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HOME RANGE, MOVEMENTS, AND ORIENTATION IN THE EASTERN BOX TURTLE, *TERRAPENE CAROLINA CAROLINA*

by

ROBERT MADDEN

A dissertation submitted to the Graduate Faculty in Biology in partial fulfillment of the requirements for the degree of Doctor of Philosophy, The City University of New York.

1975

This manuscript has been read and accepted for the Executive Committee in Biology in satisfaction of the dissertation requirement for the degree of Doctor of Philosophy.

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ABSTRACT

This study covers the home range, homing ability, habitat utilization, and juvenile dispersal of the eastern box turtle, _Terrapene carolina carolina_. Radiotelemetry was used to track 23 adult turtles for periods of time ranging from 50 to 480 days of activity. In addition, 13 hatchlings were tracked during their initial movements from the nest, as well as two young turtles, 9 and 10 years old. Smaller amounts of data were also acquired on several other turtles. The study area was the Kalbfleisch Field Research Station of the American Museum of Natural History, in Dix Hills, Long Island.

The data acquired in this study were used to compare the principal methods currantly in use for determining home range--namely convex polygon, minimum polygon, and bivariate normal. Although home ranges calculated by the three methods differed substantially in magnitude, they correlated so highly ($r>.9$), that they must be considered to perform essentially identical functions. None of these methods was useful in measuring the actual area utilized by turtles (called "utilized home rage"), as opposed to the overall area over which patches of use were distributed (called "total home range"). A subjective estimate was made of the utilized range. In magnitude, this estimate was smaller than any of the three objective estimates, and closest to the minimum polygon estimate. Its correlations with the objective methods, though fairly high, were lower than the correlations among objective methods (r about .7). A proposal was made for an objective measure of utilized home range that weights patches of use by their intensity of occupation; however the method requires very large amounts of data on each animal.

It was found that box turtle home ranges are quite stable from year to year, and that there is considerable variability in the degree to which home ranges shift during different times of the year. Females had larger home ranges, and home ranges may be larger in areas of low habitat diversity. Home range did not appear to be related to weight of the animal, or to the population density of the area. Box turtles appear to be non-territorial, with the possibility of some aggressive interaction between males. The average area of a box turtle's 95% bivariate normal home range is 6.96 hectares.

Forty-one displacements of box turtles were made to distances 250 to 1150 meters outside of the 95% bivariate normal home range, except for one juvenile who was displaced 180 meters from its known lifetime home range. 14 adult animals, two animals 9 and 10 years old, and one 1.5-year old animal were involved. Return to the home range was observed in 38 out of the 40 releases in which the animal was successfully tracked. One adult, and the 1.5 year old turtle failed to return. The experimental design made the following mechanisms of homing unlikely: pure inertial guidance, inertial guidance with external

directional information, orientation by visual landmarks or familiarity with the terrain, random search, and bicoordinate celestial navigation. By process of elimination, it is suggested that smell may be the sensory modality involved.

Habitat preference was examined with regard to the following habitat types: forest, brush, field, grass, forest-brush ecotone, forest-field ecotone, and forest-grass ecotone. It was found that box turtles favor ecotones between forest and brush and forest and field. They avoid forest, grass, and ecotones between forest and grass. They are essentially neutral with regard to field and brush. There is some seasonal variation in habitat preference, forest being less avoided in August. In general, it was concluded that box turtles favor areas of high diversity.

The following factors were examined to determine whether they are important in affecting box turtle movements: temperature at various times of the day, precipitation, and time of year. It was found that temperature at all times of the day affects box turtle movements, including times when they are inactive. Temperatures sampled at eight-hour intervals provide about as much predictive ability as temperatures sampled at four hour intervals. However, not all sets of eight-hour samples are equally effective. The set 4:00, 12:00, and 20:00 provides a better prediction than the set 0:00, 8:00,

16:00. The reasons for this are not clear. Correlations with night-time temperatures were negative, indicating greater movement with lower temperature. Precipitation was positively correlated with distance moved. It was found that turtles move less early and late in the year than in the middle of the year. No support for previous observations of a mid-summer period of inactivity was found.

Hatchling box turtles tracked during their initial movements from the nest traveled no further than the woods surrounding the field containing their nesting site in the first three seasons of activity. Thus they did not appear to undergo any appreciable dispersal from the nesting site. Population regulation in box turtles may largely be by mortality of the young.

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The help, encouragement, friendship, patience, criticism, and cooperation of many people made this thesis possible. It is hard to say sometimes whose existence may have influenced the final outcome. With appologies then to those who perhaps should also be mentioned, I wish to express my thanks and gratitude to the following: Max Hecht, Leslie Marcus, Wesley Lanyon, Richard Zweifel, David Ehrenfeld, Horace Havemeyer, Ursula Behrens, James Gulledge, Chaim Kropach, David Ewert, Cynthia Chazotte, Mary Guillet, and all the N.S.F.U.R.P. program students at the Kalbfleisch Field Research Station. Also, I would like to thank the many graduate students at City University whose companionship and intellectual stimulation I shall always remember with pleasure. Finally, my greatest thanks go to Jacalyn Madden for all her love and all that we share. Naturally, responsibility for any deficiencies which exist in this work remains with me.

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INTRODUCTION

Background

This is a report of a study done on the home range, movements, homing behavior, and some aspects of the general ecology of the eastern box turtle, <u>Terrapene</u> <u>carolina</u>. The last complete study of this kind on this species was done by Stickel (1950). She relied primarily on the technique of mark and recapture, with supplementary, more detailed data being provided by devices containing a spool of thread that unwound as the animal walked. The mark-recapture technique has the severe disadvantage of providing limited information on each animal (Stickel's average number of recaptures per animal was 8), while the thread-trailer is quite unreliable. Usually the thread breaks or is completely run out after a relatively brief period. In short, when Stickel did her study, there was no way of obtaining detailed information on individual turtles over long periods of time. More recently, the development of miniaturized radio transmitters has provided such a method, and it was thought worthwhile to restudy the box turtle using this technique. Some idea of the relative advantage of radiotelemetry over thread-trailing may be gleaned from the fact that home ranges in this study were calculated on the basis of 50 to 480 days (about 3 seasons) of tracking, while Stickel trailed only one animal for more than 50 days (161 days) and ten other animals for periods of 1-44 days. Also transmitters, being much smaller and lighter than thread trailing devices, can be expected to interfere less with the normal behavior of the turtles, and can even be made small enough to permit attachment to hatchling turtles, providing information on a virtually unknown age class. Accordingly, this study was undertaken.

The genus Terrapene contains mostly terrestrial members of the largely aquatic family Emyidae. Milstead (1969) recognized four species in the genus, two of which, Terrapene carolina and T. ornata, are found in the United States. According to Legler (1960), T. ornata is basically a grasslands species, while T. carolina is a forest species. Certainly, their distributions indicate some such difference, T. ornata having a mid- and southwestern distribution, and T. carolina having a more eastern distribution, with considerable overlap between the two. However, one of the conclusions of this study is that T. carolina really occupies the ecotone between forest and field, and at least when given the choice is not fundamentally a forest species.

The genus shows evolutionary convergence with the Testudininae, the true land tortoises. They have high-domed shells, reduction in the size and number of the digits, reduction of the webbing between the digits, and are weak swimmers. In fact, box turtles have occasionally drowned when they fell into one of several artificial concrete ponds with straight walls that are on my study area, and were unable to climb out.

The purpose of this study was to investigate the use of space by Terrapene carolina. It was hoped that radiotelemetry would provide the means for obtaining much more detailed information on individual box turtles than has previously been possible. With such data, it seemed reasonable to suppose that a more precise picture could be obtained of the manner in which this species exploits the resources available to it. A variety of questions arise in this regard. How do box turtles distribute their activites over the available space? What habitats are used by turtles, and how specific are their habitat requirements? How does usage of space differ with season of the year? Are there specific requirements for the nesting and hibernation sites which are not met by the rest of the home range? Do the requirements of males and females differ, and do males attempt to extend their home ranges in an effort to inseminate more females? What kind of a social structure, if any, do box turtles maintain? How strong is a box turtle's attachment to its home range, and what adaptations exist for permitting it to orient with regard to its home range? What are the initial habitat requirements of young turtles, and do young turtles undertake a dispersal from the nesting site? If so, to what distances? What factors affect the movements of box turtles? Finally, it was hoped that the data obtained in this study would be of use in resolving a variety of problems that exist in the concept of home range itself.

Materials and Methods

The study area consisted of the Kalbfleisch Field Research station of the American Museum of Natural History, plus the adjoining private property of Mr. Horace Havemeyer (figure 1). The area of the field station is 94 acres, with the Havemeyer Estate representing approximately an additional 80 acres. The study area is located in the Dix Hills section of the Town of Huntington, Suffolk County, Long Island, New York, on the Ronkonkoma terminal glacial moraine. Elevation ranges from about 230-320 feet, and the topography is very gently rolling with kettle depressions in which a number of permanent and seasonal ponds occur.

The vegetation of the field station consists of a patchwork of grassy fields, herbaceous fields, brushy areas, and forest. In addition, hedgerows of trees and heavy brush cut across many of the non-forested areas. This considerable habitat diversity is the result of purposeful management of the various pastured and cultivated fields and the woodlots that made up the station prior to its acquistion by the American Museum of Natural History in 1957. Certain fields have been mowed periodically, others have had the woody vegetation killed off with herbicides, still others have been left alone to undergo normal succession. In addition, certain fields have occasionally been plowed, and others burned. The forest areas have largely been left alone, but one (BWF-2, figure 2) has been burned.

A detailed land use history and floral description is available for the field station (McCormick, et. al., 1969), portions of which will be summarized here. The property has been cultivated, pastured, and used as woodlot for at least 150 years. When the it was acquired in 1929 by Miss Augusta Kalbfleisch, it was being pastured and truck farmed. Cropping was temporarily terminated until 1938, but mowing and grazing continued. By 1954, fields AP-1 through AP-10 were again being cultivated, but after this there was no further cultivation. In 1957 the property was acquired as a field station by the American Museum of Natural History, and has since been managed as described above. During Miss Kalbfleisch's ownership, new roadways were built, including a paved main road, and extensive ornamental plantings were made, principally around the main residence hall and along the main road.

The Havemeyer Estate differs from the field station principally in that it was being grazed by cattle and horses during the study. As a result, the fields contain mainly grasses, and a large area of forest to which the livestock had access is mostly free of understory, in contrast to the dense understory of _Smilax_ _rotundifolia_, _Rhus_ _radicans_, _Lonicera_ _japonica_, _Parthenocissus_ _quinquefolia_, _Vacinium_ _vacillans_, _Gaylussacia_ _baccata_, and other species that characterizes forest areas from which livestock have been excluded. The habitats of the study area are designated as follows. Mowed or grazed areas consisting mostly of grasses are called "grass". Areas in which woody vegetation has been killed, and consisting mostly of herbaceous growth other than grasses are called "field". Areas undergoing normal succession and containing woody vegetation 5 meters or less high are called "brush". Areas containing woody vegetation more than about 5 meters high, and ungrazed are called "woods". Finally, areas containing trees more than 5 meters high, but with the understory grazed out by cattle are called "open woods".

An approximate idea of the plant species to be expected in each habitat type can be gleaned from McCormick, et. al. (1969). They class the various plant species into the following abundance groups:

Rare: Known from only one specimen or one station.

Occasional: Occurring in 10% or less of the available habitat.

Frequent: Occurring in 10-25% of the available habitat.

Common: Occurring in 25-75% of the available habitat.

Abundant: Occurring in 75% or more of the available habitat.

Species listed as "frequent" or better in the various habitats are:

"Oak Forest" areas BWF-1, BWF-2, and BWF-3, the most mature woods on the station--*Dryopterus thelypterus*, *Dennstaedtia punctiloba*, *Danthonia spicata*, *Panicum depauperatum* *P.* *sphaerocaron*, *Carex pensylvanica*, *Smilacina racemosa*, *Cypripedium acaule*, *Castanea dentata*, *Quercus alba*, *Q.* *palustris*, *Sassafras albidum*, *Acer rubrum*, *Cornus florida*, *Pyrola rotundifolia*, *Kalmia latifolia*, *Lyona mariana*, *Epigaea repens*.

"Shrubby Woodlands", less mature woods areas--*Dryopterus thelypterus* *Juniperus virginiana*, *Smilax rotundifolia*, *Mirica pensylvanica*, *Pyrus malus*, *Prunus serotina*, *Lespedeza virginica*, *Rhus radicans*, *Acer rubrum*, *Trichostema dichotomum*, *Solidago caesia*, *Aster divaricatus*.

"Shrubby Areas"--*Panicum languginosum*, *Comptonia peregrina*, *Rumex acetosella*, *Sassafras albidum*, *Lespedeza virginica*, *Rhus glabra*, *R.* *copallina*, *Hypercum perforatum*, *H.* *canadense*, *Lechea intermedia*, *Trichostema dichotomum*, *Linaria canadensis*, *Eupatorium hyssopifolium*, *Crysopsis mariana*, *Solidago nemoralis*, *Aster divaricatus*, *Hieracium pratense*, *H.* *grohovii*.

"Fallow Fields"--*Juniperus virginiana*, *Poa compressa*, *Dactylis glomerata*, *Agrostis tenuis*, *Anthroxanthum odoratum*, *Panicum lanuginosum*, *Juncus tenuis*, *J.* *effusis*, *Sisyrinchium arenicola*, *Myrica pensylvanica*, *Rumex acetocella*, *Polygonum hydropiper*, *Pyrus sieboldii*, *Potentilla norvegica*, *P.* *canadensis*, *Rubus flagellaris*, *R.* *pensilvanicus*, *Prunus serotina*, *Trifolium agrarium*, *Desmodium ciliare*, *D.* *marilandium*, *Oxalis europaea*, *Rhus* *radicans*, *Hypericum perforatum*, *H. punctatum*, *H. mutilum*, *Oenothera biennis*, *Daucus carota*, *Cornus florida*, *Apocynum androsaemifolium* *A. cannabinum*, *Asclepia tuberosa*, *Glechoma hederacea*, *Prunella vulgaris*, *Solanum carolinense*, *Verbascum thapsus*, *Linaria vulgaris*, *L. canadensis*, *Veronica officinalis*, *Plantago lanceolata*, *Lonicera japonica*, *Eupatorium hyssopifolium*, *Chrysopsis mariana*, *Solidago speciosa*, *S. juncea*, *S. nemoralis*, *S. rugosa*, *S. canadensis*, *S. graminifolia*, *S. tenuifolia*, *Aster simplex*, *Gnaphalium obtusifolium*, *Rudbeckia serotina*, *Chrysanthemum leucanthemum*, *Cirsium vulgare*, *C. arvense*, *Hieracium flagellare*, *H. pratense*, *H. florentinum*.

"Cultivated Areas"--*Setaria lutescens*, *S. faberi*, *Rumex crispus*, *Polygonum pensylvanicum*, *Polygonum hydropiper*, *P. persicaria*, *Chenopodium album*, *C. ambrosoides*, *Amaranthus hybridus*, *Phytolacca americana*, *Mollugo verticillata*, *Portulaca oleracea*, *Cerastium vulgatum*, *Rhaphanus rhaphanistrum*, *Trifolium repens*, *Euphorbia supina*, *Oenothera biennis*, *Daucus carota*, *Trichostema dichotomum*, *Solanum carolinense*, *Plantago major*, *Lobelia inflata*, *Erigeron annuus*, *E. canadensis*, *Ambrosia artemisiifolia*, *Bidens frondosa*, *Galinsoga ciliata*, *Cirsium arvense*, *Lactuca scariola*.

"Field Boarders"--*Comptonia peregrina*, *Sassafras albidum*, *Geum canadense*, *Rubus phoenicolasiasius*, *Rhus radicans*, *Vitrus labruscana*, *Vitrus aestivalis*, *Lechia intermedia*, *Lactuca canadensis*, *Hieracium gronovii*.

"Fence Rows"--Juniperus virginiana, Allium vineale, Smilacena racemosa, Smilax rotundifolia, Sassafras albidum, Pyrus malus, Geum canadense, Prunus avium, P. serotina, Rhus glabra, R. copallina, R. radicans, Vitis labruscana, Solalum dulcamara, Lonicera japonica, Solidago caesia, Aster divaricatus, Lactuca canadensis.

Grass areas are not distinguished per se in the study, but on the basis of personal observation, the principal species are: Agrostis tenuis, Agrostis alba, Anthroxanthum odoratum, Dactylis glomerata, Agropyron repens, Phleum pratense, and Holcus lanatus.

The lists above give the general species compositions of the various physiognomic habitat types recongized in this study. Actually, however, the detailed composition of different areas of the same habitat type can be quite variable. Unfortunately, no adequate description of the station vegetation on such a detailed scale exists. I have undertaken a preliminary characterizatin of this variation, which is presented here. Locality designations refer to figure 1b, taken from Martin (1958). The alphanumeric symbols refer to vegetation cover types designated in that study, which are no longer valid, but are now used by field station workers as convenient locality designations.

AP-1: The central portion contains well spaced out woody vegetation filled in by herbaceous vegetation. The woody vegetation is mostly Myrica pensylvanica, with smaller amounts of Pyrus sieboldii, Rhus copallina, and

Rosa multiflora. The herbaceous vegetation is largely Solidago rugusa, S. graminifolia, S. speciosa, S. juncea, S. canadensis, and Hieracium pratense. In addition, there is a groundstory of Lonicera japonica and Potentilla canadensis. The peripheral areas of AP-1 contain Solidago rugusa, S. graminifolia, S. speciosa, S. juncea, S. canadensis, Anthoxanthum odoratum, Rhus radicans, Lonicera japonica, and Hieracium pratense.

AP-2: This area contains well-spaced woody vegetation, filled in by herbaceous vegetation. Woody species include Juniperus virginiana, Pyrus sieboldii, Viburnum sp., Pinus strobus, and Myrica pensylvanica. Herbaceous species include, Solidago rugosa, S. speciosa, S. graminifolia, and Hieracium pratense. The woody plant Lonicera japonica can also be considered part of the herbaceous filler.

AP-3: Nearly a pure stand of Myrica pensylvanica. Some Lonicera japonica and Parthenocissus quinquefolia entwined in the branches. There is also a very light understory of Parthenocissus quinquefolia, and an occasional Solidago spp. The borders of the area contain Solidago rugusa, S. speciosa, S. juncea, and S. canadensis.

AP-4: This area was quadrat sampled in 1970 by Rabinowitz (1970) as part of a botanical research project under the direction of Jack McCormick. All species found by Rabinowitz to have an average cover greater than 1% are listed here, together with their average cover. The area can be divided into two portions, a western half managed by periodic burning, and an unmanaged eastern half. The composition of the managed half, based on 45 one meter square plots was: *Potentilla canadensis* (32.0%), *Solidago rugosa* (23.1%9, *S. speciosa* (20.0%), *Apocynum cannabinum* (16.0%), *Hieracium pratense* (14.3%), moss and lichen (11.2), *Solidago juncea* (10.4%), *S. gramminifolia* (7.7%), *S. canadensis* (7.2%), *Apocynum androsaemifolium* (6.4%), *Lonicera japonica* (4.2%), *Solidago nemoralis* (3.5%), *S. tenuifolia* (2.9%), *Myrica pensylvanica* (2.3%), *Rubus spp.* (2.0%), *Andropogon sp.* (1.5%). The composition of the unmanaged half, based on 35 one meter square quadrats was: moss and lichen (24.1), *Solidago rugosa* (22.3%), *Lonicera japonica* (17.7%), *Solidago speciosa* (13.7%), *Potentilla canadensis* (13.3%), *Myrica pensylvanica* (10.3%), *Robinia pseudoacacia* (10.2%), *Apocynum canabinum* (8.3%), *Hieracium pratense* (8.0%), *Apocynum androsaemifolium* (6.6%), *Solidago juncea* (4.4%), *S. gramminifolia* (3.5%), *S. nemoralis* (2.4%), *Anthoxanthum odoratum* (1.2%), *Rosa multiflora* (1.8%), *Prunus serotina* (1.1%), and *Pyrus sp.* (1.1%). The designation moss and lichen refers mostly to *Polytrichum sp.* and *Atrichum sp.* Several comments on the above data are in order. The use of percentage cover is not as useful an indication of the importance of a species as some more fundamental parameters, such as biomass or energy flow through the species. The importance of *Hieracium pratense*, Potentilla canadensis, and moss and lichen, are particularly exagerated by this measure, in my opinion, since these plants form essentially two dimensional layers while other species occupy three dimensional volumes. True, in theory, a single layer of foliage could capture as much sunlight as many layers, but in practice, this is not the case. In addition, these three species hug the ground closely, and so are often receiving light only after it has been filtered through the foliage of other species. Another point is that the average cover figures given above hide much variation in composition from one part of the area to another. In the managed half there is a gradual gradation from a high percentage of Apocynum and little Solidago in the western end to a high percentage of Solidago and little Apocynum in the eastern end. In the unmanaged portion, the average covers are even more misleading. As can be seen in figure 1, the managed half contains a triangle physiognomically designated as brush, while the rest is woods. The woods portion is a nearly pure stand of Robinia pseudoacacia, with an understory of Solidago spp. The brush portion contains much Myrica pensylvanica, with Lonicera japonica entangled in the branches. The space between the Myrica is filled with Solidago spp., with some Apocynum spp., and an understory of Potentilla canadensis and moss and lichen.

AP-5: Though not mown, this area contains much grass. The main species are Anthoxanthum odoratum, and Agrostis *tenuifolia*. Some *Solidago* is also present, especially *Solidago speciosa* and *Solidago juncea*. Additional species include *Potentilla canadensis*, *Rubus sp.*, *Lonicera japonica*, and small amounts of *Apocynum canabinum*.

AP-6: *Anthoxanthum odoratum*, *Solidago speciosa*, *S. juncea*, *S. canadensis*, *S. graminifolia*, *S. rugusa*, *Apocynum canabinum*, *Heiracium pratense*, and lesser amounts of *Potentilla canadensis* and *Lonicera japonica*.

AP-7: This area was plowed during the study. It quickly grew up to primarily *Solidago spp.*, including *Solidago speciosa*, *S. juncea*, *S. rugusa*, *S. canadensis*, and *S. graminifolia*. Also some *Heiracium pratense*, *Anthoxanthum odoratum*, *Potentilla canadensis*, and *Agrostis tenuifolia*.

AP-8: This is one of the mown areas, but is not as heavy in grasses as is normal for such areas. Species include *Anthoxanthum odoratum*, *Lonicera japonica*, *Apocynum cannabinum*, *Solidago rugusa*, *S. speciosa*, *S. graminifolia*, and *S. canadensis*, in approximately that order.

AP-9: A mown area containing mostly grasses. Species include *Anthoxanthum odoratum*, *Phleum pratense*, *Poa compressa*, *Holcus lanatus*, *Agropyrum repens*, and *Dactylus glomerata*.

