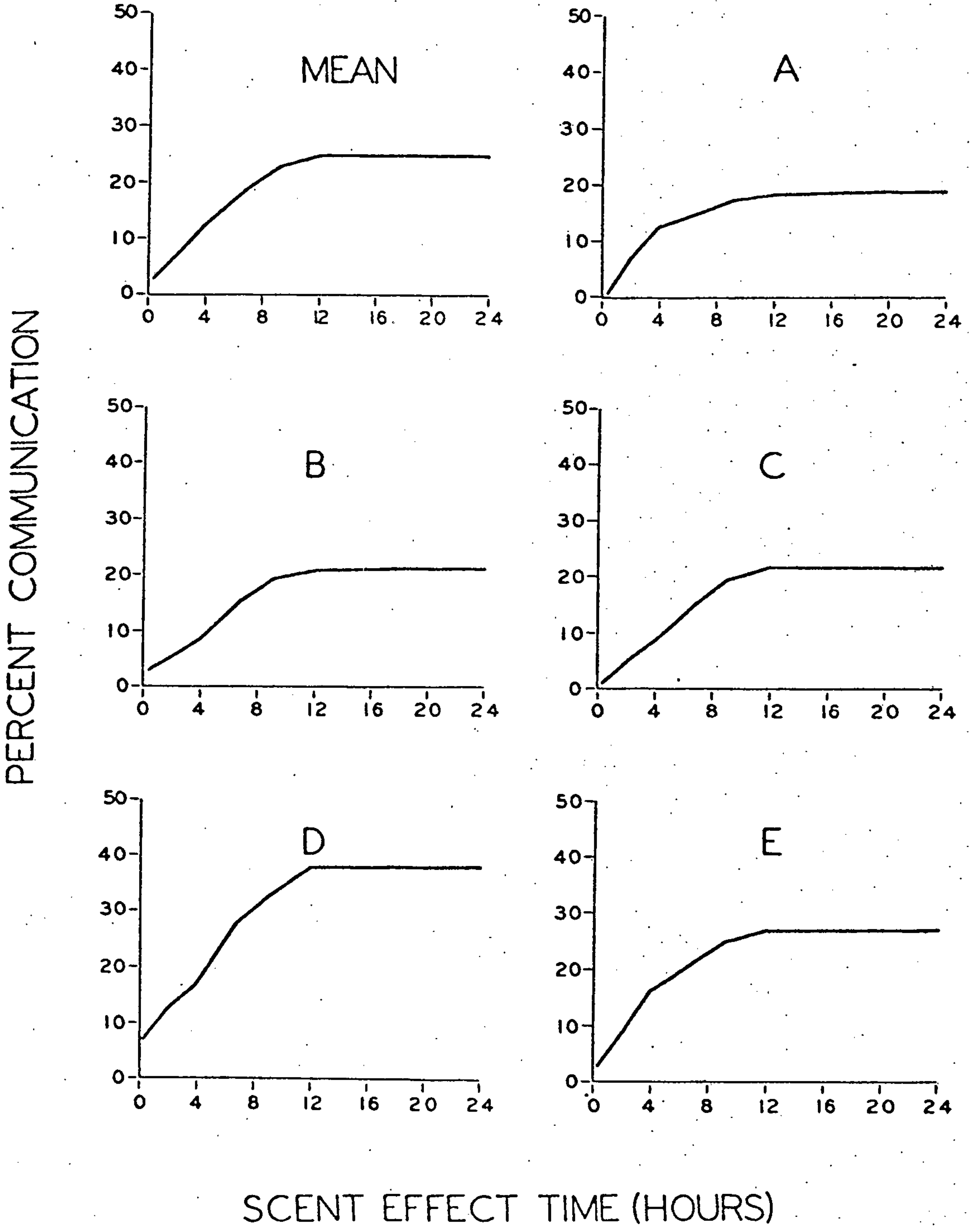
> ". . . the fox's own daily rhythm has the result that in nature the sence of sight is not a particularly important receptor to the red fox".

In general (Marler 1965:547), in spite of adaptations for improved vision in darkness, nocturnal animals can rely less on vision than other senses for communication. An additive factor which would further reduce the effectiveness of visual signalling is interference by topography and vegetation. Interference with visual signals by vegetation was shown by Bronson (1964) to seasonally decrease visual communication among woodchucks (*Marmota monax*), a diurnal mammal. Interference, when combined with darkness, would make visual communication over moderate or long distance very difficult for red fox. Visual communication is thus probably of little importance in maintaining social bonds in red fox dyads, not because movements prevent it, but because fox are primarily nocturnal and because the habitat interferes with visual signals.

Scent Path Communication:

Increasing the scent effect time, which increased the length of the path of effective scent which was available at any time, increased levels of communication for all dyads (Fig. 10). However, amounts of communication afforded by longer-lasting scent quickly reached an upper limit. On the average, scent path signalling provided communication no more than 25 percent of the time, even when scent remained effective for 12 hours or more. At the extremes for the five dyads, the upper limit in level of communication was reached with 18 hours of scent effect for dyad A and 10 hours for dyads B, C, and D. At the upper limit in level of communication for the dyads

Figure 10. Levels of scent-path communication which occurred in five simulated red fox dyads (A-E) with scent effect times of 0.33 to 24 hours, and the mean levels of communication for the five dyads. Note that an increase in level of communication with increasing scent effect times occurred only until scent was effective for about 12 hours, and further increases in scent effect time did not give further increases in communication. On the average, the animals communicated 20 percent of the time when scent remained effective for 7.6 hours.


MEAN
A
B
C
D
E
PERCENT COMMUNICATION
0
10
20
30
40
50
0
4
8
12
16
20
24
SCENT EFFECT TIME (HOURS)

considered separately, the maximum level was 38 percent for dyad D and the minimum level was 19 percent for dyad A. Dyad A, which could communicate no more than 19 percent of the time by scent path signalling regardless of the scent effect time, required a longer scent effect time to reach its maximum level of communication. Dyad D, in contrast, needed a shorter scent effect time to reach a higher maximum level of communication.

A limit on the effect of increasing scent effect times was approached as these times increased (Fig. 10). The limiting factor(s) are unknown; no scent path signal was wasted by emission outside the boundary of the elliptical area which included the home range spaces. However, the home range spaces of the two members of each dyad depended on where within the elliptical area each animal actually moved. The home range spaces of dyad members may have diverged enough so that some scent path signal could not be received, and was wasted.

As with the other means of communication, only differences in movement patterns among the dyads could account for the different levels of communication with the same scent effect time (Fig. 10). On the average, the dyads communicated 20 percent of the time when scent was effective for 7.6 hours. Variation among the dyads with a scent effect time of 7.6 hours ranged from 15 percent communication for dyad A to 28 percent for dyad D. For a particular scent effect time, the dyads consistently ranked as follows with respect to levels of communication: D = 1; E = 2; C = 3; B = 4; A = 5.

The variation among dyads, and the consistency in relative level of communication with each of many scent effect times shows that the movements of one or both dyad members influenced the level of scent path communication. In contrast to visual signalling, the way in which signallers moved about while signalling with scent paths apparently influenced the level of communication (Table 4). Signallers which had a relatively high rate of travel, and particularly those which tended to travel straight ahead at a rapid rate, were more successful in signalling the receiver of their dyad. A critical factor in scent path communication is the total length of path which carries effective scent at any time, because a longer effective path increases the probability that the receiver will move across it before the scent becomes ineffective. Where the animals move over large areas, a second critical factor is the total area in which scent paths are effective. Given the same length of effective scent path, the probability of communication would be lower when that path is concentrated in one small part of the receiver's home range space because the receiver may be moving in an entirely different part of the space while the scent is effective. A movement pattern in which the signaller moves rapidly and seldom turns would provide both a longer effective scent path at any time, and a tendency to distribute that path over a large portion of the receiver's home range space.

Table 4. A comparison of the level of scent path communication provided by the pairs of movement patterns which formed each of the five dyads with 4 parameters of the movement patterns of signallers and receivers within each dyad. Criteria for ranking the levels of communication among the dyads, and for ranking the movement patterns among signallers and among receivers are given in the text.

Dyad	Communication Rank	Rate of Movement (mean)		Straight Ahead Travel ±30°		Contagion of Locations (K)		Total Number Grid-squares	
		Signaller	Receiver	Signaller	Receiver	Signaller	Receiver	Signaller	Receiver
D	1	2	1	1	2	2	2	3	2.5
E	2	1	3	2	1	1	3	3	2.5
C	3	3	5	3	3	4	4	3	1
B	4	5	2	5	4	5	5	1	4
A	5	4	4	4	5	3	1	5	5

Scent path signalling is potentially an efficient means for providing moderate levels of communication in red fox dyads. Red fox have interdigital glands which produce odor distinguishable even to humans, and which may contribute to leaving a scent trail as the animals move about (Fox 1971:201). Anal and other scent glands may also produce odors which are left as a trail, along with distinctive chemical substances from non-glandular parts of the fox's body surface. Because a scent trail is left as the animal moves about, incidental to its other activities (Ewer 1968:112-113), a fox need not spend much additional time and energy in communication. Scent trails can carry information about the identity and state of the individual which leaves them (cf. Wilson 1968:90) and, because of concentration gradients along a trail, about the direction of travel and the amount of time which has passed since the trail was laid (Bossert and Wilson 1963:458-463). Information inherent in scent trails could thus allow fox to maintain a degree of spacing or help to bring them together.

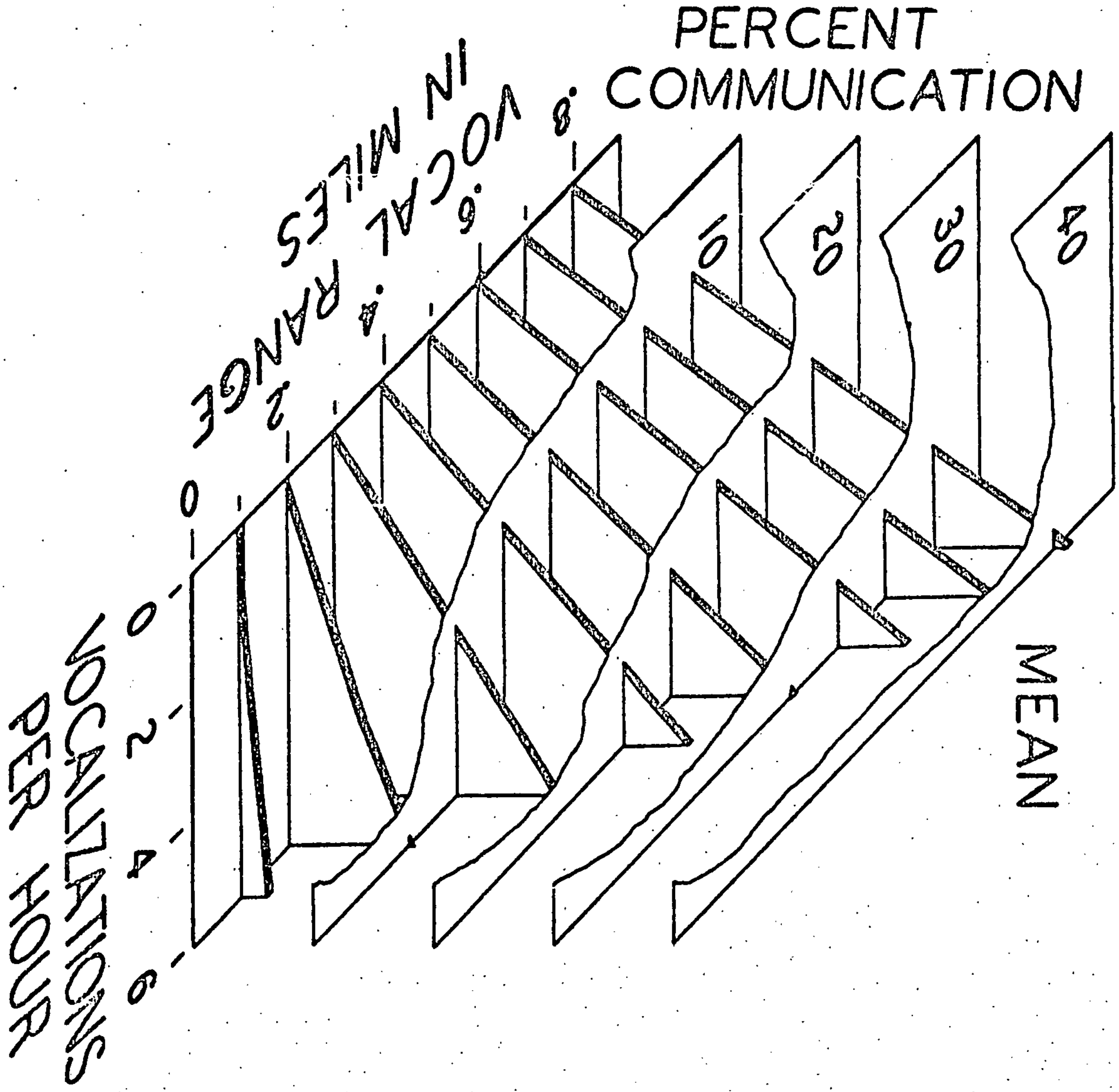
Red fox almost certainly can use information from scent trails, although good evidence for them doing so is lacking. Certain breeds of the domestic dog (Canis familiaris) have outstanding ability to discriminate among and to follow scent trails (reviewed by Fuller and Fox 1969:472-474). That this ability is generally developed in canids is indicated by observations of timber wolves following the scent trails of conspecifics (Mech et al. 1971:23; Jordan et al. 1967:243).

