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Differential Behavior of Coyotes with Regard to Home Range Limits

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DIFFERENTIAL BEHAVIOR OF COYOTES WITH REGARD TO HOME RANGE LIMITS

by

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Approved:

Major Professor	Committee Member
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Charles E. Harris

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ABSTRACT

Differential Behavior of Coyotes with Regard to Home Range Limits

by

Charles E. Harris, Doctor of Philosophy

Utah State University, 1983

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This study was conducted to examine coyote behavioral responses to novel stimuli in familiar and unfamiliar environments and the implications of this behavior with regard to specific coyote management and research techniques. A series of pen studies with captive coyotes was undertaken at the U.S. Fish and Wildlife Service's Predator Ecology and Behavior Project research site, Logan, Utah, to observe the range and type of behaviors coyotes showed towards small novel objects and standard scent stations in familiar and unfamiliar 1-ha enclosures. The initial response to these novel stimuli in familiar environments was one of neophobia and caution, whereas in the unfamiliar environment these same stimuli were readily approached and investigated. Field studies were undertaken at the Idaho National Engineering Laboratory and Freer, Texas, to examine coyote visitation to scent stations inside, peripheral to, and

outside their defined home ranges. Radio-collared coyotes were monitored to determine home range use and movement patterns, with relocations plotted on computer graphic maps and gridded base maps. Modified scent-station survey lines were run and visitations by marked coyotes plotted with respect to home range zone. Marked coyotes visited a greater percentage of scent stations peripheral to and outside their home ranges than inside. The socio-spatial distribution of coyotes, home range size, and percentage of road comprising home range zones influenced differential scent-station visitation rates. The importance of understanding the influences of animal behavior on wildlife management and research techniques is discussed.

(132 pages)

INTRODUCTION

It is generally assumed that mammals limit their movements and activity to a particular area within which they acquire the necessary resources for growth, maintenance, and reproduction. Such an area is commonly referred to as a home range (Burt 1943).

Certain advantages can accrue to individuals living in familiar environments. The term familiar suggests a detailed knowledge of the nature and spatial relationships of objects, resources, pathways, and potential dangers within a specific area has been acquired. Animals probably obtain much of their knowledge of the environment in which they live by exploratory behavior. Familiarity is maintained through frequent exposure, whereby change is detected, resulting in recognition and investigation of novel stimuli (Sheppe 1966).

Exploratory behavior, i.e., those behaviors in which an animal appears to take a certain initiative in finding out more about its environment (McReynolds 1962), has been studied in a variety of animal species (for general review see Berlyne 1960, Welker 1961, Fowler 1965). Most of the investigations concerning exploratory behavior have involved wild and laboratory rats (Rattus norvegicus) placed in various maze types, exposed to novel stimuli, or allowed access to open-field exploratory boxes (Berlyne 1950, Barnett 1958a, 1963, Cowan 1976, 1977). Such behaviors have also been studied in laboratory environments for several other species including: rhesus

monkey (Macacca mulatta) (Butler 1953, 1954, Butler and Alexander 1955, Harlow et al. 1956, Menzel 1962), chimpanzee (Pan troglodytes) (Welker 1956a, b, Menzel et al. 1961), lower primates (Ehrlich 1970), marsupials (Russell and Pearce 1971), the dog (Canis familiaris) (Thompson and Heron 1954, Fox and Spencer 1969), black bear (Ursus americanus) (Bacon 1980), deer mouse (Peromyscus maniculatus baridii) (Price 1972), white-footed mouse (P. leucopus) (Sheppe 1966), canyon mouse (P. crinitus) (Brant and Kavanau 1965), short-tailed vole (Microtus agrestis) (Shillito 1963), domestic fowl (Murphy 1978), and wild fowl (Hogan and Degabriele 1982).

Laboratory rats spend more time investigating new things than things they have previously encountered, and the second time they encounter the same situation they spent less time examining it than the first (Berlyne 1950, Montgomery 1951, Dember 1956). Investigatory behavior is also prominent in wild rats when exposed to totally new environments (Barnett and Spencer 1951, Barnett 1958b). However, neophobia (new object reaction), or avoidance behavior, frequently results from relatively minor changes in familiar environ-ments such as placing a familiar food dish in a new location or the addition of a new food dish (Barnett 1958a, c, Cowan 1976, 1977).

Few studies have examined the behavioral responses of animals to novel stimuli in their natural environment. Chitty and Shorten (1946), Shorten (1954), and Calhoun (1962) discussed the neophobic responses of Norway rats to novel stimuli in their respective natural environments. Balph (1968) provided a detailed discussion

of the behavioral responses of Uinta ground squirrels (Spermophilus armatus) to various live-trapping experiences. Exploratory behavior and responses to novel stimuli are likely common among most mammalian species. However, the responses are by no means universal nor can typical reactions to novel stimuli be described for all species.

Metzgar (1967) found transient white-footed mice engaged in more exploratory behavior than residents and subsequently were more vulnerable to owl predation than residents. Mice in familiar terrain seemed less vulnerable to avian predators than those in unfamiliar areas. Barnett (1963:31) found wild rats were more vulnerable to predation by cats (Felis domesticus) when in unfamiliar surroundings. Errington (1946, 1967) noted wandering, migrating, or displaced prey were more vulnerable to predation. Dr. C. C. Smith (pers. commun. 1978) stated red squirrels (Tamiasciurus hudsonicus) were more vulnerable to trapping when raiding food caches in neighboring territories than within their own territories. Similarly, Hibler (1977) reported coyotes to be more vulnerable to trapping along the margins and outside their defined home ranges than inside. None of his coyotes were killed within their respective home ranges, and more were killed well outside their home range than along the periphery. He also stated that coyotes spent relatively little time outside their home ranges yet seem to be very vulnerable during the short time that is involved.

Coyotes appear to be more vulnerable to trapping and man-induced

mortality in areas less familiar to them. Rucker (1975), Woodruff (1977), Althoff (1978), and Litvaitis (1978) noted similar patterns in their respective coyote studies. Mech (1977) reported 8 of 10 wolves (Canis lupus lycaon) trapped between 1968 and 1976 were known to have been outside their pack's territory when caught, and most were at least 16 km away.

These studies imply a differential behavior or vulnerability of animals within and outside familiar environments. In some instances unfamiliarity with the environment subjects the animal to increased levels of predation and mortality. In other cases an animal's vulnerability to traps depends upon whether they are encountered in familiar or unfamiliar surroundings. The potential influence of such behavior patterns on research and management techniques is little understood. Balph (1968) emphasized the importance of considering a species behavior in the use of various population estimators. Most animals exhibit some exploratory behavior, strange-object response, and are subject to conditioning. If a population estimation procedure involves use of a novel object, animals may have a specific response to the novelty. If a technique includes repetitive stimuli, animals may become conditioned. The design and interpretation of population estimation and indexing techniques could be improved through better understanding of species behavior and ecology and knowledge of the basic learning concepts of animals.

Salmon and Marsh (1977) suggest that with tests involving measuring the response of animals to olfactory stimuli, the biology

of the animals must be understood so as to measure as natural a behavior of the animal as possible. Two important aspects to consider are the neophobic and exploratory characteristics of the animal.

Ecologists generally pay little attention to the role of exploratory behavior and novel object response, although both affect the animals and the results of techniques used in studying the animals. Trap success is likely influenced by the balance between neophobia and neophilia (Chitty and Kempson 1949, Geis 1955, Sealander et al. 1958, Crowcroft and Jeffers 1961, Calhoun 1963, Sheppe 1966, Balph 1968). In routine collecting and population estimation processes it is important that the responses of the animals to novel objects be considered.

OBJECTIVES AND APPROACH

The objective of this study was to investigate coyote responses to novel stimuli in familiar and unfamiliar environments and to examine implications regarding specific coyote management and research techniques. I also wanted to address the four possibilities put forth by Hibler (1977) with respect to why coyotes appeared more vulnerable to trapping and man-induced mortality along the margins and outside of their defined home ranges than within, namely that: (1) during the habitual travel of a coyote about its home range it may repeatedly and inadvertently bypass trap sets without detecting or responding to the scent stimulus; (2) coyotes are more attentive to stimuli when they are in unfamiliar areas than when in familiar areas; (3) upon detecting a trap scent coyotes may avoid rather than approach it when within an area familiar to them but approach it when in areas less familiar to them; and (4) coyotes change or shift their use of space as a result of the trapping experience making subsequent analyses appear as if the animals were trapped outside their defined home ranges.

Behaviorial responses of coyotes to novel stimuli were initially studied in a series of pen experiments using captive animals to assess the type and range of responses shown by coyotes. Based on findings of previous studies of animal response to novel stimuli in familiar and unfamiliar environments, null hypotheses were formulated and tested to ascertain the amount and type of attention

coyotes directed to novel stimuli.

H1: There is no difference in the relative number of avoidance and nonavoidance behaviors directed towards novel stimuli in familiar and unfamiliar environments.

H2: There is no difference in the number of investigative approaches directed towards novel stimuli encountered in familiar and unfamiliar environments.

H3: There is no difference in the amount of time spent within 5 m of novel stimuli in familiar and unfamiliar environments.

Field studies were subsequently undertaken to examine the response of coyotes to a potentially novel stimulus (scent stations) in a natural environment and whether or not scent stations would evoke contrary behaviors in familiar and unfamiliar portions of coyote's environment. The corresponding null hypothesis tested, given exposure to scent stations in different situations, was:

H4: There is no difference in the relative response rates to scent stations placed inside, peripheral to, or outside areas familar to a coyote.

The first 3 of Hibler's (1977) potential explanations of differential behavior of coyotes associated with home range limits can be discussed in conjunction with the results from H1-H4. To address his fourth possibility, coyotes were trapped well within their areas of frequent use and subsequently released to assess

whether or not they shifted their movement and/or spatial utilization patterns as a result of being trapped. The null hypothesis tested was:

H5: There is no difference in the relative frequency of use of the home range segment in which a coyote was trapped before and after that event.

DEFINITIONS

Terminology

The Problem Of Semantics.--Terminology such as novel, odd, and familiar require definition (Ruggerio et al. 1979). Incorrect translations of terms can lead to misunderstanding and misinterpretation of experimental findings. Ruggerio (1975) and Ruggerio et al. (1979) discuss the semantic problems of the terms novelty and oddity as they relate to prey characteristics, their effects on predatory behavior, and how various authors have used the same terminology but with different meanings.

Definition of Terms.--Before defining the terms used in this discussion, it is appropriate to quote Menzel (1963:1).

> "The 'innate response' to a given stimulus object is a potential sequence of behavior patterns which, strictly speaking, is neither elicited by the stimulus nor emitted in vacuo by the subject; it is a product of a complex interaction in which the properties of the stimulus, the history of the subject, and present circumstances must all be taken into account."

Novel: A novel stimulus is one that the organism has not previously encountered, does not remember, and does not relate to previous experiences (Weisler and McCall 1976). A stimulus can be novel only once; novelty, by definition, must decrease as a function of repeated exposure. In studies with repeated trials, total novelty must dissipate as familiarity increases (Menzel 1963).

Discrepancy: Discrepancy, in contrast to novelty, implies that the new stimuli bear some magnitude of physical or conceptual similarity to events remembered by the organism but are at variance

with those events (Weisler and McCall 1976).

Familiar: The term familiar denotes stimuli which, by virtue of experience, are no longer novel. Habituation (the gradual loss of responsiveness to repeated stimuli) is a function of experience so it can be said that a familiar stimulus is one which has been habituated to, i.e., accepted as normal and thereby rendered familiar (Ruggerio 1975).

Neophobia (new object reaction): The avoidance of unfamiliar (novel) stimuli in a familiar environment (Barnett 1981).

The Concepts of Home Range and Territory

Movements in and use of space by mammals are areas of study that have received much attention. Data from such studies furnish basic information useful to taxonomists, behaviorists, ecologists, and wildlife managers. Spacing patterns are brought about largely by the manner in which different individuals of a species react to each other. The dispersion of animals in space and time results, in a proximate sense, from the direct response of individuals to features of the environment and to the presence or absence of conspecifics (Brown and Orians 1970).

Seton (1909:26) noted "No wild animal roams at random over the country; each has a home region, even if it is not an actual home." Burt (1943) formally defined home range as "that area traversed by the individual in its normal activities of food gathering, mating, and caring for young." He excluded specific types of movements (migration, dispersal, sallies) that were not considered normal or

routine. Variations and alternatives to Burt's definitions are numerous. Historical development of the home range concept and various definitions are adequately covered elsewhere (Brown 1962, 1966, Jewell 1966, Sanderson 1966, Hibler 1977).

The home range concept is different from, although frequently associated with, the concept of territory. The two concepts are not identical nor are they alternatives in any way (Brown 1975:61). Territory is most commonly defined as any defended area (Noble 1939). Such a definition is purposely flexible and to some extent arbitrary since the meaning of defended is not specified (Brown and Orians 1970). Several alternatives to Noble's definition have arisen depending upon the research question being asked and whether one's orientation is behavioral (Brown 1975) or ecological (Pitelka 1959, Schoener 1968). General reviews of the territory concept, its historical development, and various definitions are given by Nice (1941), Eisenberg (1966), Fisler (1969), Stokes (1974), and Wittenberger (1981).

The degree to which most canids, specifically coyotes, are territorial can only be established by long-term observations of small known populations. Territoriality can be assumed if animals have a stable limited home range that changes little over time, and acts of defense by the possessor, whether direct attacks, threats or some form of advertisement (e.g., scent marking, vocalizations) evoke escape and/or avoidance in conspecifics (Kleiman and Brady 1978).

Although there are only limited data to confirm or deny territoriality for most canids, it is generally believed these species are territorial (Kleiman and Brady 1978). The behavioral flexibility of many canids allow for changes in social organization to meet changing environmental demands such that territoriality may or may not exist at different times and places within a species. Coyote territoriality has been documented or inferred from the data in several studies (Chesness and Bremicker 1974, Hibler 1977, Camenzind 1978, Andelt and Gipson 1979, Bowen and Cowan 1980, Althoff and Gipson 1981, Wells and Bekoff 1981, Bowen 1982), although only those studies of Bowen and Cowan, Camenzind, and Wells and Bekoff included actual observations of coyotes scent-marking, fighting, and chasing at territorial boundaries.

The relevance of the concepts of home range and territory to this research are twofold: (1) they are areas where the animal can become familiar with its surroundings, and (2) the socio-spatial distributions of animals can potentially influence sampling and population estimation procedures.

Definitions of terms used to describe spatial utilization patterns in this study are as follows:

Home range: The area or volume that is habitually occupied or traversed by an animal in pursuit of routine activities within a specified period of time (Hibler 1977). The home range may or may not be defended; those portions that are defended constitute the territory.

Territory: An area occupied more or less exclusively by an

animal or group of animals by means of repulsion through overt defense or advertisement.

Core area: The area of most frequent use within the home range or territory.

Total area: The entire area covered by an individual during the course of this study.

Hibler (1977) defined a peripheral zone as an area 0.5 km on either side of his defined home range boundaries. The area circumscribed by this peripheral zone was inside the home range and that area beyond the peripheral zone was considered outside the home range. For purposes of this study the three respective zones were defined on the basis of both quantitative and qualitative characteristics since no boundary was specifically drawn. Percent of total relocations within a grid cell (grid cell techniques and analyses are explained in the Methods section) and relative position of the grid cell with respect to adjacent animals and/or physical features of the environment acting as potential boundaries between adjacent coyotes (primarily roads) were the variables. Initially, grid cells with 0.1-0.5% total relocations were considered outside, 0.5-1.5% total relocations were considered peripheral, and >1.5% inside. Adjustments were sometimes made between outside and peripheral designations with respect to the grid cells relative position in the home range rather than adhering strictly to the percentage criteria.

METHODS

Study Locations

Millville Facilities.--Pen studies were undertaken at the U.S. Fish and Wildlife Service's Predator Ecology and Behavior Project research site 12 km south of Utah State University and 2 km south of Millville, Utah. The 50-ha research facility consists of 6 pen complexes, 2 40-animal kennels, and an office/laboratory building.

INEL Field Site.--The Idaho National Engineering Laboratory (INEL), a National Environmental Research Park (NERP) located in Bingham, Bonneville, Butte, Clark, and Jefferson counties, Idaho, is approximately 56 km northwest of the city of Idaho Falls. The study area comprised about 300 km^2 of the 2,300-km^2 INEL site (Figs. 1, 2). Topography of the study area is characterized by rolling to broken plains interspersed with lava flows, craters, cinder cones, and sandy ridges. The vegetation is typical of the northern cool desert type with big sagebrush (Artemisia tridentata)-grass communities as the dominant association (Atwood 1970). More detailed discussions of the INEL site, its vegetative and soil characteristics are given elsewhere (Harniss and West 1973, McBride et al. 1978, Davison 1980). Mean annual precipitation is 18-20 cm, occurring mainly as snow in winter and rain in early spring. Mean annual temperature is approximately 5.5 C, but ranges from -16 C in January to 31 C in July.

The principal mammalian fauna of the study area include black-

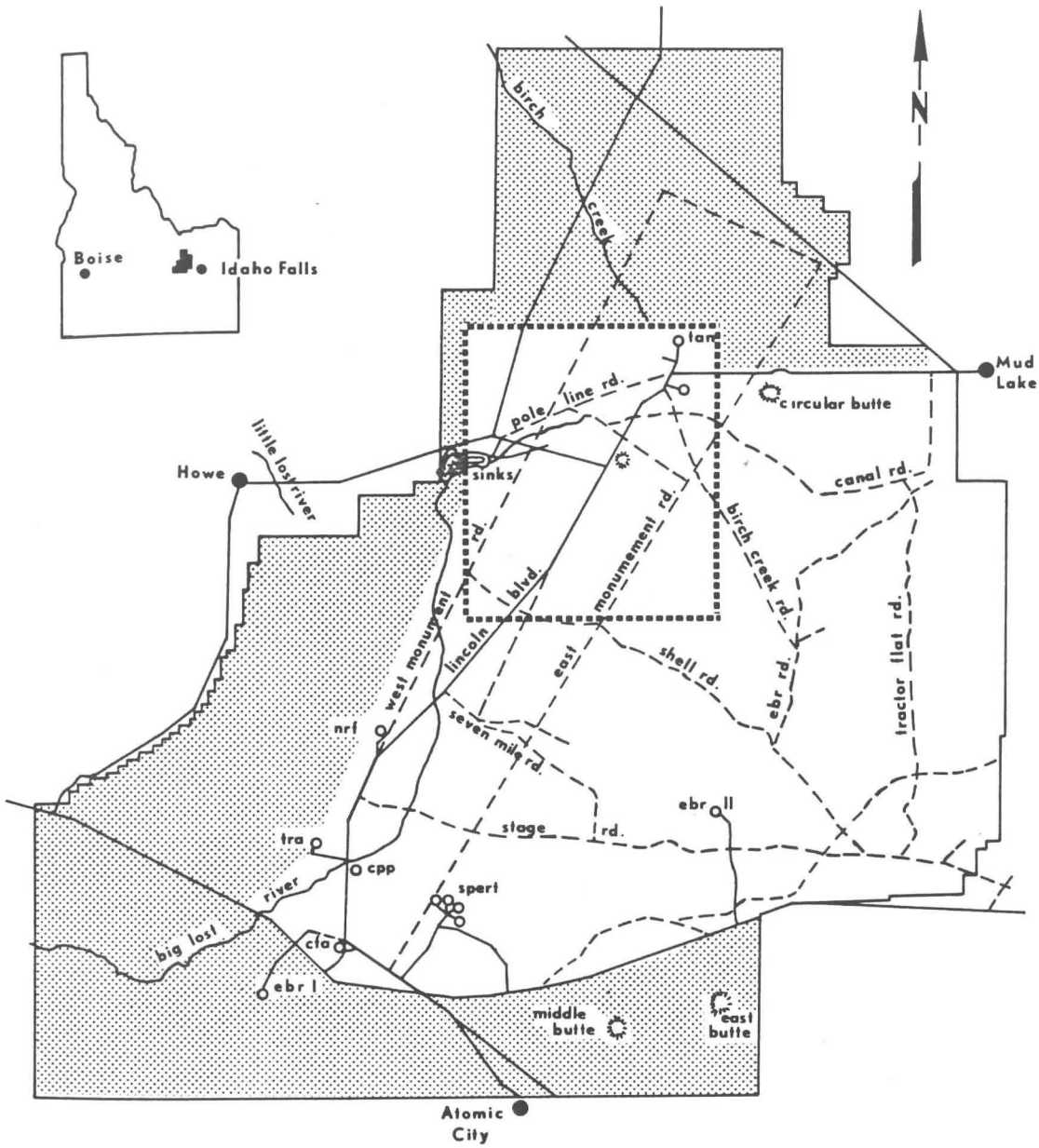

Fig. 1. Map of the 300 km^2 study area (dashed line) within the U.S. Fish and Wildlife Service research area (unshaded) of the Idaho National Engineering Laboratory (INEL).

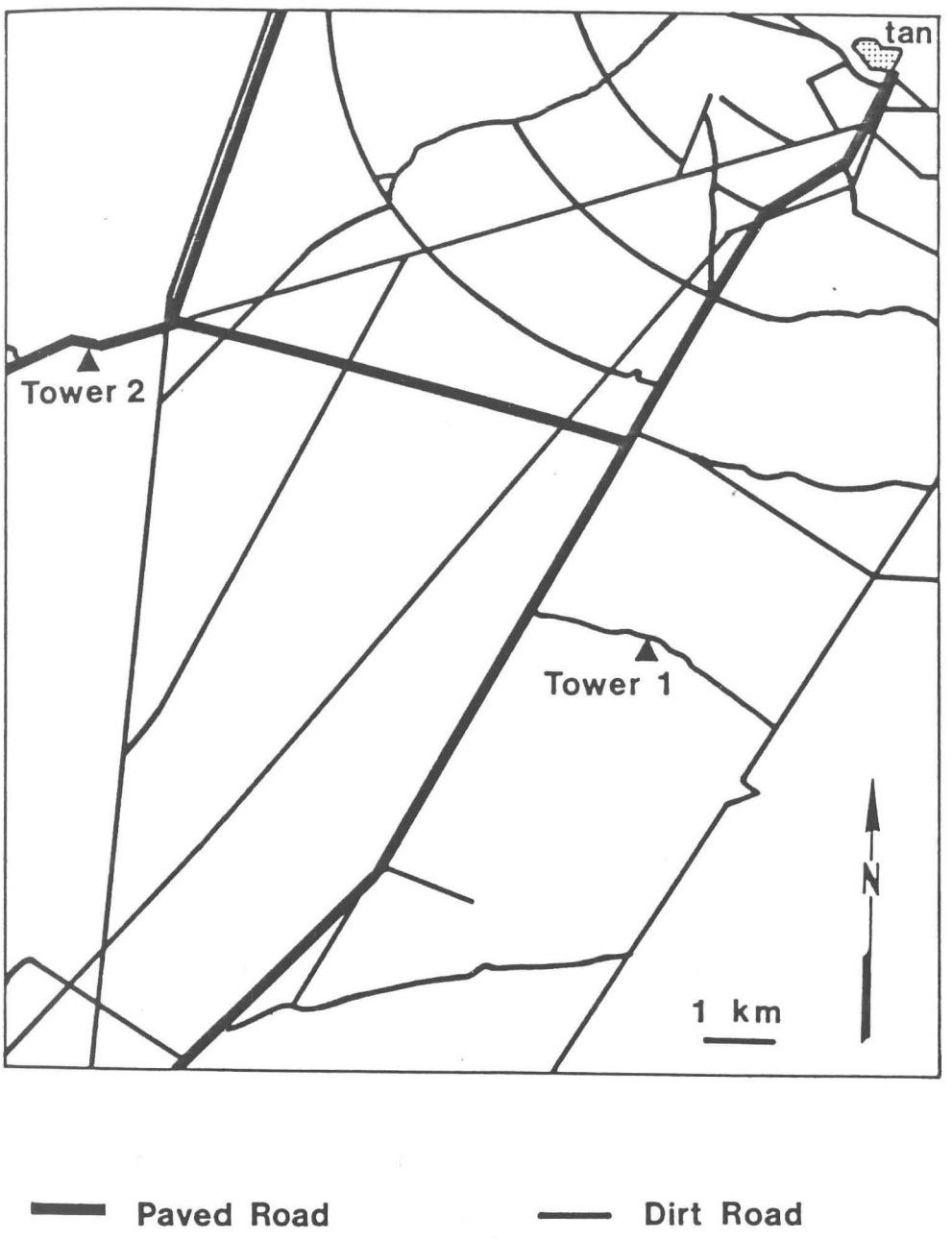

Fig. 2. Map of the 300 km^2 INEL Study area.

tailed jack rabbits (Lepus californicus), mountain and pygmy cottontails (Sylvilagus nuttalli and S. idahoensis), pronghorn (Antilocapra americana), mule deer (Odocoileus hemionus), badger (Taxidea taxus), bobcat (Felis rufus), and approximately 17 species of rodents with the deer mouse (Peromyscus maniculatus), Great Basin pocket mouse (Perognathus parvus), Ord kangaroo rat (Dipodomys ordii), least chipmunk (Eutamias minimus), and Townsend's ground squirrel (Spermophilus townsendii) the most frequently trapped (Davison 1980).

Freer Field Site.--The Clinton Manges ranch located about 10 km southwest of Freer, Texas, in Duval and Webb counties was a second field study site (Fig. 3). The study area comprised roughly 250 km^2 of the 400-km^2 ranch. The topography was level to rolling and the vegetation characterized as a mesquite-acacia savannah. The mean annual precipitation of 45 cm is erratic between and within years (Gould 1962).

Principal mammalian fauna of the study area include white-tailed deer (Odocoileus virginianus), collared peccary (Dicotyles tajacu), badger, raccoon (Procyon lotor), black-tailed jack rabbit, desert and eastern cottontails (S. auduboni and S. floridanus), southern plains woodrat (Neotoma micropus), and hispid cotton rat (Sigmodon hispidus).