AP-10: This area was quadrat sampled in 1967 under the direction of Dr. Jack McCormick (field station records). It is divided into two sections. The southern half is unmanaged, while the northern half is managed by killing off all woody vegetation with herbicides. Physionomically, the northern area is designated "field", while the southern area is designated "brush", reflecting the considerable growth of woody vegetation. All species with average covers greater than 1% are listed here, together with their average covers. Unmanaged section (based on 72 one meter square plots): Lonicera japonica (43.0%), moss and lichen (36.9%), Hieracium pratense (31.9%), Potentilla canadensis (17.7%), Solidago rugosa (16.7%), Juncus tenuis (9.6%), Betula populifolia (9.6%), Myrica pensylvanica (8.9%), Solidago juncea (7.8%), S. canadensis (5.1%), Pyrus sp. (sieboldii?-RCM), Solidago speciosa (3.6%), Betula lenta (2.8%), Solidago nemoralis (2.6%), Trifolium agrarium (2.2%), Chrysanthemum leucanthemum (2.0%), Rumex acetocella (1.9%), Solidago tenuifolia (1.9%), S. graminifolia (1.7%), Juniperus virginia (1.7%), Andropogon scoparius (1.4%), Pinus rigida (1.4%), Veronica officinalis (1.4%), Eleagnus commuta (1.2%), Anthoxanthum odoratum (1.0%), Trifolium repens (1.0%). Managed section (based on 76 one meter square plots): Lonicera japonica (58.3%), Solidago rugosa (20.6%), moss and lichen (16.8%), Hieracium pratense (14.5%), Potentilla canadensis (6.4%), Solidago canadensis (5.1%), S. juncea (4.2%), Juncus tenuis (3.9%), Apocynum canabinum (3.6%), Chrysanthemum leucanthemum (3.2%), Solidago speciosa (1.7%), S. graminifolia (1.6%), Rumex *acetocella* (1.1%), and *Andropogon scoparius* (1.0%). The term "moss and lichen" refers mostly to *Atrichum* and *Polytrichum*. The same comment that was made under the description of AP-4 with regard to the usefulness of average cover as a measure of species importance applies here. There appears to be less variation within a section in this area than in area AP-4. It should be noted however that the northern most third of the managed area contains an especially heavy growth of *Apocynum spp*.

BWF-1: The "BWF" areas are the most mature habitats on the station. They are dry black oak (*Quercus velutina*) forests. BWF-1 is an unmanaged area. Its species include: *Quercus velutina*, *Quercus alba*, *Quercus palustris*, *Acer rubrum*, *Carya ovalis*, *Betula lenta*, *Nyssa sylvatica*, *Cornus florida*, *Sassafras albidum*, *Viburnum acerifolium*, *Kalmia latifolia*, *Castanea dentata*, *Smilax rotundifolia*, *Lonicera japonica*, *Rhus radicans*, *Parthenocessus quinquefolia*, *Vaccinium vacillans*, *Gaylussacia baccata*, *Aralia nudicaulis*, *Solidago rugosa*, *Dryopteris noveboracensis*, *Carex sp*., *Chimaphila maculata*, and *Lysimachia quadrifolia*.

BWF-2: This area has had the understory burned out. Species include: *Quercus velutina*, *Quercus alba*, *Quercus palustris*, *Cornus florida*, *Carya ovalis*, *Sassafras albidum*, *Rhus copallina*, *Viburnum acerifolium*, *Vaccinium vacillans*, *Gaylussacia baccata*, *Carex sp*, *Solidago rugosa*, *S. speciosa*, *Parthenocissus quinquefolia*, and *Rubus spp*.

WFR-1: *Carya ovalis*, *Quercus velutina*, *Prunus* *serotina*, *Cornus florida*, *Rhus glabra*, *Carya ovalis*, *Sassafras albidum*, *Smilax rotundifolia*, *Lonicera japonica*, *Rubus spp*., *Solidago rugosa*, *S*. *graminifolia*, *S*. *canadensis*, *S*. *speciosa*, *Vitus sp*.

WFR-3: *Carya ovalis*, *Rhus glabra*, *Quercus alba*, *Quercus velutina*, *Prunus serotina*, *Smilax rotundifolia*, *Lonicera japonica*, *Rubus spp*.

Area North of AP-5 and G-1: This shrubby forest area includes ISW-4, G-2, P-1, IFR-1, P, S-3, and LW-1. Species are: *Quercus velutina*, *Pyrus sieboldii*, *Prunus serotina*, and *Rhus radicans*. The south-east corner contains a pine plantation with *Pinus strobus*, and *Pinus sylvestris*.

ISW-1: *Prunus serotina*, *Picea glauca*, *Pyrus sieboldii*, *Sassafras albidum*, *Fagus sp*., *Juniperus virginiana*, *Quercus alba*, *Quercus velutina*, *Carya ovalis*, and *Rhus radicans*.

ISW-2, WFR-2, S-5: *Cornus florida*, *Tsuga canadensis*, *Fagus sp*., *Juniperus virginiana*, *Pyrus sieboldii*, *Prunus serotina*, *Pinus strobus*, *Quercus velutina*, *Rhus radicans*, *Myrica pensylvanica*, *Solidago rugosa*, *Smilax rotundifolia*.

P-3: Pine plantation--*Pinus strobus*.

SW-4: *Robinia pseudoacacia*, *Prunus serotina*, *Rhus radicans*, *Solidago rugosa*.

SW-2: *Pinus strobus*, *Betula populifolia*, *Rhus radicans*, *Kalmia latifolia*.

ISW-13: Similar to BWF-2, but with some *Tsuga canadensis* and *Parthencissus quinquefolia*.

ISW-6: *Picea glauca*, *Tsuga canadensis*, *Cornus florida*, *Pinus strobus*, *Rhus radicans*, *Parthenocissus quinquefolia*.

SW-2, IFR-2, ISW-5, SW-3: *Carya ovalis*, *Cornus florida*, *Pyrus sieboldii*, *Agropyrum repens*, *Quercus velutina*, *Rhus radicans*, *Smilax rotundifolia*, *Vitus sp.*, *Lonicera japonica*.

P-2: Pine plantation--*Pinus strobus*, *Pyrus sieboldii*, *Parthenocessus quinquefolia*, *Rhus radicans*.

LW-2, S-4: *Carya ovalis*, *Pyrus sieboldii*, *Quercus velutina*, *Betula populifolia*, *Viburnum acerifolium*, *Smilax rotundifolia*, *Rhus radicans*, *Parthenocissus quinquefolia*.

Y-6: *Pyrus sieboldii*, *Quercus velutina*, *Juniperus virginiana*, *Vitus sp.*, *Lonicera japonica*, *Rhus radicans*.

P-4: *Pinus strobus*.

IFR-3 North half--*Acer rubrum*, *Betula populifolia*, *Juniperus virginiana*, *Prunus serotina*, *Solidago spp.*, especially *Solidago rugosa*, *Rhus radicans*, *Lonicera japonica*. South half--*Robinia pseudoacacia*, *Solidago rugosa*, *Lonicera japonica*, *Rhus radicans*.

LW-3: *Prunus serotina*, *Carya ovalis*, *Agropyrum repens*, *Robina pseudoacacia*, *Quercus velutina*, *Rhus radicans*, *Parthenocissus quinquifolia*, *Lonicera japonica*.

S-7: *Agropyrum repens*, *Pyrus sieboldii*, *Juniperus virginiana*, *Robinia pseudoacacia*, *Rhus radicans*, *Rosa multiflora*.

ISW-8: *Sassafras albidum*, *Rhus radicans*, *Carya* *ovalis*, and *Quercus velutina*.

SW-1, SF-1, Y-3, Y-4: *Robinia pseudoacacia*, *Picea glauca*, *Prunus serotina*, *Rhus radicans*, *Solidago canadensis*, *Rosa multiflora*, *Rubus sp*.

ISW-7, LW-4: *Acer rubrum*, *Pyrus sieboldii*, *Quercus velutina*, *Robinia pseudoacacia*, *Rhus radicans*, *Parthencissus quinquefolia*.

SW-6, IFR-4: *Juniperus virginiana*, *Rhus copallina*, *Quercus velutina*, *Carya ovalis*, *Betula lenta*, *Prunus serotina*, *Sassafras albidum*, *Myrica pensylvanica*, *Dryopteris noveboracensis*, *Lonicera japonica*, *Rhus radicans*, *Smilax rotundifolia*, *Rubus sp*., *Vitus sp*., and *Agropyron repens*.

WFR-6: *Prunus serotina*, *Carya ovalis*, *Quercus velutina*, *Q. alba*, *Sassafras albidum*, *Rhus radicans*, *Lonicera japonica*, *Rubus sp*., and *Solidago rugosa*.

This study took place during the summers of 1969, 1970, 1971 and 1972, with 1970, 1971, and 1972 being the years of most intensive field work. Field work was carried on during the entire period of turtle activity for these years--from about mid-April, to early November. Occasional spot checks on the condition of the animals were made during the winter as well.

As mentioned, the method of tracking turtles was to attach small radio transmitters to their shells. Two different transmitters were used. The larger weighed about 15 grams, including batteries and potting compound, had a life expectancy of 2-3 months, and a reliable range of about 100 meters. It was used for tracking adults and older juveniles, weighing at least 150 grams. The other transmitter weighed 1.5 grams, had a life expectancy of about one month, and a range of about 20 meters. It was used in tracking younger turtles, principally hatchlings. Although even this very tiny transmitter represented about 20% of the weight of a newborn turtle, it did not seem to create any problems. It is quite certain that the larger transmitter, representing only about 3% of the weight of a small adult, had little effect on the animals carrying them. Turtles of both sexes were observed mating without difficulty while equiped with transmitters, and females constructed normal nests. Details on the transmitters are as follows:

The larger transmitter was a crystal-controlled Hartley oscillator with direct radiation from the tank coil, one loop of which was extended to run around the shell of the turtle. The oscillator was pulse-modulated by a complementary transistor-pair astable multivibrator, controlling the bias to the oscillator transistor. Duty cycle was about 2%, and pulse interval about one second, resulting in a reasonable battery life. Peak power input was about 2 mW. Two Mallory MS76 silver-oxide cells hooked in series supplied power. Silver oxide cells were found to be more reliable than mercury cells, and deliver a slightly higher voltage, 1.5v as compared to 1.4v. Although the shelf-life of silver oxide cells is not supposed to be as great as that of mercury cells, this posed no problem, since batteries were expected to perform for only 2 months. The transmitters radiated in the citizens' band. The design of the smaller transmitter was similar, but crystal control was not used. Transmission was in the FM band, and a single, much smaller battery was used (Mallory RM312 mercury cell). To obtain better battery life, the duty cycle was shortened to 1%, and power input was reduced to about .5 mW. In the smaller transmitter, there was no antenna loop around the shell. All radiation was from the tank coil and associated circuitry. Figures 2a and 2b give circuit diagrams, and a complete list of components for both transmitters.

Because all available plastic materials for coating transmitters are unacceptably permeable to water (Mackay, 1968), a coating of beeswax was used for waterproofing, followed by a coating of epoxy for mechanical strength. In addition, the smaller transmitter had a coating of polystyrene under the beeswax to minimize frequency shift during potting, and to improve the efficiency of transmission. Transmitters were attached to the turtles with General Electric RTV-108 translucent self-curing silicon rubber. If the shells were completely dry before the tranmitter was put in place, adhesion was excellent, and the bond was quite water resistant, though prolonged immersion, as occasionally happened when turtles hibernated in dry kettle depressions that later in the winter filled with water, could loosen the bond. Normally, the silicon rubber would hold the transmitter in place for its entire expected battery life, but occasionally repair was needed. On warm days, the silicon rubber would cure sufficiently in one hour to permit release of the turtle.

A Lafayette HA-305 was the tracking receiver for the larger transmitter, and a Heathkit GR-98 receiver, somewhat modified, was used for the smaller transmitter. Adequate range of reception for tracking box turtles was obtained with this equipment. One difficulty with an animal that lives as close to the ground as a box turtle, is that signal strength can be very erratic, necessitating some moving on the part of the tracker to get into a good signal area. Triangulation with a directional antenna was not found to be sufficiently accurate as a method for determining the position of the turtles, so all positions were determined by following the signal to its source.

Once a turtle was located, its position was plotted in one of several ways. The field station has been surveyed into 50 meter by 50 meter grid squares, marked by a post at each corner. On the field station, the location of a turtle was designated wherever possible by taking compass azimuths on two grid posts with a Suunto compass. The accuracy of this compass is better than plus or minus 1/4 degree. When vegetation made the taking of compass readings impractical, the distances to the nearest grid lines were paced. As a compromise, compass direction was sometimes taken to a single grid post, and the distance to that point paced. Locations based on compass locations should be accurate to within about a 1 meter radius, while paced distances are accurate to within about 3 meters. On the Havemeyer estate, there was no grid system. Instead, compass and tape surveys were made of a variety of conspicuous objects--distinctively shaped trees, rocks, dirt road intersections, the corner of a barn, and a wooden man-made structure of unobvious function. The turtles were then located with regard to these objects by compass azimuth and pacing. Accuracy in this case is lower, on the order of 6 meters.

In general, efforts were made to disturb the animals as little as possible. Normally, they were not handled, and if vegetation was thick, it was frequently impossible even to spot them. Occasional handlings were made to record cloacal temperature with a Schultheis quick-reading thermometer, and to check the condition of the transmitter. At about two month intervals, the animals were returned briefly to the laboratory to change transmitters, at which time they were weighed. All turtles brought into the laboratory, whether in conjunction with this project or not, were marked by filing notches or drilling holes into the marginal scutes, and had basic shell measurements taken. This was done by assistants of Dr. Richard Zweifel as part of an ongoing project. Because of the long-standing nature of this latter project, some mark-recapture data for previous years are available for many of the animals used in this project.

Unless otherwise stated, results in this thesis are based on a group of 23 adult animals for which a minimum of 20 observation points were available extending over a minimum of 50 days. For most of these animals, considerably more data is available. The maximum is 233 points, obtained over 480 days of tracking, which is equivalent to nearly 3 complete seasons of activity. For analyses where detailed information on individual turtles is not needed, data from additional animals, for whom the data is less complete is also used. In addition to the adults, 13 hatchling turtles were tracked. Several juveniles were also tracked, and enough data collected on two of them to be useful in establishing their home ranges.

SOME GENERAL ASPECTS OF BOX TURTLE BIOLOGY

This section covers some aspects of box turtle biology that will be useful later in interpreting the major topics of this thesis. It also presents some miscellaneous data acquired in the course of field work on the main topics.

Diet

T. carolina appears to be quite omnivorous. Workers have differed in their assessment of the relative importance of animal and vegetable matter in the diet of this species. Schmidt (1953) considered them to be of about equal importance. Allard (1935) indicated a preference for animal matter, while Cahn (1937) believed that vegetable material was favored. The most extensive study of box turtle diets is that of Klimstra and Newsome (1960). They confirm Schmidt's belief that animal and vegetable matter are equally favored. Their study is based on an analysis of 117 stomach contents. The major items in the turtles' diets were unidentified plant material (34.2%), insects (19.6%), seeds (17.4%), gastropods (10.6%), carrion (4.8%), isopods (3.5%) and diplopods (2.5%). About 51.6% of the diet, by volume, was plant material, 46.3% was of animal origin, and 2.1% was undetermined. Thus, the reliance on plant and animal sources of food was just about equal. There was some seasonal variation in the kinds of food consumed. Also, total volume of the stomach contents increased from March to June, and decreased from June to October. By contrast, Legler (1960) considered <u>T</u>. <u>ornata</u> to be a largely insect-eating species. He did not give the average percentage of plant and animal material in the stomach contents of the 23 <u>T</u>. <u>ornata</u> he looked at, but states that they contained "up to 20%" vegetable matter. This implies considerably less reliance on plants than is the case for <u>T</u>. <u>carolina</u>. Casual observations on the Kalbfleisch turtles do not indicate any deviations from the situation found by Klimstra and Newsome. Turtles were at various times observed eating raspberries, blueberries, caterpillers, sow bugs, dung and the associated insects, and carrion (dead birds). One box turtle spent several days in the vicinity of a herring gull corpse.

Ages of Box Turtles

It is not known exactly how long box turtles live. Up to a point, it is possible to estimate the age of a turtle by counting the more or less annual growth lamellae of the plastral scutes. Usually the annual rings are quite clear, but irregularities in growth rate during the season of activity always produce secondary rings which could, if unusually well-defined, occasionally be confused with an annual ring. It also appears that turtles may fail to grow some seasons (Nichols, 1939). However, this is not the most severe limitation of this method for aging turtles. As the turtle gets older, growth slows down, and the annual rings get crowded increasingly close together. Eventually, individual rings can no longer be distinguished. This normally happens around the 15th to 20th year of life. Thus one can often only say that a turtle is at least 15-20 years old, but how much older cannot be determined. Wear on the scutes can provide some information. In a fifteen to 20 year old animal, there is usually only rather incipient wear. However, some turtles have been found in which the scutes are polished smooth, and the growth lines nearly obliterated. Such turtles must be very old. There are a number of records in the literature that give some idea of the minimum ages to which box turtles may live in the wild. These records are based on the recapture of turtles that have had initials and dates carved into their shells, turtles being frequent victims of the pen knife. In a few cases, it has been possible to obtain verification of the carved date, and such records can be considered reasonably reliable. In all reported cases, the animal was of adult size when marked, and therefore probably at least 15 years old at the time. Here are some ages that have been determined in this way: Cahn (1937) gives a case of a turtle recaptured 61 years after being marked; Edney and Allen (1951) report a 64 year record; and Price (1951) a 46 year record. Oliver (1953) claims a record of 110 years apparantly the oldest known. For the purposes of this study, a turtle was called adult if it was beyond the age where the later lamellae were far enough apart to count. Sexual maturity, however, takes place at an earlier age.

The actual ages of younger animals, as determined from lamellar counts are always given. The following observations on hatchling turtles followed during this study may be of use. Box turtle eggs hatch in the fall. The young turtles may emerge from the nest in the fall, or may wait to the following spring. In either case, no growth ring is formed the season the animal hatches. Formation of the first growth ring begins the following spring. Thus a turtle with three lamellae beyond the original scute is in its third full season of activity, not counting the season it was born in. This differs from the situation found by Legler (1960) for T. ornata, where hatchlings sometimes showed appreciable growth the year they were born. In this study, when a turtle is called X years old, it is in its Xth full season of activity, not counting its season of birth.

Season of Activity, Mating, Nesting, and Hibernation

In the Long Island area, box turtles are active for about 6 months out of the year, from May to October, inclusive. There may, however, be limited activity in Late April and early November, depending on the weather. The earliest movement observed in the course of this study was between April 8th and 9th, and the latest was between November 15 and 22. Table 1 shows the dates of earliest and latest movements for all turtles for which this information is available. Hatchlings become active considerably later than adults and cease activity considerably earlier. Figure 4a shows the known hibernation sites of all adult animals. As can be seen, hibernation sites are very constant from year to year. Hibernation is always in the woods (with the exception of one hatchling) but not necessarily very far into it. During hibernation, turtles were never observed to burrow much below the leaf litter. Usually they would dig into the ground only to the point where the top of the carapace was about level with the bottom of the leaf litter layer. Depth of hibernation of box turtles seems to vary considerably from region to region depending on winter temperatures. Dolbeer (1971) found that turtles in Tennessee behaved similarly to the Kalbfleisch turtles, digging in only until the top of the carapace was level with the bottom of the leaf litter. Cahn (1937) however, found that turtles in Illinois dug in increasingly deeply as the winter progressed, reaching their maximum depth of 19" by November 30.

Mating appears to be possible throughout the season of activity. In this study, the earliest mating was observed on May 31, and the latest on October 3. The number of matings observed during each month were as follows: May (1), June (3), July (1), August (1), September (2), October (1). Box turtles can therefore be considered "oportunistic copulators". This agrees with observations by other workers, including Ewing (1933) and Legler (1960). There is no evidence for pair-bonding, as the same individual was observed mating with more that one individual during the course of a summer. One attempt at homosexual copulation between males was observed (see HOME RANGE) This has also been reported by Ewing (1935). Female box turtles are apparantly capable of storing sperm. Finneran (1948) reports a case of a female producing fertile eggs two years after being isolated from all males, and Ewing (1943) a case of a female producing fertile eggs four years after isolation. Thus, though nesting occurs in June, sperm obtained during copulation at any time of the year would be useful to a female. Good descriptions of copulation can be found in Evans (1953), and my observations agree with his. The process begins with the male nudging and biting at the edges of the female's shell. He eventually works his way around to the rear of the female, and mounts. As long as she keeps her shell closed, he will reach his head over the top of her carapace, and nip her. Eventually, she opens her shell, he hooks his legs under the edges of her carapace, leans back, and inserts his penis. Following copulation, he falls back, and the female crawls off.

The time of nesting is from about mid-June to early July. Twenty-two nesting attempts were observed in the course of this study, the earliest being on June 11 and the latest being on July 5. Table 2 gives the dates and other data on all observed nesting attempts. Turtles appear to return to the same nesting site in succesive years. Only one exception to this rule was found (see figure 4b). The location of nesting sites in relation to home range will be discussed in the chapter on home range. Digging of the nest, and laying of the eggs always occur in the evening. The exact time of commencement of nesting cannot be given, since turtles were not usually found at the very start of the nesting process. Table 2 gives the time of discovery of all nesting attempts, and the state of completion of the nest. It appears that nesting may begin any time between about sundown to just before darkness. As table 2 shows, the time required for nesting varies considerably. In some cases, the turtle finished by darkness; one female did not complete her nest until 0:40 EST. The nesting process itself was described in detail by Allard (1935), and there is little I can add. Sixteen initial nesting attempts were observed. Eleven of these were successful, in the sense that the female finished the entire nesting process, including digging the nest, laying, and covering. In the five failures, the turtle abandoned the attempt prior to laying eggs. In four of these cases, the female attempted a second nesting. In the fifth case, there was no further nesting effort by that female that season. Two of the four reattempts were successful. In one of two failures, the female layed, but did not cover. Examination of the eggs showed them to be badly malformed. They were twisted into odd shapes, broken, and two were only about half the size of normal eggs. In the case of the other failure, the female made a third attempt, which was successful. Out of the final total of 14 successful nests, 10 nests eventually produced young. Three did not hatch, and one was eaten.

Hatching occurs in late summer. The exact time cannot be stated, because young often do not emerge as soon as they hatch, and nests were left undisturbed as much as possible. Emergence may even be delayed until the following spring. For nests in which emergence occurred in the spring, it is known that hatching occurred in the fall, since any nests from which young had not emerged were dug up in the autumn, once it seemed unreasonable to expect that emergence would occur that year. Table 2 gives the time of emergence for all nests located during this study. A tempscribe recorder was used to record nest temperature for one nest, beginning two days after it was built, and continuing throughout the period of incubation, with a few days lost due to ink-flow problems. Average temperature was 24.7 degrees Celsius (s.e.=.11, n=912). Range was 15.6 to 37.2. The exact incubation time is not known, since young do not necessarily emerge as soon as they hatch. Emergence took place on October 3, 1969. The nest was constructed on June 26, so the time between laying of the eggs and emergence was 100 days. Two tempscribes were used to record winter temperatures on two nests in which emergence did not occur until the following spring. Minimum observed temperature was -1 degrees Celsius for both. The young in both nests survived.

Temperature Preference of Box Turtles

A total of 104 temperature readings were taken on adult turtles. 63 of these were on turtles believed to be active at the time the temperature was taken. 41 were taken on turtles that appeared to be inactive. A turtle was considered active if it was on top of the substrate, and if its feet and head were out of the shell. A turtle retracted into its shell, buried in the leaf litter, or occupying a form, was considered inactive. Turtles, of course, tended to retract into their shells at the approach of an observer, but usually only a little way, and only very temporarily. Generally, if a turtle was reluctant to emerge, it was considered inactive. It is possible, however, that some turtles classed as inactive were actually exceptionally shy, active individuals. The temperature given below for active turtles is therefore more reliable than that for inactive turtles.