Simulation indicates that moderate levels of communication are possible with red fox movements when scent remains effective for about 9 hours, but that further increases in scent effect time are inefficient in terms of increasing communication. Thus, the optimal level of scent emission is that which provides communication over a time approximately equal to the length of the daily activity period. It seems possible that the primary function of scent path signalling is to reveal the location of the signaller during the same daily activity period that scent trails are left. Ambiguity introduced by scent persisting from one daily activity period to the next may be avoided by the signaller emitting only that kind or amount of scent which provides an optimal scent effect time.

Vocal Communication:

Changes in the communication variables which tended to increase the area covered by signal, the time covered by signal, or both resulted in higher levels of communication for all dyads in the complex relationship among vocal range, vocalization frequency, and communication (Fig. 11). Vocal communication would have occurred 100 percent of the time for all dyads with a vocal range of 1.50 miles (2,413 m) and a vocalization frequency of 12 per hour. With those values a signal from anywhere on the home range space covered the entire elliptical area, and vocalizing 12 times per hour (once per 5 minutes) was equivalent

Figure 11. Mean levels of vocal communication which occurred in five simulated red fox dyads with vocal ranges of 0.10 to 0.80 miles (161 to 1,287 m) and vocalization frequencies of 0.33 to 6.00 per hour (one per 1-1/2 hour to one per 10 minutes). Note that a linear increase in vocalization frequency gave a linear increase in level of communication for each simulated vocal range. Several vocal ranges and vocalization frequencies gave an average of 20 percent communication, including 2.8 vocalizations per hour with a vocal range of 0.80 miles (1,287 m), and 4.7 vocalizations per hour with a vocal range of 0.40 miles (644 m).


PERCENT COMMUNICATION
10
20
30
40
VOCAL RANGE IN MILES
0
.2
.4
.6
.8
VOCALIZATIONS PER HOUR
0
2
4
6
MEAN

to continuous vocalization in the communication model. With the maximum values which I simulated, a vocal range of 0.80 miles (1,287 m) and a vocalization frequency of 6 per hour (once per 10 minutes), three dyads communicated more than 40 percent of the time and the remaining two dyads more than 30 percent of the time. The maximum rate of communication with these values was 45.9 percent for dyad D and the minimum was 34.6 percent for dyad A.

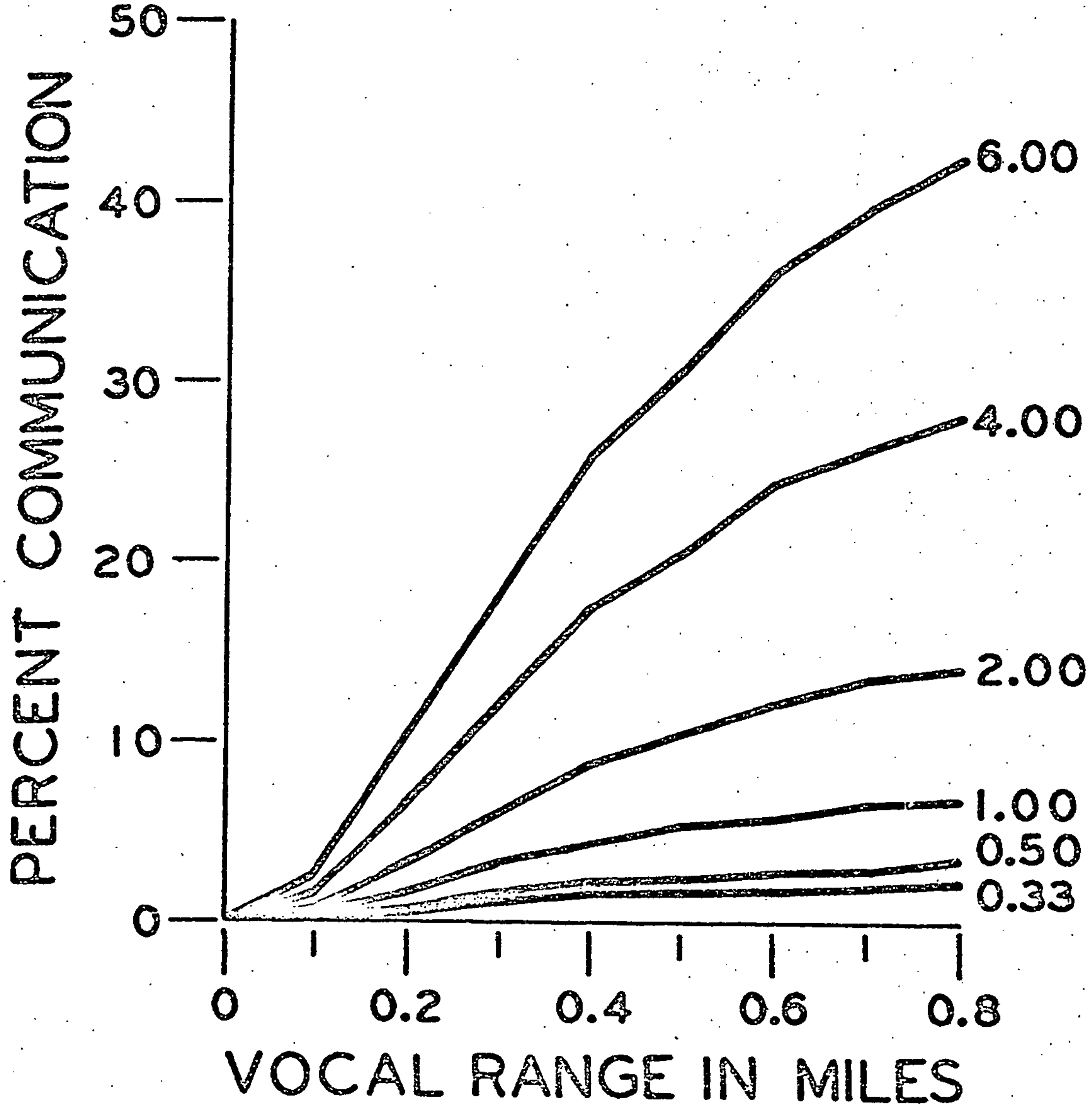
There was a linear increase in communication with linear increase in vocalization frequency (Fig. 11) for each vocal range from 0.10 to 0.80 miles (161 to 1,287 m). Vocal range and vocalization frequency interacted such that, as vocal range increased the effect of increasing vocalization frequency became more pronounced. For example, an increase of one vocalization per hour with a vocal range of 0.20 miles (322 m) gave 1.6 percent more communication, while an increase of one vocalization per hour with a vocal range of 0.80 miles (1,287 m) gave 7.0 percent more communication. This result indicates that an increase in the frequency with which a fox vocalizes will have a greater effect on the level of dyadic communication when the vocalizations are emitted such that they can be heard from far away.

The effect of increasing vocal range on level of communication was non-linear, becoming more and more limited as the vocal range increased with a given vocalization frequency

(Fig. 12). Wastage of vocal signal emitted beyond the boundary of the elliptical area accounts for a part of this limit. As with visual communication, signal was wasted when it went into space not used by the receiving animal, and a similar set of threshold locations existed for such wastage of vocal signal. In contrast to visual signalling, the signaller could move outside these threshold locations without reducing the efficiency of signalling, so long as it did so between the times when it emitted vocal signals. Given that a signaller is aware of the location of a potential receiver, vocal signalling may be made more efficient by directional emission of signal toward the receiver (Busnel 1963), which reduces wastage of signal. Directional emission was excluded from the communication model when I assumed that all communication was unidirectional.

For a particular combination of vocal range and vocalization frequency, only differences in movement patterns could account for the different levels of communication shown among the dyads. On the average (Fig. 11) the minimum values of vocal range and vocalization frequency which gave communication 20 percent of the time were: 2.8 vocalizations per hour with a vocal range of 0.80 miles (1,287 m), and 4.7 vocalizations per hour with a vocal range of 0.40 miles (644 m). There was considerable variation among the dyads in the levels of communication which occurred with these sets of values. With 2.8 vocalizations per hour and a vocal range of 0.80 miles (1,287 m),

Figure 12. The relationship between increasing vocal range and mean amount of communication which resulted for five dyads with the 6 vocalization frequencies indicated at the right of the figure. The inflection of the curves for vocalization frequencies greater than 0.50 per hour illustrates the limit which wastage of vocal signal placed on the effectiveness of increasing the vocal range.


PERCENT COMMUNICATION
50
40
30
20
10
0
6.00
4.00
2.00
1.00
0.50
0.33
0
0.2
0.4
0.6
0.8
VOCAL RANGE IN MILES

communication ranged from 16.0 percent for dyad A to 21.2 percent for dyads D and E. Communication ranged from 13.5 percent for dyad A to 26.0 percent for dyads D and E with 4.7 vocalizations per hour and a vocal range of 0.40 miles (644 m). The relative amount of communication per dyad was consistent among the dyads for these two and many other sets of values of the communication variables. Levels of communication among the dyads ranked as follows: D = E = 1.5; B = 3; C = 4; A = 5.

Although the way in which the animals moved about influenced their ability to communicate vocally, there were no obvious correlations between ways of moving about and levels of communication (Table 5). However, dyads whose members tended to travel at greater speeds and tended to turn less often (both members) ranked highest in levels of vocal communication. Lowest levels of communication resulted when both members of a dyad traveled slowly and turned frequently. Theoretically, either pattern of movement could have resulted in higher levels of communication if the movement patterns of the animals had been coordinated such that they used the same portions of the elliptical area at the same times. Where the movements were not coordinated, the probability that they were close together depended on chance alone, and the chance that both animals would be in the same part of the elliptical area at the same time was apparently increased when both animals traveled at high rates in fairly straight lines.

Table 5. A comparison of the level of vocal communication provided by the pairs of movement patterns which formed each of the five dyads with 4 parameters of the movement patterns of signallers and receivers within each dyad. Criteria for ranking the levels of communication among the dyads, and for ranking the movement patterns among signallers and among receivers are given in the text.

Dyad	Communication Rank	Rate of Movement (mean)		Straight Ahead Travel ±30°		Contagion of Locations (K)		Total Number Grid-squares	
		Signaller	Receiver	Signaller	Receiver	Signaller	Receiver	Signaller	Receiver
D	1.5	2	1	1	2	2	2	3	2.5
E	1.5	1	3	2	1	1	3	3	2.5
B	3	5	2	5	4	5	5	1	4
C	4	3	5	3	3	4	4	3	1
A	5	4	4	4	5	3	1	5	5

Parameters which summarize the distribution of locations resulting from a pattern of movement should show less correlation with levels of communication than do parameters which describe the pattern of movement per se. Communication by any means of signalling depends on the individuals being at certain places at certain times, and the over-all distribution of locations does not reflect the timing of the animal's movements. For example, both members of a dyad might concentrate a portion of their activity on the same part of the elliptical area without enhancing vocal communication if they were not both in that part at the same time.

There was an indication, however, that movement patterns which resulted in maximum dispersion of locations (high K values) gave more vocal communication than patterns which resulted in greater clumping of locations (Table 5). Unless the two members of a dyad were mutually aware of locations used by the other member and had clumps of locations in the same portion of the home range space, or unless clumping in the same portions occurred by chance, there should have been an advantage in maximizing dispersion of locations used by both the members. This is because clumps of locations for the two animals located in distal portions of the elliptical area, when combined with short vocal ranges, would have resulted in low levels of communication regardless of when the animals used these clumps.

Vocal signalling could be an effective means for maintaining social contact in red fox dyads. As shown by simulation, movements of the animals allow them to communicate a reasonably high proportion of the time with relatively low emission intensities and frequencies of signalling. Vocal signalling is efficient in terms of energy cost to the animal, relative to other means of communication (Sebeok 1967:368) and may require less interference with ongoing behavior of the animal than do other means of signalling (Marler 1967:773). In the total energy budget for a red fox, the cost of vocalizing a few times per hour is probably not important, regardless of the emission intensity. High frequencies of signalling with greater vocal ranges might allow a potential predator of red fox to better locate its prey (Hall 1965), and thus promote selective pressure against such vocal signalling. However the most probable predator, the timber wolf, generally locates its prey by scent or sight (Mech 1966:118-125).

Red fox probably are capable of emitting vocalizations which can be heard over distances at least as great as the vocal ranges which I simulated. Fox (1971:48) indicates that auditory signals are well developed in the more solitary canids for communication over greater distances, notably in the red fox. That author, however, presents no data on absolute vocal ranges. The loud vocal signals are highly stereotyped (Fox 1971:185) as predicted (Marler 1965:583; Marler 1967:772; Nottebohm 1972:131;

Lancaster 1968:442) for signals which transmit information over relatively long distance. Timber wolves (Rutter and Pimlott 1968:138) respond by vocalizing to the howls of wolves which are at least 0.50 miles (804 m) away, and farm dogs by barking to the baying of hounds which are 1 mile (1,609 m) or more away (personal observation). Spotted hyenas (Crocuta crocuta) respond to tape-recorded vocalizations from as far as 3,000 m (Kruuk 1972). At least from distances of 10 m and less, red fox can very precisely locate slight noises made by prey on the basis of hearing alone (Osterholm 1966:57). Localization from both short and long distance is enhanced (Busnel 1963) by repetition of signalling which allows a receiver to "home in" on the direction of the signal source. Red fox are thus probably capable of both emitting loud vocal signals and using these signals for communication over long distance. As indicated by simulation, these loud vocalizations when emitted often enough could provide high levels of dyadic communication when red fox move about as they do.