Pen Studies: Response to Novel Objects

Subjects.--Eleven captive coyotes at least 18 months of age and naive to the research site's "pi pen" complex were used in the

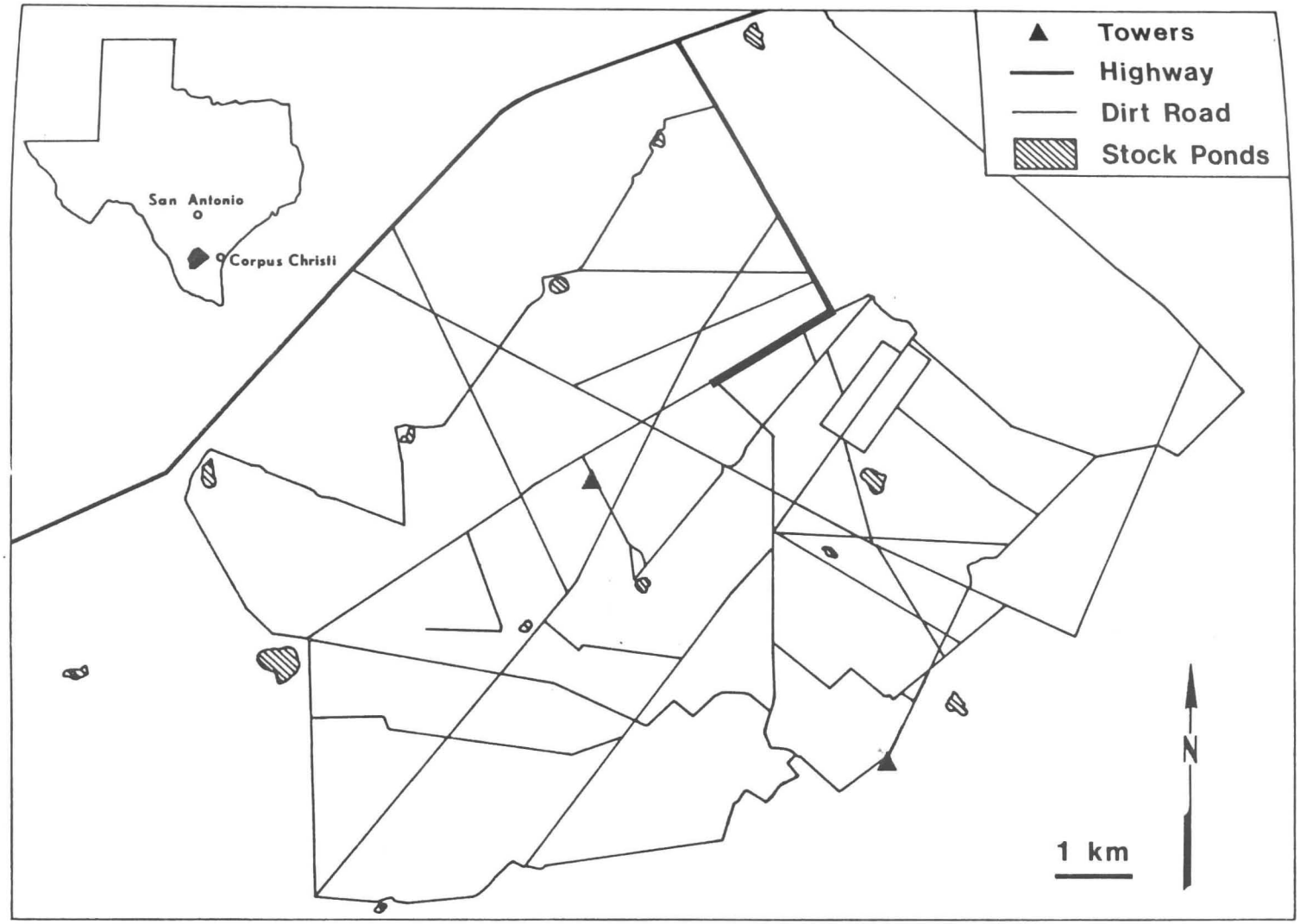

Fig. 3. Map of the 250 km^2 study area on the Clinton Manges ranch near Freer, Texas.

initial series of pen studies January through May 1979. All animals had been born in captivity; some had been hand-reared.

Hand-reared coyotes were removed from their mothers when approximately 10 days of age and bottle fed a bitches milk replacer formula before being weaned to a solid food diet of softened puppy chow, ground rabbit, or commercial mink food. Littermates were reared together in vegetated 0.1 ha teardrop-shaped pens with access to den boxes and shade shelters. Litters were in visual contact with other coyote litters in adjacent pens and could hear adults, other pups, and wild coyotes in the area. When 36-40 weeks of age, littermates were separated into individual kennels but were still in visual, auditory, and olfactory contact with each other and/or other coyotes. Coyotes handled by humans at an early age habituate to observers more readily and resume normal activities within 5 minutes of the arrival of an observer in an observation building (Knight 1978).

Experimental Facilities.--Two adjacent 1-ha wedge-shaped enclosures of the "pi pen" complex were utilized to study behavioral responses of coyotes to novel objects. Each pen radiated out 160 m from a central elevated observation building to an outer circumference of 125 m. The pens were enclosed with a 2-m chain-link fence topped with two electrified fence wires. Vegetative cover of the pens was a grass-alfalfa (Medicago sativa) mixture. A polar coordinate system employing color-coded steel stakes was established in each pen to aid in recording location data. Experimental animals were housed beneath the observation building in

kennels which opened into their respective 1-ha pens. A plywood wall prevented coyotes from viewing activities in the pens while they were in the kennels.

Experimental Procedures.--One coyote per enclosure constituted an experimental trial, with 2 trials being run concurrently in adjacent pens. Each coyote was placed in the kennel and given a 3-day acclimation period. On day 4 the coyote was given access to the adjoining 1-ha pen into which a small novel object, either a black cube or pyramid 15 x 15 x 15 cm, had been placed. This situation constituted a novel stimulus in an unfamiliar environment. Animals were observed for 8 hours on the 4th and 17th days of their respective experimental trials and 2-4 hours on alternate intervening days, with location and activity recorded at 1 minute intervals. On the evening before day 17 of a trial the coyote was kenneled and a second novel object, different from the initial object, placed in an area of the pen frequented by the coyote. This situation constituted a novel stimulus in a familiar environment. The animal was released the following morning and observations continued as before.

All coyote behaviors directed towards the novel objects during the entire trial were recorded on video tape to later quantify the number of approaches to and the time spent within 5 m of the objects. The types of behavior patterns coyotes directed toward novel stimuli in familiar and unfamiliar environments could also be studied in more detail.

Differences in relative and absolute numbers of avoidance and nonavoidance behaviors in familiar and unfamiliar environments were determined with chi-square analysis of a 2 x 2 contingency table (Zar 1974:60-67) and the Fisher exact test (Zar 1974:291-293). Differences in number of approaches and the time spent within 5 m of the object were determined with a Mann-Whitney test (Zar 1974:109-114) and a Wilcoxon rank sum test (Hollander and Wolfe 1973:676-75).

Pen Studies: Response to Scent Stations

Subjects.--Twenty-two captive coyotes at least 12 months of age and naive to the "pi pen" complex were used in studies between August and November 1980 and May through August 1981. All animals had been born in captivity; none had been hand-reared.

Experimental Procedures.--As before, 1 coyote per enclosure for a 17-day period was used for an experimental trial. Following a 3-day acclimation period, the coyote was released into the adjoining 1-ha pen on day 4 in which a single standard scent station (Linhart and Knowlton 1975, Roughton and Sweeny 1982) had been prepared the previous evening. The scent capsule was not placed on the scent station until 1-2 hours prior to beginning observations. Observations and data were recorded as previously described. This experimental procedure constituted a novel stimulus in an unfamiliar environment. The response to a scent station in a familiar environment was studied by giving another group of coyotes access to the pen for 10 days. On the evening of the 10th day the coyote was kenneled and a scent station prepared in an area of the pen

frequented by the coyote during the 10-day observation period. A scent capsule was placed on the scent station the following morning and observations resumed upon release of the coyote 1-2 hours later. Data were recorded as previously described. Statistical analysis procedures were the same as those described for the respective responses to novel objects. Animals used in the unfamiliar environment experiments were not reused in the familiar environment experiments as the scent stations would not have been as novel the second time they were encountered.

Field Studies

Coyotes were darted from a helicopter using a Cap-Chur gun and darts (Palmer Chemical and Equipment Co., P. O. Box 867, Douglasville, GA 30134) loaded with ketamine hydrochloride (Ketaset, Bristol Laboratories, Syracuse, NY 13101) or a ketamine hydrochloride-xylazine mixture (Baer et al. 1978, Cornely 1979). The search area was restricted within specified bounds defined in association with the location of the fixed-location tracking shelters to optimize signal reception and triangulation. Attempts were made to selectively dart adult animals as these were most likely to have well established territories and less prone to disperse from the immediate study area. Captured animals were ferried to a central processing area and fitted with a radio transmitter (Kolz et al. 1973) operating on 1 of 12 frequencies in the 164 mHz range, emitting signals at rates of 60, 90, or 120 per minute. A single toe was surgically amputated from a fore foot to

enable individual track identification at scent stations (Andelt and Gipson 1980). Other data recorded included sex, weight, general physical condition, capture location, and estimated age based upon tooth wear. Animals less than 1-year old were classified as juveniles and all others as adults. A lower premolar was extracted for verification of age by radiographs and/or cementun annuli analysis (Linhart and Knowlton 1967, Davison 1980). Animals were held overnight to allow the effects of the drugs to wear off and released the following day at the capture location.

Instrumented coyotes were monitored from fixed-station tracking shelters equipped with 2 5-element yagi antennas stacked horizontally and coupled out-of-phase with a sum-and-difference hybrid junction. Antenna orientation was established and maintained with a "beacon" transmitter. Baseline distances between the tracking shelters in the Idaho and Texas study areas were 9.75 km and 5.75 km, respectively.

Relocations, using standard triangulation techniques (Heezen and Tester 1967), were taken at 10-minute intervals in Idaho and 15-minute intervals in Texas, 16 hours per day from 1600 hr to 0800 hr to enable a detailed assessment of movement patterns in a relatively short time period. Data were read as azimuths from each antenna set, recorded on modified FORTRAN coding forms, key punched onto computer cards, and later processed at the Los Alamos Scientific Laboratory (LASL), Los Alamos, New Mexico.

Base maps for each study area were entered into a computer from 7.5 minute U.S. Geological Survey maps with a Tektronics Model 4954

Graphics Tablet and MAPPER (Dahl 1979), a computer graphics software package developed at LASL. Azimuth readings were converted by a FORTRAN program to Universal Transverse Mercator (UTM) x-y coordinates compatible with the base maps and plotted. Using an FR-80 film recorder, 35 mm slides of each coyote's daily movement patterns and total area of use were produced (White 1979). Other methods used in the analysis of spatial utilization were HOMER, a computer software package developed by the Cedar Creek Laboratory, University of Minnesota (Rongstad and Tester 1969), and an SPSS crosstabs program to overlay the study area base maps with 0.25 km^2 or 0.01 km^2 grids that would depict the number of relocations and percent of total relocations in each grid cell. Use of grid cells to assess spatial utilization have been described by Rongstad and Tester (1969), Fossey (1974), Caro (1976), Waser and Wiley (1979), and Laundre and Keller (1981).

After the initial 2-3 week monitoring period to assess each coyote's movement patterns, modified scent-station survey lines (Linhart and Knowlton 1975, Roughton and Sweeny 1982) were established and run for 10 days in Idaho and 2 10-day periods in Texas to assess whether or not differential vistitation rates to the scent stations in different parts of each coyote's home range occurred. Monitoring of the coyote movement patterns continued throughout this period.

Scent-station survey lines consisted of artificial scent stations located immediately adjacent to the edge of a road and

0.48 km (0.3 mi) apart along predetermined routes. Each scent station consisted of a 0.91 m (3 ft) circle of sifted earth with a small perforated plastic capsule in the center supported 1.27-2.54 cm (0.5-1.0 in) above the surface by a small stick. Capsules were filled with about 1 g of FAS attractant (Roughton 1982) and were consecutively numbered. The stations were alternated between left and right sides of the road to reduce influence of prevailing winds. Capsules that were carried off or destroyed by animals, clogged with blowing dirt, washed out by rain, or disturbed by humans or vehicles were replaced as needed. All capsules were replaced on the 5th day of the 10-day surveys. Scent-station lines were checked daily and coyote visits by tagged and untagged animals (based upon tracks) were recorded. Visited scent stations were smoothed over so that new tracks could be distinguished on succeeding days. Since it is impossible in most cases to distinguish the number of individuals leaving tracks at a scent station, only 1 visit per scent station per night was recorded.

Following completion of the scent station phase of the study, #3 Victor traps with off-set steel jaws and tranquilizer tabs (Balser 1965) were selectively set within the core areas (Kaufman 1962) of each coyote's home range to ascertain whether or not coyotes shifted their movement patterns and utilization of space as a result of being trapped. Captured animals were held overnight to allow the effect of the tranquilizer (Tranvet, propriopromazine hydrochloride) to wear off and released at the capture site the following day. Traps were operational until the target animal was captured or for a

maximum of 30 days. After all traps were removed from the study area, telemetric monitoring of movement patterns resumed for 10 days. Potential changes in movement patterns and spatial utilization were determined by comparing relative frequency of use during the post-trapping period within a 200 m and 500 m radius of the site of capture with the relative frequency of use of these respective areas during the pretrapping period.

Differences in scent station visitation and shifts in spatial utilization as a result of trapping were analyzed with a Mann-Whitney test (Zar 1974:109-114) and a Wilcoxon rank sum test (Hollander and Wolfe 1973:67-75).

RESULTS

Pen Studies

Response to Novel Objects.--Type of coyote response, the amount of time spent within 5 m, and the number of approaches to the novel objects in familiar and unfamiliar environments are given in Table 1. The neophobic or avoidance category of response included circling the object, approach-withdrawal, examination (visually and olfactorally) from a distance, and non-use of the pen in the vicinity (<10 m) of the object after initial detection. Nonavoidance behaviors included direct approach to the object with close (<1 m) visual and olfactory examination. Some coyotes exhibited a "cautious demeanor" characterized by a direct but slow approach to the object, then when within 1 to 2 m stretching forward for visual and olfactory inspection and continuing to advance in this fashion. They seldom circled the object or showed the approach-withdrawal behaviors of the neophobic category.

With the exception of the amount of time spent within 5 m of the novel objects in familiar environments ($U = 28$, $P < 0.02$) there were no significant differences in the behaviors of the hand-reared and nonhand-reared coyotes. Coyotes 2835 and 2837 (Table 1) spent the greatest amount of time within 5 m of novel objects in familiar environments, but their behaviors were at opposite extremes. Coyote 2835 showed no avoidance of the object and spent considerable time pawing and chewing the object. Coyote 2837 responded neophobically

Table 1. Response of captive coyotes to novel objects in familiar and unfamiliar environments.

Coyote	Sex	Unfamiliar environment			Familiar environment		
		Behavioral response[a]	No. seconds within 5 m	No. of approaches	Behavioral response	No. seconds within 5 m	No. of approaches
2704 H[b]	♀	II	26	2	II	113	3
2631	♀	I	19	2	III	89	5
2833 H	♂	II	117	4	III	378	17
2879	♀	II	147	6	III	20	4
2875	♀	I	154	7	III	84	7
2760 H	♂	II	49	2	II	226	9
2754 H	♂	I	46	3	III	426	10
2835 H	♂	I	96	2	I	1143	12
2837 H	♂	I	116	7	III	1472	28
2639	♀	I	56	5	I	320	9
2724	♀	I	32	2	III	0	0
Mean			78.0			388.27	9.45
SE			14.9			145.11	2.32

[a] I = Nonavoidance

II = Cautious

III = Neophobic

[b] Hand-reared coyotes

with numerous approach-withdrawal bouts. Nonhand-reared coyotes demonstrated the same behavioral extremes. With no consistent and demonstrated differences in behaviors of the two groups of coyotes with respect to the variables measured in this study, subsequent analyses were done without regard to rearing history.

Differences in the 3 behavioral categories within familiar and unfamiliar environments were significant ($X^2 = 10.44$, $\underline{P} < 0.01$, Table 2), with coyotes showing more avoidance behaviors in the familiar than unfamiliar environment. In chi-square analyses of the contingency tables it is recommended that no more than 20% of the expected values be less than 5.0 (Zar 1974:66), a recommendation violated in this data set due to the small sample size. The behavioral categories of caution and neophobia were combined and a 2 x 2 contingency table constructed of the data (Table 3).

Differences in the behavioral categories of caution and nonavoidance in familiar and unfamiliar environments were significant (Table 3, $X^2 = 4.70$, $P < 0.05$) with coyotes showing more cautious behaviors in the familiar than unfamiliar environment. Sample sizes, however, were again too small to comply with the above recommendation for contingency table analyses. The Fisher exact test is more applicable to 2 x 2 contingency table analyses when cell frequencies are small (Zar 1974:63). Analysis of the data in Table 3 by this procedure was significant ($P = 0.0373$). A greater proportion of time was spent investigating novel objects (time within 5 m) in the familiar than unfamiliar environment ($W = 2.18$, $P < 0.02$). The number of approaches towards the novel objects were

Table 2. Two x three contingency table of frequencies of types of coyote behavioral responses to novel wooden objects.

	Nonavoidance	Cautious	Neophobic
Unfamiliar environment	7	4	0
Familiar environment	2	2	7

$X^2 = 10.44$

$P < 0.01$

Table 3. Two x two contingency table of frequencies of types of coyote behavioral responses to novel wooden objects.

	Cautious	Nonavoidance
Unfamiliar environment	4	7
Familiar environment	9	2

$X^2 = 4.70$

$\underline{P} < 0.05$

also greater in the familiar than unfamiliar environment ($W = 2.92$, $P < 0.02$) due to the approach-withdrawal behavior frequently exhibited in the familiar environment. In light of these results, H1, H2, and H3 are rejected.

Response to Scent Stations.--Type of response by coyotes, amount of time spent within 5 m, and the number of approaches to artificial scent stations in familiar and unfamiliar environments is given in Table 4. Differences in the 3 behavioral categories within familiar and unfamiliar environments were not significant ($X^2 = 5.14$, $P < 0.10$, Table 5). Expected cell frequencies were again too small to comply with the previously cited recommendation for contingency table analyses. When the behavioral categories of caution and neophobia were combined into a 2 x 2 space on both sides contingency table differences in the behavioral categories of caution and nonavoidance in familiar and unfamiliar environments were significant ($X^2 = 4.19$, $P < 0.05$; Fisher Exact Test $P = 0.0483$, Table 6), with coyotes showing more avoidance behavior in the familiar than unfamiliar environment. More time was spent investigating the scent stations in the familiar environment ($W = 2.64$, $P < 0.01$), but there was no difference in the number of approaches to the scent stations ($W = 0.96$, $P < 0.34$). Hypotheses 1 and 2 are thus rejected, but I was unable to reject #3.

Comparison of Coyote Response to Novel Objects and Scent Stations.--In the unfamiliar environment novel objects elicited a significantly greater amount of time spent within 5 m than did the

Table 4. Response of captive coyotes to scent stations in familiar and unfamiliar environments.

Unfamiliar environment					Familiar environment				
Coyote	Sex	Behavioral response[a]	No. seconds within 5 m	No. of approaches	Coyote	Sex	Behavioral response	No. seconds within 5 m	No. of approaches
2928	♀	I	21	1	2912	♀	I	80	1
2748	♂	I	9	1	2920	♂	III	71	1
2729	♀	I	5	1	2891	♀	III	87	1
2910	♂	I	9	1	2904	♂	III	310	4
2889	♀	I	3	1	2916	♀	III	62	2
2894	♂	I	10	1	2926	♂	I	15	1
2918	♀	II	36	2	2906	♀	III	28	1
2908	♂	I	3	1	2924	♂	I	13	1
					2567	♀	II	90	2
					2573	♀	II	27	2
					2569	♂	I	13	1
					2261	♂	III	125	2
					2575	♂	I	4	1
					2565	♀	I	8	1
Mean (SE)			12.0 (3.99)	1.13 (0.12)				66.64 (21.32)	1.50 (0.23)

[a] I = Nonavoidance

II = Cautious

III = Neophobic

Table 5. Two x three contingency table of frequencies of types of coyote behavioral responses to artificial scent stations

	Nonavoidance	Cautious	Neophobic
Unfamiliar environment	7	1	0
Familiar environment	6	2	6

$X^2 = 5.14$

$\underline{P} < 0.10$

Table 6. Two x two contingency table of frequencies of types of coyote behavioral responses to artificial scent stations.

	Cautious	Nonavoidance
Unfamiliar environment	1	7
Familiar environment	8	6

$X^2 = 4.19$

$\underline{P} < 0.05$

scent stations (U = 79, P < 0.005) as well as the greater number of approaches (U = 85.5, P < 0.001). Results were the same in the familiar environment with more time spent within 5 m of the novel objects (U = 140, P < 0.001) and a greater number of approaches (U = 124, P < 0.01). Although quantitatively different, response to the 2 types of novel stimuli were qualitatively similar with response to the scent stations being less intense than those elicited by the small black objects.

Field Studies

INEL.--Five adult coyotes were telemetrically tagged on the INEL study area August 20-22, 1979 (Table 7). Monitoring of the coyotes between August 27 and September 22 provided 4,837 relocations ($\bar{x}$ = 976, SE = 12.2) upon which to determine each coyote's movement patterns. Figures 4 and 5 are examples of the plotted relocations and grid cell frequencies, respectively. Maps and grid cell frequencies of the other INEL coyotes are given in Appendix A. Scent-station survey lines were run October 18-28, resulting in 49 coyote visits in 1,963 scent-station nights. Three visits were by marked coyotes. Coyote 03 visited 2 sequential scent stations approximately 4.8 km outside of its defined home range on the 3rd night of the survey. Coyote 04 visited a scent station peripheral to its home range on the 6th night.

The results of the INEL scent-station survey were inconclusive due to heavy rain the 1st and 2nd nights of the 10-day survey period that potentially washed out or obliterated tracks. The 3 visits were insufficient for statistical analysis and hence inadequate to

Table 7. INEL coyote telemetry relocations.

Coyote	Age/sex	Number of relocations		
		Aug 27 - Sep 22	Oct 18 - Oct 28	Total
01	adult ♀	1,004	805	1,809
02	adult ♂	959	758	1,717
03	adult ♂	967	633	1,600
04	adult ♂	929	668	1,597
05	adult ♀	978	777	1,755
Total		4,837	3,641	8,478
Mean (SE)		967.4 (12.2)	728.2 (33.0)	1,695.6 (42.2)

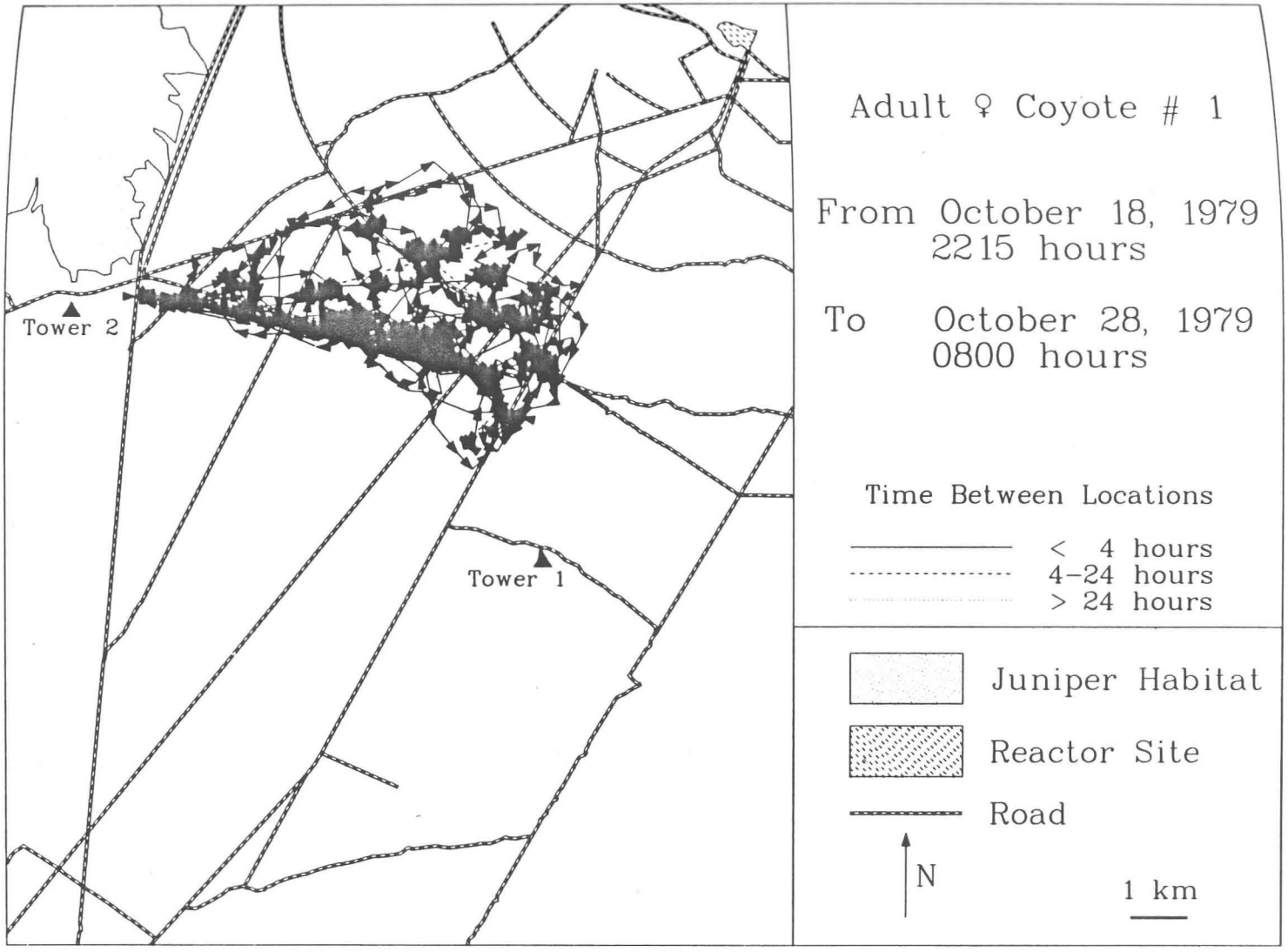

Fig. 4. Distribution of telemetry relocations for coyote 01 on the INEL.