Mean temperature of active turtles was 25.0 degrees Celsius (s.e.=.60, range=20.0-30.9, n=63). Mean temperature of inactive turtles was 21.3 degrees (s.e.=.54, range=16.3-26.5, n=41). The active temperature given above compares with a temperature of 28.8 degrees (s.e.=.30, n=153) found by Legler for _T._ _ornata_. Thus _T._ _carolina_ seems to be active at a slightly lower temperature than T. ornata. This makes sense, considering the more woodland nature of _T._ _carolina_'s habitat. A question that arises is the extent to which box turtles thermoregulate. This can be answered by comparing the variance of temperatures of active turtles with the variances of temperatures of objects that are definitely not thermoregulating. One possibility is to compare the variances of active and inactive turtles. When this is done it is found that the the variance is greater for active turtles (20.1 as compared to 12.2). The difference is not quite significant at the .05 level by an F test. Even the variance of air temperature, 16.9 , did not exceed that of active turtles. It must be concluded that turtles are rather indifferent temperature regulators. Legler (1960), however, has observed that box turtles will avoid extremes of temperature. When he tied an ornate box turtle out under full sun, it quickly overheated, and would undoubtedly have died had he not rescued it. Aside from such avoidance of extreme temperatures however, box turtles seem to function well over a wide range of temperatures.

Box Turtles and Water

Allard (1935) and Cahn (1937) both report instances of box turtles purposely entering water in hot weather. In addition, Cahn reports instances of box turtles hibernating in water. In all cases the water was shallow enough for the turtles to be able to breath by extending their necks. One instance of a box turtle purposely entering water was observed by me. Turtle #82 was found under water in a kettle depression on the Havemeyer property shortly after dark on July 12, 1971. It was in about an 8 inch depth of water, and probably could not have reached the surface by extending its neck. Presumably, it intended to spend the night in this location. A case of accidental winter submersion was also noted. Hatchling B4 spent its first winter submerged when a dry kettle depression it hibernated in in the fall subsequently filled with water. It is not known whether it survived, since the long submersion loostened the silicone rubber bond of its transmitter, causing the transmitter to detach.

HOME RANGE-THEORY

Problems in the Measurement of Home Range

The term "home range produces a definite construct in the minds of most biologists who deal with the behavior and ecology of animals. Yet, it is not a simple idea to deal with, as evidenced by the plethora of theoretical discussions and methodologies that greet one upon perusal of the home range literature. My rationale for embarking on still another such discussion is the fact the much previous theorizing has taken place in the absence of adequate information about how animals actually distribute their activities, and my belief that the data provided by the box turtles I have studied is of value in designating the factors that have to be considered in any theory or methodology relating to home range.

A widely used definition of home range is that of Burt (1943) namely, ". . . that area traversed by the individual in its normal activites of food gathering, mating, and caring for young. Occasional sallies outside the area, perhaps exploratory in nature should not be considered as in part of the home range." Implicit in Burt's definition seems to be the assumption that the home range consists of an area over which the probability of encountering the animal is relatively uniform, limited by a relatively sharp boundary beyond which the probability of encountering the animal becomes virtually zero, though the animal may occasionally explore beyond this boundary, and thus be encountered. No doubt he excludes the area covered by these explorations because he believes that it does not supply the animal with significant resources. Many species of animals are quite difficult to observe in the wild, and in such species it is unusual to have, for any one individual, more than a few points where the animal was known to have visited. With such limited data, it is impossible to confirm or deny the assumptions in Burt's definition. Certainly, one could imagine ways that an animal could distribute its activities over an area that might make Burt's definition hard to apply, or even meaningless. For example, a home range could consist of a center of activity characterized by a maximum probability of encountering the animal, away from which the probability gradually decreased. Without a sharp boundary, the distinction between the area within which the animal carries out its "normal" activities, and the area where it is merely "exploring" becomes meaningless. Another possibility is that an animal's home range could be "patchy", that is, consisting of a number of areas within which the probability of encountering the animal is high, separated by areas where the chances of encountering the animal are relatively low. In such a case, the question arises of whether the whole area over which the patches are distributed should be considered the home range, or just those areas where the animal actually carries out significant activity. Other possible distributions of activity can readily be imagined. Additional questions arise with Burt's definition. In species that do not care for their young, is the nesting site to be considered part of the home range? Stickel (1950), working with box turtles, thought it should not. Should the hibernation site? Precisely how does one decide whether a point where the animal has been observed is in the area over which the animal normally ranges, or represents an exploratory sally? Finally, how does one determine the area of normal activity with limited amounts of data, when one cannot be sure of having observation points on the boundary?

To know what we really mean by home range, it is probably best to look at the methodologies by which we determine it. There are many in the literature. To review them all, some of them occurring only in a single paper, would be an extensive task. Fortunately, most are variants on a relatively few distinct procedures, which can be described in a reasonable space.

1. Range length methods. In these methods, the distance between the most extreme points of capture is used as a measure of home range. In some cases, this distance is considered to be a diameter of a circle, the area of which is the home range. Examples of the use of this method are found in Chitty (1937), Stickel (1950), Godfrey (1954), and Brown (1956).

2. Polygon Methods. There are two main variations on these, minimum polygon, and convex polygon. The minimum

polygon is drawn by connecting all the points in either clockwise or counterclockwise order. Different polygons may result, depending on which order is chosen. The convex polygon is drawn by connecting points in order with the stipulation that the resulting polygon must be convex. Only one convex polygon can be drawn for any given set of points. Somewhat confusing is the term "minimum convex polygon" sometimes used to mean convex polygon. Worse is the fact that minimum convex polygon occasionally gets shortened to "minimum polygon". Minimum polygon as defined here has been used by Dalke (1942), Mohr (1947), and Stickel (1954). Examples of the use of convex polygon can be found in Blair (1940), Burt (1943), Sheppe (1967) and many others. The areas of polygon home ranges can be found by plotting the points by hand, drawing the polygons, and measuring their area with a planimeter. However, when large amounts of data are involved, it is helpful to have a computer determine the order of points and calculate the area using the mapmaker's formula (see appendix 1). The use of a computer is a virtual necessity in calculating minimum polygon home range when a large number of points is involved.

3. Area Points Curve Method. First proposed by Odum and Kuentzler (1955), this procedure attempts to deal with the problem that the area of a polygon, whether minimum or convex, tends to increase with increasing sample size. Their method is to observe the increase in area (A) with

increasing numbers of points (P) and to designate the home range as that area for which dA/dP equals some arbitrarily small value. Their suggestion is .01.

4. Distance Between Successive Recaptures Method: This method was proposed by Fitch (1958) and is limited to the situation where the time between recaptures is sufficiently long that each recapture can be considered an independent event. He calculates the average distance between successive recaptures and uses this as a measure of home range, reasoning that larger average distances indicate larger home ranges.

5. Bivariate normal Method: Proposed by Jennrich and Turner (1969), and Mazurkiewicz (1968, 1971), this method assumes that the observation points on an animal follow a bivariate normal probability distribution. In this case, if one draws any line through the center of gravity (average of the ordinates and abcissas) of the points, and projects the points onto the line, the distances of the points along the line from the center of gravity will follow a normal distribution. There will be more points close to the center of gravity, and increasingly few as one moves away from the center of gravity. As one rotates the line around the center of gravity, the variance of the distances changes (unless the home range is circular). There will be some direction, called the major axis, for which the variance will be maximum, and a direction at right angles to this, called the minor axis, for which the

variance will be minimum. One can draw ellipses of probability within which one expects to find the animal some given percentage of the time, for example, the ellipse within which one expects to find the animal half the time, or 90% or the time, or 95% of the time, etc. The ellipses grow larger with increasing probability of finding the animal, are concentric, and coaxial. The calculation of bivariate normal home range is shown in appendix 2.

6. Circular Normal Method. This is a special case of the bivariate normal. It assumes that home ranges are circular, that is, that the variances are the same in all directions. One can then draw circles of probability. Thus you can draw the circle within which you expect to find the animal half the time, or 90% of the time, or 95% of the time, etc. Each such successive circle will be larger in diameter, and all circles are concentric. Circular normal methods have been used by Dice and Clark (1953), Harrison (1958), and Calhoun and Gasby (1958).

Some comments on these methods are in order at this point. In methods other than the bivariate normal (and circular normal) workers sometimes throw out points which seem excessively distant from the others, on the grounds that they represent "exploratory sallies". Such a procedure is basically subjective. Also, points where special activities not part of the animal's day to day repertoire occur, such as nesting, may be discarded. Discarding excessively distant points does not make sense in the case of the bivariate normal, since its assumption is one of progressively decreasing probability of encounter away from a central point. Beyond this, there are certain theoretical characteristics of the different methodologies which are worth mentioning.

The range length method uses less of the information available from the data than do any of the others. In particular, all information on the shape of the home range is discarded. This is a serious, and unnecessary deficiency. In addition the range length method is sample-size dependent. As one gathers more data on an animal, the apparant range length home range can be expected to increase, approaching an asymptote if the real home range is sharply bounded, and increasing less and less rapidly, but indefinitely, if the probability of encountering the animal decreases gradually. The one advantage of the method is that it can be calculated when only two capture points are available. Since one is not likely to learn much from a home range based on two capture points, the range length method seems to have little application.

Polygon methods do make use of information on shape provided by the data. Like the range length method, however, they are sample-size dependent. Also, the minimum polygon method suffers from the ambiguity that it can be based on either counterclockwise or clockwise rotation, but this seems to be a minor point. A characteristic of the minimum polygon technique that might possibly be of value is that it is the most conservative of the commonly used techniques, providing the smallest estimate of home range. This could be a consideration for someone studying territoriality. The minimum polygon method is less likely than other methods to show overlap between home ranges when there really is none, though it would always show real overlap, provided enough data had been gathered. A technique proposed by Metzgar (1971) is interesting in this regard. In this technique, the amount of overlap among the home ranges on a study area is determined, and again after the home ranges have been randomly rearranged randomly by a computer. The amount of overlap between the rearranged home ranges and the amount between the original ones are compared, and if the former is larger, territoriality is suspected. Metzgar's technique was based on grid-trap data, and no polygons were drawn, but the point-by-point comparison technique he employs resembles minimum polygon. The technique could probably be adapted to non-grid data, by measuring the overlap among polygons. Either minimum or convex could be used, but minimum might be more efficient. Another possible advantage might be in determining home ranges on animals that have "patchy" distributions of activity. Since the minimum polygon must pass through all points, internal as well as external, it might be expected to reveal more of the internal structure of a home range than other methods. However, this appears to be a false hope, as will be demonstrated later.

The convex polygon method is the most widely used method for determining home range, probably because it is easier to draw than minimum polygon. Another slight advantage is that the relative variance of the convex polygon is somewhat less than that of the minimum polygon (Jennrich and Turner, 1969), but the difference is small. For many purposes, there may be no compelling reason to prefer one polygon technique over the other.

The area-points curve method solves the problem of the sample-size dependency of of the polygon methods by the expedient of essentially limiting the researcher to a single sample size--that for which dA/dP equals some arbitrarily small value. One wonders what the advantage is over just picking some arbitary number of points, such as 40. In many studies, such an arbitrary restriction is unrealistic. The amount of data that can be collected is often not easily controllable by the researcher. One would often like to determine home ranges on the basis of as much data as can be reasonably collected on an animal. The method is thus limited to those situations where the investigator can take as much data on an animal as he wishes, plots the curve as he accumulates data, and stops taking data as soon as the predetermined criterion for dA/dP is reached. Odum and Kuentzler's criterion of dA/dP=.01 was reached at between 25 and 90 points on the birds they studied. It is reached at about 40 points on box turtles. For many studies, this represents an unrealistic amount of data. Another problem is that dA/dP must be calculated on a smoothed curve. Such smoothing is essentially a subjective process.

Fitch's distance between successive recaptures method has interesting possibilities, though it needs some rethinking from its original conception. It will be discussed later in the section "The Effective Home Range". An inherent deficiency of the method is that it yields a pure area that cannot be plotted on a map.

The bivariate normal distribution has a lot of advantages which make it appealing. It is sensitive to the shape of the home range, and it is independent of sample size. Furthermore, its use makes it unnecessary to discard points that "do not seem to fit". It permits one to give a precise meaning to the phrase, "that area traversed by the animal in its normal activities", in Burt's definition. For example, one can draw the area within which one expects to find the animals 95% of the time. The circular normal method is just a special case of the bivariate normal. It is unclear that there is anything to be gained by assuming circularity, other than slightly simpler computation. Therefore, the general bivariate normal should be used in preference to it. Sometimes the circular normal is used in calculating composite home ranges. That is, the centers of gravity for data on a lot of animals are calculated, and the data from these animals are superimposed upon each other, matching centers of gravity. In this case, the use of the circular normal seems plausible, though the general bivariate normal is still at least as good.

There is only one serious question that arises in conjunction with the use of bivariate normal method, namely how valid is the assumption of a bivariate normal distribution? The validity of this assumption does not seem to ever have been tested on any species. Mazurkiewiz (1971) does attempt a preliminary test of this nature by counting the points inside and outside of her calculated 62% ellipse, and testing the observed against the expected values with a chi-square test. She accepts the bivariate normal as fitting her data. However, aside from the rather insensitive nature of the fit that results from only two groups, her test does not seem to be mathematically valid. Calculating the bivariate normal requires estimating five parameters--mean in the X direction, mean in the Y direction, variance in the X direction, variance in the Y direction, and the covariance of X and Y. In performing the chi-square test, these must be subtracted from the total degrees of freedom. Since a chi-square on two groups has only one degree of freedom even with an extrinsic hypothesis, the test cannot be performed. Therefore, at this point I would like to examine the box turtle data with regard to the question of goodness of fit to a bivariate normal distribution.

The method was as follows: for every turtle with 50 or more observation points, the number of points lying between successive 10% ellipses was determined. The expected number of points lying between successive 10% ellipses is, of course, 10% of the total number of points. For each animal, the expected and observed numbers of points were compared with a chi-square test, yielding four degrees of freedom. Table 3 presents the analysis on the 16 animals that had at least 50 observations. As can be seen from the table, the fits are not good. Only one animal, number 59, has a distribution which is not significantly different from bivariate normal at the .05 level. For two animals, $.025>p>.01$. For four animals, $.01>p>.001$. For the remaining nine animals $p<.001$. I therefore conclude that the probability of finding a box turtle does not, in general, follow a bivariate normal distribution.

The question immediately arises of whether the observed deviation from bivariate normal is regular or irregular. That is, do all animals tend to deviate in the same way, or is every animal different? The answer to this question is important both from a statistical viewpoint, and because it may indicate something about how box turtles relate to the habitat that is available to them. If most of the deviation is irregular, it suggests, from a statistical point of view, that no reasonably simple distribution is likely to fit better that the bivariate normal. From a biological viewpoint, it would indicate that box-turtle habitats are quite patchy, and that the distribution of observation points reflects mainly the response of each turtle to the distribution of habitats in its home range. On the other hand, a large regular deviation from bivariate normal indicates, from a statistical point of view, that one could obtain a better fit by using some distribution other than the bivariate normal, and from a biological point of view, the possibility of fitting any parametric distribution would suggest that the distribution of observation points is mainly a species-specific property--that is, that box turtles have an inherant tendancy to follow a particular pattern in occupying their home ranges, and that the distribution of suitable habitats is not very important. Even a superficial glance at the summary in table 3 indicates a rather irregular deviation from bivariate normal, but it is worthwhile to test this statistically. This can be done by looking at the heterogeneity and pooled chi-squares. That is, the total chi-square for all turtles is partitioned into two components, that due to regular deviation from the bivariate normal, and that due to irregular deviation. The calculations are given in table 3, and the results are as follows: chi-square for the pooled data, representing regular deviaton from the bivariate normal, is 22.4 ($p<.001$), or 5.3% of the total chi-square. Heterogeneity chi-square which represents irregular deviation from the bivariate normal is 397.3

($p < .001$), or 94.7% of the total chi-square. In other words, most of the deviation from bivariate normal is irregular. While a complex multinomial might be found that fit, interpretation of the parameters would not be easy.

Though representing only a small portion of the total chi-square, the pooled chi-square is nevertheless highly significant. Examination of the pooled observations however, fails to show any particularly interesting pattern to the deviations from bivariate normal. One might have expected a general platykurtosis, since any tendency on the part of box turtles to shift their home ranges seasonally or from year to year should result in a platykurtic distribution of observation points. This does not seem to be the case. It remains true however, that certain animals have a noticeably bimodal distribution, with the animal spending most of its time in two areas and very little time in between. This is most clearly seen in animal number 34 (figure 9), which appears to have one home range centered around the west end of field AP-10, and a second home range north west of field AP-5 (figure 1). In this case, the difference between the two ranges appears to be seasonal, with the second range being occupied from the end of July through August. A second animal showing this kind of home range is animal #18 (figure 6b). It has a northern and a southern home range. The distinction between the two is less clear than the distinction between the two parts of number 34's home range. In this case, the northern range was occupied during 1970, with nesting having taken place in northern G-2 (figures 1a and 4b), while the southern range was occupied during 1971, nesting having taken place in west AP-10. This is the only example found by me of a substantial difference in home range between years. The effect of a bimodal distribution of observation points is to cause the bivariate normal estimate of home range to be much too large. Not only is a lot of unoccupied area between the two peaks included in the home range, but a considerable amount of area on each side of the peaks is included. For such animals, therefore, the bivariate normal estimate of home range is exaggerated. This is also true of the other methods used to measure home range, however (see below).

The poor fit of the bivariate normal is certainly a disappointment. On the other hand, the sample-size dependency of the polygon methods, which seem to be the best alternatives, also discourages their use. Most workers seem to have been rather sanguine about how much polygon home ranges change with sample size. Figure 3a shows the relationship between sample size and minimum polygon home range in box turtles. This graph was made by sampling increasing numbers of points from turtles for which at least 100 observations were available. For each turtle, 300 random samples of points were taken at each number of points, with replacement, and the results averaged for all turtles. As the graph shows, area is still rising noticably at 40 points. This seems to contradict the conclusion in Stickel (1950) that the apparant size of male box turtle home ranges does not increase with sample sizes greater than three. I can also find no basis for her conclusion that female home ranges based on three points are, on the average, larger than those based on four, five or six points. Stickel actually used a range length method, rather than a polygon method, but the two should be similarly sample-size dependent.

At the beginning of this chapter, it was suggested that the home ranges of animals might not meet the criterion of being a sharply bounded area of relatively uniform activity that Burt's definition seems to require. This appears to be the case with box turtles. Figure 5a illustrates this point. This presents the data on animal number 59. This is the animal for which the distribution of observation points did not differ significantly from bivariate normal when tested above. Although this animal contained approximately the expected number of points within each successive 10% ellipse, inspection of the data shows that this goodness of fit test has actually concealed a great deal. The figure shows a boundary line subjectively drawn around the observation points, which excludes certain areas within which no points are found. It also shows the 95% bivariate normal home range, and the convex polygon home range. The subjective home range is rather ameboid, and even disjunct. Clearly the animal is concentrating is activities in rather limited areas. Large portions, roughly half, of the 95% bivariate normal home range actually appear to be unused by the animal. The distribution of activity of turtle number 18 (figure 5c) provides a more spectacular example. It is distinctly patchy, with very large unoccupied areas between the patches. This is by no means a rare situation. Figures 6b, 10a, 11a, 12a, and 13a provide some additional examples. In fact, it is hard to find examples of turtles that "fill" their 95% ellipses really well. The best are in figures 8b, 9b, 10b and 11b. Almost all turtles show some degree of patchiness in the distribution of their observation points. This patchiness only really becomes evident when fairly large amounts of data are available. For example, figure 3b shows the distribution of 10 randomly selected points from the data for turtle number 59. It would be hard to guess from this figure what areas the turtle is using, and what areas it is not. Thus, mark-recapture studies, where the number of recaptures is usually small, may never hint at this patchiness.

The patchiness that characterizes the distribution of a box turtle's activity suggests that home range can be thought of in two different ways. One is the area within which the animal actually carries out most of its activity, and the other is the total area over which patches of activity are scattered. I will call the former "utilized area", and the latter "total area". The actual area utilized by an animal is important, because it is this area whose resources are available to the turtle. The total area could also be of significance, however. How large a total area a turtle had to scatter its activities over to find enough suitable habitat could be just as important as how big an actual area was required to support a turtle under various circumstances. Also, anyone whose major interest in box turtles was studying their homing abilities would want to know the total area, since this would be the area likely to be familiar to a turtle. That is, turtles could be expected to become familiar with the areas they move through in passing from patch to patch, even though they did not utilize these intervening areas for anything. Odum and Kuentzler (1955) suggest a somewhat similar distinction with what they call "utilized" and "maximum" home range, though by "maximum" home range they appear to mean specifically convex polygon home range, while they do not provide more than a very preliminary discussion of "utilized" home range. Kaufman (1962) appears also to be suggesting a related idea with his concept of the "core" area. In the coatis he worked with, however, the core area was a central, defended area of high activity, rather than an area of scattered patches. I believe this distinction between total area and utilized area may be of concern in the case of many animals other than box turtles, and that a discussion of the various methods for determining home range with regard to their ability to measure these two types of home range would be worthwhile.

It seems fairly obvious that the bivariate normal and convex polygon methods for determining home range can, at best, measure only total area. Of the two, the bivariate normal method seems preferable because of its sample size independence, even though the assumption of a bivariate normal distribution is not closely met. Since the minimum polygon has to pass through all of the data points, one might expect it to reflect better the utilized home range. Figures 5b and 5d show the minimum polygon home ranges for animals number 59 and 18. The minimum polygon home range of number 59 does seem to indicate the utilized area better than do the bivariate normal and convex polygon methods. It does not appear to do as well with animal number 18.

The best way to examine the relationships among the various home range techniques is to apply them to the analysis of data, such as that on box turtles. To provide a basis of comparison, it is useful to have some technique that clearly measures utilized area. One possibility is to evaluate utilized home range subjectively by drawing lines around the areas that reasonably seem to be utilized, as was done in figures 5a and 5c. Such a recourse is not above criticism. It is sample-size dependent in an uncertain way, and no two people would draw the exact same home ranges given the same data. Yet it may still provide a useful comparison. I have calculated box turtle home ranges by four methods then, 95% bivariate normal, convex polygon, minimum polygon, and "subjective utilized" with the following results: 95% bivariate normal home range, 6.96 hectares (s.e.=1.02, n=23); convex polygon home range, 4.05 hectares (s.e.=.538, n=23); minimum polygon home range, 2.12 hectares (s.e.=.367, n=23), subjective utilized home range, 1.76 hectares (s.e.=.137, n=23). Certainly, the minimum polygon home range is closest to the subjective utilized home range, and the smallest of the three objectively determined home ranges. It would appear, therefore to be excluding unutilized area. Unfortunately, there is a contrary indication to be found in the data. This can be seen by examining the correlation coefficients among the four methods (table 10a). In this table, the correlation coefficients among the three objective methods are enclosed in dotted lines. The correlation coefficients between the subjective method and the three objective methods are enclosed in solid lines. As can be seen, the three objective methods correlate very highly among themselves, and much less well with the subjective method. This can be seen even more strikingly if only home ranges based on forty or more observation points are used in calculating the correlations (see table 10b). Use of home ranges based on considerable data reduces random variation, and the sample-size dependency of all but the bivariate normal method. In this case, the correlations among objective methods exceed .9 and approach unity, while correlations between the subjective method and the objective methods, though quite high, are somewhat less (about .7). In view of the intensity of correlation between the minimum polygon method and the other two objective methods, it appears unlikely that the minimum polygon method is really doing anything different. The results of the three objective methods apparantly differ only with regard to scale; they all seem to measure the same properties of the data. The "subjective" approach does appear to be doing something distinctive. Performing a homogeneity of correlations test on the correlations in tables 10a and 10b confirms this. There is no significant heterogeneity in the correlations among objective methods, and also none among the correlations between subjective method and objective methods. However, when all six correlations are tested together, there is significant heterogeneity ($p<.01$).