Why then do red fox not vocalize more often with emission intensities such that they can be heard over long distances? Nocturnal animals such as the red fox might be expected (Nottebahm 1972:131) to rely on audition as the dominant modality for communication over long distances. Timber wolves (Theberge and Falls 1967) apparently use long-distance vocalizations as a means for maintaining contact among members of social units when they become separated. However, Fox (1971:184) indicates that, unlike domestic dogs, wild canids in general do not often vocalize. Red fox apparently seldom emit loud vocalizations. Sargeant (personal communication) observed pairs of red fox in a 10-acre (4 hectare) enclosure and "very rarely" heard them vocalize. On the fewer than 5 occasions during several months of observation when vocalizations were heard, the animals apparently responded either to the presence of the observer or to other disturbance. Burrows (1968:170-173) listed all fox vocalizations heard during a one-year period. Vocalizations, excluding those on 8 dates by cubs at a den, were noted on only 56 dates, and on most of these only a single vocalization was heard. There were long periods of consecutive dates when the foxes did not vocalize. For example (Burrows 1968:45): "During February 1966 I heard foxes on only three nights."

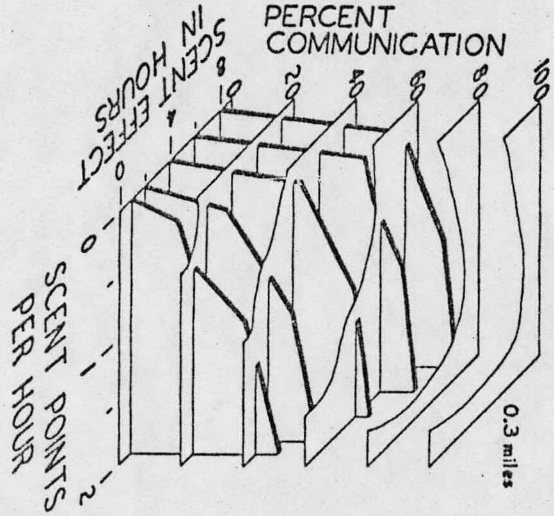
It is unlikely that red fox would depend entirely on vocal signalling, or on any other single means of communication, for maintaining social contact between members of dyads. Marler (1967:773) notes that when vision is limited there tends to be more reliance, in general, on olfaction for both close-range and distant communication. Red fox have well developed scent glands and olfactory capabilities (Fox 1971). As indicated in the previous section of this paper, and in the section which follows, the movements of red fox can provide for moderate to high levels of olfactory communication.

This study suggests that vocal communication could be effective in maintaining social contact in red fox dyads. That such communication occurs infrequently is explainable in at least two ways. Levels of communication required to maintain social bonding in red fox dyads may be very low or, more likely, other means of communication such as those provided by scent marks and trails may usually preclude the necessity for using long-distance vocal communication.

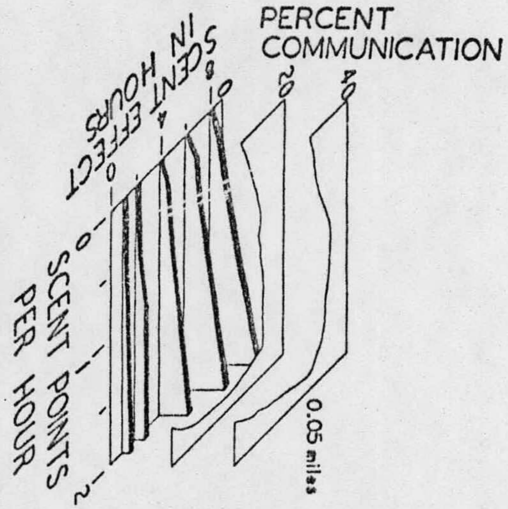
Scent Point Communication:

Combinations of the three communication variables which produced relatively sparse, small circles of scent on the home range space gave low levels of communication, while combinations which produced relatively common, large circles of scent gave high levels of communication (Fig. 13). Higher levels of communication resulted from increasing the scent range, and for each scent range from increasing the number of effective scent points. A greater number of scent points effective at any time resulted from higher scenting frequencies, longer scent effect times, or both. Scent point communication would have occurred 100 percent of the time with a scent range of 1.50 miles (2,413 m), a scenting frequency of 12 per hour, and a scent effect time of 5 minutes. With a scent range of 1.50 miles (2,413 m) other combinations of scenting frequency and scent effect time would have given 100 percent communication,

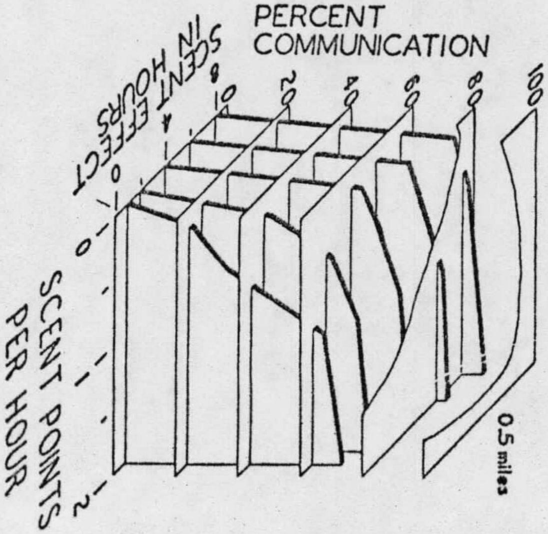
Figure 13. Mean levels of scent point communication which occurred in five simulated red fox dyads for four scent ranges (0.05, 0.10, 0.30, and 0.50 miles or 80, 161, 482 and 804 m), scent effect times from 1 to 8 hours, and scenting frequencies of 0.33 to 2.00 per hour (one per 1-1/2 hours to one per 30 minutes). Note that the average amount of communication increased with an increase in any one or more of the communication variables. Many values of the three variables resulted in an average of 20 percent communication including a set in which the signaller deposited scent once every 30 minutes (2 per hour), scent remained effective for 8 hours, and the receiver could smell scent from 0.06 miles (96 m).



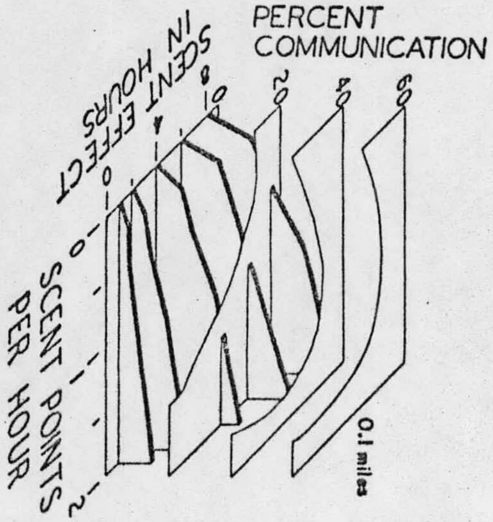
0.3 miles



0.05 miles



0.5 miles



0.1 miles

such as a frequency of 6 per hour and an effect time of 10 minutes, so long as one or more scent points were effective at any time. I simulated lower scent ranges from 0.05 to 0.50 miles (80 to 800 m), scent effect times of 1 to 8 hours, and scenting frequencies of .033 to 2.00 per hour (one per 3 hours to one per 30 minutes).

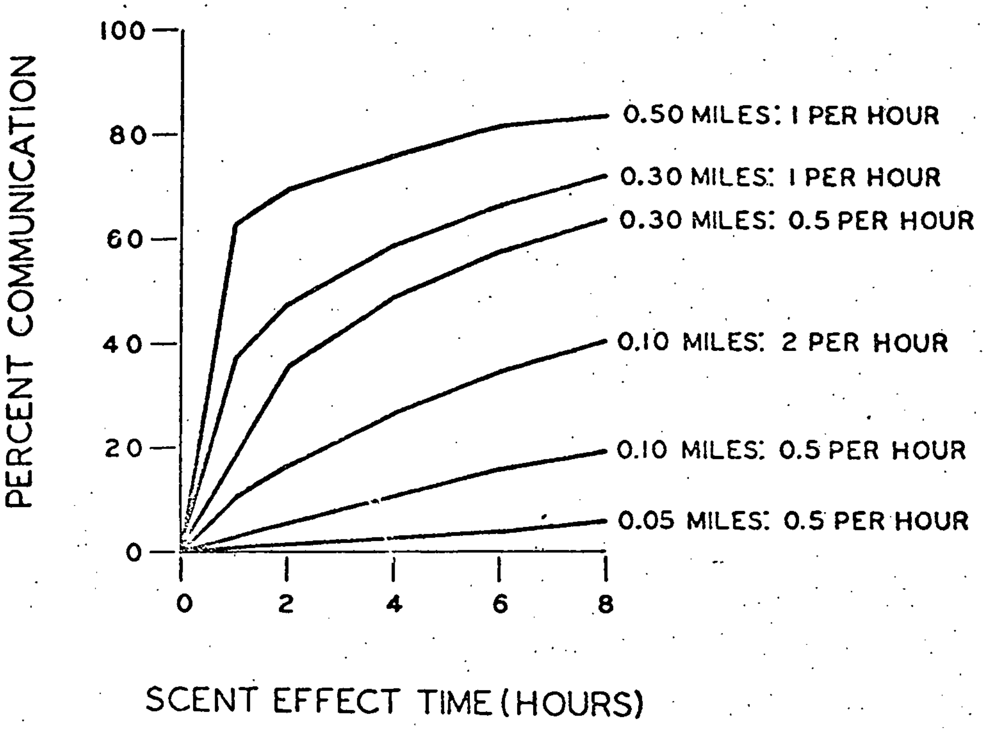
On the average with maximum values of all three variables (0.50 miles or 800 m; 8 hours; 2 per hour), the animals communicated 86.8 percent of the time. With these high values, there was considerable variation in level of communication among the dyads with dyad E communicating 99.8 percent of the time and dyad A 69.8 percent of the time. The lowest values which I simulated (0.05 miles or 80 m; 1 hour; 0.33 per hour) gave an average of 00.6 percent communication. There was negligible variation in level of communication among the dyads, with dyad A communicating 1.1 percent of the time and the remaining four dyads less than 1 percent of the time.

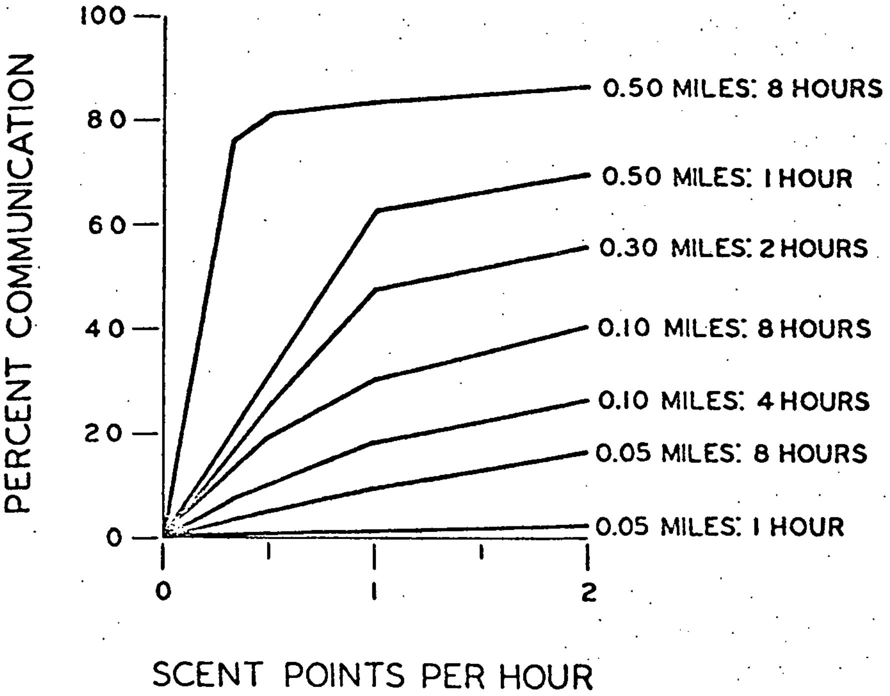
Increasing the value of any of the three communication variables while the other two were held constant did not result in expected increases in communication. Some factor(s) thus limited the effect of increasing the value(s) of the communication variable(s). The amount of communication which resulted from the scent point model, given a particular dyad's movement patterns, should have been directly related to the area covered by effective scent at any time. A change in any of the three variables which increased this area should have increased communication in direct relation to the increase in total scented area, other things being equal. When the other two variables were held constant, a linear increase in scent range (the area increased as the square) should have resulted in a non-linear increase in communication. When the other two variables were held constant, a linear increase in either scent effect time or in scenting frequency should have given a linear increase in communication.