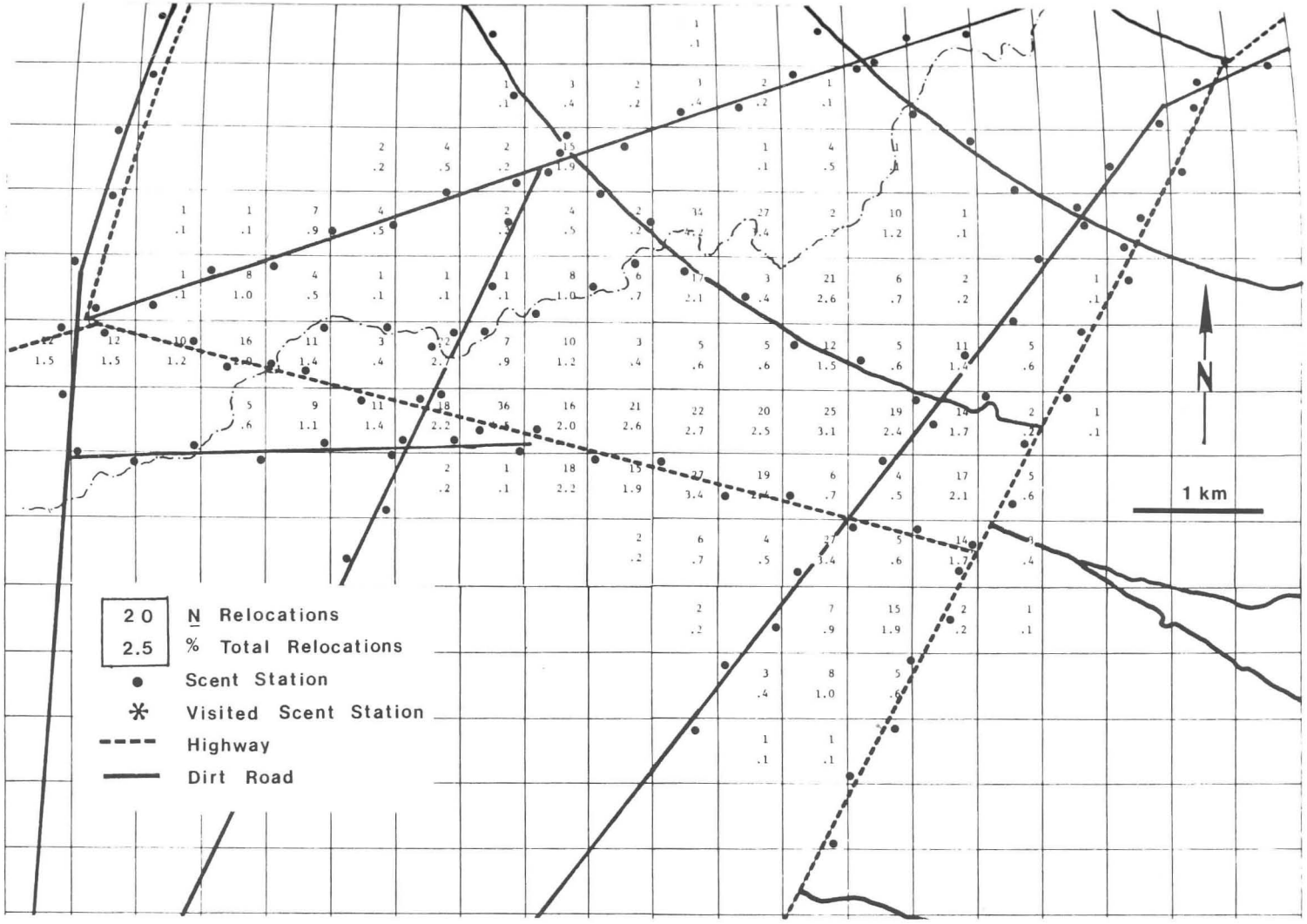

Fig. 5. Grid cell frequency distribution of telemetry relocations for coyote 01 on the INEL.

test H4.

Trapping instrumented animals to assess potential changes in movement patterns as a result of the trapping experience was omitted due to subfreezing temperatures. The risk of foot damage to trapped coyotes at such temperatures was too great. Any changes in movement patterns associated with the trapping experience would be confounded with potential injury and hence difficult to interpret. A change could have been attributable to limited ability to travel because of foot damage, a shift away from the site of the trap experience, or a combination of the two.

Freer.--Nine coyotes were telemetrically tagged on the Clinton Manges Ranch February 14-20, 1980 (Table 8). The initial monitoring period of February 21-March 6 yielded the relocations ($\bar{x}$ = 628, SE = 12.70) to determine the coyote's respective movement patterns (Figs. 6, 7 are examples). The maps and grid cell frequencies of the other Freer coyotes are given in Appendix B.

The positions of coyotes 01 and 02 within the study area with respect to the baseline between the 2 tracking shelters posed problems in plotting relocations. Using standard triangulation techniques, it is preferrable to have azimuths intersecting as close to 90 degrees as possible. Extremely acute or obtuse angles of intersection coupled with minor errors in the telemetry system result in gross misrepresentation of the actual location of the animal. For this reason telemetry analyses often discard data points when the angle of intersection of the azimuths are $<20^{o}$ or

Table 8. Coyote telemetry relocations on the Freer study area, Texas.

Coyote	Age/Sex	Number of relocations			
		Feb 21 - Mar 06	Mar 19 - Apr 10	Jun 3 - Jun 13	Total
01	adult ♀	647	1,195		1,842
02	adult ♀	578	976	295	1,849
03	juvenile ♂	551	1,278	259	2,088
07	adult ♀	652	746		1,398
08	adult ♀	659	1,180	353	2,192
09	adult ♀	662	1,258		1,920
10	juvenile ♀	636	1,214	469	2,319
11	adult ♀	636	1,197	447	2,280
12	juvenile ♂	631	1,259	492	2,382
Total		5,652	10,303	2,315	18,270
Mean (SE)		628.0 (12.70)	1,144.8 (58.0)	385.8 (39.72)	2,030 (104.0)

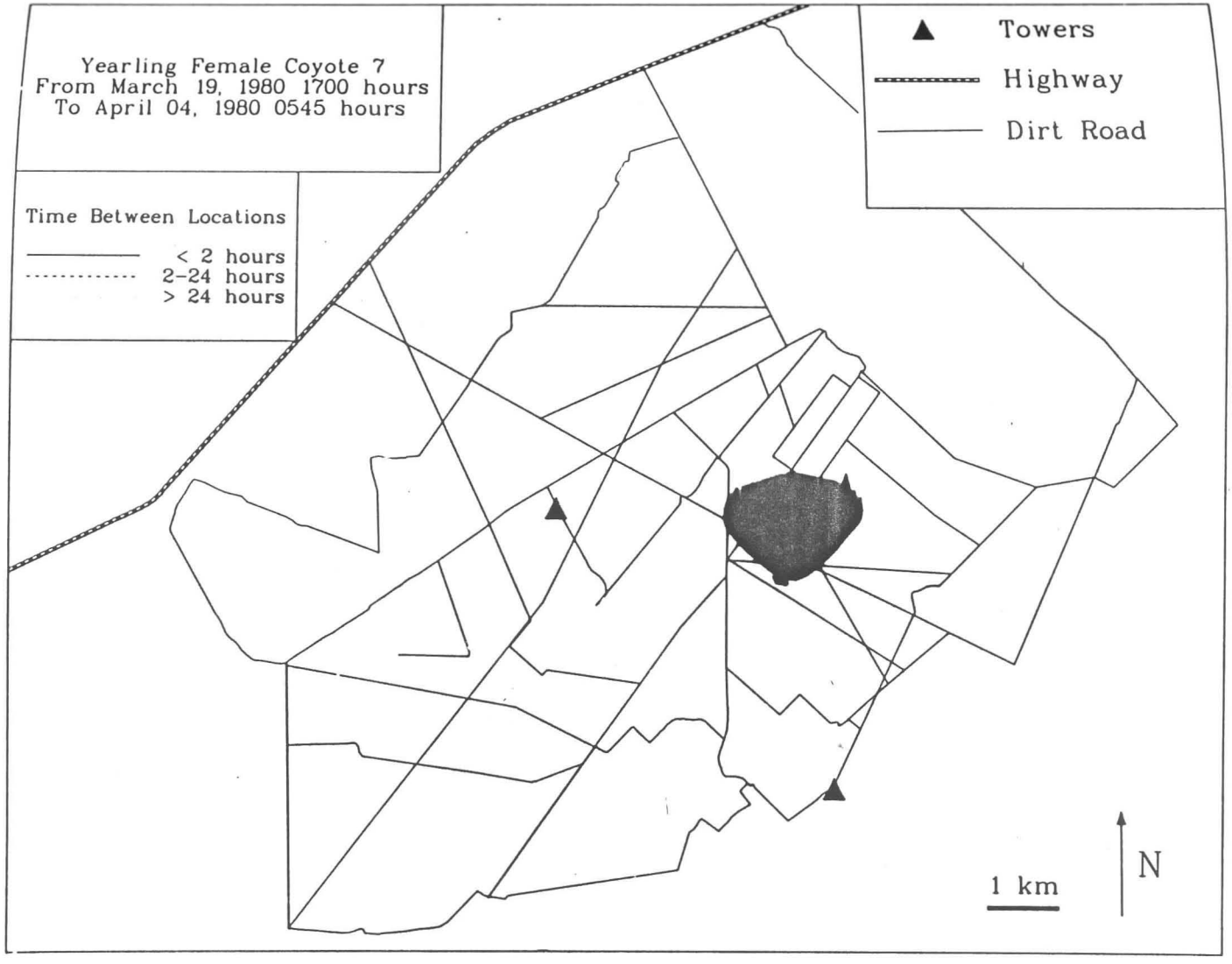

Fig. 6. Distribution of telemetry relocations for coyote 07 on the Freer study area, Texas.

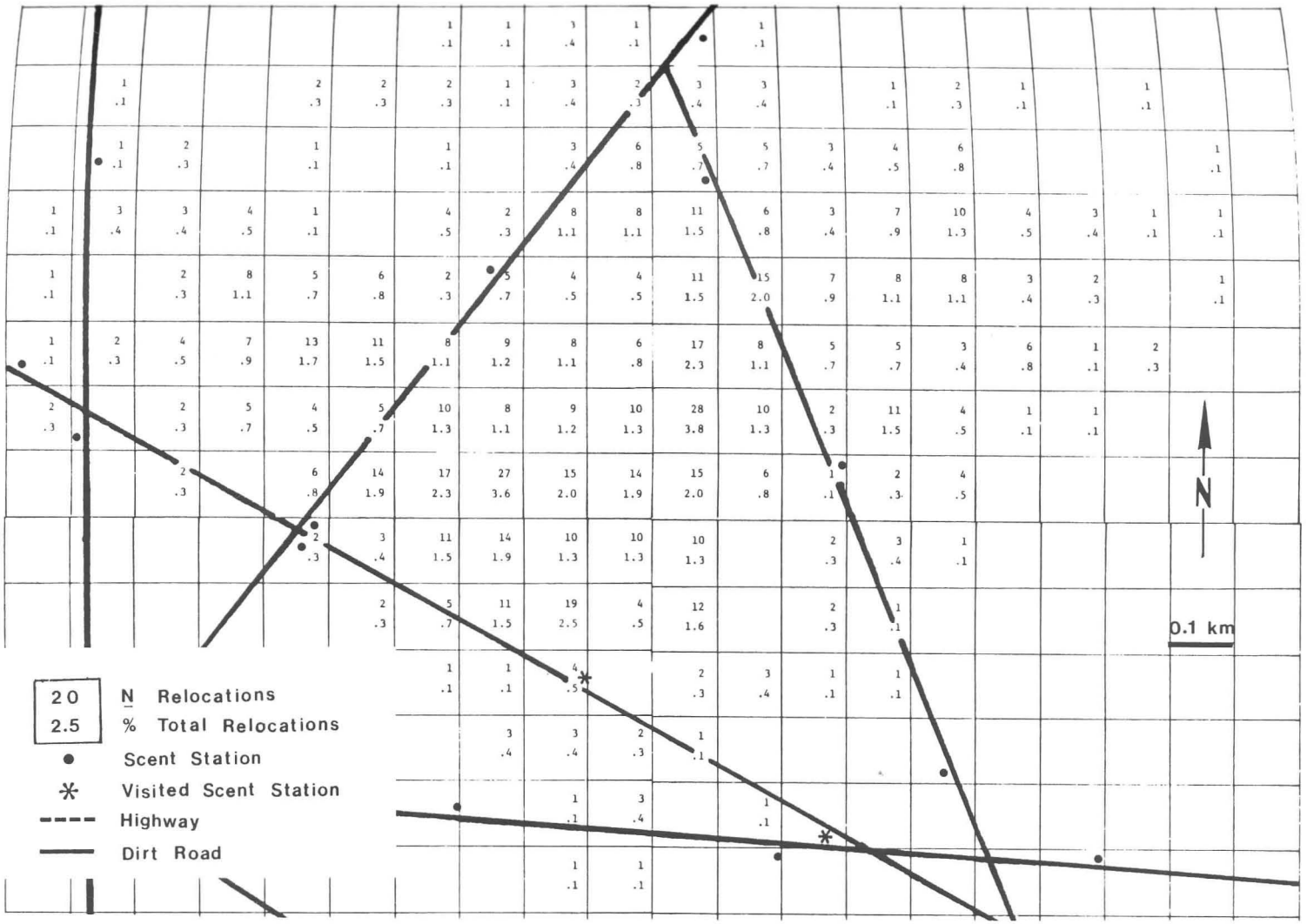

Fig. 7. Grid cell frequency distribution of telemetry relocations for coyote 07 on the Freer study area, Texas.

$>160^{o}$. Many of the relocations of coyote 02 were deleted as a consequence of such spurious data points. Similar problems occurred in portions of the home range of coyote 01.

Coyotes 01 and 10 had disjunct and/or wandering spatial utilization patterns (terminology from Hibler 1977). The larger areas used by these animals, necessitated use of 0.25 km^2 grids rather than 0.01 km^2 grids for analyses of data. In some cases analyses from the 6 coyotes with contiguous spatial use patterns are provided separately. The differences are denoted by use of the terms "6 coyotes" and "8 coyotes."

Scent-station survey lines were operated for 2 consecutive 10-day periods March 19-April 10 to adequately cover respective portions of the study area. Some coyotes, because of their proximity to the dividing line, were exposed to scent stations for more than 10 days. In 2,345 scent-station nights 462 coyotes visits were recorded, 23 by tagged animals (Table 9). All initial visits by tagged animals were either peripheral to (6) or outside (2) the defined home ranges; no initial visits were inside the home ranges. There was no significant difference in the day of first visit between juvenile ($\bar{x}$ = 5.60, SE = 1.85) and adult coyotes ($\bar{x}$ = 5.60, SE = 1.78).

Twenty-one of 23 visits were peripheral or outside the defined home ranges (Table 10). This would appear to provide evidence to reject H4. This hypothesis, however, was formulated under the assumption that coyotes would have equal or proportional exposure to scent stations inside, peripheral, and outside their home ranges.

Table 9. Relocations (N and %), day visited, and home range zone of scent station grid cells visited by marked coyotes on the Freer study area, Texas.

Coyote	Relocations[a]	% relocations[b]	Day visited	Home range zone
01	2	0.2	11	outside
	89	7.4	13	inside
03	2	0.2	8	peripheral
	4	0.3	9	peripheral
07	1	0.1	5	peripheral
	4	0.5	9	peripheral
08	9	0.8	3	peripheral
	4	0.3	5	peripheral
	7	0.6	12	peripheral
	2	0.2	13	peripheral
09	1	0.1	1	peripheral
	37	2.9	7	inside
	1	0.1	14	outside
	1	0.1	14	outside
	1	0.1	16	outside
10	1	0.1	7	outside
	1	0.1	7	outside
	19	1.6	10	peripheral
11	4	0.3	8	peripheral
12	12	1.0	2	peripheral
	1	0.1	3	outside
	12	1.0	8	peripheral
	8	0.6	10	peripheral

[a]Number of relocations within the scent station grid cell

[b]Percent of the total number of relocations the scent station grid cell contained

Table 10. Scent station visitations on the Freer study area, Texas, with respect to home range zones and coyote age/sex classes.

	Sample size	Number of scent stations visited			
		Inside	Peripheral	Outside	Total visits
Adult ♀♀	5	1[a]	8	3	12
		(2)[b]		(4)	(14)
Juvenile ♀♀	1		(1)	(2)	(3)
Juvenile ♂♂	2		5	1	6
Total		1	13	4	18
		(2)	(14)	(7)	(23)

[a]Figures for 6 coyotes

[b]Figures for 8 coyotes

This may not have been the case. Only 6 scent stations were located inside coyote home ranges while 44 were peripheral (Table 11).

The question arises whether scent-station survey lines were biased in their placement or whether coyotes were demonstrating differential responses to scent stations with regard to home range limits. Tests of association of visits and nonvisits with scent station location were not significant (6 coyotes, $X^2 = 1.05$, $0.05 < \underline{P} < 0.25$; Fisher exact test $\underline{P} = 0.34$; 8 coyotes, X^2 1.62, $0.25 < \underline{P} < 0.10$; Fisher exact test $\underline{P} = 0.08$). Coyotes then were not visiting scent stations disproportionately in any one zone given what was available to visit. Tests of the frequency of use of grid cells with visited scent stations versus frequency of use of grid cells with nonvisited scent stations were not significant (6 coyotes, $\underline{W}^* = 0.6230$, $\underline{P} < 0.54$; 8 coyotes, $\underline{W}^* = 0.3521$, $\underline{P} < 0.72$). Analzyed on an individual coyote basis, the frequency of use of grid cells with visited scent stations versus nonvisited scent stations were not significant. The location of scent-station survey lines was then not biased with respect to frequency of use of the home range, i.e., the various home range zones were representatively sampled given the roads available to use for scent-station survey lines.

Frequency of use of grid cells as small as 0.01 km^2 could be influenced by minor error in the telemetry system. To accommodate this potential error, an averaged frequency was calculated from the 8 adjacent grid cells surrounding the grid cell containing the scent station. Results of the analysis of this data set were not

Table 11. Visited and non-visited scent stations with respect to home range zones for 6 coyotes on the Freer study area, Texas.

Coyote	03		07		08		09		11		12		Scent stations per zone
	#[d]	%[e]	#	%	#	%	#	%	#	%	#	%	
Visited scent stations													
I[a]							37	2.9					1
II[b]	2	0.2	4	0.5	4	0.3	1	0.1	4	0.3	8	0.6	13
	4	0.3	1	0.1	9	0.8					12	1.0	
					7	0.6					12	1.0	
					2	0.2							
III[c]							1	0.1			1	0.1	4
							1	0.1					
							1	0.1					
Total visited	2		2		4		5		1		4		18
Non-visited scent stations													
I	10	0.8			8	0.7			12	1.0	17	1.4	5
									18	1.5			
II	5	0.4	1	0.1	2	0.2	1	0.1	1	0.1	1	0.1	31
	5	0.4	5	0.7	4	0.3	6	0.5	2	0.2	3	0.2	
	7	0.5	5	0.7	2	0.2	5	0.4	2	0.2			
	4	0.3	1	0.1	4	0.3	2	0.2					
	1	0.1	1	0.1	2	0.2	1	0.1					
			2	0.3	1	0.1	3	0.2					
			2	0.3	4	0.3	1	0.1					
III	1	0.1					2	0.2			1	0.1	7
							3	0.2			1	0.1	
							4	0.3					
							4	0.3					
Total not visited	7		7		8		11		5		5		43
Total scent stations within coyote's total area	9		9		12		16		6		9		61

[a] I = Inside home range

[b] II = Peripheral to home range

[c] III = Outside home range

[d] # = Number of relocations in the scent station grid cell

[e] % = Percent of total relocations in the scent station grid cell

significant on a grouped (W^* = 0.6994, P < 0.48) or individual coyote basis.

There was a significant difference between peripheral and inside zones with respect to the percent of total relocations in grid cells with visited scent stations (U = 28, P < 0.02, Table 12). Differences in peripheral and outside zones were also significant in this regard (U = 88, P < 0.005). No difference was noted between outside and inside zones (U = 14, P < 0.10). This was potentially due to small sample sizes in each area and the large number of tied ranks in the nonparametric analysis.

A greater number of scent stations were visited peripheral to and outside the home ranges than inside (X^2 = 147.5, P < 0.001, Table 13). Additionally, a ratio of the number of relocations in visited scent station grid cells per scent station visit could also be used as an indicator of differential behavioral response by coyotes in the respective home range zones (Table 13). Coyotes appear to require greater exposure to scent stations inside the home range (102.0 relocations/visit) than peripheral (12.0 relocations/visit) or outside (5.0 relocations/visit) before visiting a scent station. The single visit inside the home ranges, however, was confounded by the fact that the coyote had previously visited a peripheral scent station.

The paucity of scent stations in core areas of coyote home ranges on the Freer study area may be related to home range size and the relative distribution of roads in each of the home range zones. Coyote home ranges on the Freer study area were significantly

Table 12. Relocations (N and %) and day visited of scent station grid cells with regard to home range zone for coyotes on the Freer study area, Texas.

Number of relocations			% relocations			Day visited		
I[a]	II[b]	III[c]	I	II	III	I	II	III
89*[d]	2	2*	7.4*	0.2	0.2*	13*	8	11*
37	4	1	2.9	0.3	0.1	7	9	16
	4	1		0.5	0.1		9	14
	1	1		0.1	0.1		5	14
	4	1*		0.3	0.1*		5	7*
	9	1*		0.8	0.1*		3	7*
	7	1		0.6	0.1		12	3
	2			0.2			13	
	1			0.1			1	
	19*			1.6*			10*	
	4			0.3			8	
	12			1.0			2	
	12			1.0			8	
	8			0.6			10	
$\bar{X}$ 63.0	6.36	1.14	5.15	0.54	0.11	10	7.36	10.29
(37.0)[e]	(5.38)	(1.0)	(2.9)	(0.46)	(0.10)	(7.0)	(7.15)	(11.75)
SE 26.0	1.39	0.14	2.25	0.11	0.02	2.99	1.38	1.80
(0.0)	(1.07)	(0.0)	(0.0)	(0.09)	(0.0)	(0.0)	(1.03)	(2.96)

[a] I = Inside home range
[b] II = Peripheral to home range
[c] III = Outside home range
[d] * = Data points excluded in the calculations for 6 coyotes
[e] Means and SE for 6 coyotes are in parentheses

Table 13. Comparison of the number of relocations per visited scent station with regard to home range zone for 6 coyotes on the Freer study area, Texas.

Home range zone	No. relocations of marked coyotes in grid cells with scent stations			No. scent stations in grid cells used by marked coyotes	No. of visits	% of stations visited	No. relocations in scent-station grid cells per scent-station visit
	Visited stations	Non-visited stations	Total				
	(A)	(B)	(C)	(D)	(E)	F=Ex100/D	(G=C/E)
Inside	37	65	102	6	1	16.7	102.0
Peripheral	70	86	156	44	13	29.5	12.0
Outside	4	16	20	11	4	36.4	5.0
Total	111	167	278	61	18	29.5	15.4

smaller than those on the INEL (U = 39, $P < 0.05$; Tables 14, 15). Smaller home ranges combined with a higher percentage of road comprising home range boundaries resulted in less road in the core areas. Additionally, since spacing between scent stations remained constant (0.48 km), fewer were accommodated within the smaller home ranges.

Three tagged coyotes (09, 11, 12) and 15 other coyotes were trapped between May 13 and June 11 (1,057 trap nights) for purposes of assessing potential shifts in movement patterns and spatial utilization as a result of a trapping experience. The 3 tagged animals were captured during the first 3 days of trapping. Coyote 09 died 7 days after release, but the cause of death was not determined. Monitoring of coyote movement patterns resumed June 3 for 10 days.

Relative frequency of relocations within 200 m of the trap site was significantly different pre- and post-trapping for coyote 11 (W^* = 1.98, $P < 0.05$), but there was no difference in space utilization within 500 m of the trap site (W^* = 0.20, $P < 0.84$). Frequency of relocations pre- and post-trapping was significantly different within 200 and 500 m of the trap site for coyote 12 (W^* = 3.66, $P < 0.0002$; W^* = 2.87, $P < 0.004$, respectively).

A sample of 2 coyotes is an inadequate test of H5. The shifts in spatial utilization appear real and may be a direct response to the trapping experience, however, such shifts could also be the result of seasonal changes in home range use related to phenological

Table 14. Home ranges (km^2) of coyotes on the Idaho National Engineering Laboratory.

Coyote	Sex	Aug 27 - Sep 22	Oct 18 - Oct 28	Mean (SE)
01	♀	18.70	21.68	20.19 (1.49)
02	♂	12.90	14.61	13.76 (0.86)
03	♂	9.63	8.11	8.87 (0.76)
04	♂	30.25	21.23	25.74 (4.51)
05	♀	16.06	19.47	17.77 (1.70)
Mean (SE)		17.51 (3.52)	17.02 (2.55)	17.27 (2.85)

Table 15. Home ranges (km^2) of coyotes on the Freer study area, Texas.

Coyote	Sex	Feb 21-Mar 06	Mar 19-Apr 10	Jun 03-Jun 13	Mean (SE)
01	♀	23.49	11.78		17.64 (5.85)
02	♀	16.08	11.32	19.58	15.66 (2.40)
03	♂	1.49	3.00	2.43	2.47 (0.29)
07	♀	1.84	2.02		1.93 (0.09)
08	♀	2.43	2.25	2.90	2.53 (0.20)
09	♀	2.69	3.65		3.17 (0.48)
10	♀	21.81	6.89	23.43	17.38 (5.27)
11	♀	4.48	3.57	4.40	4.15 (0.29)
12	♂	1.42	2.33	2.02	1.92 (0.27)
Mean (SE)[a]		8.41 (3.09)	5.20 (1.29)	9.13 (3.96)	7.43 (2.38)
Mean (SE)[b]		2.39 (9.47)	2.80 (0.29)	2.94 (0.52)	2.70 (0.35)

[a] 8 coyotes

[b] 6 coyotes with contiguous spatial utilization pattern

or weather changes, or a change in social relationships within a coyote group. The home ranges of coyote 09 and 12 overlapped completely. Death of a potentially dominant adult may have changed how the juvenile subsequently used the area. Additionally, monitoring of the animal's spatial utilization 4 weeks post-capture may have documented only a temporary avoidance of the trap site.

DISCUSSION

Prefatory Remarks

Field Versus Laboratory Studies.--Two approaches to the research of animal behavior are commonly pursued: laboratory studies and field studies, either of which can be descriptive, correlative, or manipulative. Studies of curiosity, exploratory behavior, and response to novelty have come largely under the realm of laboratory experiments conducted by psychologists on individual animals in confined environments. Laboratory experiments have the advantage of permitting better control of variables and allowing the use of more sophisticated instrumentation and techniques. Since laboratory settings frequently differ from natural environments, observed behaviors may be aberrant or pathological, making it difficult to generalize results to natural environments (Wittenberger 1981). In contrast, field studies permit behaviors to be observed within the context of the animal's "natural" environment wherein the ecological and adaptive significance of behaviors are more readily discerned. They lack, however, the control over the myriad of variables influencing an animal's behavior and thus fall short of permitting strong scientific inference (Platt 1964). Confidence in interpretation of field data is enchanced if observed results were predicted in advance based upon theoretical considerations.