Compared with the three objective home ranges, the subjective home range has an interesting property. It is less variable than the objective home ranges. Coefficients of variation are as follows: subjective, 37.4%, bivariate normal, 70.4%, minimum polygon, 83.0%, convex polygon, 63.7%. A possible interpretation is that the amount of good habitat needed by a turtle is relatively constant from individual to individual, but that individuals have to range over varying amounts of total area to find this amount of good habitat.

An indication of the correctness of this hypothesis can be gotten from examining the relationship between sex and home range. As can be seen from table 9, all three objective methods indicate a larger home range for females than for males. The difference is significant by a t-test ($p<.05$) for all three. The subjective home range of females is only slightly larger than that of males, and the difference is not significant. I am inclined to agree with Stickel (1950) that females are likely to range wider because of the necessity of including a nesting site in their home ranges. It appears, however, that females do not actually use much more area than males--the areas they use are simply spread out more. The inclusion of a nesting site seems, at most, to increase the utilized area only slightly.

The Effective Home Range

It is apparant from the previous discussion that none of the objective methods for determining home range now in the literature can be considered measures of utilized area. Apparantly utilized area correlates quite highly with total area (r about .7), but the correlation is far from perfect. Clearly it would be useful to have an objective technique for determining utilized area. This section will present one approach to the problem. In addition to being objective, the technique improves in another way over the subjectively determined utilized home range used above, namely in weighting patches of activity by their intensities of use. A disadvantage of the technique, however, is that it requires a large number of observation points on each animal.

Figure 17a shows two hypothetical home ranges, both consisting of two equal-area patches of use, separated by areas of non-use. The only difference between the two home ranges is the amount of unused area separating the areas that are being used. It would not be unreasonable to feel that the two animals should be assigned equal home ranges, since the area that is being used, and whose resources are therefore available to the animal, is the same in both cases. All present objective methods of designating home range, however, would assign a larger range to the animal whose two patches were more widely separated. They would include the unused space between the two used areas, and the bivariated normal would include areas on either side of the used areas. The hypothetical example is not without precedent in the real world, as note for example, the home ranges of animals 34 and 161 (figures 6b and 11a). Let us look at another hypothetical example. In the case shown in figure 17b, another two home ranges are depicted. Again, they both consist of two equal area patches, but in one case, the patches are equally utilized, while in the other case, the animal spends 80% of his time in one patch, and only 20% of its time in the other. Here, it is reasonable to feel that the animal that divides its time equally between the two areas has a larger home range. The turtle that spends most of its time in one area would seem to be relying mostly on the resources of that area, and therefore to have effectively less resource available to it. Real home ranges are much more complex, but the principles involved in these two examples still apply. In short, one would like to have a measure of home range that counts only those areas where the animal actually occurs, and counts even these areas in such a way that the areas which are less heavily used are allowed to contribute less to the calculated home range. This section makes an attempt at formulating such a definition. Unfortunately, as will be seen, the amount of data required in actually measuring a home range defined in this way, is very large.

In general, if one takes n observations of an animal's location, these observations will be closer together, on the average, the smaller the home range is. Furthermore, disregarding edge effects, the average distance between points will be the same, for a given home range, whether the home range consists of a single large patch, or many little ones. In other words, the distance between each point and its nearest neighbor can be used to estimate home range. One could pick just one point, find its nearest neighbor, and use this as an estimate of density, but obviously a more accurate estimate would result from averaging the estimates of many points. Such an average has the property that the less a given subdivision of the total home range is used, the fewer points it will contain, and the less it will contribute to the overall average. Thus it would appear that a nearest neighbor estimate of home range has the two required properties; it is not affected by the division of the home range into patches, i.e. it counts only areas where the animal actually occurs, and it counts less areas that are used less. Such an estimate of home range reflects better the actual availablility of resources to the animal. I will refer to it as the "effective home range". The formula and formal derivation are shown in appendix 3.

The problem that arises with this estimate of home range is this: it is within-patch distances, not between-patch distances that are required for making the estimate. Thus a patch must contain at least two points. If a patch contains only one point, the nearest neighbor for that point will be a point in another patch. If one tries to estimate home range with only a few points, most of the patches will contain only one point, the calculated home range will reflect mostly between-patch distances, and will be an overestimate of the real home range. As the number of points increases, an increasingly high percentage of the patches will contain at least two points, and the home range estimate will approach a limit asymptotically from above. The question is, how many points are needed to give a reasonable estimate of the asymptote? This can only be answered with empirical data. Accordingly, effective home range estimates were made on animals number 47 and 59, the two animals with the largest amount of data in this study. Estimates were made from 300 random samples of 5, points. The results are plotted in figure 18a. As can be seen, the number of points required is large, and very few studies yield adequate data. In general, it will probably require automated telemetry systems to gather the amounts of data that will be needed to make estimates of home range in the way suggested here. Other methods of gathering data do not provide enough information to determine the area whose resources are actually available to the animal, except to the extent that between-patch estimates of home range correlate with within-patch estimates. Present methods of measuring home range primarily reflect between-patch distances and will continue to be useful to those interested in homing behavior, or in social interaction, but of less use to those interested in resource availability. The failure, sadly, is not just one of mathematics, but also data.

The distance between successive recaptures method proposed by Fitch (1958) has certain conceptual similarities to the effective home range method suggested here. One could achieve essentially Fitch's measure by measuring the distance between each point and a randomly selected point, instead of the closest point. The problem with Fitch's approach is that it results essentially in measuring between-patch distances, rather than within-patch distances. Thus it does not really reflect the amount of area being used by an animal, but rather the total area over which the patches are spread. Other methods such as the polygon methods do the same thing, but at least yield something that can be plotted on a map, while Fitch's method yields only a pure area. Since the total area over which the observation points are spread would mostly be interesting to those studying homing behavior or territoriality, where a knowledge of the shape and location of the home range, as well as its pure area is required, Fitch's method does not seem very appropriate. The effective home range method also yields a pure area, but at least it is one that indicates how much area is actually being used by the animal.

Conclusions and Summary

It is evident that much work remains to be done before a fully satisfactory concept of home range can be arrived at. I believe that a useful distinction can be made between the area whose resources are actually used by an animal (utilized home range), and the overall area over which the animal's activites are spread (total area). The concept of utilized area is one that especially needs to be explored. No satisfactory objective method now exists for designating it. Furthermore, it appears that its complete characterization requires very large quantities of data. It is not clear whether a useful concept of utilized area based on smaller quantities of data can be arrived at. The fact remains, however, that examination of the data presented in this thesis strongly suggests a distinction between utilized and total area. A sufficiently full analysis of what a human being does when he draws a subjective home range ought to enable a computer to do the same thing.

Methods now in the literature are probably better at determining total home range. The major methods, minimum polygon, convex polygon, and bivariate normal seem to accomplish virtually the same thing. Since the bivariate normal method is sample-size independent, I suggest its use, despite the poor fit of data to the bivariate normal distribution. It is true that the minimum polygon method encloses less area than do the others, and might be of interest to those looking for territoriality, since it would be less likely to produce an appearance of overlap when none existed than the other methods. However, it correlates no more closely with a subjectively determined utilized home range than any other objective method.

HOME RANGE RELATIONSHIPS OF <u>T</u>. <u>CAROLINA</u>

Size of Home Range

I have already calculated the home ranges of turtles involved in this study by several methods. An inevitable comparison is that between the home ranges of my animals and those of Stickel (1950), who did the last major study of home range in this species. Unfortunately, it is not possible to do this in a very satisfactory way. Since Stickel used a range length method, a comparison can be made only by calculating the range length home ranges of the animals in my study, despite the fact that this is a poor measure of home range. For females, this equals 373 meters (s.e.=32.4, n=13), compared to Stickel's value of 113 meters (s.e.=8.8, n=27). For males, my value is 284 meters (s.e.=36.1, n=10), compared to Stickel's value of 101 meters (s.e.=7.9, n=28). It appears that the turtles on my study area had substantially larger home ranges than did those studied by Stickel. However, the comparison is not completely valid. The average number of observation points used by Stickel to calculate a home range was only 8, whereas my home ranges are based on an average of 84 observation points. Range length is a sample-size dependent measure of home range. To make possible a more valid comparison, the following simulation procedure was followed. From the data on each of my animals, 100 random samples of 8 points was taken, the sampling being done with replacement. The average range length of these 100 samples was then used as the range length for each animal. The actual sampling was done by an XDS Sigma 7 computer, with the random number generator from XDS's Numerical Subroutine Package used to pick the random samples. The program was written in FORTRAN IV. The means of the resulting home ranges were: females, 266.1 (s.e.=23.6, n=13), and males, 185.8 (s.e.=31.3, n=10). These home ranges are still larger than those obtained by Stickel, and the difference, for both males and females, is significant by a t-test ($p<.001$). The range length method can reasonably be interpreted to yield a total home range. It is not possible to compare my data and Stickel's with regard to utilized home range.

The question arises of why Stickel's home ranges differ from mine. One possibility is the difference in habitat between her study area and mine. Stickel conducted her study on a river flood plain in Maryland. Compared to my study area, hers was more heavily forested, and considerably wetter. Temperature for the region would naturally be higher. On my study area, turtles did not especially favor heavily forested areas (see chapter on habitat preference), though there is some indication that they tended to move into the forest more during hot parts of the year. Stickel chose her study area because, out of several habitats available to her (the others on higher ground and drier), it had the highest population of box turtles. It is interesting that the moist, diverse wooded area between AP-5 and AP-6 on the Kalbfleisch Station (see figures 1a and 31c), sustained more box turtle activity than did other forest areas, and is the area of the station most closely resembling Stickel's study area. Compared to my study area, Stickel's was generally more uniform. It is possible that box turtle home ranges were less "patchy" on her study area, and that less total area was needed to contain the same utilized area. Stickel presents several maps showing the wanderings of turtles on her study area based on thread trailer records. Because there are relatively few of these maps, and some cover quite short periods of time, I have not attempted a formal comparison of them with my data. It appears to me, however, that distributions of box turtle activity are quite patchy even in her study area. I am therefore inclined to believe that the utilized home range of the turtles on her area was also less than the utilized area of the Kalbfleisch turtles, as well as the total area.

There also appears to be a difference in population density between her study area and mine. Population density for my study area for the year 1970 was estimated as follows. From the records of the field station, an estimate of the number of living adult turtles was made. This was done by counting the number of turtles appearing in the field station records between 1966 and 1973, but not counting turtles first marked in 1970 and later. Turtles whose last appearance was previous to 1966 were assumed to be no longer alive. For this estimate, turtles were classed as adults if they weighed more than 200 grams. Two sources of error are involved in this estimate. Some turtles last seen prior to 1966 might still have been alive in 1970, and some turtles last seen in the years between 1966 and 1969 may have died. These errors are in opposite directions, and I can only hope they were fairly small, and approximately compensating. The estimate of marked adult turtles alive in 1970 is 85. During the summer of 1970, 40 turtles were captured, of which 31 were marked. A Lincoln index puts the estimated population of the field station at 110. Of the 94 acres of the station, 75 were considered to be reasonable box turtle habitat. The main area eliminated was the heavily wooded BWF-1 (see figure 1a), for which very little box turtle activity was recorded. The estimated population density of the station is then 1.5 per acre. Stickel estimates the density on her study area to be 4-5 per acre. Despite the notoriously low accuracy of population estimates, it seems likely that there is a real difference between the two areas. At high population densities, aggressive interactions between box turtles could result in smaller home ranges, though I can find no evidence that this is true (see below), or the lower density may be an indication of poorer habitat, and turtles may have to spread their activities wider to obtain adequate resources. My leaning is toward the second hypothesis.

I will now examine some of the factors that could affect box turtle home ranges. Sex has already been mentioned, and it was noted that the total home ranges of female turtles was significantly larger than those of males, but that utilized home range, subjectively determined, was only slightly larger for females, and the difference was not significant. Stickel also found that female home ranges were larger than male, but the difference was not significant. Other factors I have examined are weight of the animal, habitat diversity, and population density.

One might suppose that larger animals would require more food, and that in order to acquire this food, they would need a larger home range. Alternatively, larger animals might be expected to be more mobile. The product-moment correlation coefficients between weight and the various home range measures are: subjective utilized, .349; bivariate normal, -.145, minimum polygon, .01, convex polygon, .07. All are based on 23 home ranges, and none is significantly different from 0.0 ($p>.05$). It is interesting that the largest animal in the study, female number 132, weighing an exceptional 860 grams, had a relatively small home range (see table 4). This is a highly accurate home range, based on 120 observations over 257 days of tracking. One is forced to conclude that the availability of food, or any other resource that might be needed in greater quantities by larger animals, is not an important factor in determining box turtle home ranges.

Habitat diversity was evaluated in the following way. 95% bivariate normal home ranges for animals were plotted on a map showing the five principal physiognomic vegetation types on the station (see INTRODUCTION). The area of each vegetation type within the home range was determined with a polar planimeter. The Shannon-Weaver formula commonly used to calculate species-diversity was then used to calculate habitat diversity (appendix 4). The Shannon-Weaver formula assigns minimum diversity (0.0) to the situation where the entire home range is covered by a single habitat type. Maximum diversity is assigned to the situation where all habitat types are present in equal proportions. Correlations between habitat diversity and home range measures were as follows: subjective utilized, .14; bivariate normal, -.14; minimum polygon, -.17, convex polygon, -.23. All are based on 23 home ranges, and none is significant. The lack of correlation is somewhat surprising, in view of the tendency of box turtles to occupy areas of high diversity (see chapter on habitat preference). It is possible that box turtles simply occupy large enough total home ranges to provide adequate diversity. Therefore, variation in diversity would be fairly small, and there would be little correlation with home range size. An indication that this might be true can be gotten from measuring habitat diversity over a constant area centered on the box turtle's home range, and comparing this with home range. This was done by centering a circle whose area was equal to the average 95% bivariate normal home range (6.96 hectares, radius=149. meters) on the center of gravity of each animal's home range, and determining the habitat diversity within this circle. Correlation coefficient between 95% home range and this measure of habitat diversity is -.44, which is significant (.02.>p>.05). Correlations with other measures of home range were not significant, though they approach it for the objective measures. The negative correlation is in the direction one would expect--smaller for areas of higher diversity.

Although I cannot find evidence for territoriality in box turtles (see below), aggressive interactions might still influence the size of home range. Where population density was high, turtles might seek to minimize abrasive contacts with other individuals by restricting the size of their home ranges. On the other hand, frequent encounters with other turtles could cause individuals to move around more, and thus have larger home ranges. Thus either a positive or negative correlation between home range and population density would indicate that social interaction was important in determining the home ranges. Such an effect was searched for in the following way. All known points of capture for box turtles in the field station records were plotted on a map. The number of such points within the 95% ellipse of each turtle used in this study was counted, and this number was divided by the area to give a measure of density. The product-moment correlation coefficients between this measure and the various home range measures are: subjective utilized, -.16; bivariate normal, -.31; minimum polygon, -.28; convex polygon -.32. Correlations are based on 20 home ranges (densities could only be estimated for animals whose home ranges were substantially confined to the field station), and none are significant. Thus it cannot be shown that social interactions affect home range. It should be noted that the concentration of captures of box turtles on the field station reflects the activity of workers on the station as well as the actual population density, but there is no reason to believe that the activity of workers would be related in any way to the size of box turtle home ranges, so it should still be valid to look at the relationship between concentration of captures and home range.

Territoriality

_T_. _carolina_ and _T_. _ornata_ are generally considered non-territorial (Stickel (1950), Legler (1960), and Metcalf and Metcalf (1970)). My data support this. Figure 19a shows the superimposed minimum polygon home ranges for females, and figure 19b the superimposed minimum polygon home ranges for males. It is evident that there is considerable overlap between the home ranges of different animals, suggesting no defense of territory. As pointed out before, minimum polygon home range is the best procedure to use when looking for territoriality. Overlap of home ranges does not prove lack of territoriality, though the extreme degree of overlap found here points in that direction. It remains possible that certain core areas are defended, with overlap of parts of the home range outside of these areas. In the case of box turtles, such areas, if they exist, would have to be quite small.

There is some evidence for aggressive interactions between male box turtles. Various observers have witnessed what have been characterized as "aggressive" encounters including Latham (1917), Penn and Pothurst (1940), and Stickel (1950). Three additional instances were observed in the course of this study. Two of the encounters observed by me, and that observed by Stickel follow a common pattern. One turtle faced the other, and nipped around the edges of its shell. The turtle on the receiving end of these "attentions" remained partly withdrawn into its shell. The behavior observed here strongly resembles the normal initial courtship pattern of this species (see Some General Aspects of Box Turtle Biology). It is possible that what is being witnessed is not really aggression, but an erroneous attempt at courtship. This impression is reinforced by a clear attempt at a homosexual mating observed by me. In this case I encountered male #59 facing male number #215 and nipping at its shell. When I returned to the pair 15 minutes later, #59 was attempting to mount #215. #215 eventually crawled off, followed a short distance by #59. The third aggressive encounter observed by me took place between a resident male, and another male that had been transported into the area in conjunction with a homing experiment. In this case, the resident turtle chased the non-resident, nipping at the rear part of its shell. The non-resident attempted to flee. The encounter observed by Latham was considerably more violent than any of those observed by me or that observed by Stickel. In this case, there was a considerable difference in size between the two turtles, and the larger one was apparantly transported into the area by Latham. The smaller, resident, turtle approached the larger one. The larger attacked the smaller, grabbed it by the neck, and held it for two minutes. After the larger animal released the smaller one, the former started to crawl off, and the smaller one followed it for a short distance. These two observations by Latham and myself may suggest that male turtles recognize non-resident males, and attempt to drive them off. In the case of Latham's observation, the smaller resident faired rather badly in its attempt, but nevertheless persisted in approaching the non-resident. In view of the resemblance of courtship to aggression, however, one wonders if there really is such a thing as aggression in box turtles, and whether the so-called "aggressive" encounters between males really have any effect in reducing the population density of an area. Interaction between non-resident females and resident males appears to be perfectly normal, since I observed a case of a resident male mating with a non-resident female that had been transported into his home range in conjunction with a homing experiment. I also observed a mating between a male and female both of whom had been carried off their home ranges. So far as I know, aggressive encounters have never been observed between two females in the wild.

While it is possible that encounters between males have some function in dispersing the population, it is difficult to find any evidence of this in the home range data. "Dominance heirarchies" have been observed among box turtles in captivity, under very crowded conditions (Legler (1960), citing Evans (1954); Boice (1970)), but apparantly never in the wild. It is doubtful that the situation observed in captive turtles has much relevance to wild animals. My tendency is to conclude that aggressive interactions are of minor importance in the biology of box turtles, at least under the conditions present during this study.

The possibility should be pointed out that the Kalbfleisch population may not be at carrying capacity. The comparatively recent conversion of cropland and grazing land to weedy and brushy fields probably increased the suitability of the field station for box turtles. In view of the long generation time of box turtles, it is possible that the population may be well below its equilibrium value. Aggression and territoriality might increase as population densities rose. Aggressive interactions cannot, therefore, be excluded as a regulating mechanism. It should be noted, however, that Stickel (1950) found little evidence for aggressive interaction despite the apparantly considerably higher population density on her study area. She reports turtles foraging within a few feet of each other, and in some cases nearly touching shells, without evidence of aggression even when of the same sex. Stickel cites two collecting trips when respectively 35% and 63% of the animals captured were "near one or more others." On the Kalbfleisch Station, I found turtles in close proximity to each other much less frequently.

It is interesting that _T. ornata_ seems to be considerably less aggressive than T. carolina. Legler (1960) specifically looked for instances of aggression in the population he studied, and observed none. Turtles paid little attention to each other even when foraging in bare open areas where they could easily see each other. Metcalf and Metcalf (1970) also fail to report any instances of aggression. I have no theories to explain this apparant difference in behavior between the two species.

Stability of Home Range

I would now like to examine the question of whether the home range of a box turtle is constant or shifts with time. This can be looked at from two points of view. First whether a turtle's home range shifts during a season of activity, so that it uses different areas at different times of the year, and secondly, whether there are shifts in home range from year to year.

The season of activity for box turtles runs from about May through October. There is sometimes activity during April and November, but this is generally minor. There appears to be considerable variability in the extent to which turtles use different areas on a seasonal basis. Figures 20 through 26 show the home ranges of box turtles plotted on a monthly basis. Only those monthly ranges for which a minimum of 10 points were available were plotted, and only the monthly ranges for those turtles for which a minimum of 3 months could be calculated were used. In all figures the data are presented in two ways. The left figure shows the actual 95% bivariate normal home ranges. The right figure shows the 95% confidence ellipse for the center of gravities of the home ranges (appendix 5). It is easier to visualize the changes in location of home range with time of year by looking at the centers of gravity. Turtle #47 (figures 20c and d) illustrates an animal with considerable seasonal movement. This animal was followed over four complete seasons of activity, and showed a similar pattern of movement every year. The animal hibernates in the woods just north of AP-4. In the spring, it moves gradually toward its summer range, which revolves around the hedgerow between AP-1 and AP-2. By mid June, it is down in this area, and enters AP-1 in order to nest. It spends the rest of the summer around the hedgerow, sometimes moving a short way into AP-2. In the autumn, the animal gradually moves back towards its hibernation site. The reason for this annual migration is unclear. The boundary between AP-4 and the woods north of it is perfectly good box turtle habitat, and in fact is occupied by several turtles tracked in this study. Similarly, there does not appear to be any reason why the animal could not hibernate in the woods east of AP-2 and AP-1, far closer to the animal's summer range. An even more extreme example of seasonal changes in home range is shown by animal number 82. Unfortunately, the data on this animal are somewhat limited, covering less than 50 days of tracking, but enough is available to document a rather remarkable pattern of migration (figure 27a). This animal has been picked up regularly by the field station personnel since 1964. The animal is always found in the early part of the summer, mostly in June, but there is one record for May, and one for July. The locations where the animal has been recaptured are also plotted in figure 27a. During the course of this study, several attempts were made to radiotrack the animal. It was found that it nested in field AP-5 (see figure 4b, but on the first two attempts to track it, it was lost shortly after nesting. The reason became evident the third summer, when the animal was finally tracked to its summer range. This is well off the field station, down on the Havemeyer estate (see figure 27a). It is clear that previous failures to track the animal resulted from the exceptionally long distance that the animal moved from the site of original capture. Also, its appearance in the field station records only in the spring is explained. Other animals showing considerable shifting of home range with season are #34 (male, figures 20a and b), #76 (female, figures 21c and d), #147 (female, figures 24c and d), and #155 (female, figures 25c and d). Some animals, like #34 and #76 show essentially bimodal home ranges, while others, like #147 and #155 show home ranges that shift progressively through the season.

On the other hand, seasonal variation in home range is not evident in other animals. Number 59, (figures 21a and b) for example, a male, ranges quite freely over its home range at all times of the year. Other animals showing little evidence of seasonality are #106 (female, figures 22c and d), #124 (male, figures 23c and d), #132 (female, figures 24b and c), #154 (female, figures 25a and b). Therefore, I have to consider box turtles rather variable with regard to the degree to which their home range shifts with season. In some cases the shifts are fairly minor, in other cases, quite substantial. One is tempted to speculate that historical reasons may be responsible for those situations where home ranges shift from month to month. It is possible that shifting patterns of vegetation have caused certain animals to shift their home ranges, but that they return to old areas to carry out certain functions. One wonders if turtle #82, for example, might not have been hatched from a nest in AP-5 from which area it later had to migrate in order to find some necessary resources, but to which it still returns for the purposes of nesting. The documentation of such speculations is, of course, not simple. In any case, home ranges measured over less than a season of activity may or may not reflect the full area utilized by an animal. To be fully reliable, it is important to track the animal near the time of hibernation, that is either spring or fall, and for females, near the nesting time, from mid-June to the first week in July, as well as during mid-summer.