A unit increase in scent effect time gave less and less communication as more and more of the home range space was covered with scent because of higher scent ranges and scenting frequencies (Fig. 14, top). For a particular combination of scent range and scenting frequency, the relationship between scent effect time and percent communication was linear as expected, but only for low scent ranges and scenting frequencies. A signaller could thus increase the level of communication by increasing the scent effect time, but would do so more efficiently when scent ranges and scenting frequency were held relatively low. This could be accomplished by scenting with a chemical which had a low diffusion coefficient and low volatility, as would be given by a substance with high molecular weight (Bossert and Wilson 1963:454). The resulting slow fade-out time would have the disadvantage of limiting the rate of information transfer (Wilson 1968:77), but could increase the overall level of communication in the dyad.

Figure 14. *Top*. The relationship between scent effect time and mean amount of communication which resulted for five dyads with the sex combinations of scent range and scenting frequency shown at the right of the figure. The inflection of the curves for ranges greater than 0.10 miles (161 m) and frequencies greater than 2 per hour illustrates the limit which overlap of effective scent circles placed on the effectiveness of increasing the scent effect time.

Bottom. The relationship between scenting frequency and mean amount of communication with the seven combinations of scent range and scent effect time shown at the right of the figure. The inflection of the curves illustrates the limit which overlap of effective scent circles placed on the effectiveness of increasing the number of scent points deposited per unit time.

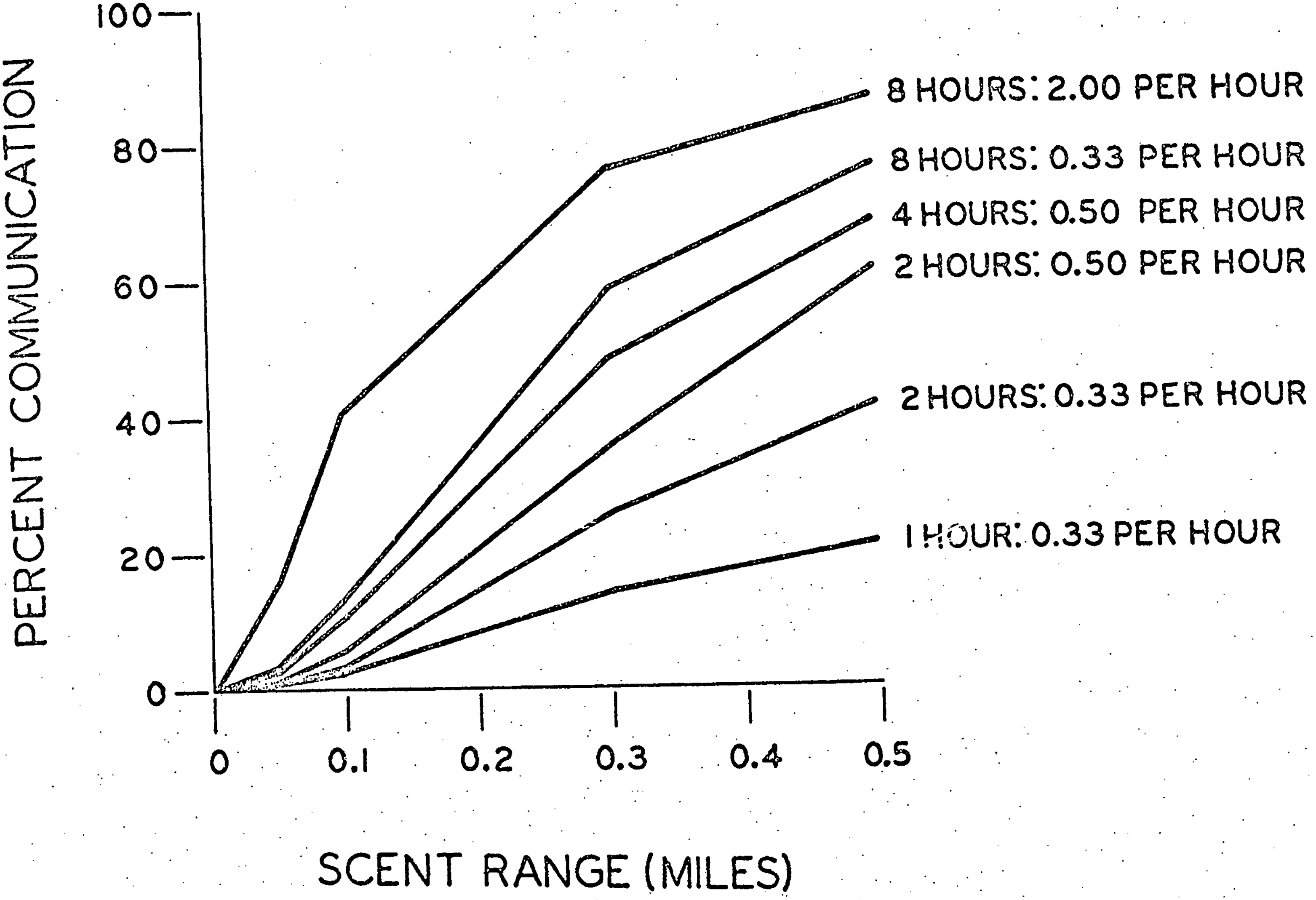

PERCENT COMMUNICATION
100
80
60
40
20
0
0
2
4
6
8
SCENT EFFECT TIME (HOURS)
0.50 MILES: 1 PER HOUR
0.30 MILES: 1 PER HOUR
0.30 MILES: 0.5 PER HOUR
0.10 MILES: 2 PER HOUR
0.10 MILES: 0.5 PER HOUR
0.05 MILES: 0.5 PER HOUR


PERCENT COMMUNICATION
100
80
60
40
20
0
0
1
2
SCENT POINTS PER HOUR
0.50 MILES: 8 HOURS
0.50 MILES: 1 HOUR
0.30 MILES: 2 HOURS
0.10 MILES: 8 HOURS
0.10 MILES: 4 HOURS
0.05 MILES: 8 HOURS
0.05 MILES: 1 HOUR

As with scent effect times, a unit increase in scenting frequency gave less and less communication as more and more of the home range space was covered with scent because of greater scent effect times and scent ranges (Fig. 14, bottom). The expected linear increase in level of communication with linear increase in scenting frequency, for a particular combination of scent effect time and scent range, was shown only for low scent ranges and scent effect times. A factor which may have limited the effect of increasing scent effect time, scenting frequency, or both was overlap of circles of effective scent. As each scent point remained effective for a longer time, or particularly as scent points deposited one after the other as the animal moved about were placed closer together in both time and space, the probability that two or more effective scent circles would overlap increased. When effective scent circles overlapped, the effect of a unit increase in the number of scent points on the home range space was reduced because each scent point covered less than the expected area around it with effective scent (there was no additional effect on communication in areas where effective scent circles overlapped).

The effect of increasing scent range on levels of communication was limited by at least two factors. These were overlap of scent circles, as discussed above, and wastage of signal emitted outside the home range space. A combination of these limiting factors resulted in deviations (Fig. 15) of the

Figure 15. The relationship between increasing scent range and mean amount of communication which resulted for five dyads with the six combinations of scent effect time and scenting frequency shown at the right of the figure. The inflection of the curves illustrates the limit which a combination of wastage of scent signal and overlap of effective scent circles placed on the effectiveness of increasing the scent range.


100
80
60
40
20
0
PERCENT COMMUNICATION
0
0.1
0.2
0.3
0.4
0.5
SCENT RANGE (MILES)
8 HOURS: 2.00 PER HOUR
8 HOURS: 0.33 PER HOUR
4 HOURS: 0.50 PER HOUR
2 HOURS: 0.50 PER HOUR
2 HOURS: 0.33 PER HOUR
1 HOUR: 0.33 PER HOUR

relationship between scent range and percent communication from the expected increases.

Scent point signalling could be made most efficient by the signaller adjusting the scent range and scent effect time to give moderate fade-out times and moderate scent ranges, by scenting at least some threshold distance from the boundary of the home range space, and by moving such that non-overlapping effective scent points were distributed over a relatively large part of the home range space, rather than being placed within a small portion of it. That a red fox moves over a large portion of its home range space in a single night's travel indicates that at least the last qualification for efficient scent point signalling may be met by the animals.

Because of the interaction of the three communication variables, there were many sets of values which, on the average, resulted in 20 percent communication. I used one such set: 2 scent points per hour; 8 hours of scent effect; scent range 0.06 miles (96 m), for ranking scent point communication among the five dyads. With those values, communication ranged from 15.2 percent for dyad B to 30.8 percent for dyad D. Communication ranked as follows among the dyads: D = 1; E = 2; C = 3; A = 4; B = 5. For at least those values of the communication variables which produced moderate to high levels of communication, ranking was generally consistent over a wide range of values of all three variables. The variation in level of communication among the dyads with particular combinations of the communication variables, and the consistency shown over a range of values shows that the way in which the animals moved about influenced their ability to communicate with scent point signalling.

Dyads in which the signaller had a relatively high rate of movement combined with straight ahead travel had higher levels of scent point communication (Table 6). There was a good correlation between level of communication and both these movement parameters. The speed and directness with which the receiver moved showed no correlation with level of communication within the range of speeds and directivity which I simulated. Likewise, there were no apparent correlations for either signallers or receivers between level of communication and parameters which describe the overall distribution of locations (K or total number of grid-squares). When the signaller moves about rapidly and in straight lines, it tends to both distribute effective scent points over a large portion of its home range space and to reduce the overlap in effective scent points. Both effects would tend to increase the probability that a receiver would encounter an effective point and increase the level of scent point communication.

Scent point signalling with red fox movement patterns can provide dyads moderate to high levels of communication, as indicated by simulation. Red fox are known to scent mark regularly as they move about, the odor persists for several days, and other fox can detect scent marks from reasonable distances.

Table 6. A comparison of the level of scent path communication provided by the pairs of movement patterns which formed each of the five dyads with 4 parameters of the movement patterns of signallers and receivers within each dyad. Criteria for ranking the levels of communication among the dyads, and for ranking the movement patterns among signallers and among receivers are given in the text.

Dyad	Communication Rank	Rate of Movement (mean)		Straight Ahead Travel ±30°		Contagion of Locations (K)		Total Number Grid-squares	
		Signaller	Receiver	Signaller	Receiver	Signaller	Receiver	Signaller	Receiver
D	1	2	1	1	2	2	2	3	2.5
E	2	1	3	2	1	1	3	3	2.5
C	3	3	5	3	3	4	4	3	1
A	4	4	4	4	5	3	1	5	5
B	5	5	2	5	4	5	5	1	4

Field observations of the number of scent marks left on snow allow estimation of the rate at which such marks are placed, because marks left during the first activity period following snowfall are attributable only to that activity period, and distances which the animal is tracked can be converted to travel times by using average rates of fox movement. Murie (1936:11) reported that a fox urinated 10 times along one-half mile (804 m) of track. Sargeant (unpublished) followed the tracks of a radio-marked male for a total of 3 miles (4,827 m) on 2 dates, finding 41 places where the animal urinated and 2 where it defecated. For urine marks, these convert to 20 and 13 marks per mile, respectively, and for feces marks to 1 per 1.3 miles. Sargeant et al (in ms.), for radio-tracked red fox, report an average rate of nocturnal travel of 1.1 miles per hour (1,770 m per hour). Using these figures, I estimate that the animals urine marked 18 and 11 times per hour, respectively, and marked with feces once per 57 minutes. Interpretation of these rates is confounded because the data on rates of urination and defecation were collected during the time of year when foxes breed. These estimated rates may thus be inflated because scent marking by red fox increases during the breeding season (Fox 1971:186).

Red fox scent persists, even to humans, for at least several days after it is placed (Murie 1936:13). Feces, in particular, can serve as scent marks for a long period but may require that a potential receiver break the scat to increase the scent level (Scott 1943:435). As with scent trails, scent marks containing large molecules with low diffusion coefficients would increase the time over which a mark is effective, but would generally reduce the effective range (Bossert and Wilson 1963:458-463) and the amount of information transferrable to a receiver (Wilson 1968:77).

The range of effect of red fox scent marks has not been experimentally determined. Penned red fox are able to detect the odor of meat from 1.5 meters (Osterholm 1966:56), and would probably detect fox scent from greater distance. The range would depend in part on wild direction and air flow. Busnel (1963:74) reported the upper limit in range of scent perception for wolves and dogs as 1500 to 2000 m but did not indicate, as seems likely, that wind had influenced this range. Heavy molecules can be carried (Van Arsdel 1967:1228) by light winds and air flow over much greater distances, reaching to at least 5 to 10 miles (8,045 to 16,090 m).

I did not simulate conditions in which a large number of small scented areas remained effective for periods of several days. Extensive modification of the computer program (Appendix A) would be necessary to do so. Higher scenting frequencies with short scent ranges were not simulated, but are possible with the program shown in Appendix A. However, it can be inferred from the simulation results (see particularly the upper curve of Fig. 15) that scenting frequencies of 10 or more per hour would give 50 percent communication or more, even with scent effect times as short as 8 hours and scent ranges of 0.025 miles (40 m) or less.

If that is its major function, scent marking could be an effective means for dyadic communication in red fox. Leyhausen and Wolff (1959:670) proposed that such scent marks can allow the individuals to time their respective movements, and thus provide spacing and "territorial" responses even when home range spaces overlap. Timing based on scent marks could provide for spacing between mated pairs which occupy the same space as well.