Discussion of Results

Pen Studies.--Nine of 11 captive coyotes responded in a neophobic or cautious manner to the small novel objects when encountered in a familiar environment while only 4 of 11 coyotes did so in an unfamiliar environment. The findings are consistent with those of other mammalian studies regarding novel object response, but the degree of neophobia was generally less than that found in wild rats (Barnett 1958a, c, Cowan 1976, 1977). In only 1 instance (coyote 2724, Table 1) did a coyote fail to approach within 5 m of the object during the 8-hour observation period. One other coyote (coyote 2879, Table 1) avoided the object until the final 30 minutes of observation and then made a few approaches of very short duration before retreating. At the other extreme, coyote 2835 (Table 1) showed no avoidance and spent a considerable amount of time pawing and chewing the novel object, even though he was in a familiar environment. Coyote 2835 was part of a litter hand-reared at the Millville Predator Research Site for a study of coyote dominance hierarchies (Knight 1978) and was thus potentially exposed to a wider variety of stimuli than captive coyotes reared by their mothers. Stokes and Balph (1965) stated that because captive animals frequently live in improverished environments (one low in diversity of stimuli), they characteristically lack the wariness of their wild counterparts. Organisms reared in captive environments may also have a smaller fund of experience to draw upon and perhaps a more limited ability to process information (Weisler and McCall 1976). Glickman and Sroges (1966) noted captive coyotes (and

carnivores in general) explored novel objects with little or no hesitation, attributing such behavior to the food-seeking habits of those species that require an immediate fearless response to a variety of forms.

The variability in behavior towards the novel objects in this study could be due, in part, to differences in rearing conditions. It could also be due to individual differences in coyotes. Littermates of coyote 2835 (coyotes 2833 and 2837, Table 1) showed neophobic responses to the novel object in the familiar environment. Dominance status of an individual may also influence a variety of behavioral responses. Summerlin and Wolfe (1971, 1973) reported that social subordination in cotton rats (S. hispidus) was directly correlated with a decrement in exploratory activity and increased neophobic response. Bekoff (1977) noted dominant coyote pups reared in captivity approached novel objects more readily than subordinates. Knight (1978), working with hand-reared coyotes, found no general relationship between rank and response to novel objects placed in familiar environments. She felt responses to novelty were individual differences rather than correlates of rank. Results of Brown's (1973) work with captive coyote pups were similar to those of Knight (1978) in that response to novelty was not consistent with rank.

The response of captive coyotes to scent stations in familiar and unfamiliar environments paralleled that of novel objects. Seven of 8 coyotes readily approached the scent stations in the unfamiliar

environments while only 2 of 14 coyotes readily did so in the familiar environment. Avoidance of scent stations was not as strong, however, as of the novel objects. Different stimuli may arouse an animal to different levels, depending upon the properties of the stimuli and the experience of the animal. In discussing his approach-withdrawal hypothesis Schneirla (1965) suggested strong stimuli caused withdrawal whereas weak stimuli caused approach. By varying prey characteristics (in terms of novelty) Coppinger (1969, 1970) and Ruggerio et al. (1979) elicited differing attack or avoidance behaviors by their respective avian predators, with familiar prey generally being attacked more frequently than unfamiliar prey. For an attack response to be elicited by a given prey item the level of arousal must exceed some lower threshold but not exceed an upper threshold resulting in avoidance.

Scent stations appear not to be as strong or discrepant a stimulus to captive coyotes as the small wooden objects in terms of the variables measured in this study. Coyotes spent more time investigating the wooden objects, approached or investigated the objects with greater frequency, and demonstrated more approach-withdrawal behaviors than with the scent stations. In the unfamiliar environment scent stations were visited on the first approach by 7 of 8 coyotes with no apparent approach-withdrawal conflict. In the familiar environment scent stations were visited on the first approach by 8 of 14 coyotes. Two of the 8 showed no hesitation in approaching the scent stations while 6 paused or circled the scent station before scoring a visit. Four other

coyotes scored on their second approach after walking beyond the 5 m mark and then returning to the scent station. One could speculate whether or not the coyotes would have returned to investigate the scent station had they not been in a confined environment.

That scent stations do not tend to produce a strong neophobic response is encouraging. Much research has gone into making the lure used in the scent stations attractive to coyotes (Linhart et al. 1977, Roughton and Bowden 1979, Roughton 1982, Roughton and Sweeny 1982). In spite of the initial neophobic response to scent stations in the familiar environment, 64.0% of the captive coyotes scored on their first approach. Lehner et al. (1976) noted initial neophobic responses of coyotes to novel odors in familiar environments. They suggested coyotes are likely not born with an innate fear of particular odors but learn to associate certain olfactory stimuli with aversive events encountered throughout their lives (Scott and Fuller 1965, Fox 1965).

Scent stations possess olfactory stimuli and strong visual stimuli. In the pens the 0.91 m (3 ft) diameter scent station was cut out of the grass/alfalfa sod producing a visual contrast with its surroundings. Similar contrasts are potentially produced in field situations when scent stations are placed along roadsides or if different colored earth is sifted upon the existing substrate.

The relative priority of the distance senses of vision, audition, and olfaction used by coyotes during hunting and travel probably depends upon the characteristics of the prey and the

environment. Vision seems to be the dominant sensory modality for coyote predatory behavior although the moment to moment role of the senses when hunting certainly varies according to environmental conditions (Wells and Lehner 1978). Coyotes are sensitive to a wide range of visual (Horn and Lehner 1975) and auditory (Peterson et al. 1969) stimuli, and canids in general are known for well developed olfactory capabilities (Kleiman 1966).

Shillito (1963) considered voles generalized animals in their sensory capabilities with all senses playing some part in exploratory behavior. She noted no particular difference in sensory use in familiar and unfamiliar environments, only the typical new object reaction to novel stimuli in a familiar area. Coyotes also seem to explore and investigate their environment with all sensory modalities, but are possibly more attentive when along the margins or outside their familiar areas (Hibler 1977). At any given moment, the sensory modality that returns the greatest amount of information about a given stimulus may be preferentially used. The novel objects were primarily a visual stimulus (except when marked by coyotes), whereas the scent stations possessed both visual and olfactory qualities. The importance of understanding coyote sensory modalities and response to various stimuli lies with the premise that we can better target our management and research techniques through a better understanding of coyote behavior (Knowlton 1972, Lehner 1976).

The behavioral responses of captive coyotes to novel stimuli was seldom as extreme as that found in wild rats (Barnett 1958a, c). It

is speculated that the strong avoidance of novel objects by wild rats is a product of selection caused by methods used in controlling rat populations (Chitty 1954, Shorten 1954, Barnett 1963:32, Cowan 1976, 1977). Tame laboratory rats not subject to these selection pressures do not show the neophobic responses of wild rats (Barnett 1958a, c, Cowan 1976, 1977). Coyotes reared in captivity, although not domesticated, may not respond as strongly or in exactly the same manner as wild coyotes subject to the many control efforts of man. Having few, if any, negative experiences associated with investigating novel objects, there may be less incentive for cautious or neophobic responses developing among captive coyotes. The extent to which generalizations can be made to a given population or species based upon studies of captive animals must necessarily be tempered with caution on both the part of the researcher and the reader. Despite the mechanisms involved or the potential for different behavior patterns between captive and noncaptive animals, for some species (the coyote included), captive studies may remain the most practical way to study and understand what behavioral patterns may occur in a natural environment.

Field Studies.--The low visitation rate by marked coyotes at the INEL site could be attributed to adverse weather conditions the first 2 nights of the 10-day scent-station survey period during which rain could have washed away any tracks in the scent stations. Had any marked coyotes visited scent stations on those night they may have habituated to the visual and/or olfactory stimuli to such a

degree that the scent stations would not elicit visitation on subsequent nights. Roughton (1980) felt animal reaction to scent stations was likely variable. Of those that visit scent stations, some may score the first station encountered, satisfy their "curiosity," and not approach subsequently encountered stations. Alternatively, lack of visits by marked animals may not have been influenced by rain. If one compares the mean day of first visit by the Texas coyotes ($\underline{\bar{x}}$ = 4.5, SE = 1.23; $\underline{\bar{x}}$ = 5.6, SE = 1.58 for the 6 and 8 coyotes, respectively) to that of the INEL coyotes ($\underline{\bar{x}}$ = 4.0, SE = 1.0) there is no significant difference. One could then speculate that the resident animals are less likely to visit scent stations the first few nights of a survey period due to various behavioral and spatial considerations. They may initially avoid the scent stations in a familiar environment until some degree of habituation has occurred. The lower visitation rates of INEL coyotes is also a reflection of the lower densities and/or indices of abundance of coyotes in Idaho compared to Texas (Knowlton 1972, Davison 1980, Bean 1981). Marked coyotes accounted for similar percentages of visits on the INEL (4.98) and Freer (6.12) study areas despite the discrepancies in number of visits.

Griffith (1976) estimated that only 28.8% of the coyotes that approached within 9.1 m (30 ft) of scent stations visited scent stations. The odor and/or visual aspects of the dusted scent stations attract some animals, but it seems more likely that wary individuals would avoid the disturbed ground, at least initially. Coyotes may also be less attentive to mild novel stimuli inside

their home ranges than outside (Hibler 1977). Since individuals whose home ranges includes parts of a scent-station line are not necessarily active over the entire area every night, the probability of encountering a scent station within its home range increases over time, assuming some sort of systematic travel pattern (Roughton 1980).

Comparisons between the INEL and Texas study areas should be tempered with caution because populations living under widely different habitat conditions may register different visitation rates (Roughton and Sweeny 1982). Hodges (1975) noted coyotes in more restricted (pine forest) habitats utilized roads to a greater extent than those in more open (sage brush) habitats. By virtue of the dense brush on the Texas study area, coyotes there may have spent more time traveling roads and therefore increased their potential exposure to scent stations compared to the INEL coyotes. The studies were also conducted at different times of year so seasonal differences in population size and density, movement patterns, and behavior need to be considered in any comparative evaluation.

The 3 visits by marked animals at INEL were peripheral (1) and outside (2) the defined home ranges of coyotes 04 and 03, respectively. The sample, however, was too small to adequately address the hypothesis of differential scent station visitation with respect to home range limits. On the Texas study area 21 of 23 visits by marked coyotes were peripheral or outside the defined home ranges. Significant differences in the number of visited scent

stations per number of relocations in the respective home range zones suggests coyotes require greater exposure to scent stations inside their home ranges before visitation occurs. Behavioral mechanisms underlying such differential visitation were discussed by Hibler (1977). He hypothesized coyotes in unfamiliar environments might be more attentive to stimuli and investigate and explore such areas more thoroughly. Welker (1961) found most animals became more attentive in unfamiliar environments. Rats in unfamiliar environments are known to engage in more exploratory behavior than when in familiar environments (Barnett 1958a, c). The same has been found to be true for voles (Shillito 1963). During exploratory sallies through new range, gorillas (Gorilla gorilla beringei) cease feeding in a leisurely manner and become "more attentive" to the possible presence of neighboring gorilla groups or other potential dangers (Fossey 1974). Camenzind (1974) observed coyotes to appear more alert as they approached the boundary or went outside their territory.

If coyotes are more attentive along the periphery or outside their home ranges they may be more likely to detect and respond to scent stations than when inside. This is not meant to imply that coyotes do not thoroughly explore the confines of their home range. As familiarity with a particular environment increases, attentiveness and exploration may be replaced by habituation. Upon repeated presentations, familiar stimuli fail to elicit the responses they once did (Welker 1961). A coyote could repeatedly and inadvertently bypass a scent station in a familiar environment

without detecting or responding to the stimulus. Griffith (1976) found 12.1% of the coyotes in his study passed within 0.45-1.36 m (1.5-4.5 ft) of a scent station without scoring, and an additional 35.2% passed within 2.27-5.00 m (7.5-16.5 ft) without scoring.

Detection of a scent station in a familiar environment may result in neophobia or avoidance of the station rather than approach and investigation. Wild rats avoid novel stimuli in familiar environments but readily approach these same stimuli in an unfamiliar environment (Shorten 1954, Barnett 1958a, c, Cowan 1976, 1977). Coyotes in pens respond to scent stations in a similar fashion. Coyotes in natural environments more frequently visited scent stations when near the periphery or outside their home range and may actually avoid those inside their home range until such time as they became more familiar with them. Griffith (1976) presented evidence based upon tracks in roads that some coyotes actively avoid scent stations. Young and Jackson (1951:186) felt detection of scent in an unnatural place by coyotes may arouse suspicion of the coyote resulting in a detour around the scent. They also noted fresh horse tracks along coyote runways were sufficient to cause coyotes to leave the trail for some distance. Balph and Balph (1981) noted animals in unfamiliar environments lack information about potential resources necessary for survival; and though there is some risk in investigating novelty, to remain ignorant about the environment may pose greater risks. An animal in a familiar environment is at no such disadvantage and can afford to respond to

novelty with some caution.

Previous experience with or repeated presentation of a stimulus can change or alter behavior during subsequent encounters. Both coyotes that visited scent stations inside their home ranges had previously visited scent stations peripheral to or outside their defined home ranges. Having previously investigated this stimuli and suffered no adverse consequences, they were more likely to approach it in a familiar environment. Higher scent station indices and percent coyotes scoring were found on roads more frequently traveled by humans (Griffith 1976). This was possibly due to coyotes being accustomed to investigating human litter and man-placed objects and therefore more likely to investigate scent stations.

Until recently, the documentation and behavioral significance of scent-marking in free-ranging coyotes received little attention (Barrette and Messier 1980, Bowen and Cowan 1980, Wells and Bekoff 1981). As in wolves (Peters and Mech 1975, Rotham and Mech 1979), coyotes scent-mark more frequently at territorial boundaries or areas of high intrusion (Bowen and Cowan 1980, Wells and Bekoff 1981). It has been estimated coyotes scent-mark about every 150 m while traveling. Consequently coyotes may encounter a recent scent-mark every 3 min at their normal rate of travel (Bowen and Cowan 1980). Peters and Mech (1975) calculated wolves mark an average of every 250 m and would encounter an olfactory sign about every 2 min and urine scent-marks every 3 min traveling throughout their territory. It would appear relatively easy for coyotes to recognize

territorial limits by scent alone under such conditions. Observations by Camenzind (1978), Bowen and Cowan (1980), and Wells and Bekoff (1981) of coyotes trespassing into neighboring territories and subsequent chases by resident animals document that both parties recognize the territorial boundaries and respond by actively and heavily scent-marking the boundaries and areas of intrusion. Trespassing coyotes were never observed to scent-mark at or near carcasses upon which they fed. They also appeared "anxious" with tail and hind quarters lowered, possibly resulting from being out of their own territory or from the abundance of resident scent-marks around the carcass (Bowen and Cowan 1980).

Exclusion of conspecifics and territorial integrity are possibly secondary functions of scent-marking behavior. It is speculated that the primary function of olfactory deposits may be to aid in orienting the the function of olfactory deposits may be to aid in orienting the movements of individuals in space, familiarizing the animal with its environment, and providing the animal with a "feeling" of security (Kleiman 1966, Ewer 1968, Ralls 1971, Eisenberg and Kleiman 1972, Walther 1978, Wells and Bekoff 1981).

The socio-spatial distribution of coyotes may influence their response to scent-station survey lines (Lehner 1976). Survey lines that fall on roads that coyotes treat as territorial boundaries may elicit more visitations than those through the middle (Lockie 1966). That coyotes treated roads as territorial boundaries is quite evident from studying the relocation maps of the INEL and Texas

coyotes (Appendices A, B). Roads were also treated as boundaries by coyotes in Grand Teton National Park, Wyoming (Wells and Bekoff 1981), by red foxes (Vulpes vulpes) in North Dakota (Sargeant 1972), and by wolves in Minnesota (Peters 1978). The degree to which coyotes utilize roads as travel routes and hence their potential for encountering scent stations varies with habitat (Hodges 1975). The number and distribution of roads coupled with the socio-spatial distribution of coyotes will also influence coyote utilization of roads.

Smaller home ranges and a higher percentage of roads comprising home range boundaries resulted in fewer roads and hence fewer scent stations in the core areas of coyote home ranges on the Freer study site. A higher proportion of roads acting as home range boundaries and the concomitant behaviors associated with such boundaries (scent-marking, increased attentiveness) resulted in greater scent-station visitation rates along these roads.

A potential bias in movement patterns and spatial utilization of the sample of Texas coyotes may exist in that 6 of the 9 were adult females. During the scent-station survey period (March 19-April 10) all could have been pregnant which may differentially influence movement patterns compared to those of the normal fall survey periods. Berg and Chesness (1978) and Preece (1978) found adult female coyotes to occupy 54% and 22% of their total home ranges, respectively, during the pre-denning (January 15-March 30) and denning (April 1-June 10) periods. Laundre (1979) noted female home range size was reduced by half during the reproductive season.

Movement patterns were also more restricted during this time (Laundre and Keller 1981). Andelt and Gipson (1979) also found female home ranges to be smaller during gestation through pup adolescent periods than during pre-breeding and breeding periods. Average daily distances moved were also shorter during the gestation period. It should be noted, however, that these studies were conducted in the upper midwest, intermountain west, and central plains, respectively, and may not accurately reflect conditions in South Texas.

Average daily movement distances were not calculated in the present study, so temporal influences on this variable are not known. There was, however, no significant differences in home range size between tracking periods for the adult females with contiguous spatial utilization patterns ($\underline{U} = 8$, $\underline{P} < 0.20$). Two of these coyotes were trapped in mid-May. Coyote 09 was not pregnant or lactating, and based upon the lack of hyperthrophied mammae did not appear to have been pregnant; coyote 11 was post-partum and lactating. Reproductive status of the other adult or juvenile females was unknown, hence it is difficult to infer whether movement patterns were in any way altered by reproductive condition.

A fourth possibility given by Hibler (1977) as to why coyotes appeared more vulnerable to trapping and man-induced mortality along the margins and outside their defined home ranges was that they shifted areas of use as a result of the trapping experience, making subsequent analyses appear as if the animals were trapped outside

their home ranges. Analyses of post-trapping spatial utilization by 2 of the tagged coyotes showed a significant decrease in the use of the area within 200 m of the trap site for both animals and within 500 m for one of them. The shifts in spatial utilization appear real and may be a direct response to the trapping experience, however, such shifts could also be the result of seasonal changes in spatial use or a change in social relationships within a coyote group. The home ranges of coyotes 09 and 12 overlapped completely. Death of a potentially dominant adult (09) may have influenced how a juvenile (12) would subsequently use the area. Additionally, if the resident coyotes are territorial, a shift in spatial utilization away from the site of capture may have been precluded by agonistic territorial neibhros, assuming the occupied territory was the minimum area necessary for self maintenance and the rearing of young. The changes in spatial utilization of coyotes 11 and 12 were not sufficient to alter designation of the trap site from inside to peripheral or outside. A sample of 2 is insufficient evidence for rejecting H5, but it seems unlikely that, as a result of a trapping experience, resident territorial animals would sufficiently alter spatial utilization patterns over a long enough period of time to account for Hibler's (1977) observed differential vulnerability peripheral to and outside defined home ranges.

Despite numerous studies of mammalian home range and movement patterns, relatively little published information is available addressing the responses of these species to their capture experience and how it may have influenced subsequent behavior and

home range use other than general statements about "trap shy" or "trap smart" animals. Pearson (1975) reported evidence of avoidance by grizzly bears (Ursus arctos) of areas where they had been foot snared, handled, and moved. Several adult males made long-distance, short-duration, post-trapping movements, whereas females remained relatively close to the point of capture for several days or weeks. Knight et al. (1978) reported a male grizzly bear making a post-trapping move similar to those described by Pearson (1975). However, without prior knowledge of these animal's home range and movement patterns, it is difficult to evaluate post-trapping movement behavior with respect to home range shifts or normal travel within the home range.

Many studies of home range utilization lack sufficient data or use inadequate analysis techniques to ascertain any "abnormal" post-trapping behavior or movement patterns. Lack of detection may in part be due to an initial capture and marking period lasting several weeks with little information being collected on the transmittered animals until that phase of the study is complete. By the time intensive monitoring of movement patterns is undertaken many long-distance, short-duration movements or home range shifts have already taken place and hence go undetected.

The potential effects of capture and handling on animal behavior, movement, and activity patterns need further consideration and more detailed study if we are to understand their influences on the animals and subsequent data analysis and interpretation.

CONCLUSIONS AND MANAGEMENT IMPLICATIONS

Knowledge of the behavioral aspects of various wildlife management and research techniques is essential to attaining the conventional goals of wildlife management as well as resolving the increasingly complex problems of present and future human-wildlife conflicts and interactions. It is unfortunate that many wildlife biologists appear to regard the study of animal behavior as an academic pursuit with little or no practical application (Leuthold 1969). This attitude was aptly summarized by Lopez (1978:77):

> "It occurred to me early on in my association with wolves that I was distrustful of science. Not because it was unimaginative, though I think that charge can be made against wildlife biology, but because it was narrow. I encountered what seemed to me eminently rational explanations of why wolves did some of the things they did, only to find wildlife biologists ignoring those ideas. True, some of the ideas were put forth by people who had only observed captive wolves; their explanations were intriguing and rational, but it was admittedly taking quite a leap to extrapolate from the behavior of captive animals to include those in the wild."

Recently, wildlife biologists and animal behaviorists seem to have found commonalities in the ecology, behavior, and subsequent management of wildlife species (Leuthold 1969, Geist and Walther 1974, Geist 1978). Their combined efforts provide a more sound and broad information base upon which to make wildlife management decisions. Lehner (1976) claimed lack of knowledge about the basic behavioral biology of coyotes was impeding development of effective coyote management techniques and went on to discuss various implications coyote behavior had for management and research.

Estimation of relative abundance of coyotes with scent-station survey lines was one area of consideration. Lehner (1976) raised several behavioral questions potentially influencing the scent-station survey technique, 2 of which were addressed in this study: (1) what are the range of responses individual coyotes show to scent stations, and (2) how might scent station visitation be influenced by the socio-spatial distribution of coyotes?

In the pen studies coyotes showed greater avoidance of novel stimuli in familiar than unfamiliar environments. A single species-typic response was not evident, but rather a broad range of responses from neophobia to investigation and manipulation were observed in both environments. That some coyotes turned away from scent stations upon initial detection in the familiar environment adds support to the field observations of Griffith (1976) that some coyotes actively avoid scent stations.

Results of the field studies suggest coyotes require greater exposure to scent stations inside their defined home ranges than peripheral to or outside before visiting a scent station. Whether this is due to active avoidance of a novel stimulus in a familiar environment or lack of detection in the familiar environment is not known. The smaller home range size and a higher percentage of road comprising home range boundaries resulted in 21 of 23 visits by marked coyotes being peripheral (14) or outside (7) defined home ranges. Scent-station survey lines that corresponded to home range or territorial boundaries elicited greater visitation than those inside. Coyotes peripheral to or outside their home rnages are

potentially more attentive to stimuli and therefore more likely to detect or score at scent stations.

It is interesting and encouraging that results of the pen and field studies were similar. In both instances novel stimuli evoked contrary behavior patterns depending on where they were encountered ; these stimuli were generally avoided or treated with caution when encountered in a familiar environment but approached and investigated when found in an unfamiliar environment. The readily observed behavioral differences of the pen situation lend insight to the behavioral mechanisms most likely to be operating in the coyote's natural environment.

One of 5 and 3 of 9 marked coyotes on the INEL and Freer study areas, respectively, visited scent stations within the standard 4-day survey period; 0 of 5 and 1 of 9 visited scent stations on the first night. The combined results produced 1 visit on day 1 and 4 visits on days 1-4. These data are consistent with the findings of Roughton and Sweeny (1982) and supportive of their proposed changes in scent-station survey methodology to operate survey lines for a single night using 10 stations.

The small but similar percentages of visits by marked coyotes on the 2 study areas raises the question as to the proportion of the coyote (or other carnivore) population the scent-station survey technique is sampling, and the potential differential response of residents and transients or adults and juveniles. When and how the scent-station survey is conducted depends upon what the information

is desired. The maximum response from a particular species will often be when juvenile animals are dispersing. These individuals are traveling outside the familiar environment of their natal home ranges and may be more likely to detect and investigate scent stations. Sampling the resident portion of a population may require different timing and modification of the survey technique. Knowledge of the species' behavior and ecology is therefore essential to obtaining the desired information.

Differential behavior of coyotes with regard to their home range boundaries has implications beyond this species and the scent-station survey technique. There is a general need for increased awareness of the behavioral aspects of various wildlife management and research techniques. This will hopefully lead to the refinement of present techniques and development of new techniques that make use of various aspects of animal behavior and are less biased or influenced by behavior.