The relationship between the size of the 95% bivariate normal home range and the month of the year was also investigated. Table 5 gives the monthly home ranges for May through October for all cases for which at least 10 points were available on an animal during a particular month. The monthly means and their statistics are summarized, and an analysis of variance is performed on the data. Home ranges appear to be smaller in May and October than during the intervening months, which is what one might expect. However, the analysis of variance shows the variation to be non-significant $(p>.05)$.

Figures 28 and 29 show 95% confidence regions for the centers of gravity of the yearly home ranges for those animals for which at least 2 months of overlap over at least two years is available. For the most part, home ranges from year to year are quite constant. The notable exception is animal #18, which had very different home ranges in the two years it was tracked. This is the only evidence I have of a substantial shift from one year to another in the home range of a box turtle. Animals #34 and #124 also seem to undergo some shift in home range between years, but this is largely artifactual. In the case of #34, the home range is highly bimodal, and the shift in center of gravity between he two years largely reflects simply different amounts of time spent in the two major patches of its rather elongate home range between the two years, resulting in a shift in the center of gravity. Similarly, the shift between years of #124's home range reflects more a change in intensity of use of different parts, than a shift in the overall area used.

It is also worthwhile to consider the extent to which home ranges shift over a period of years. This can be partially answered by comparing the home ranges found for animals in this study with the field station recapture records. Table 6 shows maximum distances that a field station record lies outside of the 95% ellipse home range, the date of that record, and the earliest date for which a field station record is available. The maximum distance that a field station record lies outside of the calculated 95% bivariate normal home range for any animal is 120 meters. I conclude that box turtle home ranges show a high degree of stability from year to year, at least over time periods of 5-10 years.

Conclusions

In view of the stability of box turtle home ranges, one is motivated to ask what the adaptive advantage is of maintaining a stable home range. What is especially interesting in this regard is that some turtles, at least, could easily find the necessary resources within a much smaller area. Numbers 47 and 82, mentioned before in connection with seasonal movements, pass over completely livable habitat in the course of their yearly migrations. As will be seen later, box turtles have a strong tendency to home when displaced from their home ranges, and will return to their home range even though they have been displaced to areas that can support box turtles, as evidenced by the fact that these areas contain resident turtles. Furthermore, the evidence gleaned from the previous analysis of home range indicates that the availability of such things as food is not very significant in determining box turtle home ranges. Nevertheless, it is clear that there is some strong selective advantage involved in a box turtle's remaining in familiar territory rather than venturing into an unknown area. Aggressive interaction between box turtles seems relatively mild so it is somewhat hard to see that it constitutes a problem, but perhaps under crowded conditions, frequent harassment of a foreign turtle by the residents would be deleterious. Knowledge of good nesting sites by females might be an advantage of maintaining a definite home range, but one wonders why some females will pass over what are clearly suitable nesting sites (other turtles nest there), in order to go to their own "favorite" nesting site. As mentioned, historical reasons suggest themselves as a possibility. Knowledge of the location of food sources might be advantageous, but box turtles are so omnivorous that one would expect that they could find food anywhere. Knowledge of areas of cover for escape from predators could be involved. Surprisingly enough, box turtles will often attempt to run for cover when disturbed. They will attempt to disappear into areas of heavy undergrowth, where pursuit is difficult. The technique is not as ineffective as it might seem, especially since box turtles are likely to see an enemy long before being seen. Finally, it may be somewhat misleading to think only in terms of a highly disturbed habitat like the field station, where good box turtle habitat is available over a large area. Under some conditions, suitable habitat may be much more restricted, and moving off its home range might be very likely to take an animal into unsuitable habitat. Evolving box turtles could certainly not have anticipated the advent of man!

Certain differences in results and methods impell me to reevaluate the conception of box turtle home range expressed by Stickel (1950). Stickel, following Burt (1943), thought of a box turtle's home range as being an area within which the probability of finding an animal was relatively uniform, and which the animal occasionally wandered outside of for special purposes. She believed that box turtles visit most of their home range within time spans of no more than a few days. Though there are indications in her data, had she chosen to pay more attention to them, that the situation was not so simple, she seemed to regard variations from this concept as virtual abnormalities. She did believe that female box turtles generally left their home ranges for the purpose of laying eggs. However, the methods available to Stickel did not allow her to gather enough data over a long period of time on enough turtles to appreciably shake her faith in Burt's conception of home range. She even goes so far as to claim that some turtles have "two" home ranges, each of the type described by Burt, rather than abandon the concept. My feeling is that box turtles are very variable in the way they use their habitat. Certainly there are turtles that have neat, compact home ranges, most of which they visit in a short time, but it is by no means exceptional to have other home range patterns. Furthermore, box turtle home ranges do not have sharp boundaries, but on the average fall off with close to normal probability. The discussion of home range in Stickel (1954) is especially indicative of her conception of home range as being sharply circumscribed. I have found that seasonal usage of home range is very common in box turtles and that the nesting sites of most females are not much outside of areas that females spend enough time in for the area to be considered part of her home range, though there are exceptions to this rule. The same is true of hibernation sites. This can be seen from figures 6-15 which show the nesting and hibernation sites for all animals together with the 95% bivariate normal home range, and the observation points on which this home range was based. Despite seasonal uses of various areas, it is really impossible, for most animals, to designate nesting or hibernation sites as separate from the home range. Often, when a turtle is trailed continuously for a period of several months, one finds that the animal has a very complex home range. As I have pointed out, adequately defining the area of such a home range is difficult, and requires considerable quantities of data. I can only conclude that biologists in the future will have to be less content with the data provided by recapture studies, at least as far as determining the ecological significance of home range.

Every box turtle followed during this study had a definite area over which it ranged, and to which it confined its activities. No turtle merely wandered at random over the study area. Stickel (1950) in her study frequently captured a turtle only once. She designated such turtles as "transients" since she assumed that they had merely been passing through her study area on their way to somewhere else, and were thus distinct from "residents". I can find no evidence for the existence of "transients".

There are various reasons why a turtle might only show up once in a mark-recapture study. One, recognized by Stickel, is that the turtle's home range lies mostly outside the study area and so the turtle spends little time in the study area, and hence is rarely found. Another reason is that turtles may differ greatly in the ease with which they are found. In the Kalbfleisch Field Station records, it can be seen that some turtles are picked up and brought in quite regularly, while others may only be found once. Radiotelemetric data, however, shows that turtles in both categories have home ranges well within the field station.

HOMING

Introduction--Can Box Turtles Home?

Homing ability has been claimed for many animals. Though well established for some groups, such as birds, sea turtles, and salmonid fishes, the data supporting these claims for many other groups has not always been impressive. Good experimental design in homing work requires the consideration of many factors if it is to be established that homing ability exists at all, and it is often worthwhile to keep possible mechanisms in mind even from the very outset. This introduction will attempt to outline the homing problem in general, and to examine claims being made for homing ability in box turtles.

In a widely used classification, Griffin (1952) distinguished three categories of orientation: type I, orientation on the animal's home range by the detection of visual landmarks; type II, in which an animal in unfamiliar territory heads in a fixed compass direction not necessarily related to the home direction; and type III or bicoordinate navigation, in which an animal outside of familiar territory can nevertheless establish its position in relation to the home location.

Orientation of an animal within its home range is not usually considered homing. Type II orientation can lead to homing under some circumstances. Ferguson (1965, 1967a, 1967b), for example, has shown that various species of frogs will head in a specific compass direction when released in aquatic circular arenas. The direction is one which would normally return the animal to its home shore if it were displaced toward the water from this shore. Bicoordinate navigation clearly represents homing ability. Not easily fitting Griffin's classification is the case of an animal carried outside its home range but able to return home by detecting landmarks from a distance. Such detection would not necessarily have to be visual, but could include detection by odor or sound, among other things. For the purposes of this discussion, such orientation, will be considered homing, and will be called "offrange orientation by landmarks". Thus homing mechanisms will be considered in three categories, type II orientation, bicoordinate navigation, and offrange orientation by landmarks.

Type II orientation requires that the animal have a compass sense. Time-compensated solar compasses have been described in such a wide variety of animals that it can be safely assumed that any animal with an adaptive need for one will possess it.

Offrange orientation by landmarks can be done in two ways. If an animal can detect a landmark on its home range, it can simply head towards it. More elaborate is to determine the azimuth to two landmarks detectable from both the home range and the release site, and to head in a direction that will restore the azimuths to their home-site values.

Bicoordinate navigation can be carried out in several ways. The one that has gotten the most attention, because of its apparant use by migrating birds, is celestial navigation. The theory of bicoordinate celestial navigation is briefly this. All celestial bodies, except one in a line with the axis of rotation of the earth, move in arcs across the sky. The sun is such a celestial body, and since turtles are diurnal, it is the most likely candidate for celestial navigation in turtles. If an animal sits in one place, the sun will pass through the high point (zenith) of its arc at the same time every day. The angular distance of the sun above the horizon at zenith changes each day, but in a predictable way, to a mathematically sophisticated animal. In general, it makes a higher angle each day to the summer solstice, and thereafter, to the winter solstice, a lower angle. The daily change in angle varies with proximity to the solstices, being smallest at the solstices, and greatest at the equinoxes. The average change is 45" of arc per day. If the animal moves in an easterly or westerly direction so that its longitude changes, the apparant time of passage of the sun through zenith alters, becoming later for a westerly movement, and earlier for an easterly one. It is this effect, of course, that is responsible for the adoption of time zones. If the animal moves in a northerly or southerly direction, so that its latitude changes, the angle of the sun above the horizon at zenith varies from what it would have been if the animal had not moved, allowing for the daily change in this angle. The angle increases for a southerly movement, and decreases for a northerly one. In theory, therefore, an animal with a very accurate internal clock, and a very accurate means of measuring the sun's altitude above the horizon could determine its new position after displacement in a homing experiment by observing the change in the time of the sun's passage through zenith, and the change in the angular height of this passage from the expected values. Carrying sophistication one step further, the animal might not actually have to observe the sun's passage through zenith, but after observing a short arc of the sun's movement at any time of day, could extrapolate and find the time and angle of passage through zenith.

Inertial guidance is another possible method for bicoordinate navigation. In theory, an animal in a closed container that deprives him of all information about the outside world, can nevertheless determine how far and in what direction it is being carried by measuring the magnitude and direction of all accelerations it undergoes, and taking the second integral. The sensory equipment required would be two accelerometers measuring accelerations at right angles to each other, and a rotational accelerometer. The accelerometers either have to be mounted on a platform that is kept level, or corrections must be made for gravity. Additional corrections must be made for Coriolis force (Barlow, 1964).

People who have had trouble mastering Calculus tend to be amused at the idea of a turtle integrating, so the high degree of mathematical sophistication required for inertial guidance, together with the fact that good accuracy requires very accurate measurement of acceleration, has tended to result in inertial guidance being discounted on theoretical grounds. I feel, however, the idea should not be so lightly dismissed. Analog integration is relatively easy to perform. For example, the accumulaton of lactic acid in a muscle is proportional to the work done, and is the time-integal of the muscle's power output. One could envision some neurohumor accumulating in the nervous system of a turtle, the release of which was proportional to the output of an accelerometer. The amount of this neurohumor that accumulated in a given length of time would then be the integral of acceleration over that time. Also, the accuracy required by a turtle returning to a relatively large home range after transport of a few hundred meters cannot be compared to that required of an ICBM fired from the U.S. that is to hit Moscow. It should be emphasized, contrary to what one might expect, that inertial guidance does not require memorizing every twist and turn of the outgoing route, but only accumulation (integration) of the distances moved in two different directions, most conveniently, though not necessarily, at right angles to each other. Vector addition of the distances in these two directions then gives the direction and distance the animal has been carried from home. A simple sun-compass would then suffice to return home. In fact, the animal might not have to make any estimate at all of the distance it had been carried, but only the general direction. This vastly simplifies the problem. Thus, if a turtle has been carried 1000 meters from a home range 300 meters in diameter, it need only estimate the direction it has been carried to an accuracy of plus or minus 9 degrees to be able to return home. Actually, depending on terrain, even less accuracy might be required, since an animal passing close to its home range could probably pick out landmarks from some distance.

Hybrid inertial guidance-like mechanisms are possible, in which directional information is supplied by an external cue instead of a rotational accelerometer. This might simplify the problem further. For example, an animal transported in a container that prevents it from seeing its surroundings, but is not light-tight, might sense inertial forces in relation to the direction of greatest light intensity, and determine the direction it was being carried. A sound source, or the earth's magnetic field could provide similar directional information. At one time, sensitivity to the geomagnetic field would have been discounted by most workers, but evidence is accumulating that some animals, at least, may be sensitive to it. Keeton (1972) for example, claims that the early disproof of magnetic sensitivity in birds was based on an error in reasoning. If you eliminate first one mechanism for homing and then a different one in two separate experiments, and find that in both cases the bird continues to home, you are tempted to conclude that the bird uses neither. In fact, it may be using both, and in each experiment it relies on the one that has not been eliminated. Thus in repeating the old experiment of attaching magnets to birds which are then released outside of their home ranges (Yeagley, 1947, 1951; Riper and Kalmbach, 1972; and Matthews, 1951), Keeton claims to have shown that pigeons carrying magnets can home under clear skies, but not cloudy skies, while birds carrying only dummies can home under both conditions. He therefore concludes that under clear skies birds will use celestial orientation, while under cloudy skies, they will switch to magnetic. In addition, Brown (1970) has found sensitivity to magnetic fields in animals as diverse as mud snails, planaria, and white mice, and Lindauer and Martin (1972) have evidence for sensitivity to geomagnetism in bees. Thus, obtaining directional information by magnetic means must be considered possible.

In fact, it may even be possible to base a bicoordinate orientation system completely on the earth's magnetic field. Declination of the field varies with longitude, and dip with latitude. Anomalies in the field would greatly limit the accuracy of such a navigation system.

This summarizes the main mechanisms that have been proposed for homing ability. There are some additional esoteric ones. For example, latitude can be detected by changes in the magnitude of Coriolis force, or by changes in body weight (an object is slightly heavier near the poles than it is near the equator). However these effects are small, and it would be hard to measure them with useful accuracy. I would now like to look at what the literature has to say on the question of whether box turtles can home.

Nichols (1939) appears to have been the first to suggest that box turtles are able to home when displaced from their normal home range. He marked 13 turtles found in his back yard on Long Island and displaced them to distances of 1000 to 1400 yards. During the next 10 years, 11 of the marked animals were found back on their home ranges. In an earlier experiment, Breder (1929) found that box turtles would return to their site of capture following displacement, but in this case, the animals were probably not removed from their home ranges. Metcalf and Metcalf (1970) performed a series of homing experiments on ornate box turtles (<u>Terrapene ornata</u>) and obtained returns of marked turtles from distances of up to 1.5 miles. Some of their turtles were transported in light proof containers, and some without visual deprivation (pers. comm.), but turtles transported in both ways homed. Lemkau (1970) reported on a series of homing experiments with <u>Terrapene carolina</u>, in which turtles were released carrying a "thread-trailer, radio-transmitter" package. The turtles were tracked for periods ranging from 14-73 days. Transportation was in cloth bags that prevented a view of the surroundings. Lemkau concluded that in unfamiliar territory, turtles tended to move in straight lines, sometimes following natural features of terrain. He states that their direction of movement was "clustered in the semicircle toward home", but does not support this conclusion with data. He does not report that any turtles actually succeeded in reaching their home ranges. Legler (1960) reports that out of 2 individuals of _T_. _ornata_ that were transported 1900 feet, one homed, and one did not.

The most extensive investigation of homing in box turtles was carried out by Gould (1957, 1959) on _T_. _carolina_. He transported animals in closed containers to release points .25 to 5.8 miles from the point of capture. An analysis of the initial directions moved by turtles upon release showed that they had a statistically significant tendency to head toward home, though the errors were large. This was true only in sunny weather. Under cloudy skies, the initial headings were essentially random. Gould hypothesized that box turtles were using celestial navigation of the kind that has been proposed for migrating birds. In other experiments, he released turtles at a distance of 100 miles from their home range, and obtained type II orientation.

In the 1959 paper, Gould also reported similar results for painted turtles (_Chrysemys_ _picta_). A number of other workers have reported homing ability in painted turtles, including Ortleb and Sexton (1964), Williams (1952), and Ernst (1970). However Emlen (1969), in a very careful series of experiments on painted turtles, was unable to confirm their homing ability except over very short distances (100 meters), where knowledge of local terrain could easily have been the orientation mechanism (Griffin's type I). Furthermore, he argued on theoretical grounds that bicoordinte celestial navigation, as suggested by Gould, was highly unlikely (see below). Emlen's work appeared, therefore, to cast a doubt on the entire question of homing ability in turtles. These doubts become especially troublesome when one considers that in general, experimental design in short-distance homing experiments of the kind that we are concerned with in turtles (as opposed to homing over hundreds or thousands of miles, as in birds) has not received adequate consideration. An analysis of Gould's experimental design will illustrate the point:

Turtles were "preselected" for their tendency to move homeward from at least one release site. In the 1959 paper, they were preselected for their tendency to move homeward from two directions. That is, turtles that did not move homeward were not used. This procedure would be valid provided that only data from release sites other than the one, or ones, that the animals were preselected for were used. The overall data however appears to include results from the preselection sites. This argument applies even though the preselection runs themselves were not used. The problem is that a turtle released a second time from the same site might tend to head in the same direction as it did the first time, in response to cues totally unrelated to homing ability.

Multiple releases from the same site, sometimes on the same day, were counted as separate items of data. Since there is a clear potential for lack of independence in such data, statistical tests based on them, assuming independence, lack validity. Also, there was no predetermined criterion for when to release a turtle several times from the same site, and when to release it only once. This appears to have been strictly up to the discretion of the experimenter. Obviously, an observer with a preconceived bias in favor of a certain hypothesis might have an unconscious tendency to repeat a run when the result favored the hypothesis. Again, if turtles tend to head in the same direction on successive runs from the same site, this would bias the data.

There was no clear criterion for when to terminate an experimental run. The direction of a turtle's initial heading after release was scored after the turtle had moved anywhere between 65 and 600 feet from the release site. Given a turtle moving at random, it is always true that a biased observer could make it appear that the animal oriented homeward by terminating the run at a time when the animal happened to be homeward of the release site. This could, of course, happen without the observer being consciously aware of it. In his 1957 paper, Gould presents two examples of what he calls "typical" runs. One of these shows a clear homeward heading by almost any imaginable criterion, but the other shows potential for the kind of bias I am discussing. These are reproduced here for reference (figure 27b). Notice in the right-hand example that the animal moves about 280 feet before it even enters the semicircle centered on the home direction. But when the run is terminated, the animal is heading almost straight home. Had the run been terminated any time prior to a movement of 280 feet, it would have been scored as moving in the wrong direction. Some runs were terminated after just 65 feet. The proper procedure would have been to score every turtle after it moved some arbitrary distance decided upon in advance, say after 200 feet, or to score it after some predetermined length of time. Since the two examples shown are the only two given in Gould's paper, it is impossible to say which is more "typical" and therefore impossible to evaluate the potential for bias in the results.

Turtles were placed down, upon release, facing opposite the homeward direction. While this seems at first sight to be a laudible (though unscientific) biasing of the results against the hypothesis, this is not necessarily true. Suppose for example, that turtles have a tendency to "turn in their tracks" upon, or shortly after release. The results then would be biased in favor of the hypothesis of homing ability. A better procedure is to randomize the direction in which the turtle is placed down.

Also it should be pointed out that in the case of releases from sites other than the preselected one, which are the only releases that count, as noted under 4, there is an ambiguity in the results. Only some of the turtles consistantly headed homeward. Others showed a tendency to head in the same direction, regardless of what site they were released from (Griffin's type II orientation). Interestingly, in another series of experiments on painted turtles, Gould (1966) found only type II orientation.

Finally, it must be noted that even if Gould's data were valid, his conclusion that bicoordinate celestial navigation is the mechanism for homing would not be warranted. Turtles were transported in closed, but apparantly not light-tight containers. Potentially, they could tell what direction they were being carried by sensing inertial forces in relation to the direction of greatest light intensity (presumably, the direction of the sun).

In general, it appears that any homing experiment should include at least the following elements of good experimental design:

Transport should be done in containers that prevent the animal from seeing where it is being taken. Many workers like to use light-tight containers as well, eliminating any homing mechanism based on the sensing of inertial forces in relation to the direction of the sun.

No more than one release should be made of any one animal from any one release site, and release sites should be scattered in different directions from the home range.

The animal's home range should be accurately known, so that one can be certain of being outside of it.

There should be a clear, predetermined criterion of when homing has occured.

It should be possible to eliminate random search as a mechanism. In general this means showing either that the initial orientation tends to be homeward (Gould's approach) or following the animal during its homeward movement so that the actual pathway is known. This consideration applies for example to Nichol's experiments, in which the animals were sometimes not found on their home ranges until several years after release, allowing for the possibility of a good deal of random search! It is also necessary to show that the frequency of success is better than one would expect if the animals head in random straight lines, some of them by chance picking the right direction.

No study now in the literature meets all of these criteria. Emlen (1969) showed more care in experimental design that any other worker, and his turtles failed to home. One of the most interesting papers with information on homing in box turtles is that of Metcalf and Metcalf (1970). Working with T. ornata, they performed two types of experiments. In one, they transported turtles away from their points of capture, released them, and later searched for them near the points of capture. 18.9% of the 434 turtles returned home. Although the home ranges of these turtles were not known, the relatively long distances involved in some of the releases (up to 1.03 miles) makes it seem likely that at least some of the releases were made off the home range. It is somewhat hard to interpret the fact that only 18.9% of the turtles were definitely known to have homed. Many explanations come to mind. Only some of the turtles were transported in closed containers (pers. comm.). Only the homing success of these animals is is meaningful. Obviously, some of these could have returned home just by heading in a randomly directed straight line, especially since the Kansas terrain was relatively flat and open, covered mostly by prairie grass, and turtles passing some distance from their home ranges could presumably make out landmarks. The path of homing is not known, so random search could not be eliminated. The time required for homing is not given in the paper. More interesting are the data from the second type of experiment, in which turtles were released carrying thread trailers of the type used by Stickel (1950). Four animals were used in this series. Three returned home, doing so in as little as 2 days. The fourth also returned home, but did so by a highly circuitous route. For the three that homed in a fairly straight line, the maximum distance between capture site and release site appears to have been about 800 meters. Unfortunately, the exact route of homing is not given, the home ranges of the animals were not known, so it is impossible to say how far outside their home ranges the animals were carried, and the method of transport is not given. Nevertheless, their results remain intriguing. It should also be pointed out that the openness of the terrain might make the problem of homing simpler for T. ornata than for T. carolina, living in a more wooded habitat.

In view of the doubt that is left by the previous literature about whether turtles are able to home, and the lack of information on the mechanism, it seemed worthwhile to carry out additional experiments on homing. I undertook such a series of experiments on the Kalbfleisch box turtles during the summers of 1970, 1971, and 1972. Several criteria of good experimental design not previously achieved have been realized here. Radiotelemetry permitted determination of the normal home ranges of the animals with a previously unattainable reliability, indicating, as was pointed out, that the best previous estimate, that of Stickle (1950) was too small. Since the turtles were carrying transmitters, the exact pathway of homing could be determined, which made it possible to eliminate random search as a mechanism.

In addition, the experiments were designed to eliminate from the the outset certain mechanisms of homing, including inertial guidance, and offrange orientation by visual landmarks. Animals can be prevented from using inertial guidance by rotating them rapidly during transport, overloading the inertial guidance system. In theory, rotating the animal just prior to, and just after transport is sufficient, but other considerations indicate that the animal should be rotated continuously during transport. The problem is that if the animal can receive any kind of outside directional information, it can reorient its inertial system in relation to this as soon as rotation stops. Sounds or magnetic fields could provide such outside sources of directional information, even to an animal transported in a light-proof container.