The major alternative hypothesis for the role of scent marking (reviewed by Ewer 1963:104-105 and 116-120) is that scent marking by an individual mammal serves to orient that individual on its home range space. Additional hypotheses concerning the role of scent marking are reviewed in Kleiman (1966). Scott (1967:379) notes that there is no evidence that domestic dogs respect as boundaries the scent marks left by other dogs. The usual reaction is to cover these marks with scent of their own. When a domestic dog enters a strange locality which has not previously been scent marked by any dog, it will urinate on any objects which are slightly elevated (Scott and Fuller 1965:68). Among canids, red fox especially will urinate or defecate on unfamiliar objects (Fox 1971:186).

Once these objects have been marked, they are ignored for long periods of time, but the scent may be periodically renewed. Young (1944:304) notes that timber wolves renew such scent marks each time they pass by a place which they have previously scent marked. Because they are so wide ranging (Mech et al. 1971: 13-18), wolves may not return to a scent post for several days. Scent marking could simultaneously serve the dual functions of self-communication and dyadic communication.

COMPARISONS AMONG THE MEANS OF COMMUNICATION

Movements of the animals had an effect on the level of communication in the simulated red fox dyads, regardless of the means of signalling. For all except tactile signalling, some communication was provided by all models and movement patterns. Within the range of values of the communication variable(s) which I simulated, the maximum level of communication which resulted for any dyad for each means of signalling ranged from 0 to 100 percent, for tactile and scent point signalling, respectively (Table 7). Visual and vocal communication would have reached the 100 percent level had I used appropriate values of the communication variable(s). As noted earlier, "close-range" communication was a special case of the visual communication model. Scent path communication, which reached a maximum of 38 percent for any dyad, would not have reached a higher level regardless of how long scent paths remained effective.

Table 7. Summary of the values of the various communication variables which were used to simulate communication in red fox dyads with simple models, and of the levels of communication which resulted from simulation.

Means of Signalling	Controlled* Communication Variable(s)	Maximum Value(s) Simulated	Maximum Communication for any Dyad (percent)	Value(s) for 20 Percent Communication (average)	Range of** Communication Among Dyads (percent)
Tactile	None	-	0	None	-
Close-range	Signal range	0.01 miles	1	None	-
Visual	Visual range	0.90 miles	96	0.19 miles	29(7 to 36)
Scent path	Scent effect time	24 hours	38	7.6 hours	13(15 to 28)
Vocal	Vocal range Vocalization frequency	0.80 miles 6 per hour	46	Various 0.40 miles and 4.7 per hour	13(13 to 26)
Scent point	Scent range Scent effect time Scenting frequency	0.50 miles 8 hours 2 per hour	100	Various 0.06 miles; 8 hours; 2 per hour	16(15 to 31)

* Movement of the animals was an uncontrolled variable with all means of signalling.

** Range when the value(s) which gave an average of 20 percent communication was used for each dyad.

The maximum levels of tactile and scent path communication which could be reached were limited by movements of the animals. Limitations placed by animal movement on visual, vocal and scent point communication could have been overcome by increasing the value of the appropriate communication variable which controlled the spatial area of effect of the signal. No such variable exists for tactile communication, and none was programmed into the simulation model for scent path signalling.

Movements of the animals had a greater infleunce on the level of visual communication than on vocal or scent point communication. For each communication model, when a particular value of the communication variable or a set of values of the communication variables were used in simulation, only differences among the movement patterns accounted for variability in level of communication among the dyads. Because the same five dyads were used for all means of signalling, this variability can be compared among the means of signalling, and indicates the relative importance of movement patterns on level of communication. With the value(s) of the communication variable(s) which gave an average of 20 percent communication, levels of visual communication ranged from 7 to 36 percent among the dyads (Table 7), a total range of 29 percent. Comparable total ranges were 13 and 16 percent for vocal and scent point communication, respectively. Those means of signalling which involved the fewest communication variables, i.e. tactile, scent point, were thus most severely limited by movements of the animals. This comparison suggests that where more variables which affect the level of communication are under control of the signalling animal, variables could be optimized to minimize the effects of movement on communication.

For the various means of signalling, different major factors limited the effectiveness of attempts to increase levels of communication (Table 8). Animal movement patterns limited attempts to increase communication for all means of signalling, and were the sole major factor for tactile, close-range, and scent path signalling.

With tactile and close-range signalling, communication levels could be increased by coordination of movements of dyad members such that they were seldom far apart. Without rare chance meetings, some other means of signalling would be necessary to reveal their respective locations so that they could initially come together and could find each other after being separated. Levels with scent path signalling could be increased by coordinating the movements of dyad members such that, even though the animals were apart, they tended to travel in the same path with the receiver approximately or actually following the signaller. Scent path signalling alone could maintain such a leader-follower set of movement patterns, although other means of signalling might increase the chances that the receiver would initially make contact with an effective scent path. Initial contact,

Table 8. Summary of factors which limited the effectiveness of attempts to increase levels of communication with the various simulated means of communication.

Means of Signalling	Controlled Communication Variable(s)	Optimal Range for Maximizing Increase in Communication	Major Factor(s) Limiting Increase in Level of Communication
Tactile	None	-	Animal movement only.
Close-range	Signal range	-	Animal movement only.
Visual	Visual range	0.05 to 0.40 miles	Animal movement; wastage of signal.
Scent path	Scent effect time	0.33 to 7.50 hours	Animal movement; divergence of home range spaces.
Vocal	Vocal range	0.10 to 0.30 miles*	Animal movement; wastage of signal.
	Vocalization frequency	0.33 to 6.00 per hour	Animal movement only.
Scent point	Scent range	0.05 to 0.30 miles**	Animal movement; wastage of signal; overlap of effective scent circles.
	Scent effect time	Various***	Animal movement; overlap of effective scent circles.

Table 8. Continued.

Means of Signalling	Controlled Communication Variable(s)	Optimal Range for Maximizing Increase in Communication	Major Factor(s) Limiting Increase in Level of Communication
	Scenting frequency	Various****	Animal movement; overlap of effective scent circles.

* Optimal range for a vocal range depended on vocalization frequency.
** Optimal range for a scent range depended on scent effect time and scenting frequency.
*** Optimal range for a scent effect time depended on scent range and scenting frequency.
**** Optimal range for a scenting frequency depended on scent range and scent effect time.

or scent path communication in the absence of leader-follower movement patterns, would be enhanced when the signaller seldom turned and traveled at high speed (Table 9).

For visual signalling, and for the spatial range variables of both vocal and scent point signalling, communication could be made more efficient by proper choice of emission intensity (Table 8) and modification of the signaller's movement pattern. This modification would involve use of a set of threshold locations appropriate for the emission intensity and its signal range, and travel by the signaller at a high rate of speed (Table 9).

For the temporal variables of scent point communication, communication could be made more efficient by modification of the signaller's movement pattern through avoidance of slow travel with many turnings (Table 9) so as to reduce the overlap of circles of effective scent. It would be more efficient with proper dual choices of frequency of scenting and scent effect time, such choices further reducing the probability of overlap of effective scent circles.

Modifications of movement patterns by an individual to influence levels of communication would have to be made within the range of patterns dictated by many other factors affecting fox movements. The fox obviously could not afford to move so fast or far to increase communication that it expended energy beyond that which it needed to survive, and modifications should

Table 9. Summary of some characteristics of the movement patterns of members of simulated red fox dyads which enhanced communication with various means of signalling.

Means of Signalling	Type of Movement Pattern Which Enhanced Communication
Visual	High rate of travel by receiver.
Scent path	Straight-ahead travel at high rate by signaller.
Vocal	Not clear; tendency toward straight-ahead travel at high rate by both signaller and receiver.
Scent point	Straight-ahead travel at high rate by signaller.

not be made which would drastically reduce the animal's chances for finding food.

Many interacting factors influence the movement pattern of an individual fox, and thus the movement patterns of a fox dyad. Some of these influences are genetically controlled, such as limitations which structure and metabolism place on speed and duration of movement, while some, such as responses to particular features of the individual's home range space, are learned. Selection should act to give a range of movement patterns which are possible for red fox, and the local environment should reduce this range by imposing limitations on individual movement. Still it seems likely that enough latitude in movement pattern is permissible under these constraints to allow modification, by an individual, of movement patterns to enhance communication. As an example of this latitude, Sargeant et al. (unpublished ms.) conclude from radio-tracking and concurrent field observations that food gathering rarely is the major determinant of red fox movement patterns. The animals which they studied moved much more than was apparently needed for finding and capturing prey, continued to move about after feeding, and showed similar total amounts of movement during periods of food scarcity and abundance. Their data support the view that, at least for one major factor affecting movement of foxes, there is latitude in the amount of influence which food gathering has on the pattern of movement.

SUMMARY STATEMENT

Results of this simulation study suggest that the way in which red fox move about differentially affects dyadic communication, the effect of movement depending on how one of the animals signals the other. The study further suggests that adjustments the signaller, the receiver, or both could make in their movement pattern(s), and the signaller could make in how it signals can affect both the level of dyadic communication and the efficiency of signalling. Such adjustments would require in general that the signaller be aware of the location of the receiver or have information on the receiver's previous movement pattern. This awareness of the pattern of movement of a receiver could result from bi-directional communication in which both animals of a dyad act as both signallers and receivers, one major function of communication being to maintain mutual awareness of the movement patterns of dyad members and promote further communication between them.

In general, two parameters determined by the movements of any two animals affect the potential for communication between them by determining the optimal means of signalling and by restricting information transfer via those means. These parameters are: distances between the animals at corresponding points in time, where the distance can range from 0 to a maximum determined by the dimensions and the spatial relationship of the two home range spaces, and; times between the animal's use of corresponding areas of space, where the time can range from 0 to a maximum determined ultimately by the lifespan of one or the other of the animals. Given that prior communication has given mutual awareness of the locations and movement patterns, the animals can adjust the distance between them, the time between them, or both. In so doing they can increase or decrease the opportunities for further communication and can increase or decrease the efficiency of signalling by one or more means. These adjustments require changes in the movement pattern of one or both individuals and will be reflected by changes in one or both home range spaces. The degree of mutual adjustment in movement patterns which the two animals can make to change the level of dyadic communication will be limited by factors extraneous to dyadic communication, such as communication and social relations with other individuals, and dispersion of life requirements in the respective home ranges of the dyad members.

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Appendix A: Listing of the computer program used for simulating communication in red fox dyads.

USE OF THE PROGRAM.

LISTED BELOW ARE THE CARDS USED TO CONTROL A RUN OF PROGRAM SIMCON.

IN THIS RUN, THE AMOUNT OF COMMUNICATION WHICH COULD OCCUR BETWEEN FOXES WITH 5 DIFFERENT SETS OF MOVEMENT PATTERNS, WHEN COMMUNICATION COULD OCCUR ONLY IF THE ONE FOX CROSSED THE OTHERS TRAVEL PATH WITHIN 120 MINUTES AFTER THE OTHER HAD USED THE TRAVEL PATH, WAS BEING DETERMINED. THE STARTING TIME FOR THE FIRST ANIMAL WAS DELAYED BY 10 HOURS. EVERY PATH SEGMENT WAS CONSIDERED, AND 540 LOCATIONS WERE USED FOR EACH ANIMAL.