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APPENDICES

Appendix A. Telemetry Relocations and Grid Cell Frequency Distribution of Telemetry Relocations for Coyotes on the INEL

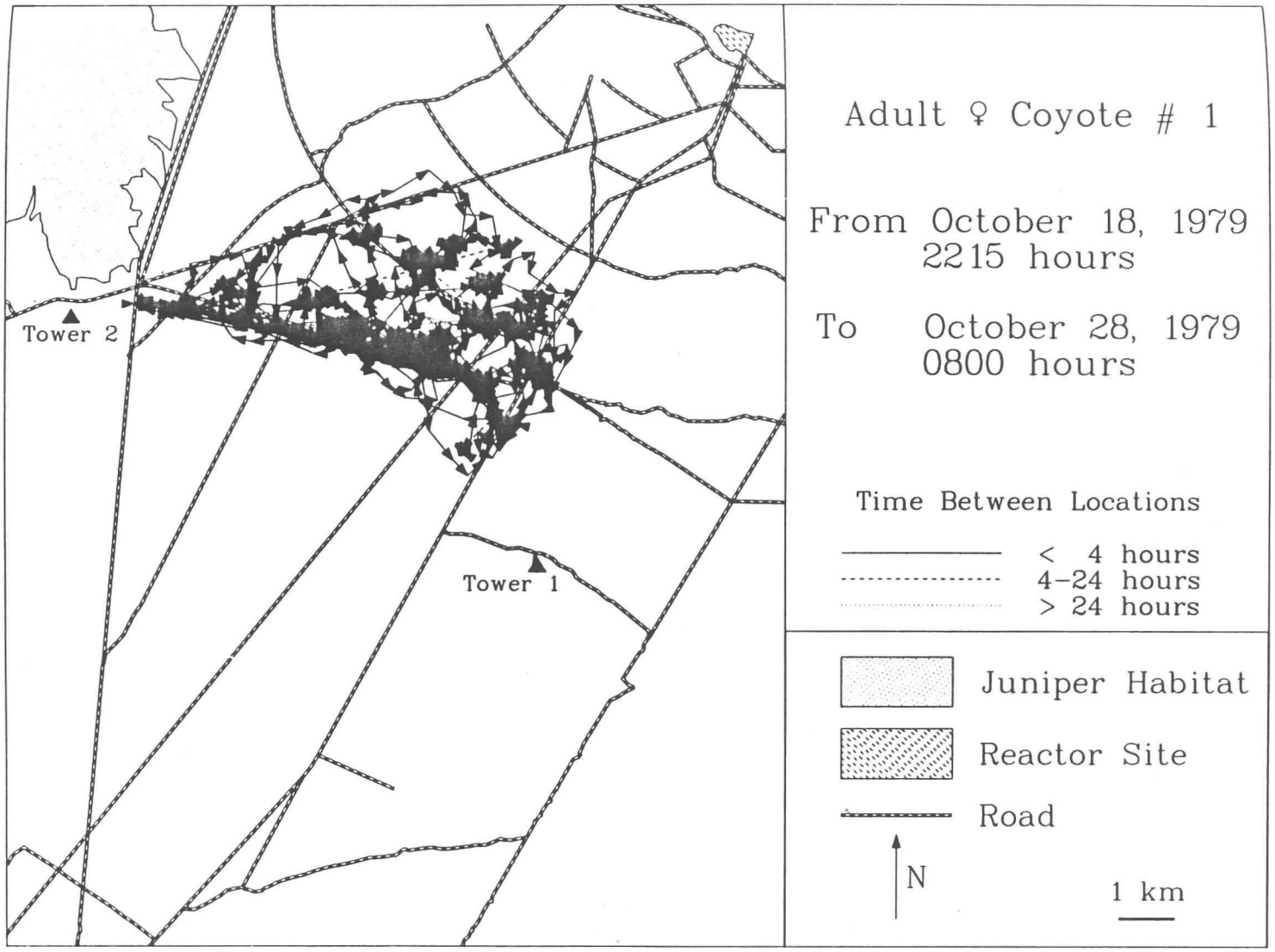


Fig. 8. Distribution of telemetry relocations for coyote 01 on the INEL.

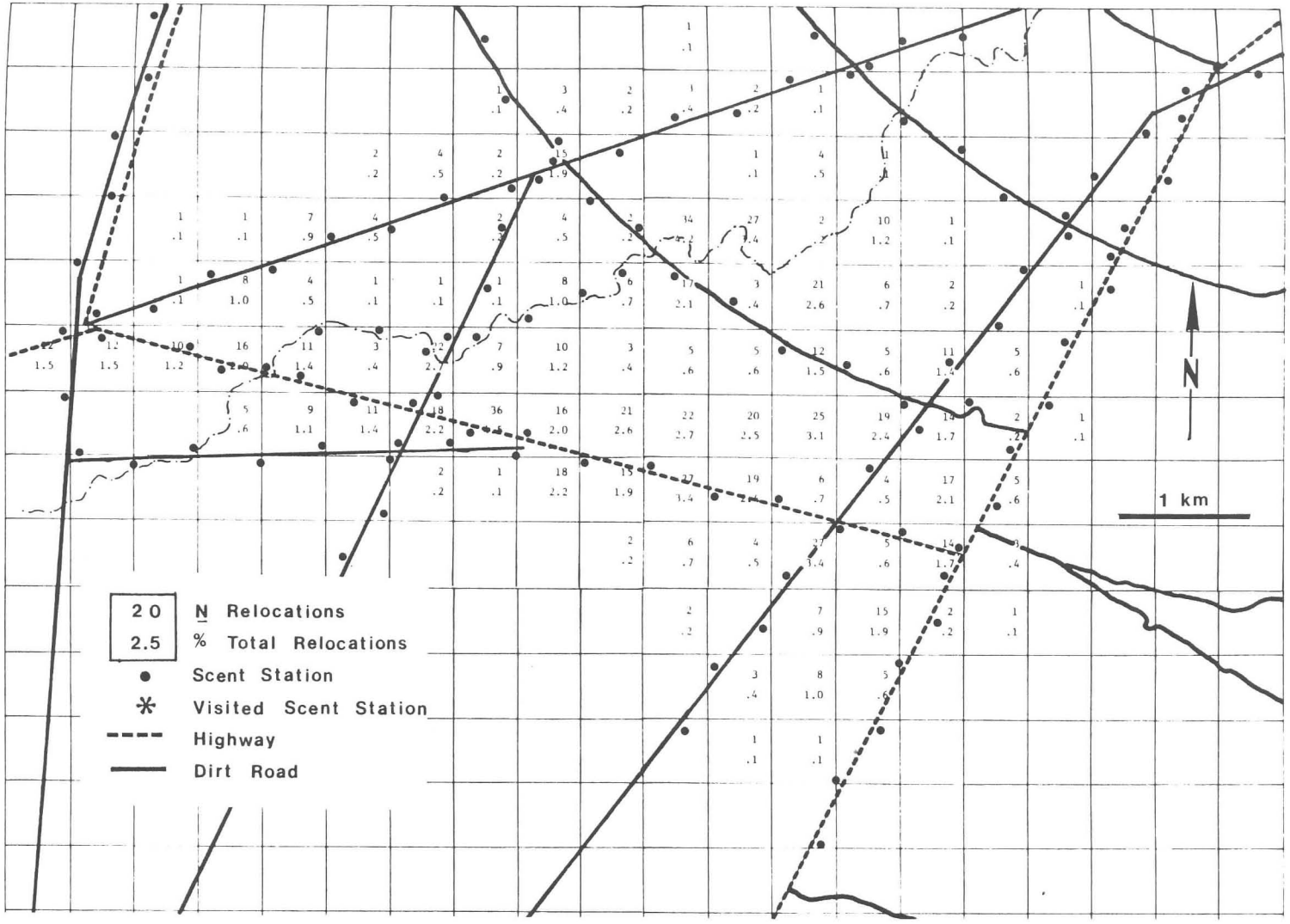


Fig. 9. Grid cell frequency distribution of telemetry relocations for coyote 01 on the INEL.

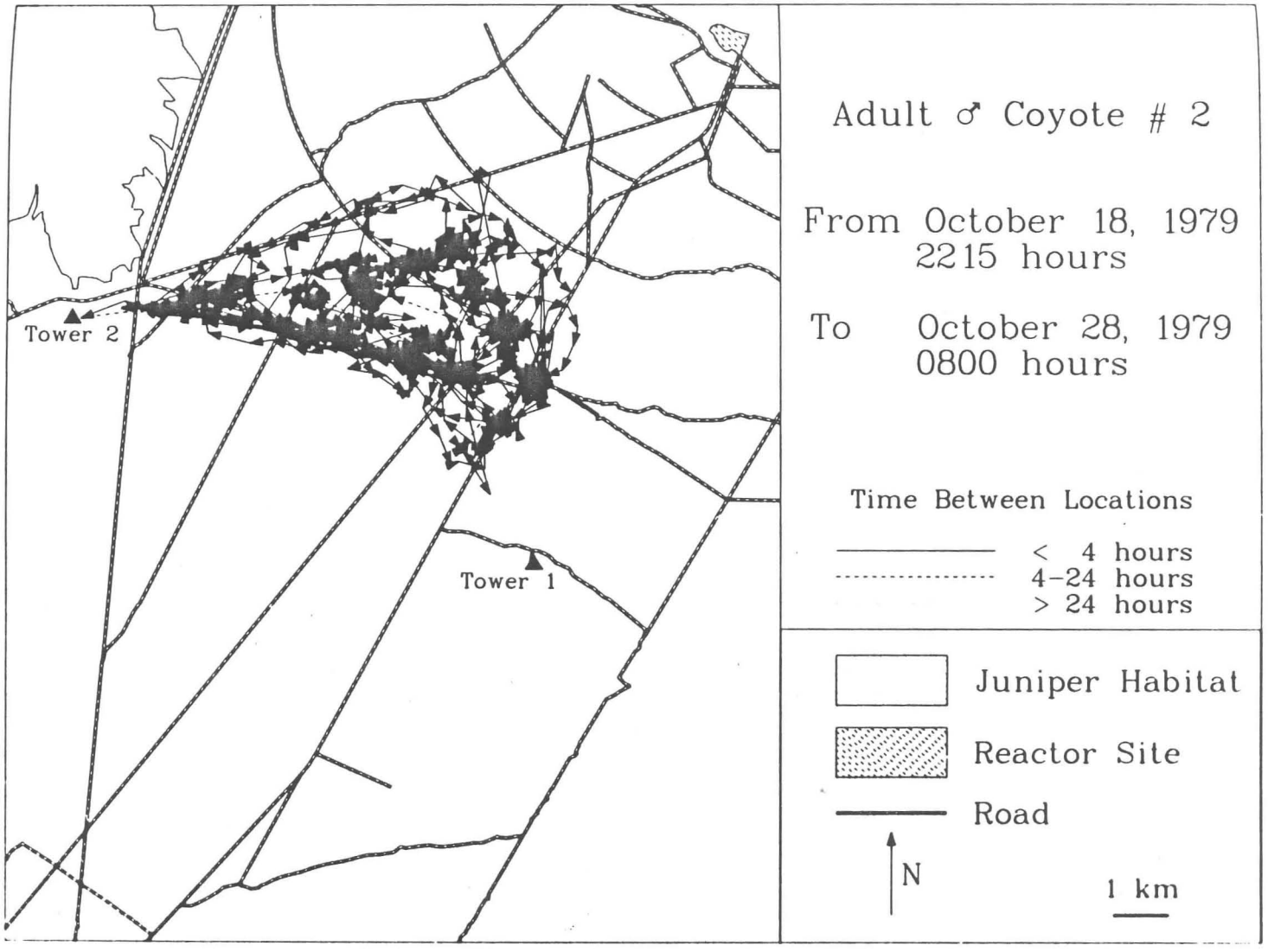
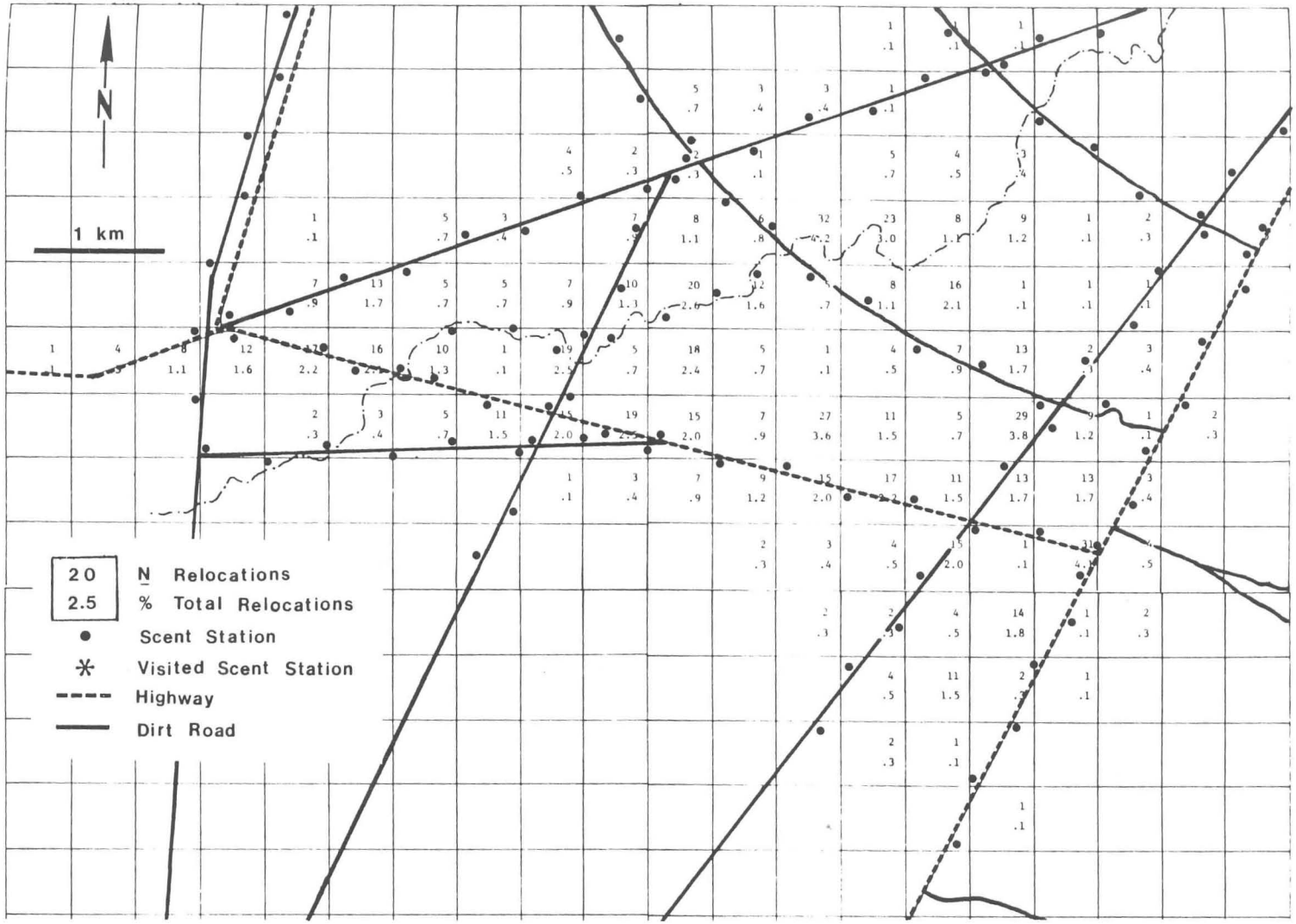


Fig. 10. Distribution of telemetry relocations for coyote 02 on the INEL.



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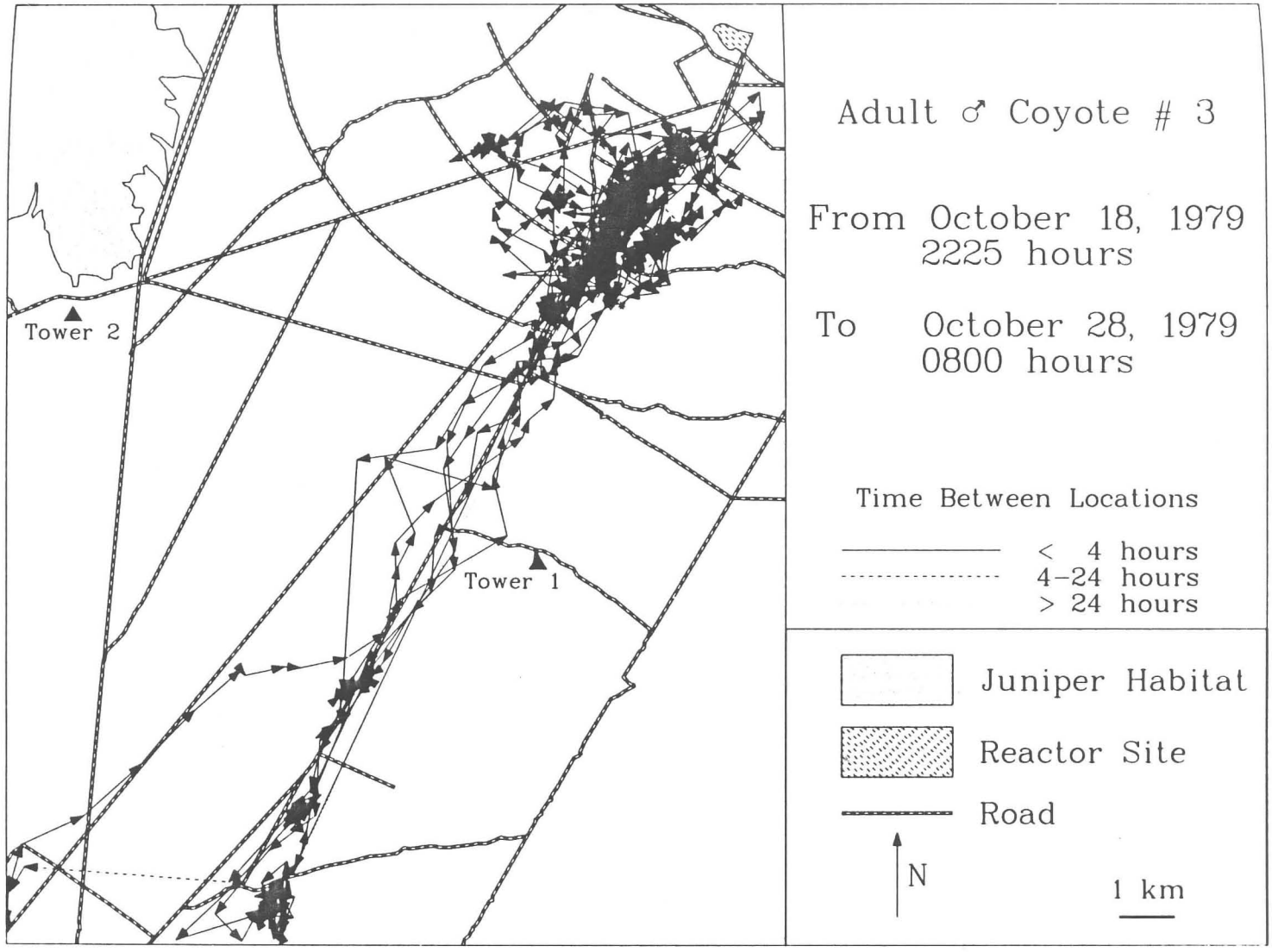

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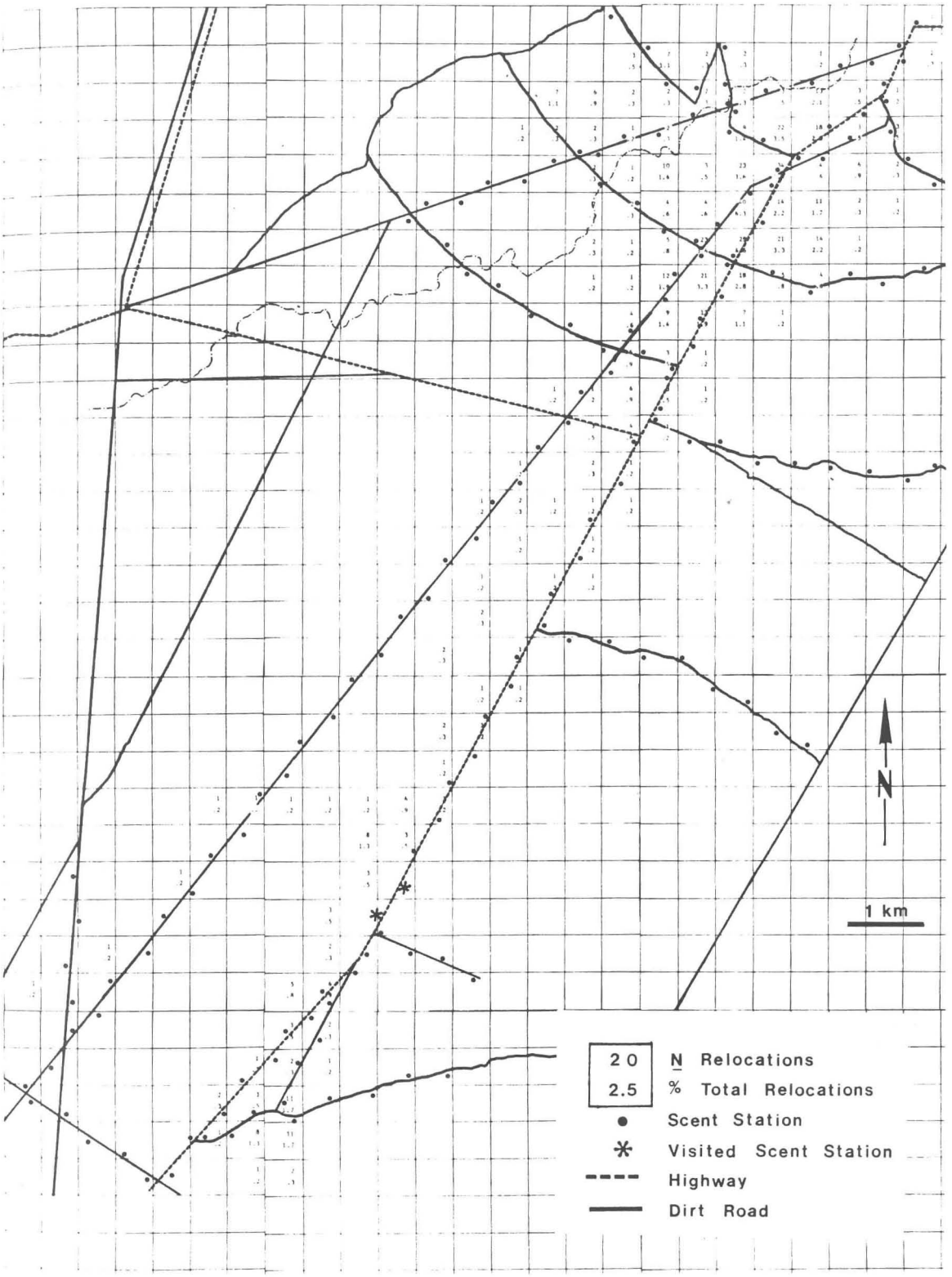

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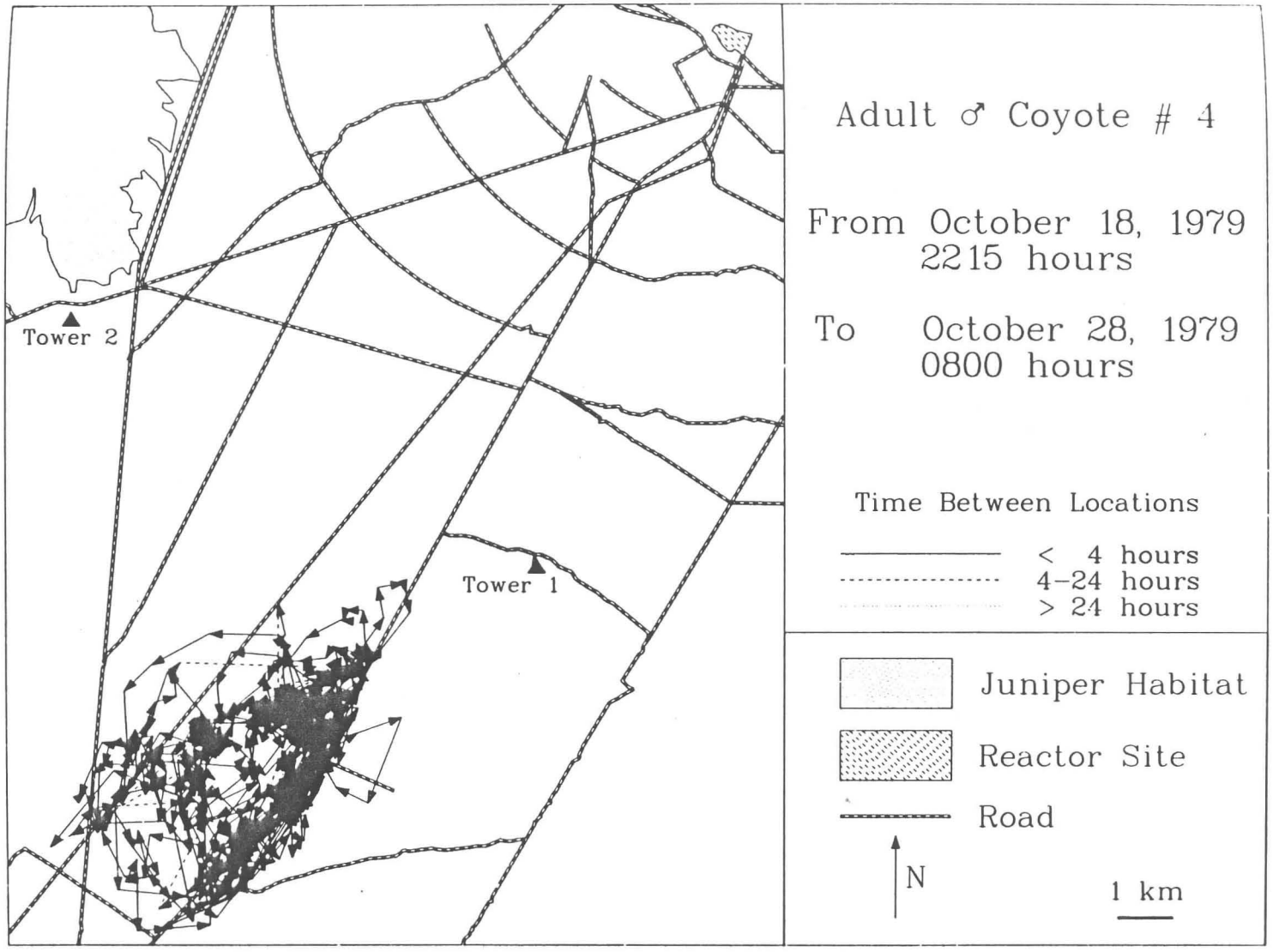

Fig. 14. Distribution of telemetry relocations for coyote 04 on the INEL.