The nature of the study area, which consisted of fields, the edges of which made good box turtle habitat, separated from each other by wooded areas that provided visual isolation of the fields, made it possible to rule out the use of landmarks visible from both the home range and the release site for orientation.

Materials and Methods:

Turtles were placed in light-proof double-layer black cloth bags on their home ranges. The light-proofness of the bags was confirmed by exposing Kodak Tri-X film in them in bright sunlight for a period of one hour. No detectable fogging resulted. In the initial releases, the advantage of spinning turtles during transport, as well as before and after to prevent hybrid-inertial guidance was not appreciated. However, begining with the 18th release, animals were spun during transport. They were spun before and after transport for several minutes on all releases. Spinning was done by twirling the animal rapidly in its sac on the end of a string. Only releases from sites more than 250 meters from the nearest edge of the 95% bivariate normal home range ellipse are counted in the final tabulaton of data. Other releases were made at distances that later turned out to be less than this, but they were discounted. The longest displacement was 1140 meters from the the nearest edge of the 95% bivariate normal home range.

A total of 40 releases were made, involving 18 turtles. Fifteen of the animals were adults. Two were young animals, 9 and 10 years old. The final animal was a 1.5-year old juvenile that had been continuously radiotracked since leaving the nest. Turtles were released by inverting the black bags and allowing them to tumble out in a random direction. In some cases, turtles were captured, transported, and released as quickly as possible. In other cases, for reasons that will be explained below, the animal was held in captivity for about 24 hours before being released. Turtles were scored as having homed successfully if they returned to within the boundaries of the 95% bivariate normal home range.

Results:

Table 7 summarizes the conditions under which each release was made, and presents the results. Figures 6a through 12b, 15b, and 15c show the actual paths followed by the turtles. The salient features of the results will be indicated here. In 38 of the 41 releases, successful return to the home range was noted. In one of the 3 failures, the animal was lost shortly after release, due to transmitter failure. However, the animal was recaptured on its home range two summers later, so it did return, though the route and length of time are not known. Another failure was that of the 1.5-year old turtle, which did not return to its home range. In the final failure, the animal did not return after 28 days, and observation was terminated. In summary then, out of the 39 releases on animals 9 years old or older, and not plagued by equipment failure, there were 38 successful returns to the home range.

Turtles that were held 24 hours before release did as well as those that were released immediately. The two young turtles 9 and 10 years old homed successfully. Turtles spun during transport, as well as before and after, homed. In some cases the turtles set out for home immediately. In other cases, the animals remained close to the release site for several days, often wandering around rather randomly, before showing homeward movement. The onset of homeward movement was generally an abrupt, easily noticed event, but the animal was arbitrarily considered to be "close to the release site" if it was within 50 meters. The average time for adults spent close to the release site was 2.2 days (s.e.=.55, n=34, range=0-14). Correlation between the distance the animal was released from home and the length in the delay in setting out for home was -.04 (n=34, p>.05). The time required from release to reattainment of the home range was 11.5 days (s.e.=1.63, n=33). Interestingly, the correlation between distance of displacement and time to return home was only 0.15 (n=33), which is not significantly different from 0.

Conclusions:

I conclude, therefore, that box turtles are able to return home when displaced from their home ranges into presumably unfamiliar territory. Of course, the determination of life-time home ranges in an animal as long-lived as box turtles, is not practical. It is possible that the home ranges of box turtles slowly shift over long periods of time. However, as indicated under the chapter on home range, the home ranges of many turtles appear be quite stable. Also, the inclusion of two younger turtles in this study, who also successfully homed tends to militate against the argument that familiarity with a large area gained over a long lifespan is important to homing. Habitats on the field station have changed over the years, and the home ranges of some turtles may have changed with these changes in habitat, but one would question whether previous knowledge was useful in a situation where such changes have taken place. For example, the now wooded area designated SW-6 (figure 1a), was once field. But it seems doubtful that a former occupant of that field would now recognize it if transported back there. There is also the question of how reliable my determination of home range was. It is true that the one animal for which a complete lifetime home range was available (#A7, 1.5 years old), did not home when carried out of its lifetime range, but it is difficult to make much of negative evidence on so young an animal. It is perfectly possible that a strong attachment to a given home range does not develop until later in life.

Therefore, while it is possible or even probable that some of the releases took place in areas that were familiar to the animals, others almost certainly did not. A moderate rate of homing success, especially if success were best from shorter distances, might be consistent with the hypothesis that the animals could only orient in areas they were familiar with, but the high degreee of success reported here, even from the farthest distances, seems to make such an explanation unlikely. In this connection, it should be noted that though observations were terminated after 28 days on the one adult animal that did not home, animals that did home took as much as 21 days to begin their homeward journey. It is possible that this animal too would eventually have homed.

Although the mechanism for homing was not determined, several frequently suggested mechanisms can be ruled out. Inertial guidance, either pure or combined with an external compass, does not seem to be involved. Offrange orientation by visual landmarks also seems unlikely. In this study, turtles were always released from fields that were visually isolated from the home field or fields by woods and hedgerows of trees. The spotting of common distant landmarks was not possible, at least for a human being. I am inclined to think that a turtle, being much closer to the ground, would be in a far worse position in this regard. Of course, sensitivity to electromagnetic wavelengths capable of penetrating foliage, such as radio waves, or x-rays is conceivable, but a bit esoteric. With regard to radio waves, the only earth-bound sources are man-made. In any case, one wonders what the effect of carrying a radio transmitter on ones back would be on a highly sensitive radio-direction finding system. Random search was also clearly not involved.

The fact that turtles with home ranges on various areas of the Kalbfleisch station were released from a variety of sites makes it improbable that homing resulted from any tendency to follow some feature of the topography or the vegetation. This can be verified by examining maps showing the homing tracks plotted together on contour and vegetation maps (figures 16a and 16b). Even when different animals are released from the same site, they follow different homing routes. For example, one site at the extreme southern end of the Havemeyer property was used for seven releases, and an eigth release was made from a site not far away. Animals released from these sites follow one of two distinct routes northward. The routes pass respectively to the east and west of the fields immediately north of these release sites. Apparently, the animals avoided moving through the centers of these large fields, and preferred to skirt the edges. This is not surprising in view of the general preference of box turtles for the edges of fields (see chapter on habitat preference). Examination of other homing tracks shows additional instances of turtles avoiding moving through fields, or at least, minimizing the distance of such movement. Topography seems to have little effect on the homing tracks. Turtles move equally readily parallel to, and at right angles to contour lines. It should be noted, however, that the topography of the station is generally very gentle. A hillier topography might have had a greater effect.

Type II orientation does not seem to be involved in turtle homing. Experimental design was such that turtles had to head in a variety of compass directions to return home. Type II orientation would not have led to such a high rate of homing success.

Bicoordinate celestial navigation was suggested by Gould as an explanation for box turtle homing. Emlen (1969) thought that it was a bit much to expect of a turtle, and I am inclined to agree with him. In fact, he underestimated the difficulty if anything. Allowing the turtle a rather generous 500 meter error in estimating its position, it would, at the latitude of the field station, have to able to measure time to an accuracy of 1.6 seconds, and angles to an accuracy of 16" of arc. Furthermore, it would have to correct for the daily change in the sun's altitude to an accuracy of one part in 170 of the average change. Emlen was able to demonstrate to his satisfaction that painted turtles cannot home, thus bringing into resolution theory and practice. I am convinced that box turtles can home, but not by bicoordinate celestial navigation. However, in an attempt to give the celestial navigation theory a severer, though not completely conclusive test, for 11 of the releases, the turtle was held in captivity for 24 hours prior to release. When a turtle is picked up and released within a period of half an hour or so, it need only estimate the passage of time to an accuracy of one part per thousand. A turtle kept 24 hours before being released must estimate the passage of time to an accuracy of one part per 50,000. This exceeds the claimed accuracy of tuning-fork timed, electronic wrist watches. Yet, as shown in table 7, turtles were successful in homing under these conditions, return being observed in 10 out of the 11 cases. I conclude that bicoordinate celestial navigation in turtles is highly improbable. This theory does seem to be compatible with what is known about the homing behavior of birds, but there the problem is quite different. Accuracies only on the order of several tens of miles are needed say to get a homing pigeon to familiar territory. Meyer (1964) was able to show that homing pigeons could distinguish angular heights of the sun to an accuracy of 1 degree, which is adequate for the task required of a pigeon. To use celestial navigation, a box turtle would have to better the performance of a good homing pigeon by more than 2 orders of magnitude.

In short, vision does not seem to be reasonable as the sensory modality involved in box turtle homing. Hearing is also unlikely. No definite auditory clues detectable to humans were available on the station, and box turtles are known to have a more restricted frequency range for the detection of sound than humans (Wever and Vernon, 1956). Sensivity to the earth's geomagnetic field is conceivable, but rotation of the animal during transport would prevent the use of a hybrid magnetic compass-inertial mechanism and it is very doubtful that the necessary accuracy could be achieved by measuring the change in dip and declination of the field.

Odor suggests itself as another possibility, and probably the best in my opinion. Odor has been well-established as a homing mechanism in Salmonid fishes (Bertmar and Taft, 1969), and there is evidence suggesting its role in the homing of amphibians (Madison and Shoop, 1970; Madison, 1969; Twitty, Grant, and Anderson, 1967, 1964; Oldham, 1967). Carr (1972) has suggested that it may be involved in sea turtle migration. Attempts to deprive box turtles of their sense of smell by plugging the nostrils in various ways were unsuccessful. Turtles with plugged nostrils did little else but work at the plugs with their front legs until eventually they succeeded in dislodging them. Meanwhile, they showed considerable distress. Because of the high value of turtles with considerable accumulated home range data, I was reluctant to try cutting the olfactory nerves. Since box turtles are reported to have musk glands (Legler, 1960), and their urine and excretion have decided odors, the possibility of scent marking must be considered. It is also possible that they could recognize distinctive aspects of the odor of their home range caused by differences in soil, or the precise mix of vegetation. This might be a more difficult problem. In any case, detection of odors at the distances involved would not seem to exceed sensory capabilities that have been demonstrated in other animals, such as Saturnid moths.

It is known that box turtles have a sense of smell (Tucker and Shibuya, 1965), however, it is not known whether their sense of smell is adequate for the task of homing. Undoubtedly, this question can only be answered experimentally. Manton, Karr, and Ehrenfeld (1972), have demonstrated in the sea turtle, Chelonia mydas, the ability to detect the presence of various water born chemicals at concentrations as low as 5 x 10 to 5 x 10 M. They also suggest the use of zinc sulfate injected intranasally to interrupt olfactory ability. The technique would probably be useful in investigating the role of olfaction in the homing ability of box turtles.

A variety of sensory capabilites have been investigated in conjunction with orientation in aquatic turtles. These include such things as infra-red sensitivity, ultra-violet sensitivity, differential sensitivity to colored light, sensitivity to polarized light, sensitivity to humidity gradients, response to the openness of the horizon, and geotropism, among other things (Anderson, 1958; Carr, 1960; Danial and Smith, 1947; Ehrenfeld and Carr, 1967; Ehrenfeld, 1968; Mrosovsky and Shettleworth, 1968; Noble and Breslau, 1938; Ortleb and Sexton, 1964). Some of these do seem to be involved in aquatic turtle orientation, but it is hard to see how they would function for terrestrial box turtles, since all are connected in some way with locating bodies of water. Sensitivity to cosmic rays, Coriolis force, gravity fluctuations, etc. not only seem unlikely, but again it is hard to see how they would be useful. I am therefore inclined to believe that odor would be the most promising sensory modality to test next.

An obvious question that arises in connection with homing ability in box turtles is the question of what the adaptive advantage is. This divides itself into two questions: what is the adaptive advantage of maintaining a definite home range for a box turtle, and when would a box turtle normally be carried off its home range? The first question has been discussed in the Home Range chapter. Two possibilites suggest themselves in answer to the latter question. Dogs have been observed to pick up and carry box turtles (Carr, 1952), and it is possible that other large carnivores do too. Second, one of the principle habitats for box turtles under undisturbed conditions is river flood plains. Stickel (1950) observed that box turtles in her Maryland population were largely confined to the flood plain of a river running through the study area. Flooding by such a river could carry box turtles out of their home ranges, and in fact, this was observed by Stickel during her study. One turtle carried 204 meters out of her convex polygon home range (determined on 15 points), was found back on her home range 11 days later.

Harder to explain, perhaps, than why box turtles home, is why painted turtles do not. Return to a pond after displacement would seem to be highly advantageous. One can only assume that painted turtles are much less likely to be displaced than box turtles. Probably they are safer from being carried by carnivores, and they are better swimmers, and might be less likely to get carried off in a flood. As noted, box turtles are almost totally ineffectual swimmers. Also, a painted turtle carried off in a flood might be expected to return by a water route. In Emlen's work, the turtles were required to home overland. It is possible that painted turtles can home over water routes, but not over land routes. This is suggested by the work of Williams (1952) and Ernst (1970), but their evidence must be considered preliminary, since the routes of homing, and the normal home ranges of their animals were not known. In both cases, however, an over-water route was possible.

On the other hand, Zweifel (pers. comm.), has found painted turtles traveling between ponds as much as 400 meters apart, with the only possible route an overland one. Though this cannot be considered "homing" from an unfamiliar area, there is at least a clear indication that painted turtles are capable of orienting on land.

HABITAT PREFERENCE AND FACTORS AFFECTING MOVEMENTS

Habitat

As was pointed out in the chapter on Home Range, a box turtle does not distribute its time uniformly over the area available to it, nor does it follow any other parametric distribution, but rather appears to be responding to localized characteristics of the habitat, resulting in a "patchy" distribution of observation points. I will now examine the characteristics of a habitat that make it favorable or unfavorable to box turtle activity. Casual examination of the distribution of observation points of box turtles (figure 31c) suggests that they are concentrating their activities in the border areas between forest and other types of habitat. The following procedure was used to test and amplify this hypothesis. Seven different habitat types were first distinguished. There were the four defined in the introduction (forest, brush, field, and grass), plus three additional habitats representing boundary areas between forest and the other three types just mentioned. These boundary habitats were taken to be a zone 25 meters on either side of the borderline. The three new habitat types are called forest-brush, forest-field, and forest-grass. The seven habitats were mapped, and their areas determined with a polar planimeter. It is necessary to be somewhat arbitrary about the area of the field station to consider in making these measurements. An area of uniform and intensive field activity must be chosen, otherwise the results may be biased by the inclusion of areas in which few observation points were available, but whose distribution of areas of habitat would nevertheless effect the expected numbers of observations. Figure 31c shows the area that was measured, and represents a reasonable choice in my opinion. It is somewhat conservative in eliminating areas of forest which could have been utilized by turtles that were being tracked had they not avoided such areas. Inclusion of such areas would have emphasized the pattern of habitat utilization discussed below; this is clear enough as it is, however, so the present procedure seems reasonable. Portions of the field station, and the entire Havemeyer Estate, on which relatively few animals were tracked, were not used in this analysis. The total number of observation points was multiplied by the proportion of the total area represented by each habitat to get an expected number of observation points per habitat, assuming random distribution. The actual number of points in each habitat was then determined, and compared with the expected numbers using a chi-square test. Data and calculations are shown in table 8 (under pooled chi-square). Chi square was 469.9 ($p<<.001$). It is quite evident that box turtles do not distribute themselves at random, which is what was expected. They spend too much time in the habitats designated forest-field and forest-brush and not enough time in the habitats designated forest, forest-grass, and grass. They spend approximatly the expected amount of time in the habitats designated field and brush, indicating that these habitats are neither shunned nor sought out.

The avoidance of grass and forest-grass is difficult to interpret. One is tempted to speculate that the principal characteristic of good box turtle habitat is high diversity, and that grassy areas lack adequate diversity. However, the paucity of observations in such areas may be artifactual. The distinction between grass and field is based on the method of management--"grassy" areas being those managed by mowing. Actual vegetational analysis (see Materials and Methods) shows considerable overlap between the vegetational contents of the two areas. For example, AP-5, managed as "field", actually contains much grass, while the western one third of G-2, which is mowed, contains considerable non-grassy herbaceous vegetation. Thus, the vegetational diversity of the two areas is probably not much different, but AP-5 supports heavy box turtle activity, while G-2 does not. Since box turtles are frequently killed by the mower, it seems reasonable to suppose that the paucity of observations in grass areas is an artifact of the method of management, and not the result of vegetational differences. Nevertheless, it does seem true that areas with high diversity are favored by turtles. Their preference for forest-field, and forest-brush is consistent with this, for these are the most varied habitats on the station. The "patchy" nature of such habitat is undoubtedly one of the factors responsible for the failure of box turtles to conform to a bivariate normal distribution.

Box turtles seem quite strongly to avoid moving very far into areas that lack fairly tall, woody vegetation. The centers of fields, grassy or herbaceous, and of the less dense brushy areas have relatively little turtle activity. The west half of AP-10, designated brush is an exception. The probable reason is that this is one of the more mature brushy areas on the station, and contains more densely growing and taller woody vegetation than do areas AP-1 and AP-2.

To the extent that wooded areas are occupied by turtles, they seem to be those areas that are moistest and most diverse. Specifically, the relatively low-lying and vegetationally complex woods between fields AP-1, AP-3, AP-5, and AP-6 (figure 1a) is more intensively occupied than the higher and less diverse BWF areas. In fact, part of IFB-3 (between AP-5 and AP-6, see figure 1b) adjacent to an intermittant pond is quite attractive to turtles.

Despite the general consistency governing the occupation of various habitats by box turtles, it is often difficult to see the precise reasons why any given individual occupies certain areas and not others. Why does animal number 34, for example, split its range between two such widely separated areas? The seemingly irrational peregrinations of animal number 82 (figure 27a) have already been discussed. Similarly, it is unclear why number 18 centered its activity in two different areas in each of two different years. Other examples can be found in the maps. In contrast, some individuals have quite compact home ranges, systematically occupying the suitable habitats in a given area. Number 59 is a good example (figure 7b), and since this animal was traced over 398 days of activity, its home range data are probably quite complete. Again, the maps supply a number of other examples. Females, as has been noted, tend to spread their activities more than males, but this is not the entire explanation.

Another question that arises is the extent to which box turtles' preference for different habitats varies with the time of year. The approach used to answer this was to determine for each month of the active season (May-October) the number of observation points in each habitat, and to compare this with the expected number of observations in each habitat, assuming proportionality to area, by means of a heterogeneity chi-square test. That is, the total chi-square was partitioned into two components, that due to regular deviation from expectation throughout the year (pooled chi-square, already discussed above), and that due to monthly variation from expectation (heterogeneity chi-square). Data for the months of September and October were pooled for the test to keep all expected numbers of observations over 5. The data and calculations are presented in table 8. Total chi-square was 624.0, pooled chi-square was 469.9 (75.3%), and heterogeneity chi-square was 154.1 (24.7%). All chi-squares are significant at p<.001. Most of the deviation from expectation is due to a uniform tendency to favor certain habitats and avoid others throughout the year (discussed above). However, there is significant variation in habitat utilization from month to month, though accounting for only about 1/4th of the total deviation. While it is somewhat difficult to characterize the seasonal variation, two things do stand out. During August, turtles appear to move deeper into the forest, and to favor forest-field ecotones less. Possibly, this is the result of a tendency to avoid the high temperatures associated with this month. The other point is that turtles actually slightly favor forest areas in September and October. No doubt, this is because they are preparing to hibernate in such areas. This pattern is consistent with that found by Reagan (1974).

As can be seen from figure 31c, showing all the observation points, box turtles never range very far into wooded areas, at least on the field station. Nevertheless, they appear capable of living in forest, for the turtles in Stickel's (1950) study did so. Unlike the field station, Stickel's study area did not have fields and brushy areas, but apparently consisted quite uniformly of forest. However, the forest in Stickel's study area was substantially different from that of the field station, for it was located on a river flood plain, in contrast to the dry oak forest of the field station.

In summary, then, box turtles on the field station prefered ecotonal areas between wood and field, and forest and brush, avoided deeper forest habitats, areas containing mostly grasses, and forest-grass ecotones, and were neutral to areas of brush and field. There was some seasonal variation in use, with forest being less avoided in August than in other months.

Factors Affecting Daily Movement

For the purposes of this section, 489 pairs of points were extracted from the data, each pair representing successive locations on the same animal taken 24 hours apart, plus or minus 1 hour. These data were examined with regard to the question of what factors might determine the distance moved by a box turtle in 1 day. It should be noted that the actual distance moved by the animal could not be determined, since box turtles do not move in straight lines. Nevertheless, the straight line distance between two successive points should, on the average increase with increasing distance moved. The average 24-hour distance moved by all turtles in the course of this study was 31.1 meters (s.e.=1.79, n=486, range=0-235.1). Thus, there was a substantial variation in the daily movements. A number of factors were looked at with regard to their possible effect on the distance moved. These include, temperatures at several times of the day, precipitation, and month of the year.

Temperatures were automatically recorded on the field station by a Honeywell Electronik chart recorder with thermocouple sensing elements. The sensing element was housed in a shaded, ventilated cage, about 1.5 meters above the ground. Temperature readings were taken at four hour intervals, beginning at 0:00 hours E.S.T. during each 24 hour period. Product-moment correlation coefficients were calculated between the distance moved and the temperature at each time of day. The results were 0:00=.202, 4:00=.245, 8:00=.243, 12:00=.224, 16:00=.169 20:00=.076. All correlations except that for 20:00 hrs. are significant at $p<.01$. Daily precipitation records taken at the field station were also compared with the distances moved. Correlation was .196 ($p<.01$). Thus rainfall and temperature at all times of the day except possibly 20:00 seem to affect box turtle activity. It is especially interesting that temperatures at times of the day when box turtles are not active seem nevertheless to have an effect on movement. The question arises of whether all of these factors really make independent contributions to determining the distance box turtles move, or whether some of the factors are correleated with distance moved only because they are correlated with other factors which in turn are correlated with distance. This was examined by running the data through the stepwise multiple regression program of the BMD Biomedical Computer Programs package

(Dixon, 1964). This program calculates the regression between distance moved, and the factor most highly correlated with distance. It then examines the other factors to determine whether a multiple regression including another factor would explain any more of the variance in distance. If so, it is added to the regression. This process is continued with all the factors, until no significant (p=.05) improvement can be obtained by adding additional factors. The program was first run with all factors "free", that is permitted to come into the multiple regression equation on their own merits. In this case, the following factors came in order: temperature at 4:00, precipitation, temperature at 12:00, and temperature at 20:00. The regression coefficient for temperature at 20:00 was negative; all others were positive. The spacing of significant temperatures at 8 hour intervals suggests the interpretation that temperatures at all times of the day are independently important in determining box turtle movements, but that a sampling interval of four hours adds little information beyond that provided by sampling temperature every 8 hours. This, together with the fact that temperature at 8:00 is nearly as highly correlated with distance as temperature at 4:00 leads to the prediction that the set of temperatures taken at 0:00, 8:00, and 16:00 should do nearly as well at predicting distance as the set of temperature taken at 4:00, 12:00 and 20:00. This can be tested by forcing the first set of factors into the regression equation. The results are rather surprising. After temperature at the three forced times, plus precipitation enter the regression equation, temperatures at the alternate three times proceed to enter in the order 20:00, 12:00 and 4:00. Furthermore, in the final equation, temperatures at 0:00, 8:00, and 16:00 are without significance. They remain in the equation only because they have been forced into it. Thus, while temperatures at 8:00 hour intervals will explain as much of box turtle movement as can be explained by temperature, not just any set of 3 temperatures will do. Certain times seem more critical than others. Why this should be true is not immediately obvious. It is also interesting that the regression coefficient for 20:00, and also 0:00 when it is forced into the equation, is negative. That is, everything else being equal, cooler night-time temperatures result in greater movement the following day. It is necessary to be somewhat careful about what is meant here. Night temperatures are positively correlated with day temperatures, which in turn are positively correlated with distance, resulting in a net positive correlation of night temperatures and distance. But when the independent effects of night temperatures are looked at, the correlation is negative. The independent correlation of night temperatures, taken at a time when turtles are not active, with movement indicates a "memory" effect--that is box turtles are not just responding to factors that immediately impinge on them, but are effected by their "memory" (not necessarily neurological), of past conditions. One is tempted to speculate that high night temperatures serve as a warning to box turtles of possible excessive day temperatures to follow, resulting in their keeping near shelter (they nearly always settle for the night in the forest side of the ecotones which are their favorite habitat). Such a retrospective speculation, when untestable, obviously has to be taken cautiously. I have no ready explanation for why the temperatures at 4:00, 12:00 and 20:00 are better predictors of box turtle movement than the temperatures at 0:00, 8:00, and 16:00. The high correlation with temperature at 4:00 makes some kind of sense--box turtles are most active shortly after dawn. My impression from field work, however, is that box turtles are more active in the late afternoon and early evening than they are in the early afternoon, which should make temperature at 16:00 a better predictor than temperature at 12:00. Such does not seem to be the case. In fact, one might expect a negative correlation with temperature at 12:00, if cooler late morning and early afternoon temperaures permitted box turtles to remain active longer. As for why 20:00 temperatures should be more important than 0:00 temperatures, the following idea is offered for what it is worth. Night temperatures, whatever the reaon, do provide box turtles with information on how far to move the next day. 20:00 is close to the time when turtles are settling in for the evening. Perhaps they are more responsive to whatever information it is that night temperatures provide at this time than a they are later, when they are, presumably, asleep. In any case, the fact that precipitation is correlated with distance independently of temperature is not surprising--this agrees with the field observation that box turtles are very active during periods of rain. Thus, the major item of interest that seems to arise from this analysis of the relationship between temperature and precipitation and distance moved is the observation that temperature at night and around noon--two periods of comparative quiescence for box turtles, are important in determining daily movements.