THE FIVE SETS OF MOVEMENT PATTERNS, REPRESENTED BY SETS OF POINT-LOCATIONS, WERE STORED AS THE FIRST 10 FILES ON A TAPE (TTECOL82), AND THE COMPILED VERSION OF THE PROGRAM WAS STORED AS THE 26TH FILE ON THE TAPE. THE REMAINING FILES ON THE TAPE CONTAINED ADDITIONAL SETS OF POINT-LOCATIONS , AND THE FORTRAN VERSION OF THE PROGRAM.

```
GENE,T10,CM100000.25026002(1)
BIN.LAD0027
REQUEST,TAPE1,HY,DW.TTECOL82
COPYCF(TAPE1,NULL,24)
COPYCF(TAPE1,NULL,1)
COPYBF(TAPE1,SIMC,1)
REWIND(TAPE1,SIMC)
SIMC(INPUT,OUTPUT,TAPE1)
END OF RECORD CARD
REW   0120.10.00000.0000120.000010540
NREW  0120.10.00000.0000120.000010540
NREW  0120.10.00000.0000120.000010540
NREW  0120.10.00000.0000120.000010540
NREW  0120.10.00000.0000120.000010540
FINISH
END OF RECORD CARD
```

```
      PROGRAM SIMCOM (INPUT,OUTPUT,TAPE8)
C
C       THIS PROGRAM AND THE SUBROUTINES DISTN AND PATHI2 ALLOW
C     SIMULATION OF THE MOVEMENTS OF TWO ANIMALS IN THE SAME SPACE,
C     ALLOW IMPOSITION OF VARIOUS MEANS OF SIMULATED COMMUNICATION
C     ON THE TWO ANIMALS, AND OUTPUT THE NUMBER OF TIMES THE ANIMALS
C     ARE WITHIN DISTANCE-TIME LIMITS WHICH WOULD ALLOW COMMUNICATION
C     TO OCCUR.
C
      DIMENSION IA(8)
      COMMON ANIM1(900,2),ANIM2(900,2),PATH,DISTN,DSW,NSPD,DELAY
C
C       THE INPUT VARIABLE-PATH-ALLOWS SIMULATION OF COMMUNICATION
C     WHICH COULD OCCUR WHEN ONE ANIMAL CROSSES THE SCENTED TRAVEL
C     PATH OF ANOTHER ANIMAL. THE TRAVEL PATH IS DEFINED AS THE SERIES
C     OF LINES WHICH CONNECT SUCCESSIVE POINT-LOCATIONS OF THE ANIMAL.
C     PATH=0, SCENT PATH COMMUNICATION IS NOT SIMULATED.
C     PATH=POSITIVE NUMBER, THEN COMMUNICATION COULD OCCUR IF
C     THE TRAVEL PATH SEGMENT FOR ANIMAL TWO CROSSES A TRAVEL PATH
C     SEGMENT OF ANIMAL ONE WITHIN PATH MINUTES AFTER ANIMAL ONE
C     USED ITS TRAVEL PATH SEGMENT.
C
C       THE INPUT VARIABLE-DISTN-ALLOWS SIMULATION OF COMMUNICATION
C     WHICH COULD OCCUR WHEN ANIMAL TWO IS WITHIN A SPECIFIED DISTANCE
C     OF ANIMAL ONE.
C     WHEN DISTN=0.0, THE DISTANCE BETWEEN THE ANIMALS IS NOT MEASURED.
C     WHEN DISTN IS A POSITIVE NUMBER COMMUNICATION COULD OCCUR WHEN
C     THE ANIMALS ARE DISTN MILES OR LESS APART.
C
C       THE INPUT VARIABLE-DSW-ALLOWS SIMULATION OF COMMUNICATION
C     IN WHICH ANIMAL ONE CAN LEAVE SCENT AT A POINT AND
C     COMMUNICATION CAN OCCUR AT SOME LATER TIME WHEN ANIMAL TWO
C     IS NEAR THAT POINT(WITHIN DISTN OF IT) BEFORE DSW MINUTES
```

```
C      HAVE PASSED SINCE ANIMAL ONE WAS AT THE POINT.
C
C      WHEN DSW=0.0, THE DISTANCE DISTN APPLIES ONLY TO DISTANCES
C      BETWEEN LOCATIONS OF THE TWO ANIMALS WHICH WERE TAKEN AT THE SAME
C      POINT IN TIME. NOTE THAT SUBROUTINE PATHI2 CANNOT BE USED WHEN
C      DSW=0. SET DSW EQUAL TO PATH.
C      WHEN DSW IS A POSITIVE NUMBER, THE DISTANCE DISTN WILL BE COMPARED
C      WITH DISTANCES FROM THE CURRENT LOCATION OF ANIMAL TWO TO ALL
C      LOCATIONS USED BY ANIMAL ONE WITHIN THE PREVIOUS DSW MINUTES, OR
C      WILL DETERMINE WHETHER OR NOT THE TWO ANIMALS WERE AT A TRAVEL
C      PATH INTERSECT WITHIN DSW MINUTES OF EACH OTHER.
C      WHEN BOTH VARIABLES DISTN AND PATH ARE USED IN A SIMULATION,
C      THE APPROPRIATE DISTANCE BETWEEN THE ANIMALS IS FIRST COMPARED
C      WITH DISTN. IF NO COMMUNICATION COULD OCCUR, THE TRAVEL PATH
C      SEGMENTS ARE CHECKED FOR COMMUNICATION WHICH COULD OCCUR VIA A
C      TRAVEL PATH INTERSECT. ONLY ONE OCCURRENCE OF COMMUNICATION IS
C      COUNTED REGARDLESS OF WHETHER IT OCCURRED VIA DISTANCE OR
C      VIA AN INTERSECT.
C        THE INPUT VARIABLE-NSPD- ALLOWS SIMULATION OF INTERMITTANT
C      COMMUNICATION SIGNALLING. FOR EXAMPLE, WHEN NSPD=1 ANIMAL ONE
C      WILL SIGNAL FROM EACH LOCATION WHICH IT USES. HOWEVER, WHEN
C      NSPD=5. ANIMAL ONE WILL SIGNAL FROM ONLY EVERY FIFTH LOCATION
C      WHICH IT USES, OR WITH EVERY FIFTH TRAVEL PATH SEGMENT.
C      IN CURRENT USAGE OF THE PROGRAM, THE ANIMALS CHANGE LOCATION
C      ONCE EVERY FIVE MINUTES.
C        THE INPUT VARIABLE-DELAY-ALLOWS PROGRAMMING OF A DIFFERENT
C      BEGINNING POINT IN THE ARRAY OF LOCATIONS FOR ANIMAL TWO. THIS
C      IN EFFECT ALLOWS SIMULATION OF RANDOMLY SELECTED STARTING
C      LOCATIONS OF THE TWO ANIMALS.
C      FOR EXAMPLE, WHEN DELAY=10.0, DATA FOR ANIMAL TWO BEGINS 10 HOURS
C      AFTER THE ACTUAL BEGINNING POINT OF DATA FOR THE ANIMAL.
C        THE INPUT VARIABLE-INP-CONTROLS THE NUMBER OF LOCATIONS
C      FOR EACH ANIMAL WHICH WILL BE USED IN THE SIMULATION.
```

```
C      RECORD AND STORE THE DATE ON WHICH THE PROGRAM WAS RUN.
       CALL DATE (IDATE)
       PRINT 1, IDATE
     1 FORMAT (1H1,//////,5X,14HSIMCON RUN OF ,A10,//)
C      INITIATE THE PROGRAM AND READ IN THE CONTROLLING VARIABLES FROM
C      A CARD.
C        ONE SIMULATION.IE. THE MOVEMENTS OF TWO ANIMALS IN THE SAME
C      SPACE UNDER ONE SET OF CONTROLLING VARIABLES, OCCURS EACH TIME
C      A HEADER CARD WITHOUT FINISH IN CMS. 1-6 IS READ.
C      THE PROGRAM LOOPS UNTIL IT ENCOUNTERS A CARD WITH FINISH IN
C      COLUMNS 1-6. THE HEADER CARD FOR EACH OF THE SIMULATIONS SHOULD
C      CONTAIN REW   IN CMS.1-3 IF THE DATA INPUT TAPE IS TO BE
C      REWOUND SO THAT THE SAME SET OF DATA ( THE FIRST TWO FILES
C      ON TAPE 8) MAY BE USED IN SUCCESSIVE SIMULATIONS. IF DIFFERENT
C      SETS OF DATA ARE TO BE USED IN SUCCESSIVE RUNS, THEN CMS.1-4
C      SHOULD CONTAIN NREW.
C      THE HEADER CARD SHOULD ALSO CONTAIN THE VALUES OF THE INPUT
C      VARIABLES AS FOLLOWS, PATH IN CMS.7-11, DELAY IN CMS.12-15,
C      DISTN IN CMS.16-24, DSW IN CMS.25-31,, NSPD IN CMS.32-33,
C      INP IN CMS.34-37.
     2 READ 3, ISWITCH,PATH,DELAY,DISTN,DSW,NSPD,INP
     3 FORMAT (A6,F5.0,F4.0,F9.5,F7.0,I2,I4)
       IF (ISWITCH.EQ.6HFINISH) GO TO 56
       IF (EOF(8)) GO TO 4
       IF (ISWITCH.EQ.6HREW   ) REWIND 8
       IF (NSPD.LE.0) NSPD=1
       DELAY=DELAY*60.
C      PRINT THE COMMUNICATION VARIABLES WHICH WILL BE USED IN THE
C      SIMULATION.
       IF (DISTN.NE.0.0.AND.PATH.EQ.0.0) GO TO 6
       IF (DISTN.EQ.0.0.AND.PATH.NE.0.0) GO TO 8
       IF (DISTN.NE.0.0.AND.PATH.NE.0.0) GO TO 10
C      THE SIMULATION WILL BE TERMINATED IF NO COMMUNICATION VARIABLES
```

```
C      WERE READ. PRINT ERROR MESSAGE BEFORE TERMINATION.
    4 PRINT 5
    5 FORMAT (46H  ERROR. NO COMMUNICATION VARIABLES WERE READ.)
      GO TO 2
    6 PRINT 7, DISTN,NSPD
    7 FORMAT (90H  COMMUNICATION FROM ANIMAL ONE TO ANIMAL TWO CAN OCCUR
     1 EACH TIME THE MOVEMENTS OF THE TWO,/,20H  BRING THEM WITHIN ,F7.5
     2,55H MILES OF EACH OTHER. THE DISTANCE IS CHECKED FOR EACH ,I5,17H
     3TH LOCATION USED.)
      GO TO 14
    8 PRINT 9, PATH,NSPD
    9 FORMAT (109H  COMMUNICATION FROM ANIMAL ONE TO ANIMAL TWO CAN OCCU
     1R EACH TIME THE MOVEMENTS OF THE ANIMALS ARE SUCH THAT ,/,58H  ANI
     2MAL TWO CROSSES THE TRAVEL PATH OF ANIMAL ONE WITHIN ,F9.5,56H MIN
     3UTES AFTER ANIMAL ONE USED THAT PORTION OF ITS PATH.,/,26H  ANIMAL
     4 ONE SCENTS EVERY ,I5,30HTH SEGMENT OF ITS TRAVEL PATH.)
      GO TO 12
   10 PRINT 11, DISTN,PATH,NSPD,NSPD
   11 FORMAT (56H  COMMUNICATION FROM ANIMAL ONE TO ANIMAL TWO CAN  OCCU
     1R,/,34H  (1) WHEN THE ANIMALS ARE WITHIN ,F7.3,24H MILES OF EACH O
     2THER OR ,/,60H  (2) WHEN ANIMAL TWO CROSSES THE TRAVEL PATH OF ANI
     3MAL ONE ,/,9H  WITHIN ,F9.5,48H MINUTES AFTER ANIMAL ONE WAS THERE
     4. ANIMAL ONE ,/,21H  SIGNALS FROM EVERY ,I5,28HTH LOCATION AND ALO
     5NG EVERY ,I5,23HTH TRAVEL PATH SEGMENT.)
   12 PRINT 13, PATH
   13 FORMAT (40H  THE COMMUNICATION SIGNAL PERSISTS FOR ,F7.2,53H MINUT
     1ES AFTER ANIMAL ONE USES A TRAVEL PATH SEGMENT.,//)
      IF (DISTN.EQ.0.0) GO TO 16
   14 PRINT 15, DSW
   15 FORMAT (40H  THE COMMUNICATION SIGNAL PERSISTS FOR ,F4.0,42H MINUT
     1ES AFTER ANIMAL ONE USES A LOCATION.,//)
C      READ X-Y LOCATION DATA FROM TAPE 8.
C      DATA FOR EACH ANIMAL ARE PRECEEDED BY PARAMETERS WHICH WERE USED
```

```
C     IN SIMULATING THE MOVEMENTS OF THE ANIMAL, AND FOLLOWED BY
C     RESULTS OF A COMPARISON OF THE SIMULATED MOVEMENTS WITH MOVEMENTS
C     OF REAL ANIMALS.
C     READ PARAMETERS FOR ANIMAL ONE.
   16 NSTART=1
      NEND=0
      READ (8,17) (IA(I),I=1,8)
   17 FORMAT (8A10)
   18 READ (8,19) INR
   19 FORMAT (I5)
C     WAS THIS THE LAST DATA SET FOR ANIMAL ONE.
      IF (EOF(8)) 25,20
C     NO, SO READ THE LOCATION DATA FOR ANIMAL ONE.
   20 NEND=NEND+INR
      READ (8,21) (ANIM1(I,1),ANIM1(I,2),I=NSTART,NEND)
   21 FORMAT (6(1X,2F6.4))
C     READ RESULTS OF COMPARISON WITH REAL ANIMAL.
      READ (8,22) CHSQ,NDF,PD,TAB1,TAB5,AEK,AEP,AEVK,AMS,AVS,IIDATE
      READ (8,22) CHSQ,NDF,PD,TAB1,TAB5,AEK,AEP,AEVK,AMS,AVS,IIDATE
   22 FORMAT (F10.5,I5,4F10.5,/,4F10.5,A10)
      READ (8,23) NRNC,NRIT,NRINP,NRMIN,NRKK,RP,RXIP,RYIP,RSZI,RXHR,RYHR
     1,NRHSW
   23 FORMAT (5I5,3F5.1,F5.4,2F5.1,I1)
      READ (8,24) RAK,RE,RXXX,RYYY,NRMM,NRLAS,NRJUM,RPATH,RDEL,RDIS,RDSW
     1,NRSPU
   24 FORMAT (4F9.5,3I5,F5.0,F4.0,F9.5,F7.0,I2)
      NSTART=NSTART+INR
      GO TO 18
   25 IF (INP.GT.NEND) INP=NEND
      PRINT 26, (IA(I),I=1,8),NRINP,NRMM
   26 FORMAT (1X,11HANIMAL ONE ,8A10,2I5)
C     READ PARAMETERS FOR ANIMAL TWO.
      NSTART=1
```

```
      NEND=0
      READ (8,17) (IA(I),I=1,8)
   27 READ (8,19) INR
C     WAS THIS THE LAST DATA SET FOR ANIMAL TWO.
      IF (EOF(8)) 29,28
C     NO, SO READ THE LOCATION DATA FOR ANIMAL TWO.
   28 NEND=NEND+INR
      READ (8,21) (ANIM2(I,1),ANIM2(I,2),I=NSTART,NEND)
C     READ RESULTS OF COMPARISON WITH REAL ANIMAL.
      READ (8,22) CHSQ,NDF,PD,TAB1,TAB5,AEK,AEP,AEVK,AMS,AVS,IIDATE
      READ (8,22) CHSQ,NDF,PD,TAB1,TAB5,AEK,AEP,AEVK,AMS,AVS,IIDATE
      READ (8,23) NRNC,NRIT,NRINP,NRMIN,NRKK,RP,RXIP,RYIP,RSZI,RXHR,RYHR
     1,NRHSW
      READ (8,24) RAK,RE,RXXX,RYYY,NRMM,NRLAS,NRJUM,RPATH,RDEL,RDIS,RDSW
     1,NRSPD
      NSTART=NSTART+INR
      GO TO 27
   29 IF (INP.GT.NEND) INP=NEND
      PRINT 30, (IA(I),I=1,8),NRINP,NRMM
   30 FORMAT (1X,11HANIMAL TWO ,8A10,2I5)
C     SIMULATE MOVEMENTS OF THE TWO ANIMALS BY SEQUENTIALLY USING THEIR
C     LOCATIONS FROM THE ARRAYS ANIM1 AND ANIM2. MEASURE THE OPPORTUNITY
C     FOR COMMUNICATION BETWEEN THE ANIMALS WITH SUBROUTINES DISTS AND
C     PATH12.
C     DETERMINE THE BEGINNING LOCATIONS IN THE RESPECTIVE ARRAYS OF
C     LOCATIONS.
C     CHOOSE THE BEGINNING POINT FOR THE ARRAY ANIM1 WHICH ALLOWS
C     ENOUGH LOCATIONS  BEFORE THE ARRAY ANIM2 BEGINS TO
C     COMPENSATE FOR THE AMOUNT OF TIME A SIGNAL PERSISTS
C     UNDER CONTROL OF INPUT VARIABLE-DSW- OR-PATH-, WHICHEVER
C     REQUIRES MORE LOCATIONS, OR FOR THE INPUT VARIABLE
C     DELAY,IF IT REQUIRES MORE LOCATIONS THAN EITHER PATH OR DSW.
C     WHEN THE INPUT VARIABLE-PATH-IS USED, THE ARRAY ANIM1
```

```
C     BEGINS SUCH THAT ANIMAL ONE CAN SIGNAL PATH MINUTES
C     BEFORE THE MOVEMENTS OF ANIMAL TWO BEGIN.
      IPATH=1
      IF (PATH.GT.0.0) 31,32
   31 IPATH=(PATH/5.)+1
C     LIKEWISE, THE ARRAY OF LOCATIONS FOR ANIMAL ONE BEGINS SUCH
C     THAT ANIMAL ONE CAN SIGNAL DSW MINUTES BEFORE THE MOVEMENTS
C     OF ANIMAL TWO BEGIN.
   32 IF (DSW.EQ.0.0) 34,33
   33 IDSW=(DSW/5.)+1
      GO TO 35
   34 IDSW=1
C     THE MOVEMENTS OF ANIMAL TWO BEGIN DELAY MINUTES AFTER THE FIRST
C     LOCATION IN THE ARRAY ANIM2.
   35 IF (IDSW.GT.IPATH) GO TO 36
      IDSW=IPATH
   36 IF (DELAY.EQ.0.0) 38,37
   37 IDELAY=(DELAY/5.)+1
      GO TO 39
   38 IDELAY=0
   39 IF (IDSW.GT.IDELAY) GO TO 40
      IDSW=IDELAY
C     PRINT HEADING FOR RESULTS OF SIMULATION.
   40 PRINT 41
   41 FORMAT (10X,17HCOULD COMMUNICATE,5X,5HTOTAL,5X,7HPERCENT)
C     LIMIT THE SIMULATION TO FIVE DAYS OF NINE HOURS EACH
C     ( FIVE DAYS EQUALS 540 LOCATIONS WITH THE ANIMALS CHANGING
C     LOCATIONS ONCE PER FIVE MINUTES).
      NEND=IDSW+539
C     ARE THERE SUFFICIENT LOCATIONS TO SIMULATE FIVE DAYS OF MOVEMENT.
      IF (NEND.LE.NRINP) 44,42
C     NO. PRINT ERROR MESSAGE AND TERMINATE THIS SIMULATION.
   42 PRINT 43, NEND,NNEND
```

```
   43 FORMAT (71H  ERROR. THERE ARE TOO FEW LOCATIONS TO SIMULATE FIVE D
     1AYS OF MOVEMENT.,/,35H  LOCATIONS NEEDED FOR ANIMAL ONE =,I5,21H A
     2ND FOR ANIMAL TWO =,I5)
      GO TO 2
C     THERE ARE SUFFICIENT LOCATIONS, SO LOOP THROUGH THE ARRAYS TO
C     TEST FOR THE OPPORTUNITY FOR COMMUNICATION.
   44 IPRINT=0
      CNT=0.
      PERCENT=0.
      COM=0.
      DO 50 I=IDSW,NEND
      II=I+1
C     I AND II INDEX THE ARRAY OF LOCATIONS FOR ANIMAL ONE.
      IDELAY=IDELAY+1
      N=IDELAY
      NN=N+1
C     N AND NN INDEX THE ARRAY OF LOCATIONS FOR ANIMAL TWO.
C     WILL THE OPPORTUNITY FOR COMMUNICATION VIA SCENT PATH SIGNALLING
C     BE TESTED IN THIS RUN.
      IF (PATH.EQ.0.0) 45,46
C     NO, SO TEST FOR COMMUNICATION WHICH DEPENDS ON A DISTANCE BETWEEN
C     THE ANIMALS.
   45 CALL DISTS (II,NN,COM,CNT)
      GO TO 47
C     YES, SO TEST FOR COMMUNICATION WHICH DEPENDS ON SCENT PATH
C     SIGNALLING. IF COMMUNICATION WHICH DEPENDS ON DISTANCE BETWEEN
C     THE ANIMAL WILL BE TESTED AS WELL. THE SUBROUTINE DISTS IS CALLED
C     FROM THE SUBROUTINE PATHI2 AFTER OPPORTUNITY FOR SCENT PATH
C     COMMUNICATION HAS BEEN TESTED.
   46 CALL PATHI2 (I,II,N,NN,COM,CNT)
   47 IPRINT=IPRINT+1
C     RESULTS WILL BE SUMMARIZED FOR EACH TENTH TIME THE OPPORTUNITY FOR
C     COMMUNICATION HAS BEEN TESTED.
```