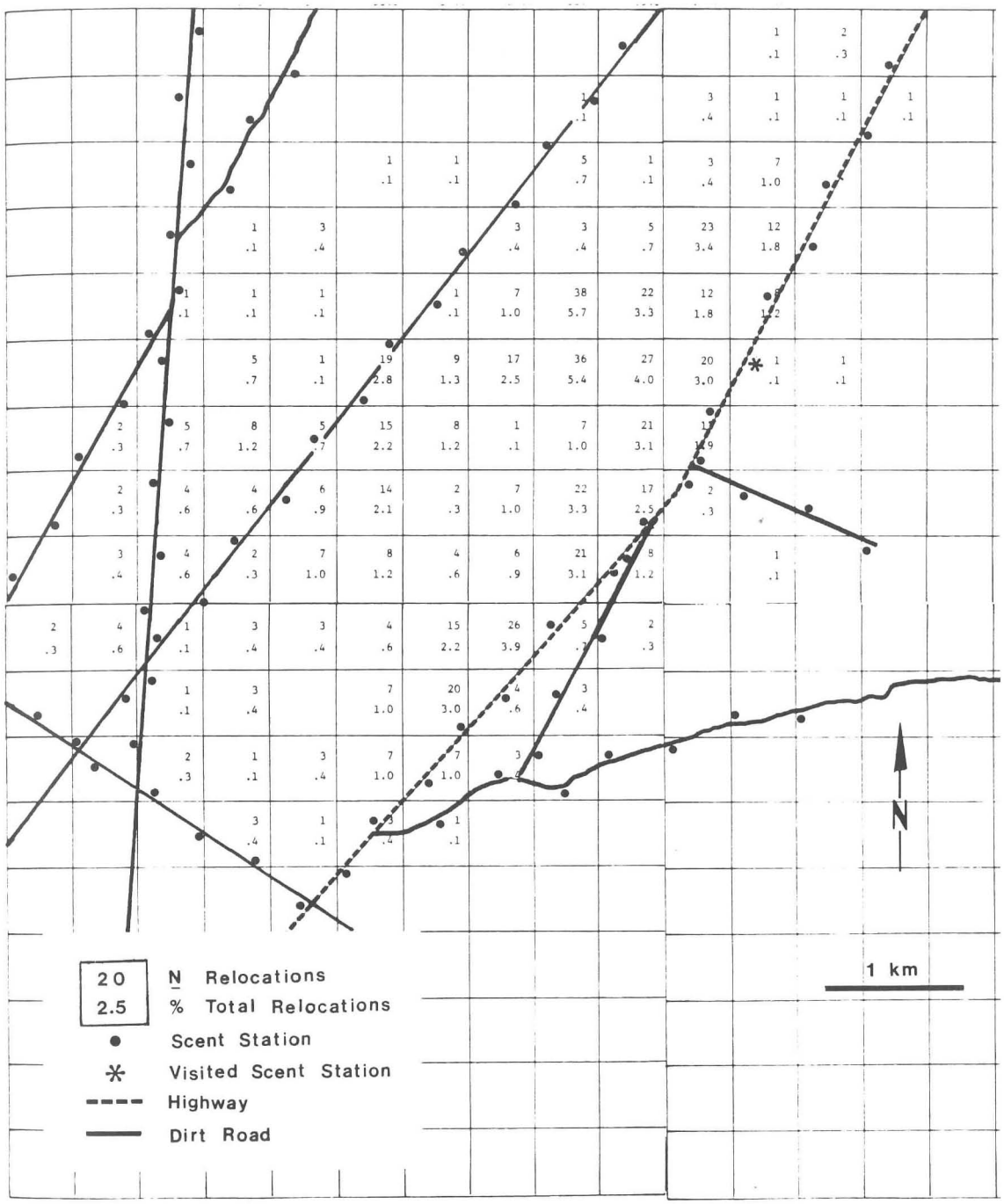

Fig. 15. Grid cell frequency distribution of telemetry relocations for coyote 04 on the INEL.

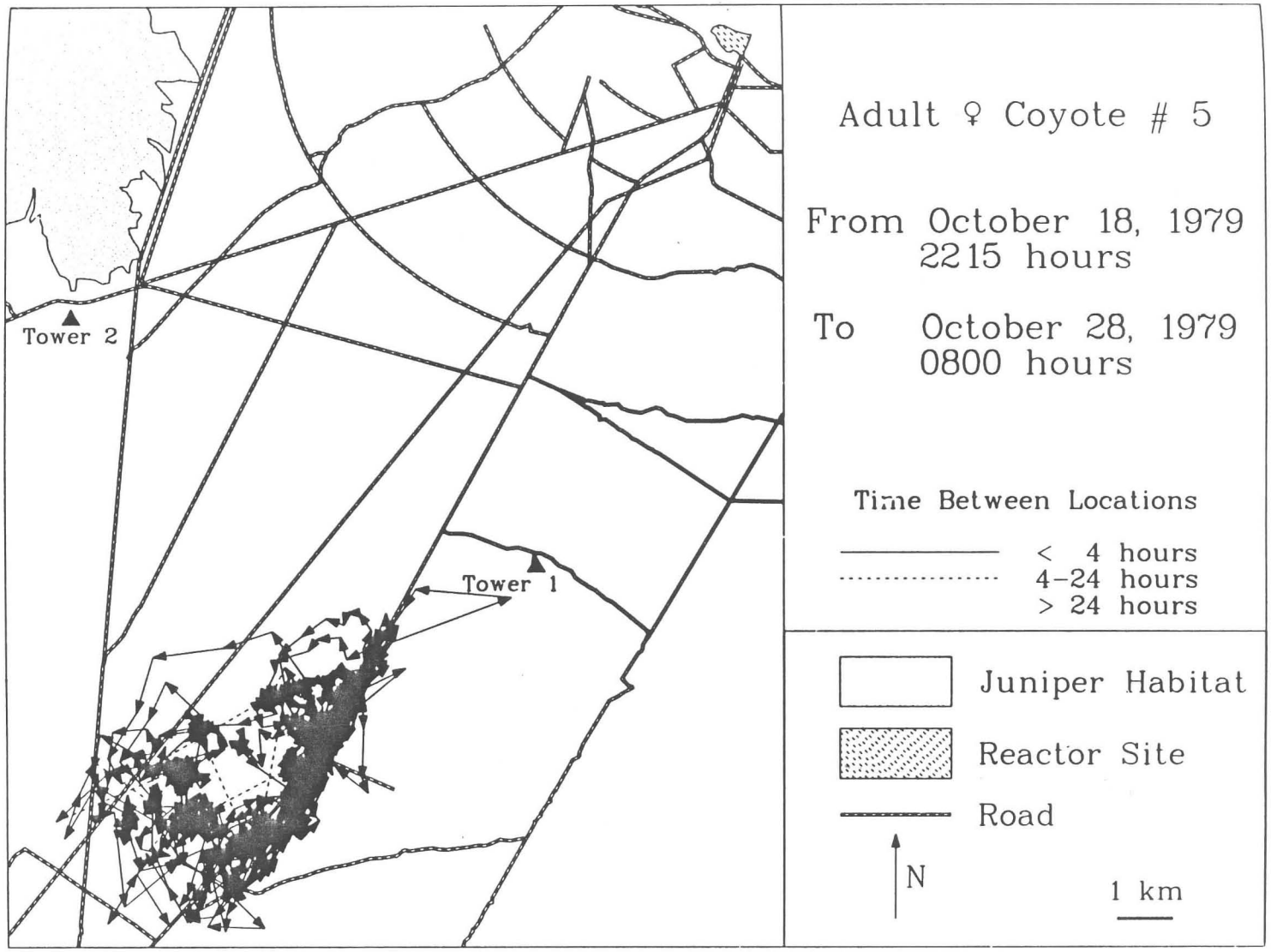

Fig. 16. Distribution of telemetry relocations for coyote 05 on the INEL.

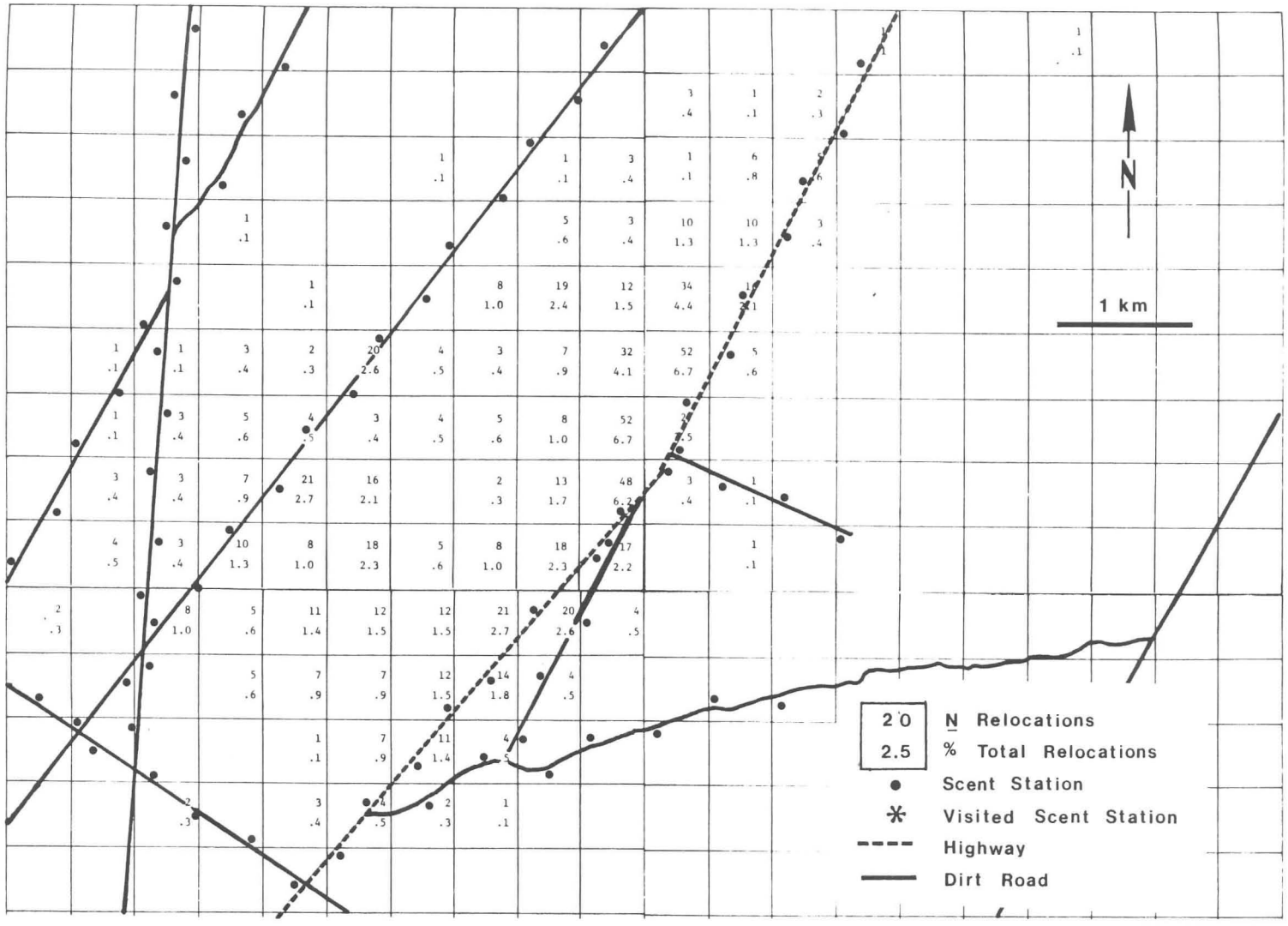

Fig. 17. Grid cell frequency distribution of telemetry relocations for coyote 05 on the INEL.

Appendix B. Relemetry Relocations and Grid Cell Frequency Distribution of Telemetry Relocations for Coyotes on the Frier Study Area, Texas

Appendix B

Telemetry Relocations and Grid Cell Frequency Distribution of Telemetry Relocations for Coyotes on the Freer Study Area, Texas

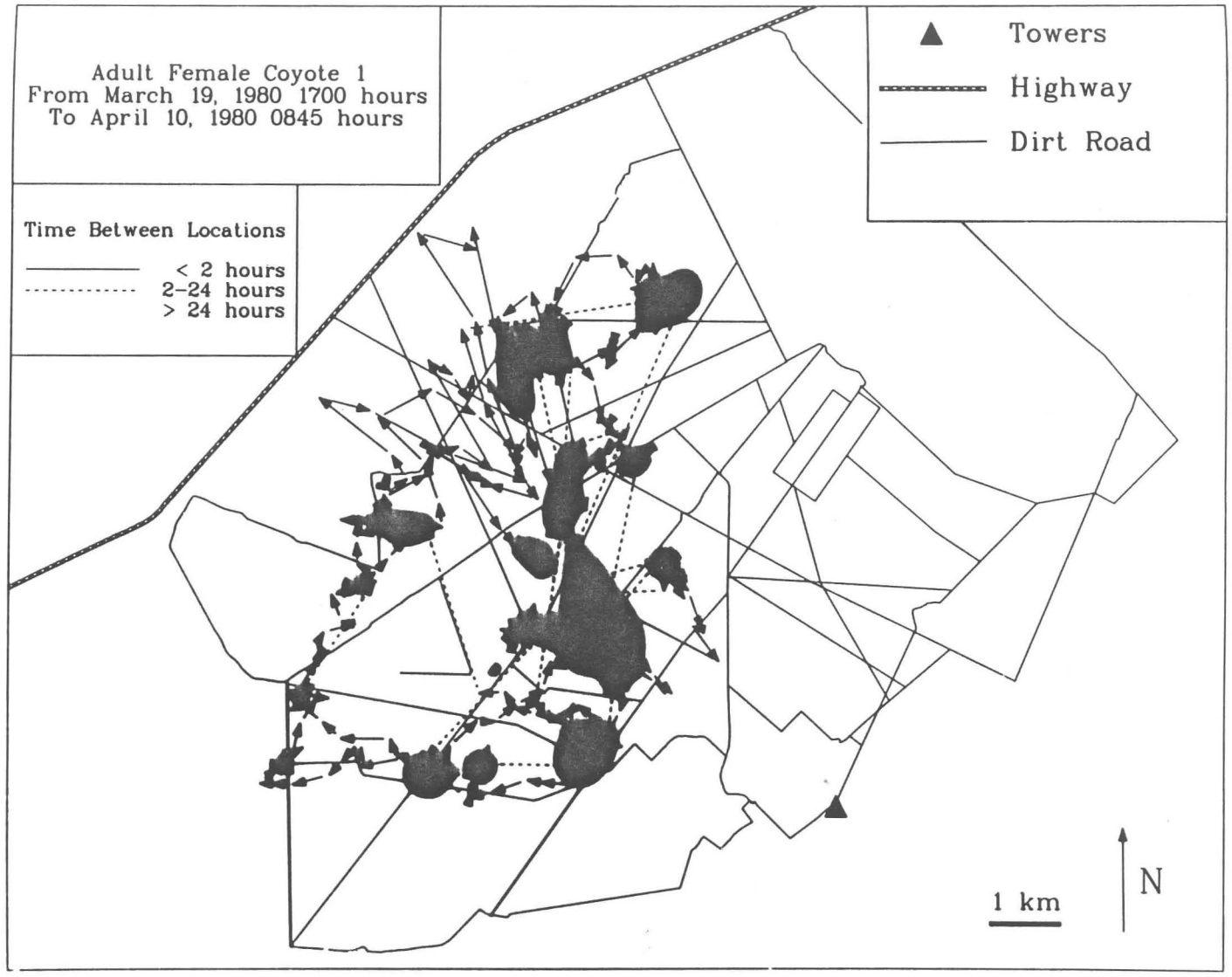

Fig. 18. Distribution of telemetry relocations for coyote 01 on the Freer study area, Texas.

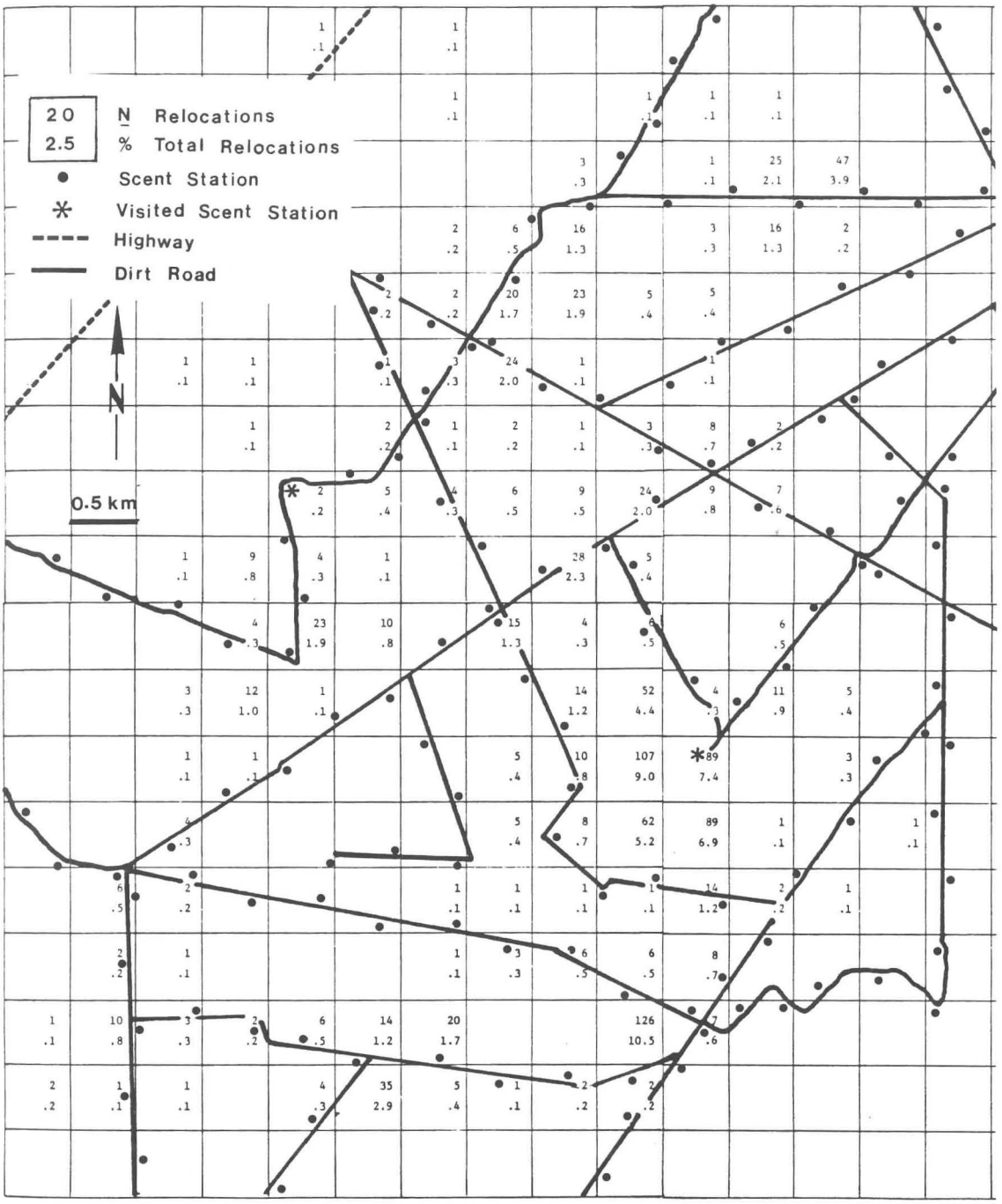

Fig. 19. Grid cell frequency distribution of telemetry relocations for coyote 01 on the Freer study area, Texas.

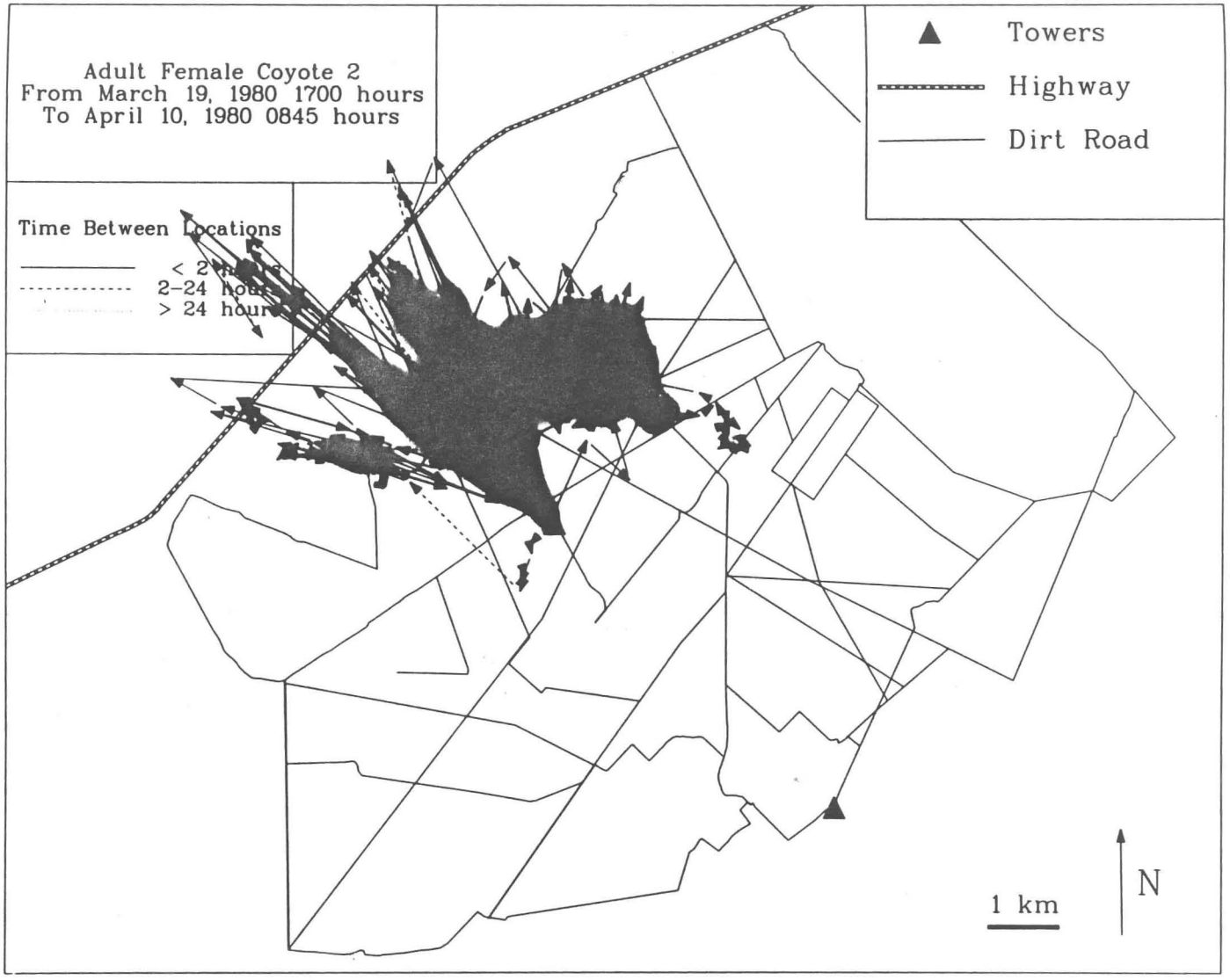

Fig. 20. Distribution of telemetry relocations for coyote 02 on the Freer study area, Texas.

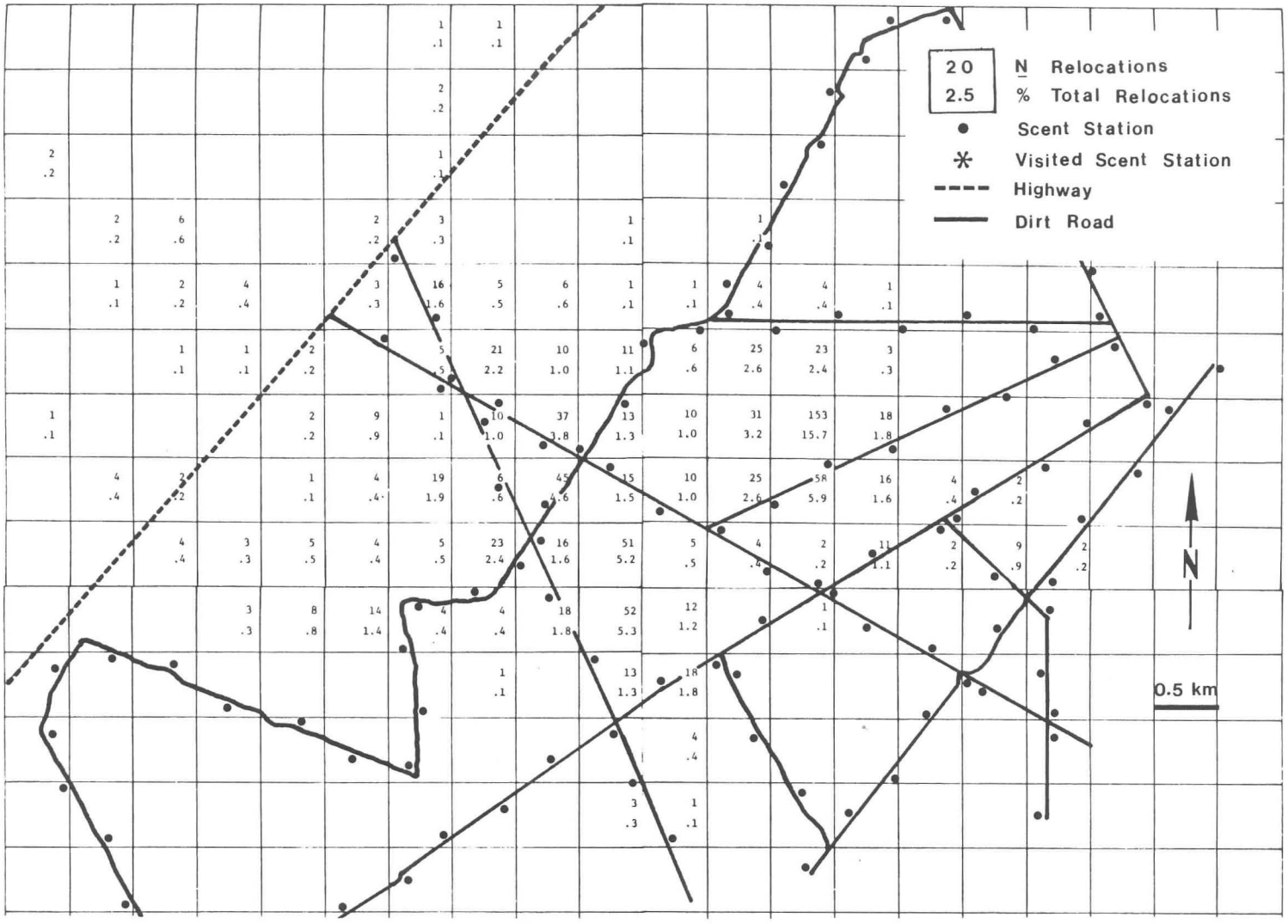

Fig. 21. Grid cell frequency distribution of telemetry relocations for coyote 02 on the Freer study area, Texas.