The relationship between time of year and daily movements was examined by running an analysis of variance on distances moved during each month from April through October. The result was significant heterogeneity between months (F=2.26, numerator d.f.=6, denominator d.f.=480, p<.05). Table 9 presents the monthly means, and their associated statistics. In general, turtles move less early and late in the season than they do in the middle of the season, not an astonishing discovery. This is in agreement with the seasonal changes in size of home ranges which are smaller earlier and later in the year, though difference was non-significant (see HOME RANGE). Cahn (1937) believed that turtles become quite inactive during the hottest months of the season, even aestivating. This was in

Illinois. I can find no evidence that Long Island turtles show decreased activity in July and August.

HATCHLING TURTLES

Three nests, designated A, B, and C, were surrounded by 1/2" mesh hardware cloth enclosures prior to emergence of the young so that the young could be collected. A total of 13 hatchlings were obtained from these three nests, equipped with radio transmitters, released, and tracked in order to obtain information on the initial movements of young turtles. All three clutches were laid in 1969. Nest A produced 5 young in the fall of 1969. Date of emergence was October 3. Two additional young were found in the enclosure surrounding the nest the following spring. The first of these (A6) was discovered on May 11. The second was discovered on May 22. These animals presumably overwintered in the nest, since the area within those enclosures was searched carefully several times prior to the appearance of the young. Nest B produced 5 young in the spring of 1970. Date of emergence was April 29. It is known that these young hatched the previous fall, because the nest contained young when it was excavated on November 12, 1969. They overwinterd without emerging, tolerating a minimum temperature of -1 degrees centigrade. Nest C produced a single offspring, which overwintered in the nest, and appeared above the ground for the first time between May 15 and May 18.

Of the five turtles that emerged from nest A in the fall of 1969, two survived to hibernate. Two of the others are definitely known to have been eaten, since the remains of their transmitters were found with toothmarks on them. The final animal was lost after five days of tracking. It is not known whether transmitter failure or mortality was involved. The two that were eaten survived 12 days and 15 days. The two that hibernated did so between October 21 and October 24, after 17-20 days of activity. One of these animals hibernated in the field without entering the forest, which is the usual hibernation site of both adult and young animals. It was the only case in this study in which an animal did not hibernate in forest. Despite the lower ground temperatures expected in such a situation, it survived. It accomplished this by digging into the ground to a depth of about 12 cm. The transmitter batteries of both animals were allowed to run down over the winter. When the two animals were excavated on April 4, 1970 to renew their batteries, it was discovered that one of the animals had been consumed. The last animal resumed activity on May 4, 1970. It was eaten on May 21, 1970, after a total, for both seasons of 34-37 days of activity.

Of the eight turtles that emerged from the nest for the first time in spring of 1970, three (#'s B1, B2, and B3) were lost within the first five days after emergence. Two of these were consumed, the fate of the third is unknown. A fourth animal was lost to unknown causes the eighth day after emergence. The four remaining turtles survived to hibernate that fall. Their dates of last movement are Ocober 11-12, October 15-18, October 15-18, and October 12-15. One of these animals (C1) froze to death that winter. It was an exceptionally small animal (10.8 grams at hibernation, compared to an average weight of 17.9, range 15.3-22.5 for the other three); probably it was not healthy and lacked the strength to dig in far enough to avoid freezing. This is also the animal that came from a nest which produced only one young, so the entire brood may have been a poor one. Of the three remaining animals, one could not be located when its site was excavated the following spring. No remains of its transmitter were found, but since the excavation was carried out well before the period of normal resumption of activity (April 7), the only likely assumption is that the animal was eaten. A second animal (#B4) hibernated in the fall in a dry kettle depression. This filled in with water during the winter. Attempts to locate the animal under the water failed, and by the time the kettle depression dried out again in June, it was past the time of normal resumption of activity. It is therefore not known whether the animal survived its immersion. The final animal (#A7) resumed activity June 3-4, 1971. It was tracked throughout the summer of 1971, and hibernated between October 25 and October 29. It became active again between May 8 and May 13, 1972, was tracked for that summer, and hibernated between October 4 and October 8, 1972. When the hibernation site was excavated in spring of 1973 to replace batteries, the animal could not be located. Possibly it was consumed. Thus, of the thirteen animals tracked, 6 are definitely known to have been eaten, one froze to death, two others were probably eaten, and the fate of the remaining four is unknown.

One of the main purposes of tracking young turtles was to determine if there is a period of dispersal shortly after hatching. This appears not to be the case. Figures 30 and 31 show the movements of the 9 turtles that managed to travel at least 5 meters from the nest before being lost or consumed. For reference to the main map, the area shown centers on field AP-5 (figure 1a). Of the four animals that were tracked during their first complete summer of activity, none traveled any further than the areas of forest that surround the field in which they were hatched (see A6, figure 30d; A7, figure 31a; B4, figure 31b; and C1, figure 31b). The average distance between the first winter's hibernation site and the nesting site was only 59.0 meters (range 38-87 meters). Furthermore, the data on animal A7 (figure 31a), which was tracked for an additional two seasons, suggests that there is no marked tendency to disperse from the nesting site in subsequent years either. Animal #A7 is the hatchling that was used in a homing experiment mentioned in the chapter on homing. This was done during its second summer, when it was displaced 180 meters northeast of its known lifetime home range, to the edge of field AP-6 (figure 1a). It was left here for about one month, during which time it wandered around within a 30 meter radius of the release site. Following this, it was returned to its capture site on its home range. The final hibernation site of this animal, following its third full summer of activity, is only 63 meters from the nesting site. Another indication of the lack of dispersal on the part of the young can be gathered from the average distances of the young from the nesting sites after various times following emergence. The average distance 5 days after emergence was 8.3 meters (n=10), 10 days after emergence it was 15.2 meters (n=8), 20 days after emergence, it was 18.0 meters (n=6), and 40 days after emergence, it was 21.8 meters (n=4).

This failure to show any dispersal is somewhat surprising. In view of the stability of adult turtle home ranges, the longevity of box turtles, and their freedom from predation, it appears unlikely that any regulation of box turtle populations takes place at the adult level. Most population regulation is probably at the level of the juveniles, and one might have expected a period of dispersal of the young. If population regulation does take place at this level however, it must be through mortality rather than dispersal. It is, of course, possible that box turtle home ranges do shift gradually over long periods of time. but it is impossible to find any direct evidence of this in the home range data of either adults or young turtles. My speculation that exceptionally large seasonal shifts in home range such as that exhibited by turtle #82 (see Home Range) are essentially recapitulations of lifetime changes in home range must remain based on circumstantial evidence. Certainly turtle #A7 showed no tendency toward a shifting home range during the period it was tracked. If box turtles do shift home ranges during their lifespan, it must only be in response to changes in habitats due to succession or disturbance. It appears that box turtles are content to stay put if conditions allow them to.

The habitat preference of young box turtles does not appear to differ greatly from that of adults. Turtle A7, tracked from May 22, 1970, to Oct. 8, 1972, shows the pattern most clearly. Like the adults, its home range is basically ecotonal. The animal follows closely the border of field AP-5, sometimes being found in the field itself, sometimes in the adjacent woods. Animals A6 and B4 support this conclusion. A6, after spending some time in field AP-5, eventually occupied the same border area as A7. B4 migrated quickly through forest, and eventually took up residence in a dry vernal pond, the bottom of which was grassy. The entire area of the pond bottom received periodic shade from the adjacent woods. This area was essentially a field-forest ecotone. Turtle C1 also headed toward the woods bordering field AP-5, though it reached the woods only shortly before hibernating. Thus this animal spent most of its life in the field. As pointed out, however, it was a weak animal, which may account for its slowness in reaching forest-field boundary. Since it froze to death that winter, it is impossible to say whether it would have continued to occupy the boundary area having once achieved it, though on the basis of the behavior of other hatchlings, it is a reasonable guess that it would have. The other animals were tracked for too short a time to establish a definite habitat preference. So, though hatchlings move less than adult turtles, and have smaller ranges, their habitat requirements are similar. Initial dispersal, at least, appears to be confined to that amount of movement necessary to achieve a suitable ecotonal habitat.

Turtles tracked in the course of this study were weighed periodically. Figure 18b plots weight against time of activity. The 0 point is the time of emergence from the nest. Only time periods during which the animal was actually active are counted. That is, periods of hibernation, during which growth obviously stopped, were not counted. Though the scatter of points is quite large, there is a suggestion of exponential growth--a not unexpected result. During approximately the first 20 days of active life, there was very little growth. Some animals actually lost small amounts of weight. Growth picked up after that, and appeared to become increasingly rapid. An attempt was also made to record body temperature, but this proved to be impractical with such small animals, and the effort was abandoned rather than risk injuring them, with subsequent possible disturbances in their movements.

SUMMARY AND CONCLUSIONS

To borrow from current jargon, box turtles can be considered a good example of a "K-selected" species. Slow-growing, long-lived, and modest in their reproductive efforts, they concentrate on being physiologically and structurally rugged. As vertebrates, box turtles have followed an evolutionary "strategy" (or "pathway", to use a less teleologic term) comparable to trees among angiosperms, according to which analogy, songbirds and small mammals would be weeds. For every species, evolution must compromise between using food resources for homeostasis in the adult, or for high reproductive rate. Box turtles seem to have chosen the former emphasis. It takes some 15 to 20 years to produce a fully mature box turtle; a small mammal matures in a matter of weeks. The difference is spectacular. The adult turtle is an unrewarding object for predators due to its heavy bone structure and musky odor, and physiologically is nearly indestructible. Box turtles operate over a wide range of temperature, can survive long periods without food or water, and have a digestive system capable of handling an extremely varied diet. Perhaps their well-developed homing ability should not be surprising. Natural selection seems to have spared little in equiping the adult animal for survival. Young animals are more vulnerable. Perhaps that is why they do not disperse from the nesting site initially. It seems likely that some individuals at least do eventually disperse, but such dispersal may be saved for an older age when the animals are less vulnerable. Young turtles are highly secretive in habit. Following emergence from the nest, they seek the cover of the forest edge, and remain out of sight. Humans rarely encounter young turtles.

It is somewhat surprising to me that male box turtle ranges are smaller than those of females. One might suppose that males, not having to produce eggs, might expend the energy wandering in search of females. Their failure to do so may be another expression of the strategy of maintaining the homeostasis of the adult, rather than expending energy on reproduction. The implication, of course, is that higher reproductive effort, at the expense of adult survival, would be unadaptive. Since little is known about what limits the population size of turtles, it is hard to guess at what factors might militate against a higher reproductive effort. Although I have shown that hatchling mortality is high, it does not follow that a greater reproductive effort would be worthwhile. Annual reproductive effort is low, but box turtles are so long-lived that the lifetime fecundity of an individual may be quite high. For example, a female who was reproductively active for 50 years, laying an average of five eggs a year, would produce 250 eggs over her lifespan, of which only two would have to give rise to adults to replace the population.

Box turtles have also avoided ecological specialization. On the field station, they are found in habitats with high diversity, offering great variety in plant physiognomy and species. Moisture may be one of their more important limiting factors. Stickel (1950) found turtles to be most abundant in the river flood plain of her study area, and less abundant on higher ground. On the Kalbfleisch Station, turtles are rarely encountered in the drier oak forested areas. Given an adequate water supply, however, they seem to be capable of utilizing nearly any food resource.

The study of box turtles should contribute to our understanding of evolutionary strategies. Certainly, the species represents an example of an unusual strategy. A knowledge of the population regulating factors for box turtles would undoubtedly be of help in understanding this strategy. It is possible that knowing more about the life-time home ranges of box turtles would contribute to such knowledge. Improvements in equipment, are making it feasible to follow turtles for years, starting with very young animals, perhaps hatchlings. Such a project would obviously be fairly costly, but could be undertaken by an institution specializing in radiotelemetric work. Reliability could be greatly enhanced by equiping animals with two transmitters--a reasonable prospect with lighter weight equipment. Automatic tracking would obviously be logical. As relatively slow-moving animals, with limited home ranges, and the capacity to carry a fair amount of equipment, box turtles are ideal subjects for studying the utilization of home range.

APPENDIX

1. Area of a polygon:

$$A=\frac{1}{2}\sum_{j=1}^{m}(X_iY_{i+1}-X_i\,Y_{i+1})$$

where (X_i, Y_i) is the ith ordered observation point, and:

$$(X_{n+1}, Y_{n+1})=(X_1, Y_1)$$

from Jennrich and Turner (1969)

2. Equation of the $(1-\alpha)100\%$ ellipse (modified from Sokal and Rohlf (1969)):

$$\bar{X}=\frac{\sum_{i=1}^{m}X_i}{n} \qquad \bar{Y}=\frac{\sum_{i=1}^{m}Y_i}{n}$$

$$s_x^2=\frac{\sum_{i=1}^{m}X_i^2-(\sum_{i=1}^{m}X_i)^2/n}{n-1}$$

$$s_y^2=\frac{\sum_{i=1}^{m}Y_i^2-(\sum_{i=1}^{m}Y_i)^2/n}{n-1}$$

$$s_{xy}=\frac{\sum_{i=1}^{m}X_iY_i-(\sum_{i=1}^{m}X_i)(\sum_{i=1}^{m}Y_i)/n}{n-1}$$

$$D=\sqrt{(s_x^2+s_y^2)^2-4(s_x^2s_y^2-s_{xy}^2)}$$

$$\lambda_1=(s_x^2+s_y^2+D)/2$$

$$\lambda_2=(s_x^2+s_y^2-D)/2$$

$$C_\alpha=(\lambda_1\,\lambda_2(n-1)2\cdot F_{\alpha[2,\infty]})/(n-2)$$

and the equation of the ellipse is:

$$C_\alpha=s_y^2(Y-\bar{Y})^2-2s_{xy}(X-\bar{X})(Y-\bar{Y})+s_x^2(X-\bar{X})^2$$

3. Effective Home Range:

μ =density of points

The probability that a circle of radius r will contain one point is:

$$F(\mu) = \pi r^2 \mu e^{-\pi r^2 \mu}$$

from the Poisson distribution.

Taking r as the distance between a point and its nearest neighbor, we require μ for which $F(\mu)$ is maximum:

$$\frac{F(\mu)}{d\mu} = \frac{1 - \pi r^2 \mu}{d\mu}$$

$$0 = 1 - \pi r^2 \mu$$

$$\mu = \frac{1}{\pi r^2}$$

Let: $E = \frac{n}{\mu} = \pi r^2$

Then: $\bar{E} = \frac{n \sum_{i=1}^{n} \pi r_i^2}{n-1}$ =effective home range

since n points yield n-1 independent r's.

4. Shannon-Weaver Formula:

$$H = \sum P_i \ln P_i$$

where P_i=proportion of the whole represented by the ith habitat.

5. Confidence region for the center of gravity of a bivariate normal distribution: Same as 2, except:

$$C_\alpha = (\lambda_1 \lambda_2 (n-1) 2 \cdot F_{\alpha[2,n-2]})/((n-2)n)$$

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TABLE 1: Dates of earliest and last movements.

No.	Earliest Movement	Last Movement
34		October 5-10, 1970
47		November 11-18, 1969
	April 8-9, 1970	November 8-14, 1970
	April 10-16, 1971	November 15-22, 1971
	April 23-29, 1972	November 11-15, 1972
59		November 3, 1969
	April 27-29, 1970	October 21, 1970
	May 3-5, 1971	November 10-15, 1971
	April 16-23, 1972	October 14, 1972
92		November 10-15, 1971
106		September 29, 1971
124		October 21-25, 1972
132		November 4-10, 1968
		October 27-November 2, 1969
	April 23-27, 1970	
154		October 15-20, 1969
	April 23-27, 1970	November 2, 1970
155		November 10-15, 1971
	April 30-May 2, 1972	
170	April 16-20, 1971	

TABLE 2: Nesting data. No.=number of animal. Time Found=time nest was discovered. If two times are given, the animal had not started when checked at the first time, but was nesting by the second time. Done=time of completion of nest. State=state of completion of nest when found. S?=yes if nest was successfully covered, no otherwise. Date Emerged=date of emergence of young.

No.	Date	Time Found	Done	State	S?	Date Emerged
18	June 17, 1970	19:25	23:30	starting	yes	no young
	June 21, 1971	18:55	?	1/2 dug	yes	Sept. 28-30, 1971
30 (C)	June 23, 1969	18:15	19:45	3/4 dug	yes	May 15-18, 1970
47	June 23, 1969	18:35	?	starting	yes	October 7-10, 1969
	June 11, 1970	19:30	0:15	starting	yes	eaten June 16, 1970
	June 18, 1971	20:00	---	3/4 dug	no	---
	June 19, 1971	21:15	22:30	1/2 dug	yes	Sept. 25-28, 1971
76	June 20, 1971	18:45	23:45	1/4 dug	yes	Oct. 1-4, 1971
82	June 26, 1969	19:30	---	1/2 dug	no	---
(A)	June 26, 1969	23:45	0:40	covering	yes	Oct. 3, 1969
	June 28, 1970	19:00-10:15	0:30	1/2 dug	yes	Oct. 8-10, 1970
92	June 27, 1971	19:00	?	starting	yes	no young
147 (B)	June 30, 1969	18:00-19:30	21:40	1/2 dug	yes	April 29. 1970
	July 4, 1970	20:30	?	3/4 dug	yes	Oct. 4-5, 1970
	July 1, 1972	19:30	?	1/4 dug	yes	no young
155	July 5, 1971	19:00	---	1/2 dug	no	---
167	June 10,1970	17:50-19:15	---	starting	no	---
	June 11, 1970	16:00-20:15	---	starting	no	---
	June 12, 1970	18:10	0:10	starting	yes	Sept 20, 1970
M14	June 24, 1969	19:30	---	starting	no	---
	June 25, 1969	19:05	---	starting	no	eggs defective

TABLE 3: Goodness of fit of *T. carolina* data to a bivariate normal distribution. o1-10 give the observed number of points in successive 10% elipses. e gives the expected number of points in each elipse. Chi-sq. lists the value of chi-square for each animal. Total, pooled and heterogeneity chi-squares are given at the bottom.

No.	e	o1	o2	o3	o4	o5	o6	o7	o8	o9	o10	Chi-sq.
106	13.2	32	14	8	8	7	3	16	21	9	14	48.3 ***
92	8.4	11	5	10	7	12	13	5	7	3	11	12.7 *
59	17.4	15	22	12	17	18	17	19	14	21	19	5.0 n.s.
47	23.3	23	38	30	21	30	13	16	20	19	23	21.5 ***
34	11.1	15	30	11	6	8	9	4	15	2	11	50.5 ***
18	10.2	10	20	5	2	5	23	12	7	9	9	39.0 ***
147	8.1	5	13	16	6	5	4	8	11	10	3	20.4 ***
76	8.5	2	3	9	7	10	13	19	12	6	4	29.0 ***
155	8.4	15	13	5	5	7	4	8	8	12	7	14.8 **
170	12.4	10	8	12	22	8	14	11	14	12	13	11.6 *
154	10.7	15	7	12	6	9	6	20	10	11	11	15.7 **
132	12.9	15	7	8	12	22	17	13	17	10	8	16.5 **
124	10.7	2	5	9	8	28	20	7	8	15	5	53.8 ***
122	5.6	2	8	1	4	9	5	16	1	5	5	32.9 ***
237	5.5	2	3	6	4	6	8	6	13	5	2	17.5 **
M12	6.5	4	12	4	8	15	3	1	3	4	11	30.5 ***
Totals	172.9	178	208	158	142	199	172	181	181	153	156	

Total Chi Sq.=419.7
Pooled Chi Sq.= 22.4 (5.3%)
Heterogeneity Chi Sq.=397.3 (94.7%)

n.s.=p>.05
*=.025>p>.01
**=.01>p>.001
***=p<.001

TABLE 4: Home ranges, and related factors. (No.=number of individual, n=number of observation points, t=time animal was tracked in days, Sub=subjective utilized home range, 95%=95% bivariate normal home range, Min=minimum polygon home range, Con= convex polygon home range, Wt.=weight in grams, Density=population density in animal's home range, H=Shannon-Weaver index for habitat diversity). Home ranges are in hectares.

No.	$\bar{n}$	t	Sub	95%	Min	Con	Sex	Wt.	Density	H
18	102	192	2.6	13.5	6.3	9.9	F	640.	39.	1.08
34	111	166	2.0	10.0	3.7	6.8	M	545.	os	.95
47	233	480	3.1	6.2	1.6	5.8	F	553.	48.	1.02
59	174	398	2.7	6.4	1.9	4.9	M	561.	59.	.70
70	21	50	1.9	8.1	3.3	4.2	F	480.	52.	.98
72	27	59	1.6	19.2	4.1	6.2	F	475.	51.	.92
76	85	106	3.0	13.6	4.7	7.1	F	504.	51.	.78
91	35	54	1.8	6.1	1.8	2.6	M	704.	33.	.80
92	84	133	1.9	2.8	1.2	3.0	F	542.	60.	.77
104	20	53	.6	7.1	.6	2.8	M	342.	41.	1.15
106	132	189	1.7	2.3	.5	2.0	M	612.	40.	.72
122	56	77	1.0	1.7	.4	.8	M	510.	81.	1.08
124	107	224	2.0	3.3	.9	2.4	M	512.	67.	.64
132	129	257	1.5	2.1	.7	1.7	F	859.	77.	1.16
147	81	157	2.2	11.0	3.6	9.4	F	601.	51.	.56
154	107	218	1.3	1.8	.5	1.4	F	452.	34.	.56
155	84	96	1.6	4.4	.8	2.9	F	375.	40.	1.06
161	36	51	.8	14.8	5.4	6.2	F	378.	os	.53
167	40	73	1.1	1.4	.4	.7	M	440.	74.	.84
170	124	162	2.2	6.2	2.0	3.6	M	498.	52.	.92
237	55	68	1.6	6.0	1.5	3.4	F	501.	-	.56
M12	65	70	1.0	2.1	.5	1.6	M	526.	54.	1.30
M14	27	57	1.4	10.2	2.3	3.7	F	530.	49.	.80
Mean			1.76	6.95	2.12	4.05				
s.e.			.14	1.02	.37	.54				

TABLE 5: Areas of monthly 95% bivariate normal home ranges in hectares.