3

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      IF (IPRINT.NE.10) GO TO 50
      IF (COM.EQ.0.0) GO TO 48
      PERCENT=(COM/CNT)*100.
   48 PRINT 49, COM,CNT,PERCENT
   49 FORMAT (20X,F7,5X,F5,5X,F7.1)
      IPRINT=0
   50 CONTINUE
C     THIS SIMULATION HAS BEEN COMPLETED.
      IF (COM.GT.0.0) 52,51
   51 PERCENT=0.0
      GO TO 53
   52 PERCENT=(COM/CNT)*100.0
   53 PRINT 54, COM,CNT,PERCENT
   54 FORMAT (1X,19HSIMULATION SUMMARY ,F7,5X,F5,5X,F7.1)
      PRINT 55
   55 FORMAT (1H1)
C     LOOP TO READ A NEW HEADER CARD.
      GO TO 2
   56 CONTINUE
      END
```

```
      SUBROUTINE DISTS (II,NN,COM,CNT)
C     THIS SUBROUTINE MEASURES THE DISTANCE BETWEEN THE LOCATIONS OF
C     TWO ANIMALS, EITHER WHEN THE LOCATIONS WERE TAKEN AT THE SAME
C     POINT IN TIME, OR WHEN THE DISTANCE OCCURS BETWEEN THE CURRENT
C     LOCATION OF ANIMAL TWO AND A LOCATION WHICH ANIMAL ONE HAD
C     PREVIOUSLY USED. THE DISTANCE BETWEEN THE LOCATIONS IS THEN
C     COMPARED WITH AN INPUT VARIABLE-DISTN- TO DETERMINE IF THE ANIMALS
C     WERE CLOSE ENOUGH TO EACH OTHER FOR COMMUNICATION TO OCCUR.
      COMMON ANIM1(900,2),ANIM2(900,2),PATH,DISTN,DSW,NSPD,DELAY
C     IS INTERMITTANT COMMUNICATION IN WHICH THE SIGNAL DOES NOT LAST
C     BEYOND THE TIME ANIMAL ONE IS AT A LOCATION TO BE SIMULATED.
      IF (DSW.GT.0.0) GO TO 2
      IF (NSPD.EQ.1) GO TO 1
C     YES. DETERMINE IF THIS LOCATION OF ANIMAL ONE IS A LOCATION
C     AT WHICH IT SIGNALLED.
      AII=II
      ANSPD=NSPD
      AA=AII/ANSPD
      NAA=AA
      AAN=NAA
      AO=AA-AAN
      IF ((ABS(AO)).GT.0.000000001) 5,1
C     WHEN THIS WAS NOT A LOCATION FROM WHICH ANIMAL ONE SIGNALLED,IE.
C     WHEN THE PROGRAM BRANCHES TO 85, THEN IT IS COUNTED AS A LOCATION
C     FROM WHICH COMMUNICATION DID NOT OCCUR.
C     WITH INTERMITTANT SIGNALLING AND WHERE THE SIGNAL DOES NOT
C     PERSIST AFTER ANIMAL ONE LEAVES THE LOCATION. THIS SET OF
C     LOCATIONS OF THE TWO ANIMALS AT A POINT IN TIME IS A SET
C     FROM WHICH COMMUNICATION MIGHT OCCUR. MEASURE THE DISTANCE
C     BETWEEN THE ANIMALS.
    1 D=DIST(ANIM2(NN,1),ANIM1(II,1),ANIM2(NN,2),ANIM1(II,2))
C     WERE THE ANIMALS CLOSE ENOUGH TO EACH OTHER FOR COMMUNICATION
C     TO OCCUR.
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```
      IF (D.LE.DISTN) GO TO 8
C     NO. IS COMMUNICATION THROUGH SIGNALS WHICH LAST AFTER ANIMAL ONE
C     LEAVES A LOCATION BEING SIMULATED.
      IF (DSW.LE.0.0) GO TO 5
C     YES. CHECK THE DISTANCES FROM THE CURRENT LOCATION OF ANIMAL TWO
C     TO THE APPROPRIATE LOCATIONS USED BY ANIMAL ONE.
C     DETERMINE THE INDEX FOR THE FIRST PREVIOUS LOCATION FROM WHICH
C     COMMUNICATION COULD OCCUR.
    2 MOX=(DSW/5.)
      MOX=II-MOX
C     WITH A COMMUNICATION SIGNAL WHICH PERSISTS, DID ANIMAL ONE
C     USE INTERMITTANT SIGNALLING.
      IF (NSPD.EQ.1) GO TO 6
C     YES. SET THE FIRST PREVIOUS LOCATION WHICH WILL BE CHECKED
C     SO THAT IT IS A LOCATION FROM WHICH ANIMAL ONE SIGNALLED.
    3 AMOX=MOX
      ANSPD=NSPD
      AAMOX=AMOX/ANSPD
      NA=AAMOX
      AN=NA
      AMOX=AAMOX-AN
      IF ((ABS(AMOX)).GT.0.000000001) 4,6
    4 MOX=MOX+1
      IF (MOX.LT.II) GO TO 3
C     THERE WERE NO APPROPRIATE PREVIOUS LOCATIONS, AND NO COMMUNICATION
C     COULD OCCUR FROM THIS SET OF LOCATIONS.
C     COUNT THE OPPORTUNITY FOR COMMUNICATION, BUT DO NOT COUNT THE
C     OCCURRENCE OF COMMUNICATION.
    5 CNT=CNT+1.
      RETURN
C     THE FIRST APPROPRIATE LOCATION OF ANIMAL ONE HAS BEEN DETERMINED.
C     CHECK THE DISTANCE BETWEEN THE LOCATIONS FROM WHICH ANIMAL ONE
C     SIGNALLED AND THE CURRENT LOCATION OF ANIMAL TWO.
```

```
    6 DO 7 KO=MOX,II,NSPD
      D=DIST(ANIM2(NN,1),ANIM1(KO,1),ANIM2(NN,2),ANIM1(KO,2))
C     COULD COMMUNICATION OCCUR WHEN THE ANIMALS ARE THIS DISTANCE
C     APART.
      IF (D.LE.DISTN) GO TO 8
C     NO. CONTINUE TO LOOP TO CHECK THE OTHER APPROPRIATE LOCATIONS.
    7 CONTINUE
C     NO COMMUNICATION COULD OCCUR FROM THIS SET OF LOCATIONS.
      GO TO 5
C     COMMUNICATION COULD HAVE OCCURRED BECAUSE THE ANIMALS WERE CLOSE
C     ENOUGH TO EACH OTHER AT APPROPRIATE TIMES. COUNT THE OPPORTUNITY
C     FOR COMMUNICATION TO OCCUR AND THE OCCURRANCE OF COMMUNICATION.
    8 CNT=CNT+1.
      COM=COM+1.
      RETURN
      END
```