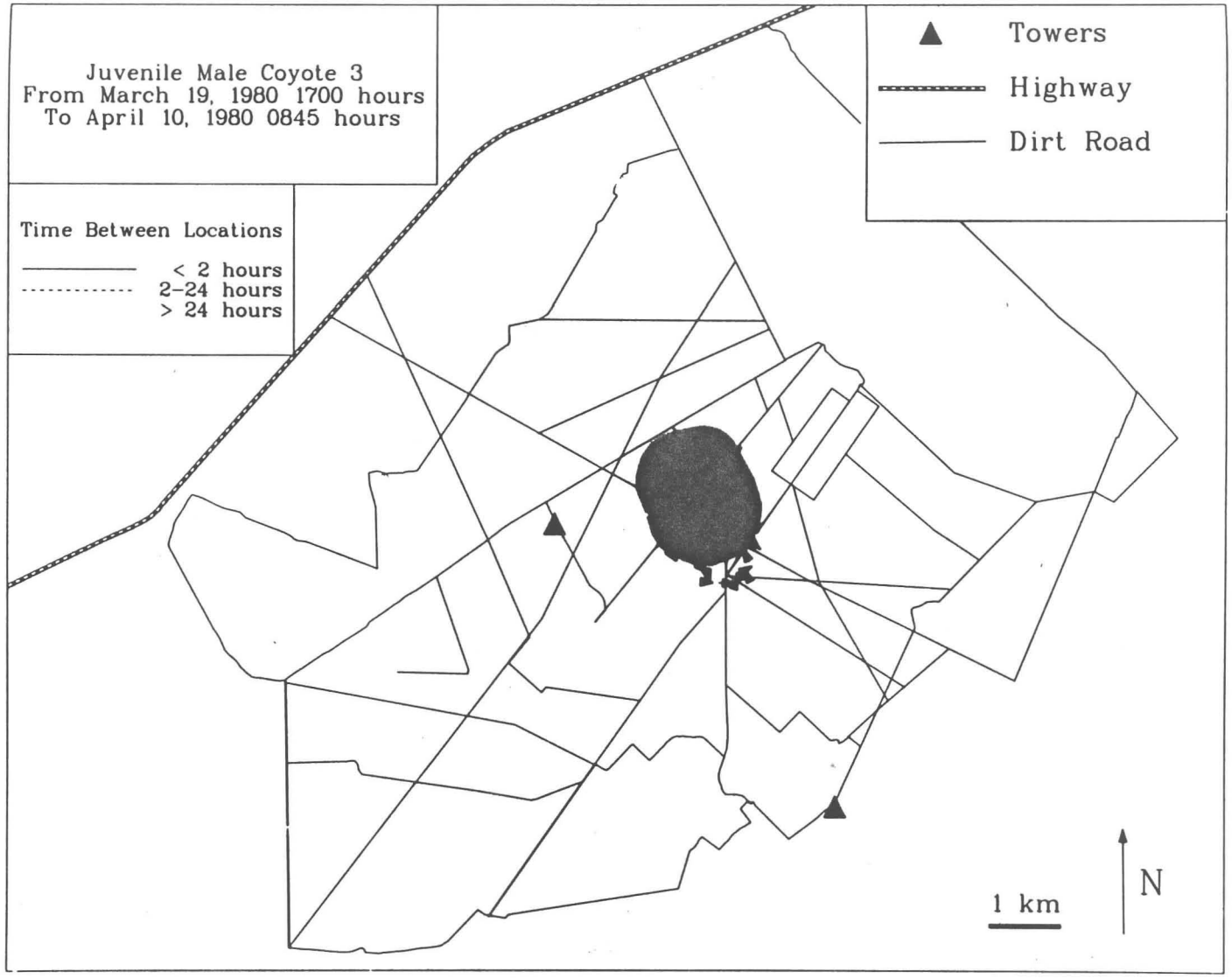

Fig. 22. Distribution of telemetry relocations for coyote 03 on the Freer study area, Texas.

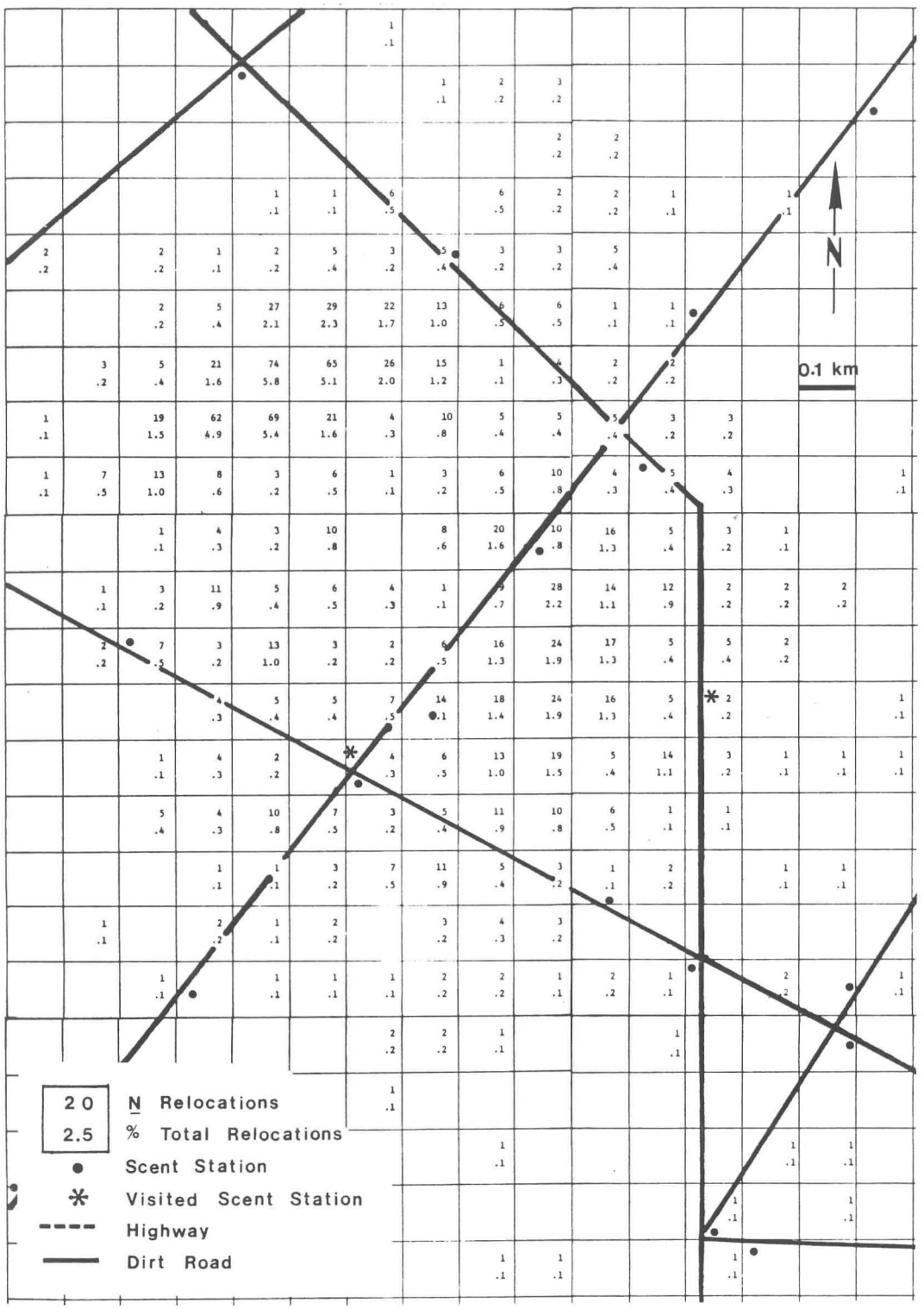

Fig. 23. Grid cell frequency distribution of telemetry relocations for coyote 03 on the Freer study area, Texas.

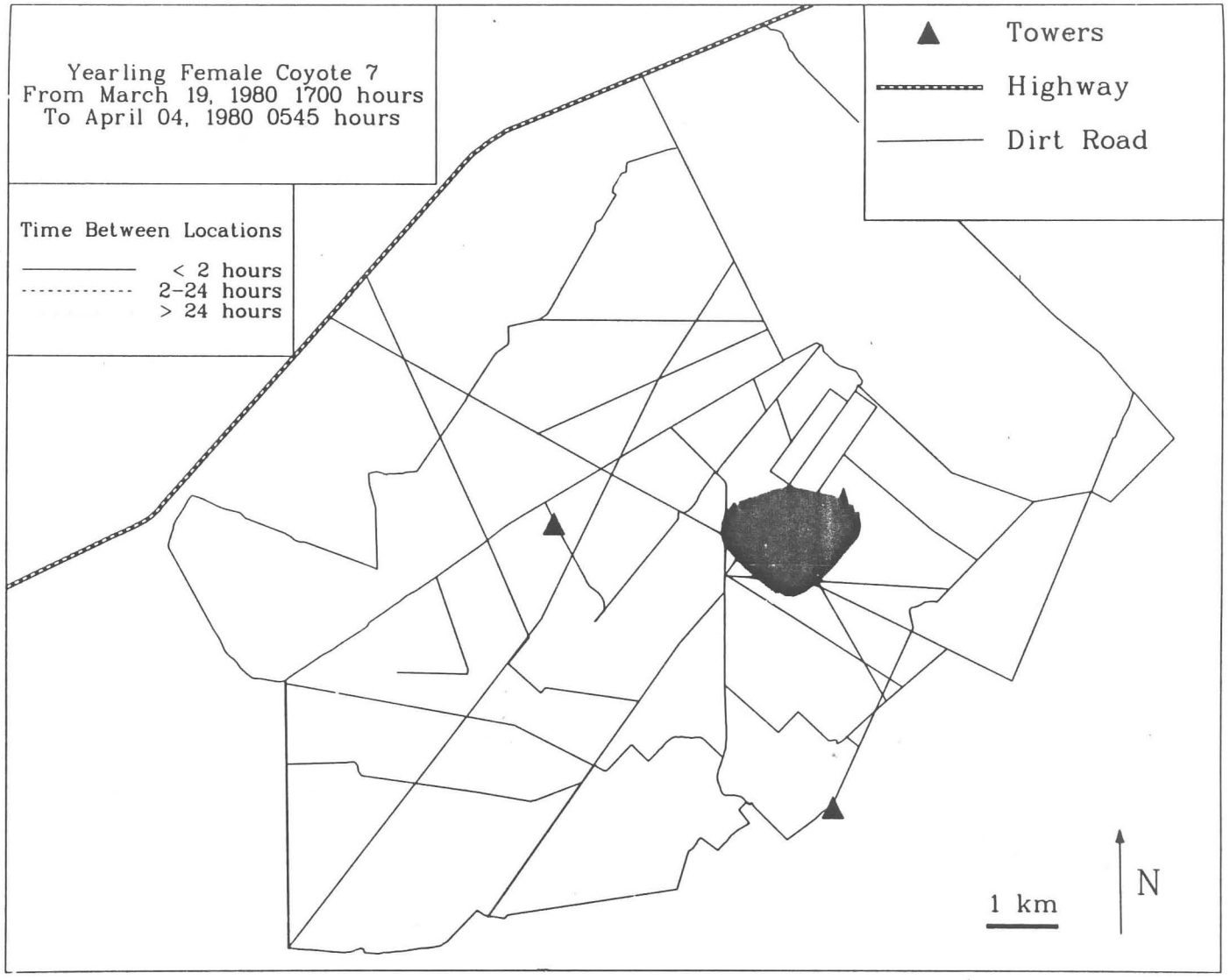

Fig. 24. Distribution of telemetry relocations for coyote 07 on the Freer study area, Texas.

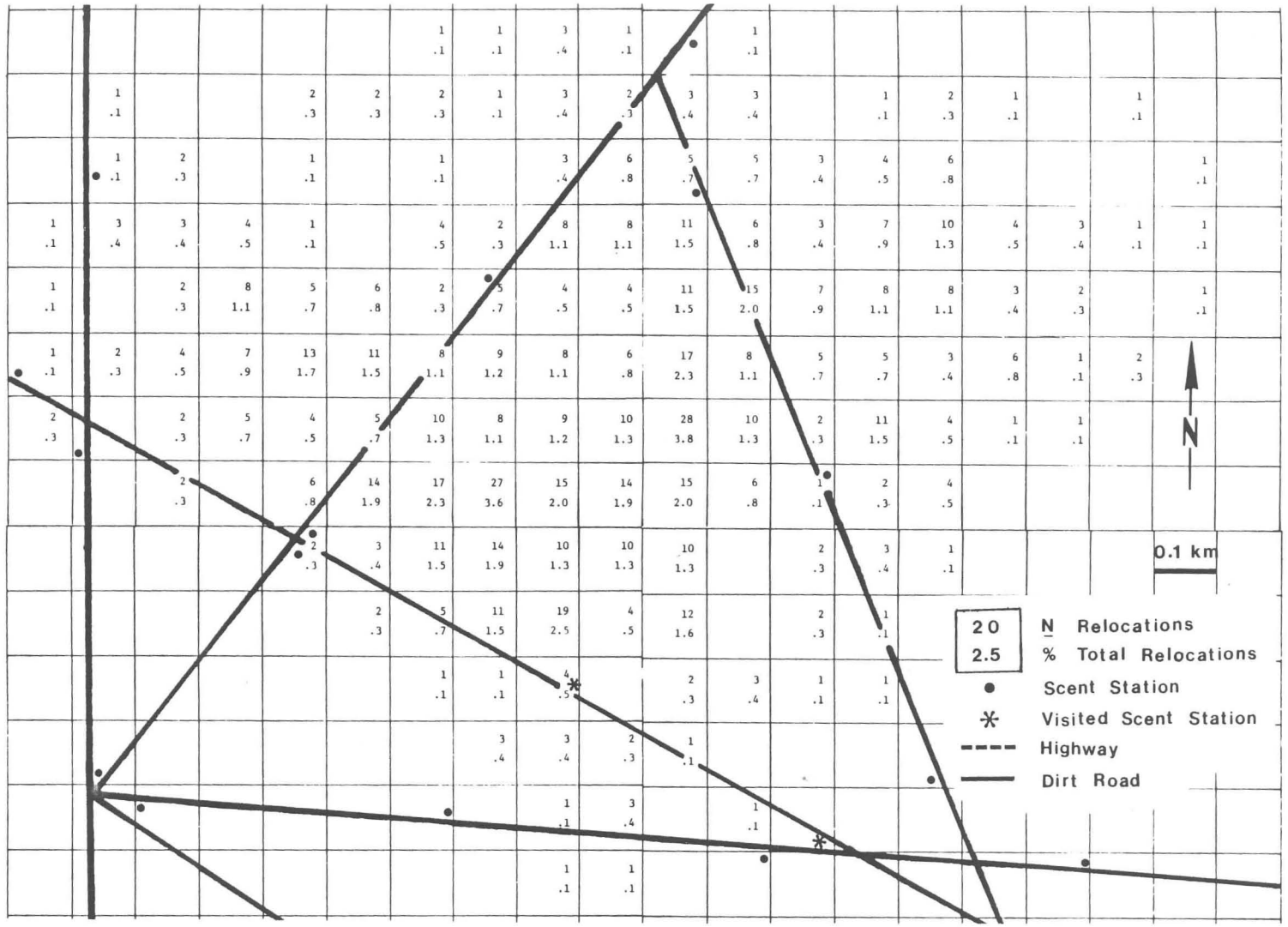

Fig. 25. Grid cell frequency distribution of telemetry relocations for coyote 07 on the Freer study area, Texas.

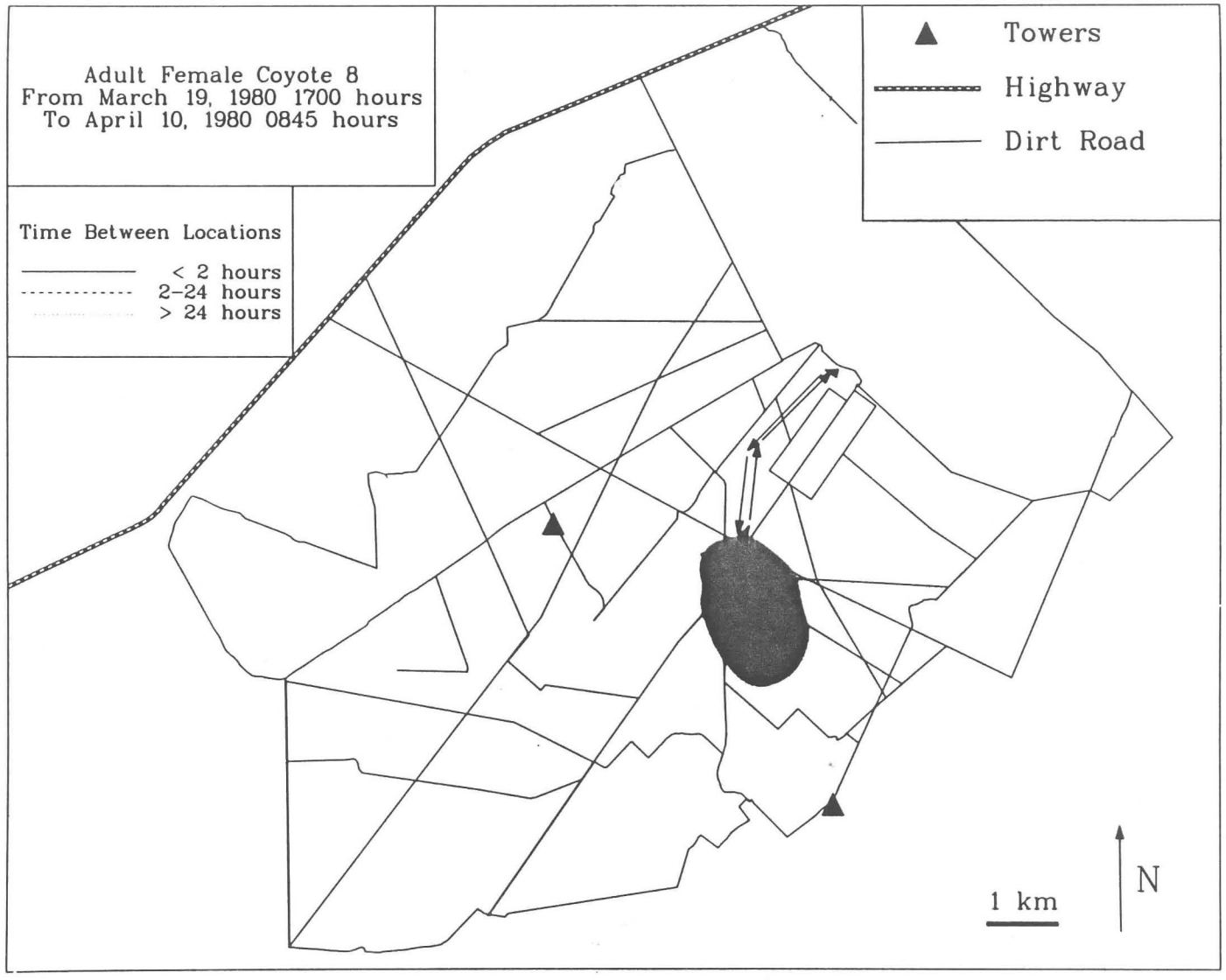

Fig. 26. Distribution of telemetry relocations for coyote 08 on the Freer study area, Texas.

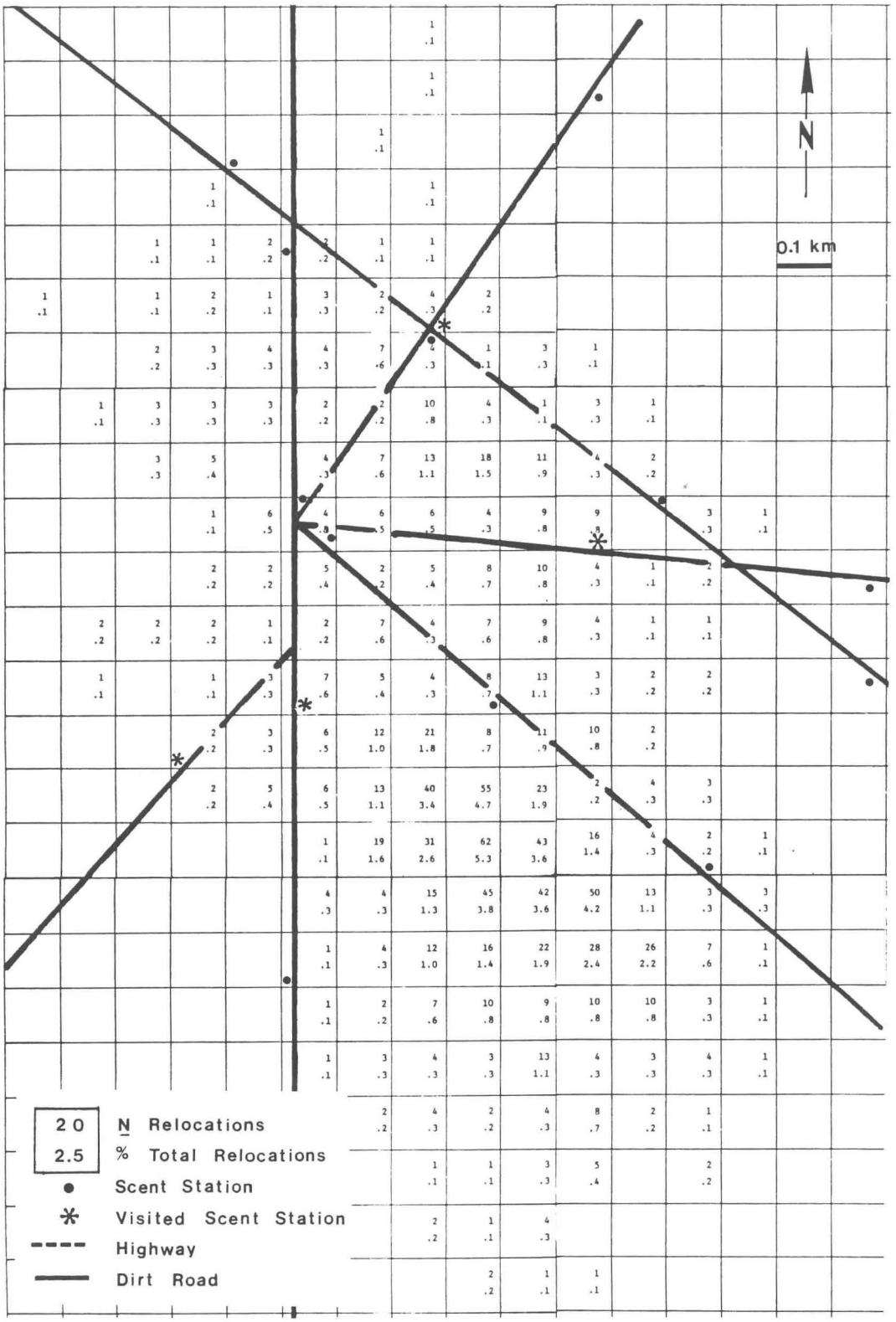

Fig. 27. Grid cell frequency distribution of telemetry relocations for coyote 08 on the Freer study area, Texas.

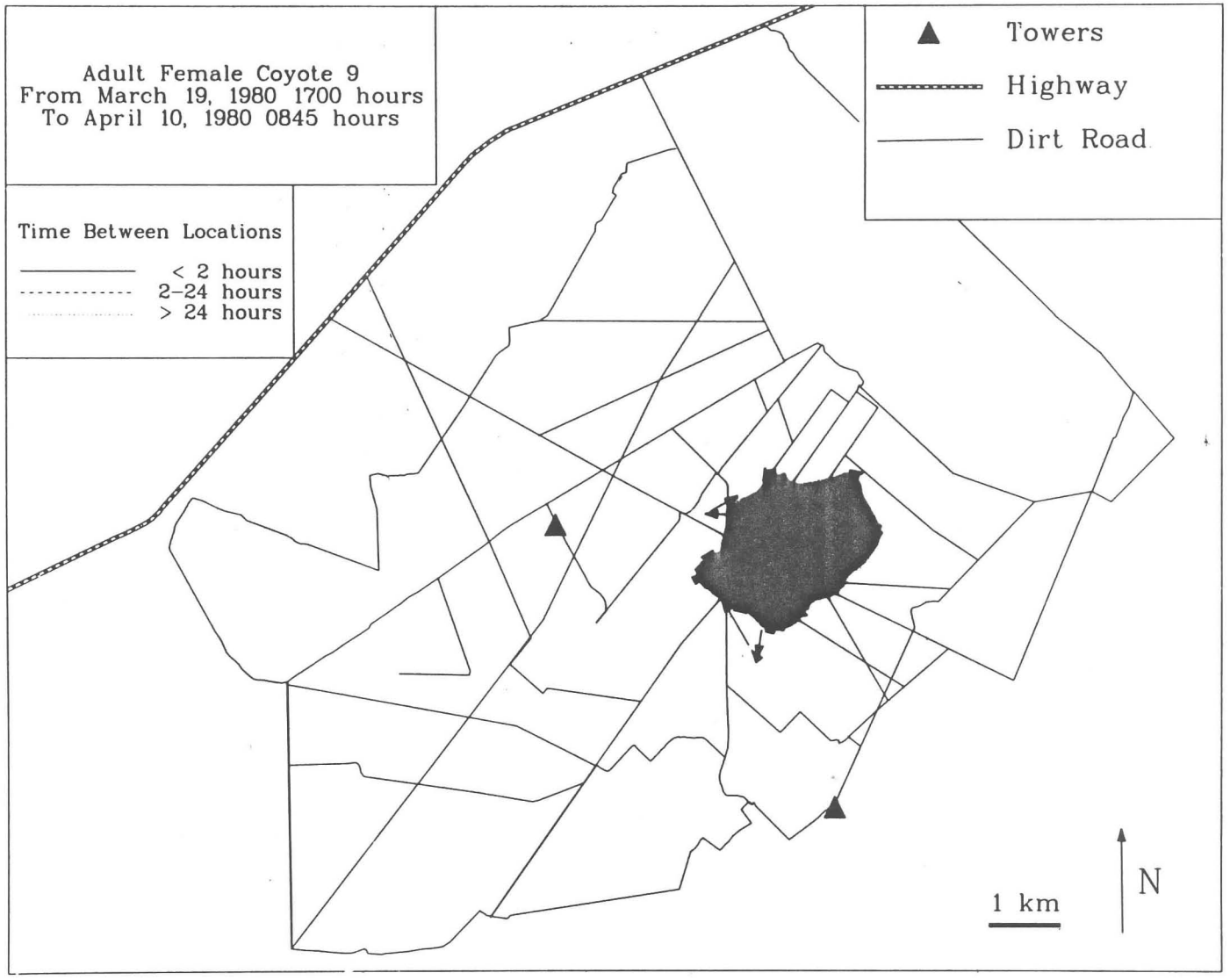

Fig. 28. Distribution of telemetry relocations for coyote 09 on the Freer study area. Texas.

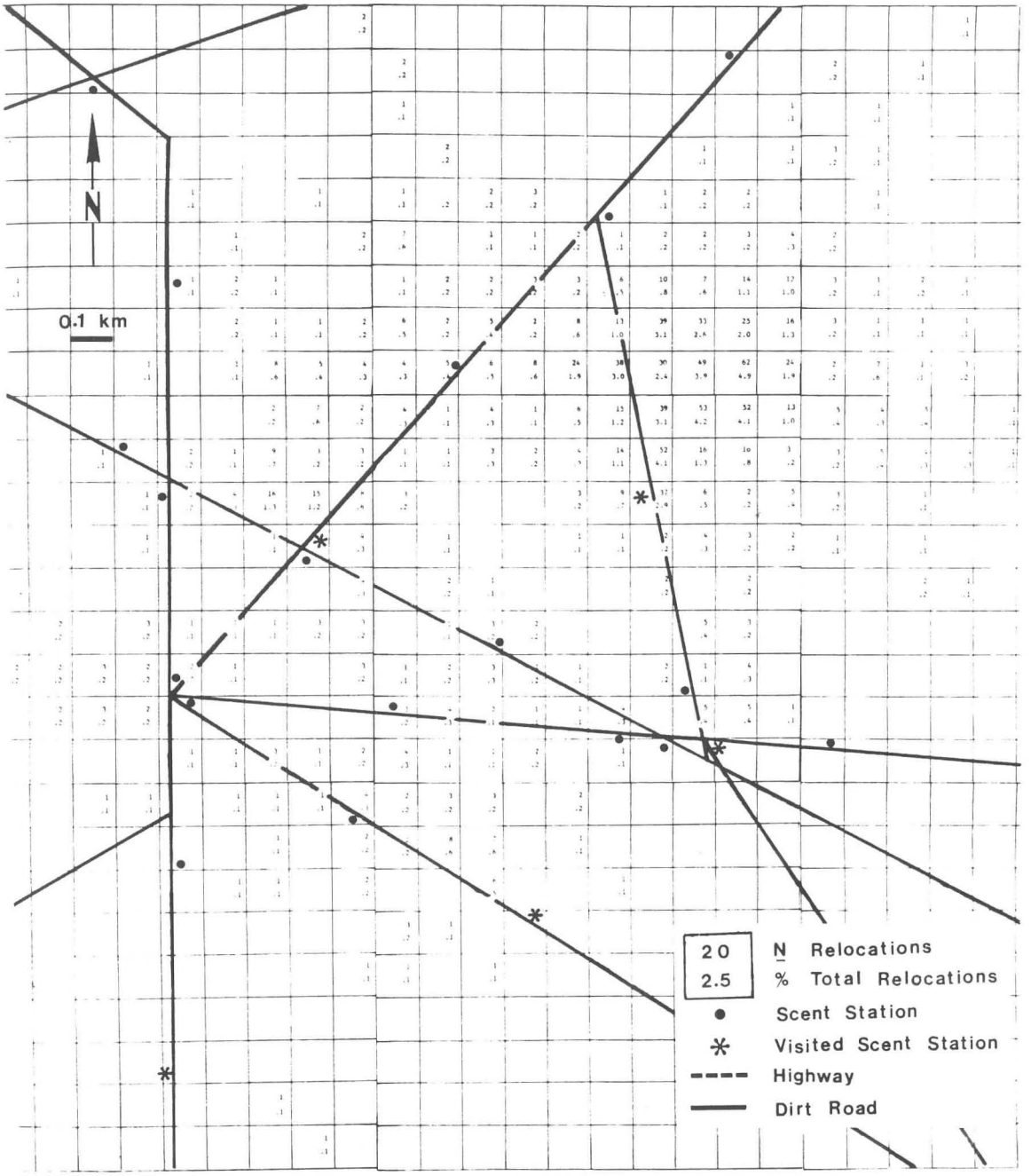

Fig. 29. Grid cell frequency distribution of telemetry relocations for coyote 09 on the Freer study area, Texas.

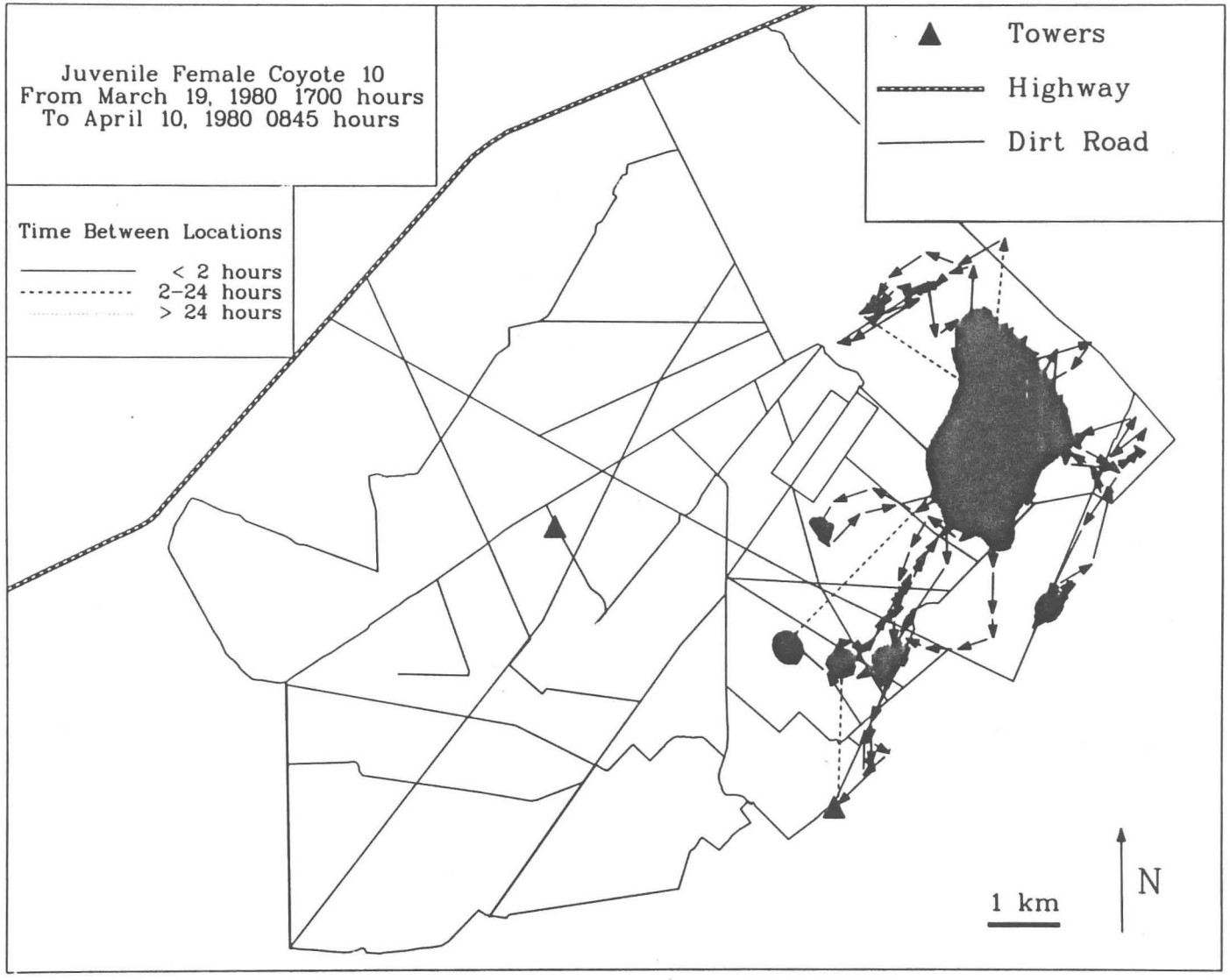

Fig. 30. Distribution of telemetry relocations for coyote 10 on the Freer study area, Texas.

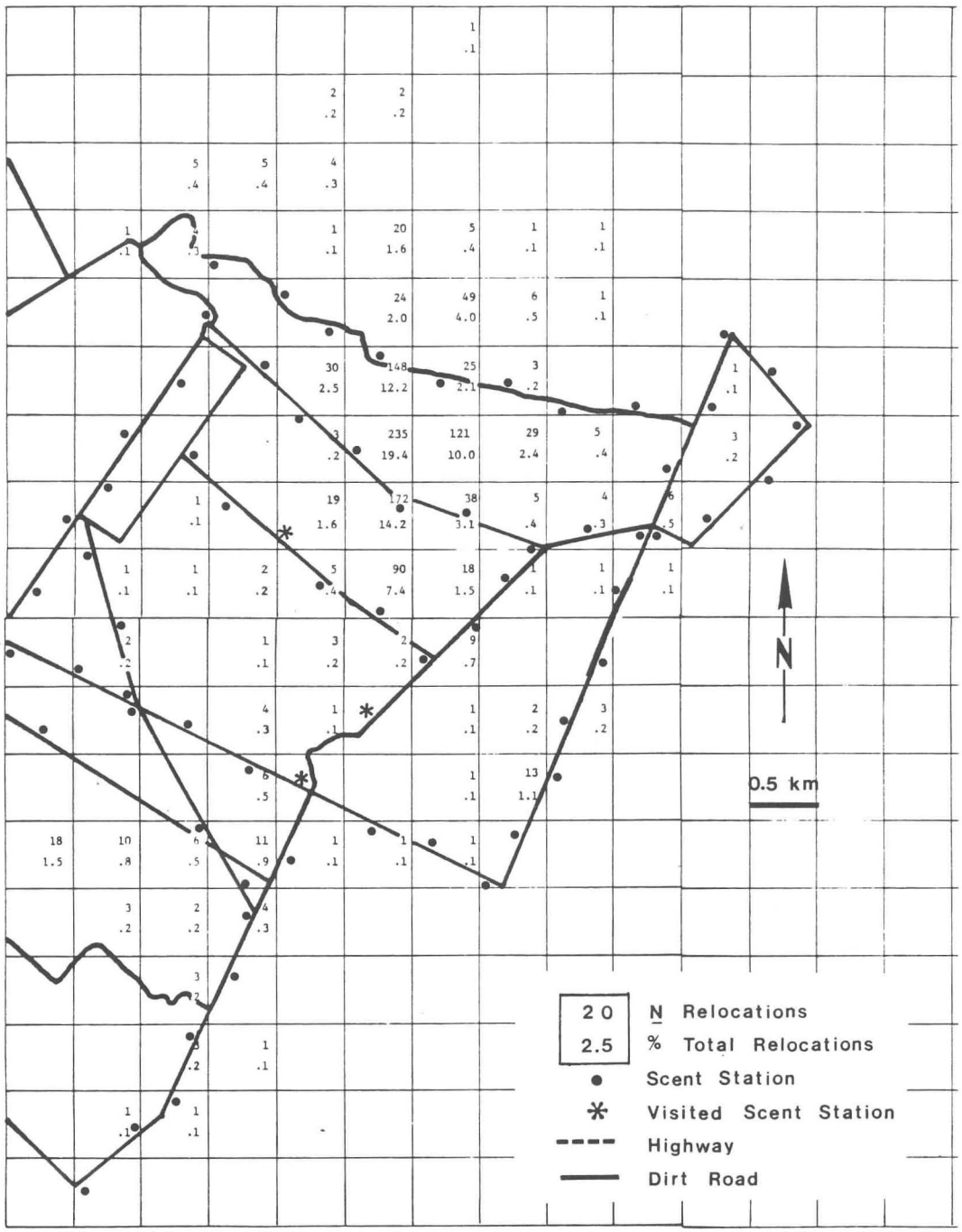

Fig. 31. Grid cell frequency distribution of telemetry relocations for coyote 10 on the Freer study area, Texas.

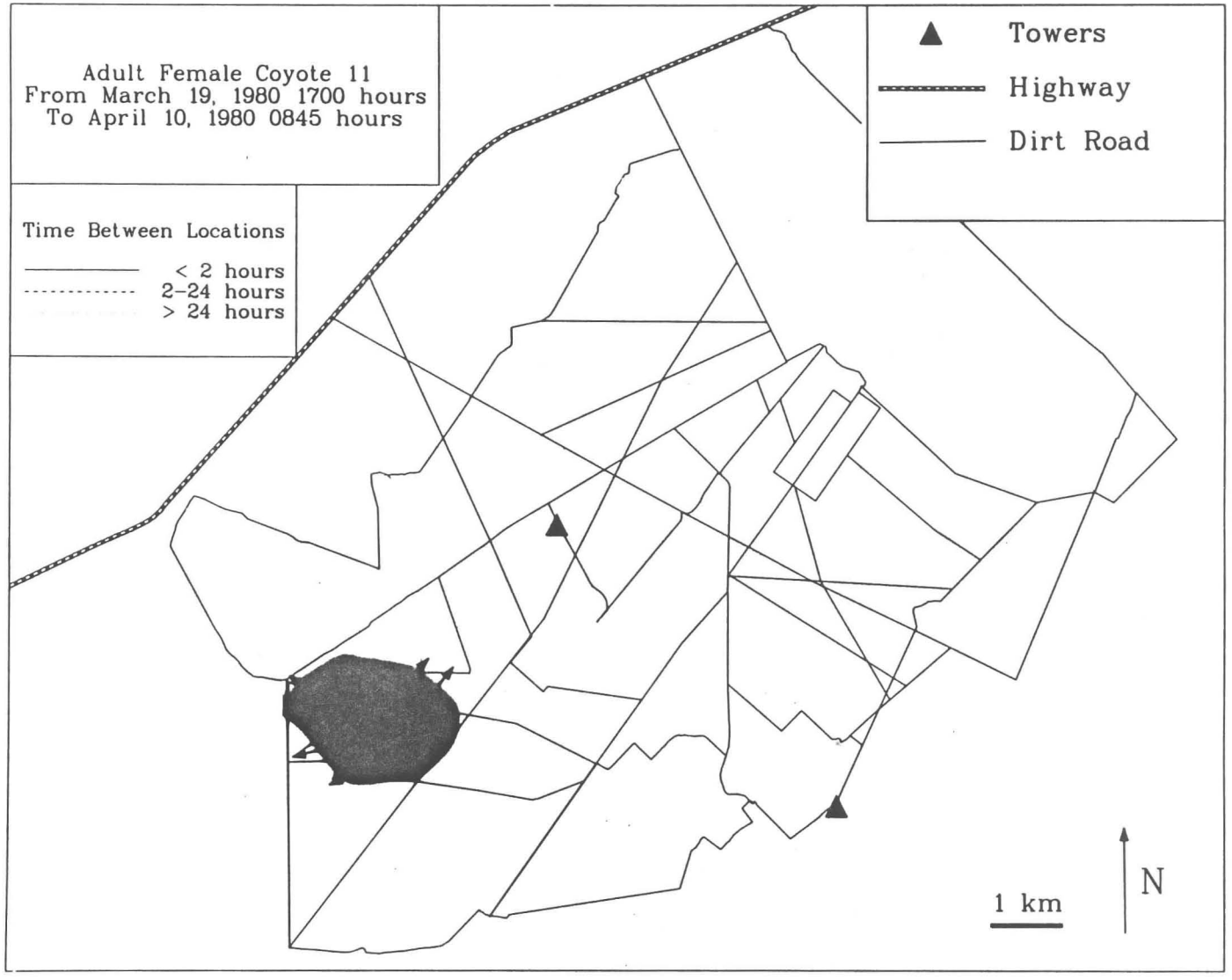

Fig. 32. Distribution of telemetry relocations for coyote 11 on the Freer study area, Texas.

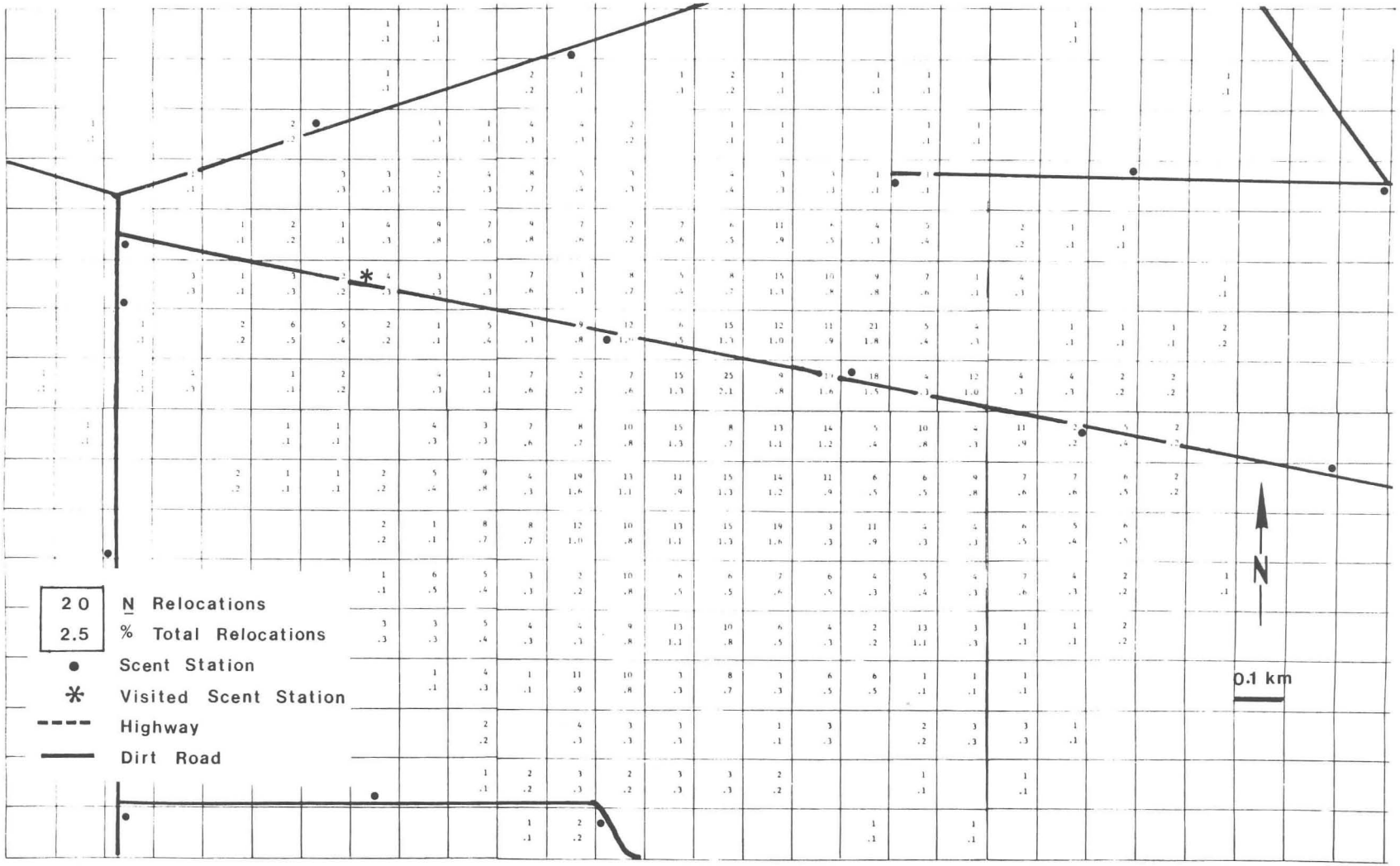

Fig. 33. Grid cell frequency distribution of telemetry relocations for coyote 11 on the Freer study area, Texas.

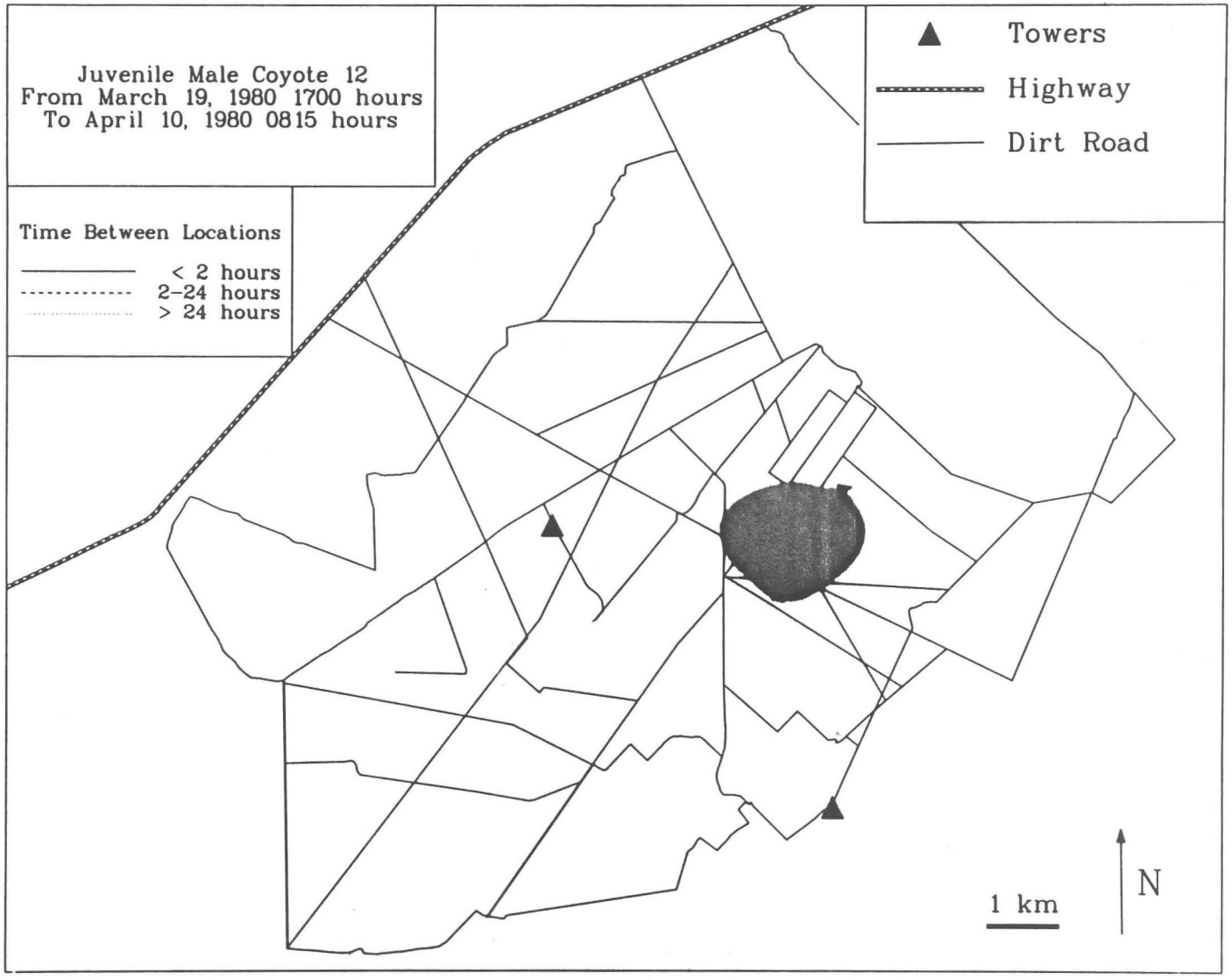

Fig. 34. Distribution of telemetry relocations for coyote 12 on the Freer study area, Texas.

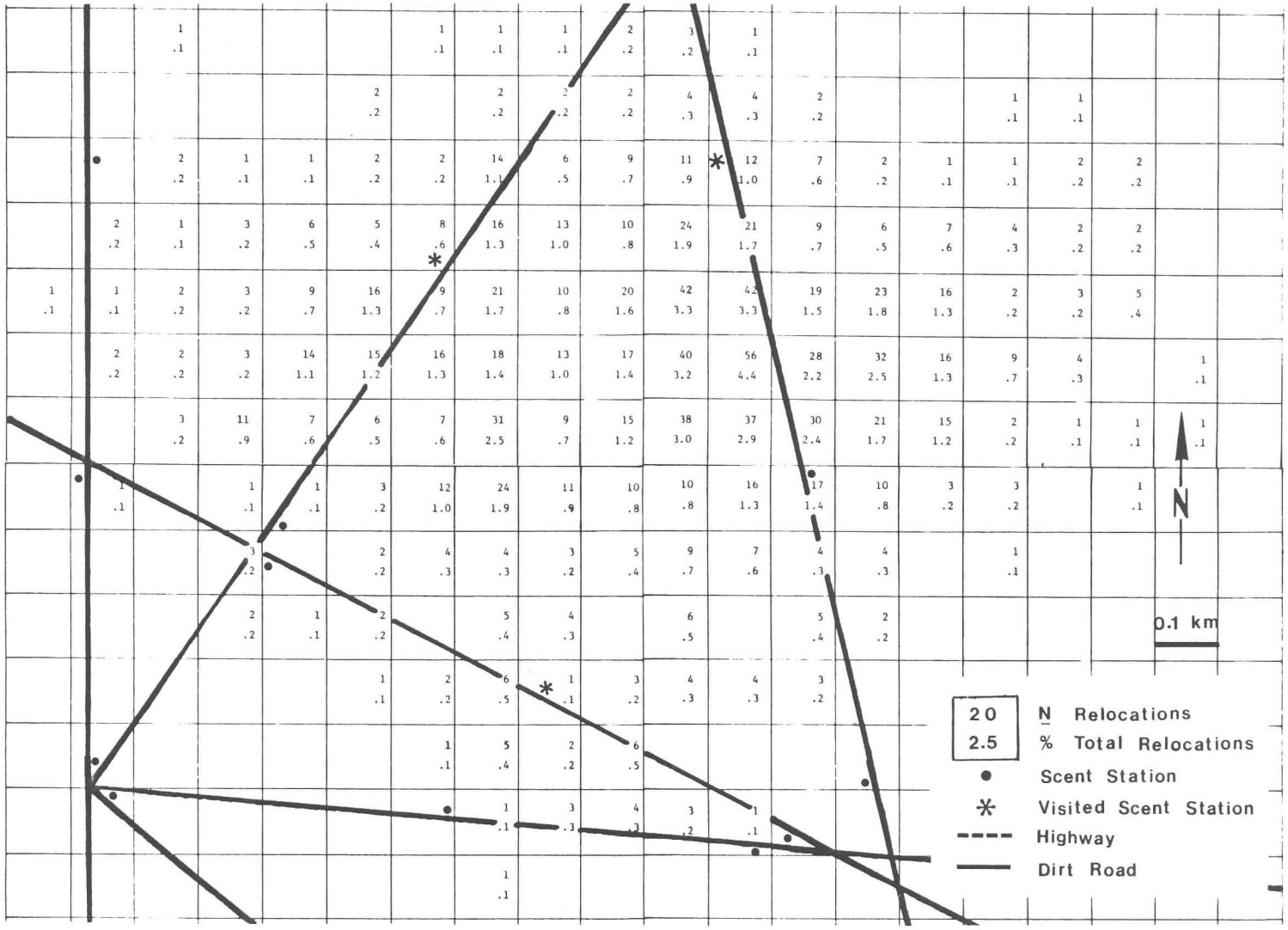

Fig. 35. Grid cell frequency distribution of telemetry relocations for coyote 12 on the Freer study area, Texas.

VITA

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Doctor of Philosophy

Dissertation: Differential Behavior of Coyotes with Regard to Home Range Limits

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