```
      SUBROUTINE PATHI2 (I,II,N,NN,COM,CNT)
C     THIS SUBROUTINE PROJECTS SEGMENTS OF THE TRAVEL PATHS
C     (EACH SEGMENT CONNECTS THE SUCCESSIVE LOCATIONS USED BY AN
C     ANIMAL) OF EACH OF TWO ANIMALS. IT ASKS WHETHER THE TRAVEL PATH
C     SEGMENT USED BY ANIMAL TWO CROSSES A TRAVEL PATH SEGMENT USED BY
C     ANIMAL ONE.
C     IF SO, THE DIFFERENCE IN TIMES OF ARRIVAL AT THE INTERSECT POINT
C     IS COMPARED WITH THE INPUT VARIABLE PATH TO DETERMINE IF THE
C     ANIMALS WERE CLOSE ENOUGH IN TIME TO COMMUNICATE AT THE
C     INTERSECT POINT.
      COMMON ANIM1(900,2),ANIM2(900,2),PATH,DISTN,DSW,NSPD,DELAY
C     SCENT PERSISTS FOR PATH MINUTES AFTER ANIMAL ONE USES ITS TRAVEL
C     PATH SEGMENT.
C     DETERMINE THE INDEX OF THE LIMIT OF SCENTED TRAVEL PATH SEGMENTS.
      MMM=(PATH/5.)
      MOX=I-MMM
      IF (MOX.LT.1) MOX=1
C     IS INTERMITTANT COMMUNICATION, IN WHICH ANIMAL ONE SCENTS ONLY
C     EVERY NSPD TH TRAVEL PATH SEGMENT BEING SIMULATED.
      IF (NSPD.LE.1) GO TO 3
C     YES. DETERMINE THE INDEX NUMBER OF THE BEGINNING OF THE FIRST
C     TRAVEL PATH SEGMENT WHICH WAS SCENTED WITHIN THE PAST PATH
C     MINUTES.
    1 MOX=(PATH/5.)
      MOX=I-MOX
      AMOX=MOX
      ANSPD=NSPD
      AA=AMOX/ANSPD
      NAA=AA
      AAA=NAA
      AO=AA-AAA
      IF ((ABS(AO)).GT.0.000000001) 2,3
    2 MOX=MOX+1
```

```
      IF (MOX.GT.I) GO TO 38
      GO TO 1
C     LOOP TO CHECK FOR INTERSECT OF ANIMAL TWOS TRAVEL PATH
C     SEGMENT WITH ALL APPROPRIATE SEGMENTS OF ANIMAL ONES TRAVEL
C     PATH.
    3 DO 37 J=MOX,I,NSPD
      JJ=J+1
C     ARE BOTH COMMUNICATION WHICH DEPENDS ON DISTANCE BETWEEN THE
C     ANIMALS AND COMMUNICATION WHICH DEPENDS ON A SCENTED TRAVEL
C     PATH BEING SIMULATED.
      IF (DISTN.EQ.0.0) GO TO 4
C     YES. FIRST CHECK THE DISTANCE BETWEEN THE ANIMALS AT THE END OF
C     THE CURRENT MOVE.
C     WHEN BOTH MEANS OF COMMUNICATION ARE BEING SIMULATED, ONLY
C     ONE OCCURRENCE OF COMMUNICATION IS COUNTED, REGARDLESS OF
C     WHETHER IT OCCURRED VIA A DISTANCE OR A PATH INTERSECT.
      D=DIST(ANIM2(NN,1),ANIM1(JJ,1),ANIM2(NN,2),ANIM1(JJ,2))
C     DID COMMUNICATION OCCUR VIA A DISTANCE BETWEEN THE ANIMALS.
      IF (D.GT.DISTN) 4,39
C     NO. WERE ANIMAL ONE AND ANIMAL TWO AT THE SAME POINT.
    4 IF (ANIM1(J,1).EQ.ANIM2(N,1).AND.ANIM1(J,2).EQ.ANIM2(N,2)) 5,6
C     THE ANIMALS WERE AT THE SAME POINT AT THE BEGINNING OF THE MOVE.
    5 XI=ANIM1(J,1)
      YI=ANIM1(J,2)
      GO TO 36
    6 IF (ANIM1(JJ,1).EQ.ANIM2(NN,1).AND.ANIM1(JJ,2).EQ.ANIM2(NN,2)) 7,8
C     THE ANIMALS WERE AT THE SAME POINT AT THE END OF THE MOVE.
    7 XI=ANIM1(JJ,1)
      YI=ANIM1(JJ,2)
      GO TO 36
C     THE ANIMALS WERE NOT AT THE SAME POINT.
C     COMPUTE THE SLOPES OF THE LINES OF MOVEMENT OF ANIMAL ONE AND
C     ANIMAL TWO.
```

```
C     SLOPE OF ANIMAL ONES LINE OF MOVEMENT.
    8 AG=100000000.
      SM=0.000000001
      AGN=-AG
      SMN=-SM
      DENR=ANIM1(JJ,1)-ANIM1(J,1)
      DENI=ANIM2(NN,1)-ANIM2(N,1)
C     WAS THE SLOPE OF ANIMAL ONES LINE OF MOVEMENT EQUAL TO ZERO OR
C     INFINITY. IF SO CHANGE THE SLOPE BY A VERY SMALL AMOUNT TO
C     REDUCE COMPLICATIONS IN COMPUTING INTERSECT POINT.
      IF (DENR.LT.0.0) 9,10
    9 IF (DENR.GT.SMN) DENR=SMN
      GO TO 11
   10 IF (DENR.LT.SM) DENR=SM
C     CHECK THE SLOPE OF ANIMAL TWOS LINE OF MOVEMENT.
   11 IF (DENI.LT.0.0) 12,13
   12 IF (DENI.GT.SMN) DENI=SMN
      GO TO 14
   13 IF (DENI.LT.SM) DENI=SM
C     COMPUTE THE SLOPE OF ANIMAL ONES LINE OF MOVEMENT.
   14 SLOPR=(ANIM1(JJ,2)-ANIM1(J,2))/DENR
C     WAS THE SLOPE EQUAL TO ZERO.
      IF (SLOPR.LT.0.0) 15,16
   15 IF (SLOPR.GT.SMN) SLOPR=SMN
      IF (SLOPR.LT.AGN) SLOPR=AGN
      GO TO 17
   16 IF (SLOPR.LT.SM) SLOPR=SM
      IF (SLOPR.GT.AG) SLOPR=AG
C     CHECK SLOPE OF ANIMAL TWOS LINE OF MOVEMENT.
   17 SLOPI=(ANIM2(NN,2)-ANIM2(N,2))/DENI
      IF (SLOPI.LT.0.0) 18,19
   18 IF (SLOPI.GT.SMN) SLOPI=SMN
      IF (SLOPI.LT.AGN) SLOPI=AGN
```

```
      GO TO 20
   19 IF (SLOPI.LT.SM) SLOPI=SM
      IF (SLOPI.GT.AG) SLOPI=AG
   20 IF (SLOPR.EQ.1.0) 21,22
   21 SLOPR=SLOPR+SM
   22 IF (SLOPI.EQ.1.0) 23,24
   23 SLOPI=SLOPI+SM
C     WERE THE LINES OF MOVEMENT OF THE TWO ANIMALS PARALLEL.
   24 A=SLOPR*1000.
      NSLOP=A
      A=SLOPI*1000.
      KSLOP=A
      IF (NSLOP.EQ.KSLOP) 37,25
C     YES. THE LINES OF MOVEMENT WERE PARALLEL,THUS THERE COULD HAVE
C     BEEN NO COMMUNICATION THROUGH A TRAVEL PATH INTERSECT.
C     NO. COMPUTE THE INTERSECT POINT OF THE TWO LINES OF TRAVEL.
C     WHERE AX+BY=E AND CX+DY=F ARE THE POINT-SLOPE FORMULAE FOR THE
C     TWO TRAVEL PATH SEGMENTS, IN THE FORM Y-Y1=M(X-X1), THE
C     SIMULTANEOUS SOLUTION FOR THE POINT OF INTERSECT IS
C     COMPUTED AS X=(DE-BF)/(AD-BC)  Y=(AF-CE)/(AD-BC).
   25 DE=-1.0*((SLOPR*ANIM1(J,1))-ANIM1(J,2))
      BF=-1.0*((SLOPI*ANIM2(N,1))-ANIM2(N,2))
      AD=-1.*SLOPR
      BC=-1.0*SLOPI
      AF=SLOPR*((SLOPI*ANIM2(N,1))-ANIM2(N,2))
      CE=SLOPI*((SLOPR*ANIM1(J,1))-ANIM1(J,2))
C     WAS THERE A ZERO DETERMINATE.
      DEN=AD-BC
      IF (DEN.EQ.0.0) 26,27
C     YES. ADD A SMALL AMOUNT TO THE DIFFERENCE.
   26 DEN=DEN+SM
C     COMPUTE THE COORDINATES OF THE POINT OF INTERSECT.
   27 XI=(DE-BF)/DEN
```

```
      YI=(AF-CE)/DEN
C     REMOVE ROUND-OFF ERRORS.
      NON=(XI*1000.)
      XI=(NON/1000.)
      NON=(YI*1000.)
      YI=(NON/1000.)
C     DID THE INTERSECT FALL ON THE TRAVEL PATH SEGMENTS.
      IF (XI.GT.ANIM1(J,1).AND.XI.GT.ANIM1(JJ,1)) 35,28
   28 IF (XI.LT.ANIM1(J,1).AND.XI.LT.ANIM1(JJ,1)) 35,29
   29 IF (YI.GT.ANIM1(J,2).AND.YI.GT.ANIM1(JJ,2)) 35,30
   30 IF (YI.LT.ANIM1(J,2).AND.YI.LT.ANIM1(JJ,2)) 35,31
   31 IF (XI.GT.ANIM2(N,1).AND.XI.GT.ANIM2(NN,1)) 35,32
   32 IF (XI.LT.ANIM2(N,1).AND.XI.LT.ANIM2(NN,1)) 35,33
   33 IF (YI.GT.ANIM2(N,2).AND.YI.GT.ANIM2(NN,2)) 35,34
   34 IF (YI.LT.ANIM2(N,2).AND.YI.LT.ANIM2(NN,2)) 35,36
C     THERE WAS NO TRAVEL PATH INTERSECT.
C     THUS THERE WAS NO COMMUNICATION.
   35 GO TO 37
C     THERE WAS A TRAVEL PATH INTERSECT. DID ANIMAL TWO ARRIVE
C     AT THE POINT OF INTERSECT WITHIN PATH MINUTES AFTER ANIMAL
C     ONE WAS AT THE POINT.
C     ASSUME THAT THE ANIMALS TRAVELED AT A CONSTANT RATE BETWEEN
C     THEIR RESPECTIVE LOCATIONS.
C     THEN THE TIME WHEN EACH ANIMAL WAS AT THE INTERSECT IS
C     PROPORTIONAL TO THE DISTANCE TO THE INTERSECT POINT
C     FROM THE BEGINNING POINT OF THE TRAVEL PATH SEGMENT.
C     DETERMINE THE DISTANCE WHICH EACH ANIMAL TRAVELED TO THE
C     INTERSECT.
   36 DRI=DIST(XI,ANIM1(J,1),YI,ANIM1(J,2))
      DII=DIST(XI,ANIM2(N,1),YI,ANIM2(N,2))
C     FIND THE LENGTHS OF THE TRAVEL PATH SEGMENTS.
      DRT=DIST(ANIM1(J,1),ANIM1(JJ,1),ANIM1(J,2),ANIM1(JJ,2))
      DIT=DIST(ANIM2(N,1),ANIM2(NN,1),ANIM2(N,2),ANIM2(NN,2))
```

```
      DRI=DRI/DRT
      DII=DII/DIT
C     ESTIMATE THE TIME WHEN EACH ANIMAL WAS AT THE INTERSECT POINT.
C     ANIMAL ONE.
      A=J
      TIR=(A*5.0)+(5.0*DRI)
C     ANIMAL TWO.
      A=N
      TII=(A*5.0)+(5.0*DII)
C     DETERMINE THE DIFFERENCE IN TIME OF ARRIVAL AT THE INTERSECT.
      TD=TIR-TII
C     DID ANIMAL ONE ARRIVE AT THE INTERSECT POINT FIRST.
      IF (TD.GT.0.0) 37,39
C     WHEN ANIMAL TWO ARRIVED AT THE INTERSECT FIRST,
C     THERE WAS NO POSSIBILITY OF SCENT COMMUNICATION FROM ANIMAL ONE
C     TO ANIMAL TWO.
C     WHEN ANIMAL ONE ARRIVED FIRST, COMMUNICATION OCCURRED. ALL TRAVEL
C     PATH SEGMENTS WHICH ARE BEING CHECKED BEGAN WITHIN THE TIME
C     LIMIT PATH OF THE CURRENT TIME.
C     LOOP TO TEST ADDITIONAL TRAVEL PATH SEGMENTS OF ANIMAL ONE.
   37 CONTINUE
C     NO COMMUNICATION CAN HAVE OCCURRED.
C     RECORD THE OPPORTUNITY FOR COMMUNICATION TO OCCUR BUT NOT
C     THE OCCURRANCE OF COMMUNICATION.
   38 CNT=CNT+1.0
      RETURN
C     COMMUNICATION HAS OCCURRED.
   39 CNT=CNT+1.0
      COM=COM+1.0
      RETURN
      END
```

```
      FUNCTION DIST (X1,X2,Y1,Y2)
C     THIS FUNCTION MEASURES THE DISTANCE BETWEEN TWO POINTS X1-Y1 AND
C     X2-Y2.
      DIST=SQRT((X1-X2)**2+(Y1-Y2)**2)
      RETURN
      END
```

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