No.	May	June	July	Aug.	Sept.	Oct.
2		.4				
18		4.6	7.3	8.97		
30		6.20				
34		1.9	4.3	1.2	3.3	
47	2.5	7.0	1.2	4.2	4.5	.7
59	3.2	8.2	4.4	3.5	5.6	3.4
70		3.2				2.5
72		3.9	8.3			
76		3.9	1.2	1.5	1.5	
82		5.2	8.0			
91			5.4			
92		2.1	3.4	1.8		
104		1.9				
106	2.9	2.4	.49	1.9	1.2	
122	.7	1.2	.4			
124			2.3	2.5	2.7	4.2
132	.6	.9	1.6	1.8	2.30	
147		3.9	7.7	5.0	1.9	
154	.9	1.2	1.4	.5	2.2	.4
155		4.0	2.6	1.8	.8	
161		8.6				
167		.8	2.2			
170	7.2	4.0	1.6			
237			1.8	9.4	3.1	
M12		2.2	.9			
M14			3.3		2.2	
mean	2.57	3.53	3.32	3.36	2.60	2.22

Anova Table

	SS	DF	MS	F
Among	14.657	5	2.932	.52 (P>.05)
Within	414.710	74	5.604	

TABLE 6: Deviations in meters of field station records from 95% bivariate normal home ranges. No.=number of animal, Max Dev=maximum distance a field station record lies outside of the 95% bivariate normal home range, Date=date of field station record with maximum deviation, Records=number of field station records on animal, Earliest=earliest capture on animal.

No.	Max Dev	Date	Records	Earliest
18	0	-	6	July, 1960
34	40	June, 1961	6	June, 1961
47	120	June, 1962	4	June, 1962
59	20	July, 1963	3	July, 1963
72	0	-	3	August, 1963
76	0	-	7	August, 1963
91	0	-	10	July, 1964
92	0	-	3	July, 1964
104	20	July, 1972	5	August, 1964
106	10	June, 1967	4	August, 1964
122	15	July, 1965	1	July, 1965
124	0	-	3	August, 1965
132	0	-	3	June, 1966
147	0	-	8	August, 1966
154	80	June, 1967	3	June, 1967
155	20	June, 1971	5	June, 1967
161	30	July, 1972	3	June, 1967
167	0	June, 1967	1	June, 1967
170	0	-	4	July, 1967

TABLE 7: Results of homing experiments. No.=number of animal; Exp.=number of experiment; Dis.=distance in meters of release site from nearest edge of 95% bivariate normal home range; 24?=y if animal was held for 24 hrs. before release, n if not; S?=y if spun during transport as well as before and after, n if not; H?=y if animal returned to within the boundary of its 95% bivariate normal home range, n if not; D=time animal spent within 50 meters of release site; T=time required to return to within the boundary of the 95% bivariate normal home range, not including D. (*=animal overwintered 250 meters from edge of 95% bivariate normal home range, completed journey in spring.) Number 230 is 10 years old; number M01 is 9 years old.

No.	Exp.	Date	Dis.	24?	S?	H?	D	T
18	1	July 10, 1970	310	n	n	y	0	3
	2	July 22, 1970	315	n	n	y	0	2
	3	August 25, 1970	570	n	y	y	2	6
34	1	July 30,1970	425	n	y	y	1	11
	2	August 15, 1970	410	n	y	y	0	5
	3	August 27, 1970	600	n	y	y	4	26
47	1	July 22, 1970	400	n	n	y	7	23
	2	August 22, 1970	950	n	y	y	0	27
59	1	August 1, 1970	340	n	y	y	10	2
	2	August 22, 1970	780	n	y	y	0	9
	3	August 22, 1971	760	y	y	y	0	3
92	1	August 21, 1972	330	y	y	y	0	4
	2	August 26, 1972	380	y	y	y	2	7
	3	September 2, 1972	380	y	y	y	4	10
	1	July 15, 1971	1150	y	y	y	0	14
	2	August 1, 1971	410	y	y	y	2	5
	3	September 13, 1971	360	y	y	y	6	18
124	1	July 1, 1970	325	n	n	y	1	8
	2	July 23, 1970	380	n	n	y	2	29
132	1	July 4, 1969	380	n	n	y	0	3
	2	July 16, 1970	360	n	n	y	2	4
	3	August 4,1970	330	n	y	y	1	11
	4	September 3, 1970	700	n	y	y	14	*
147	1	July 5,1972	330	y	y	y	2	14
154	1	July 19,1970	350	n	n	y	6	43
	2	September 1, 1970	450	n	y	y	0	12
170	1	August 17, 1970	330	y	y	y	2	12
	2	Setember 11,1970	870	n	y	y	4	14
161	1	July 9, 1970	420	n	n	y	0	10
167	1	July 2, 1970	470	n	n	y	0	2
	2	July 7, 1970	260	n	n	y	0	1
	3	August 9, 1970	630	n	y	y	1	9
237	1	August 3,1971	530	y	y	y	0	6
	2	August 17, 1971	880	y	y	y	1	19
m12	1	August 2, 1971	550	y	y	n	-	-
230	1	July 5, 1971	460	n	y	y	4	53
	2	September 12, 1971	270	n	y	y	3	13
M01	1	July 5, 1970	500	n	n	y	3	10
	2	July 25, 1970	260	n	n	y	2	3

TABLE 8: Number of observation points, and expected number of observation points based on relative area in seven habitats. FG=ecotone between forest and grass, FF=ecotone between forest and field, FB=ecotone between forest and brush, G=grass, FD=field, B=brush, FT=forest.

Month		G	FD	B	FT	FG	FF	FB	Chi-sq
May	e	6	7	7	75	21	70	30	120.9
	o	0	4	13	23	2	125	49	
June	e	15	19	18	193	54	178	76	247.4
	o	4	35	40	48	30	269	126	
July	e	12	15	15	158	44	146	62	160.3
	o	0	7	7	69	32	225	114	
August	e	8	10	10	106	29	98	42	68.1
	o	0	2	8	93	3	123	75	
Sept-Oct	e	6	8	7	78	22	72	30	27.3
	o	0	2	9	84	7	92	29	
Pooled data:									
	e	47	59	58	610	170	563	240	
	o	4	50	77	317	74	834	393	

Total Chi-sq.=624.0
Pooled Chi-sq.=469.9(75.3%)
Heterogeneity Chi-sq.=154.1(24.7%)

TABLE 9: Distances moved in 24 hours by months.

Month	Mean	s.e.	n
April	6.0	3.44	4
May	12.2	4.71	24
June	30.9	2.37	221
July	31.9	3.77	120
August	34.2	4.49	98
September	47.4	13.93	18
October	6.0	6.01	4

Anova Table

	SS	DF	MS	F	
Among	20854.1	6	3475.7	2.26	(.05>p>.025)
within	737451.6	480	1536.4		

TABLE 10: Correlations among methods of determining home range. S=subjective utilized, 95=95% bivariate normal home range, Min=minimum polygon, Con=convex polygon. A gives correlations for 23 animals whose home ranges were based on at least 20 points, B gives correlations for 18 animals whose home ranges were based on at least 40 points.

A

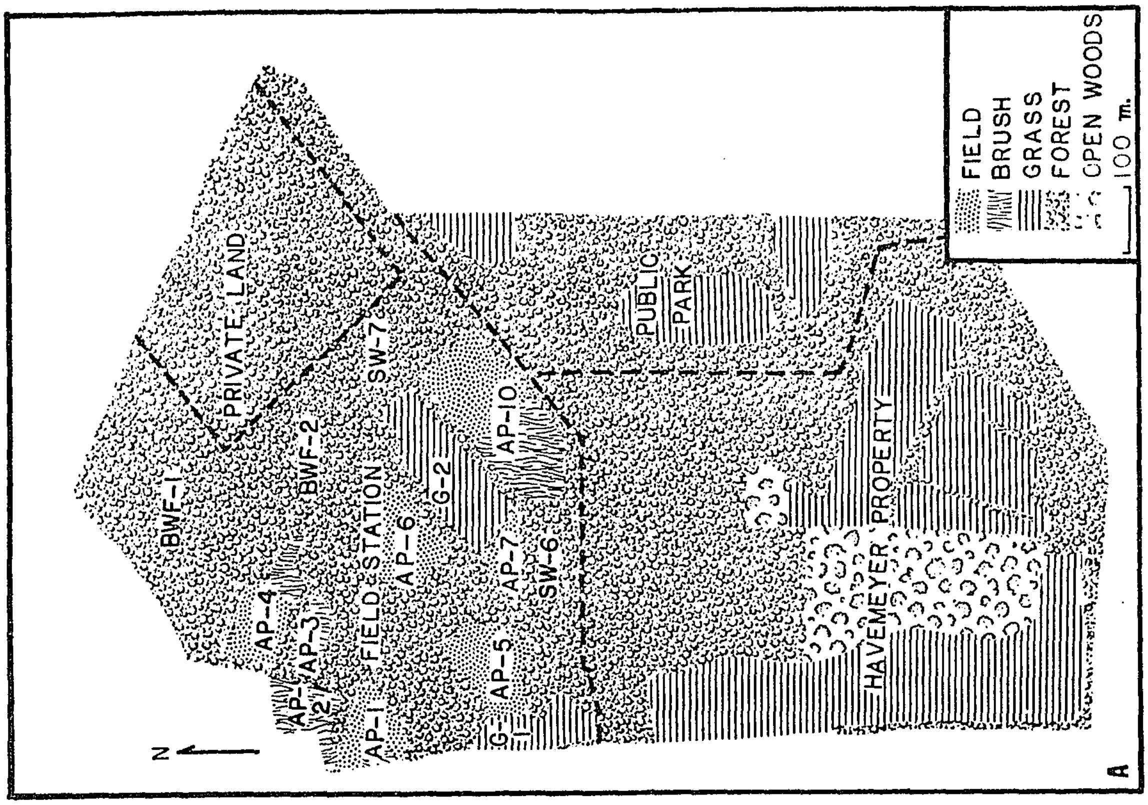
	95	Min	Con
S	.26	.40	.59
95		.89	.81
Min			.89

B

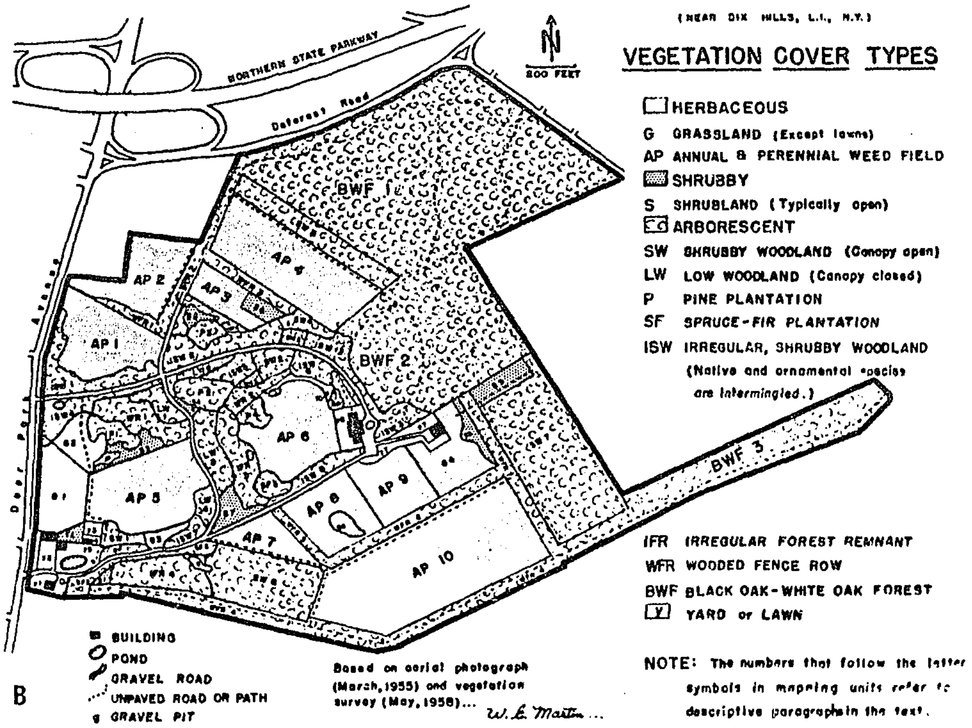
	95	Min	Con
S	.73	.66	.76
95		.97	.95
Min			.93

Figure 1a: Map of study area, showing main habitats distinguished in this study.

Figure 1b: Map of Kalbfleisch Field Research Station, showing plant physiognomy from Martin (1958).



AMERICAN MUSEUM OF NATURAL HISTORY, FIELD STATION & WILDLIFE SANCTUARY:

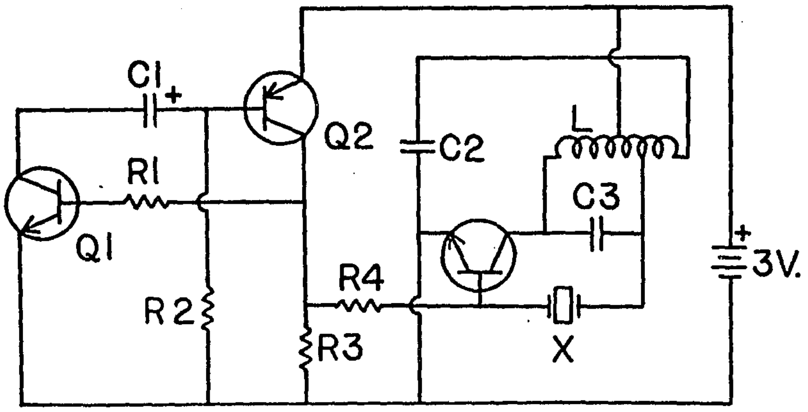


Based on aerial photograph (March, 1955) and vegetation survey (May, 1958)... W. E. Martin...

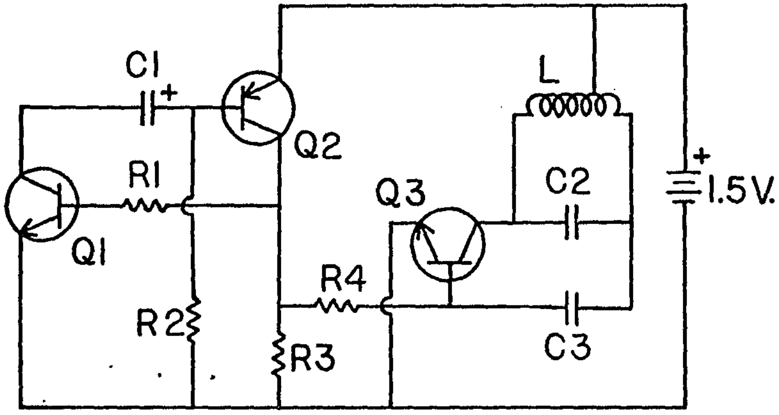
NOTE: The numbers that follow the letter symbols in mapping units refer to descriptive paragraphs in the text.

Figure 2a: Circuit diagram of large transmitter. C1=1.0mf (Sprague 162D); C2=5pf; C3=39-56pf to resonate with L1 at 27mhz.; L1 depends on size of animal's shell; Q1=General Electric D26C-1; Q2=General Electric D30A-1; Q3=General Electric D26G-1; R1=2.2kohms; R2=1Mohm; R3=10kohms; R4=10kohms.

Figure 2b: Circuit diagram of small transmitter. All components as above except C2=22pf, and C3=.005mf.



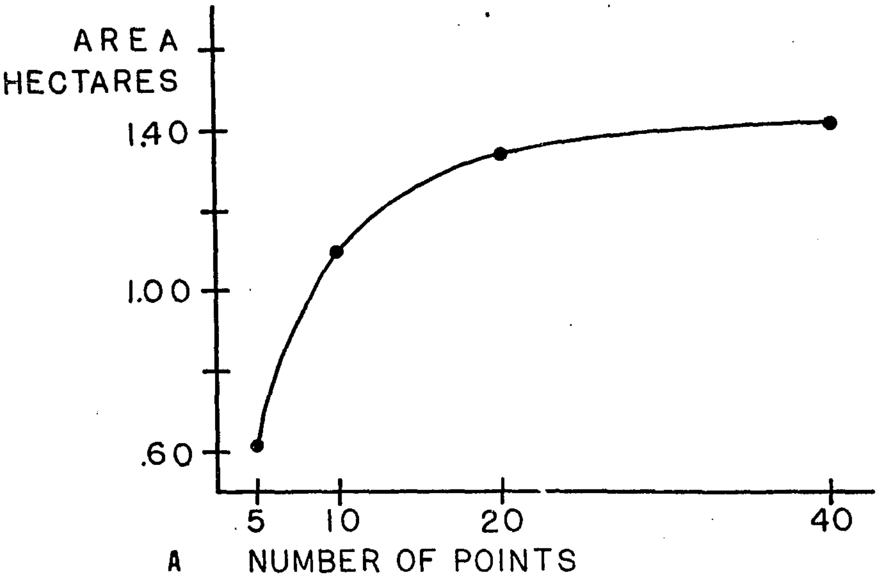
A



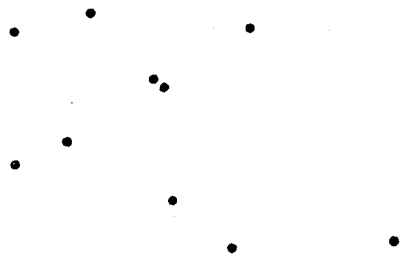
B

Figure 3a: Area-points curve for minimum polygon.

Figure 3b: 10 random points from the home range data on animal #59.



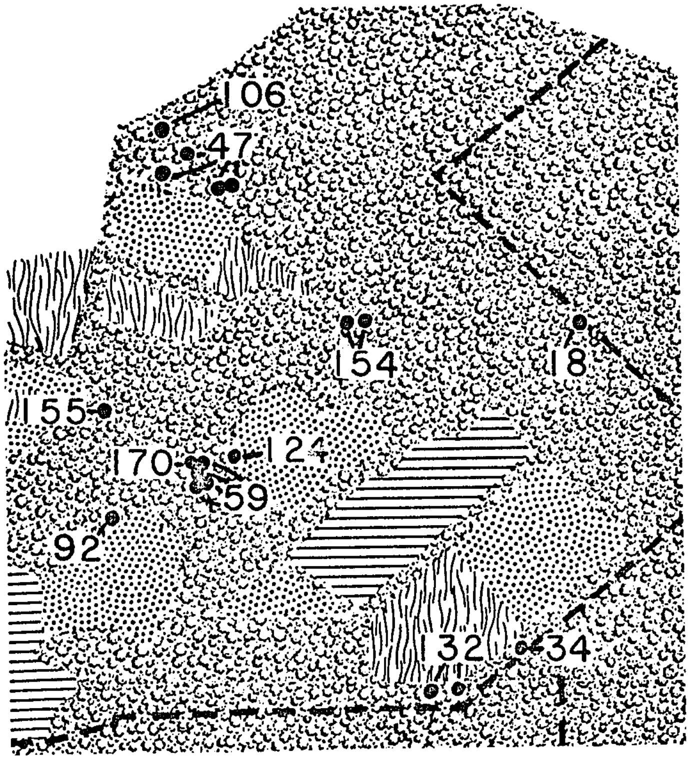
A



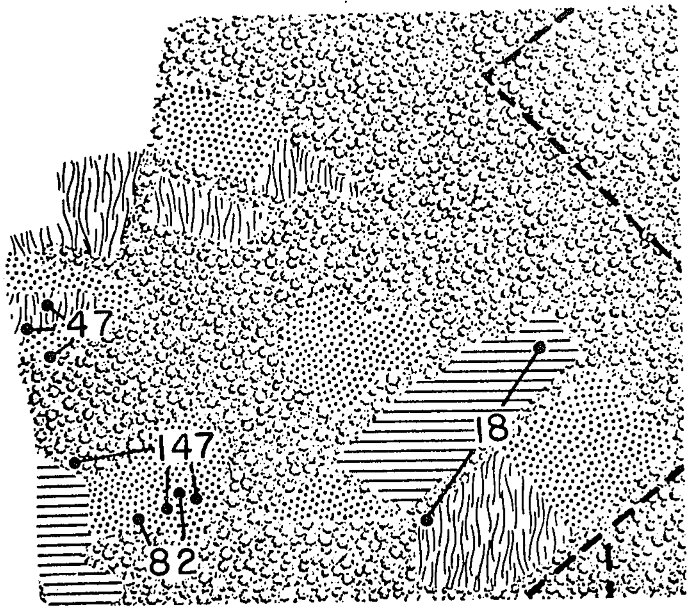
B

Figure 4a: Hibernation sites.

Figure 4b: Nesting sites for females whose nesting sites are known for more than one year. Only sucessful nestings are shown.

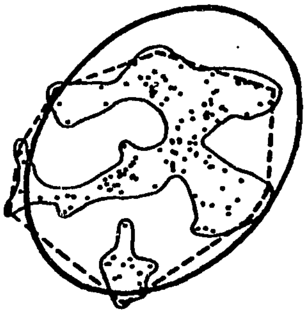


A

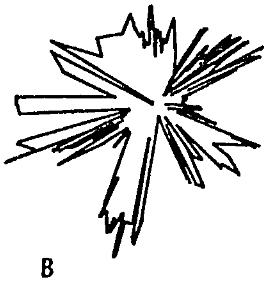


B

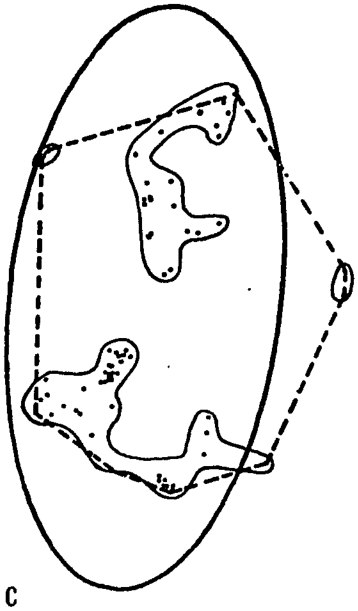
Figure 5: Home ranges by various methods. Dots show observation points. A: Subjective utilized, convex polygon, and 95% bivariate normal home ranges for animal #59. B: Minimum polygon home range for animal #59. C: Subjective utilized, convex polygon, and 95% bivariate normal home ranges for animal #18. D: Minimum polygon home range for animal #18.



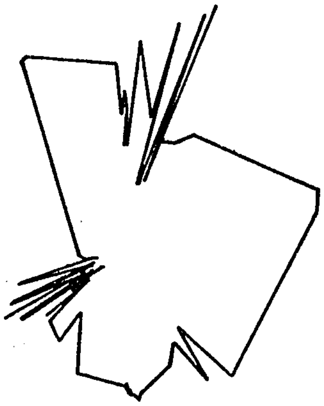
A



B



C



D

Figure 6: Basic data. Dots show observation points, Squares show nesting sites, triangles show hibernation sites, ellipse shows 95% bivariate normal home range, heavy lines show routes of homing.

A: Animal #18. B: animal #34

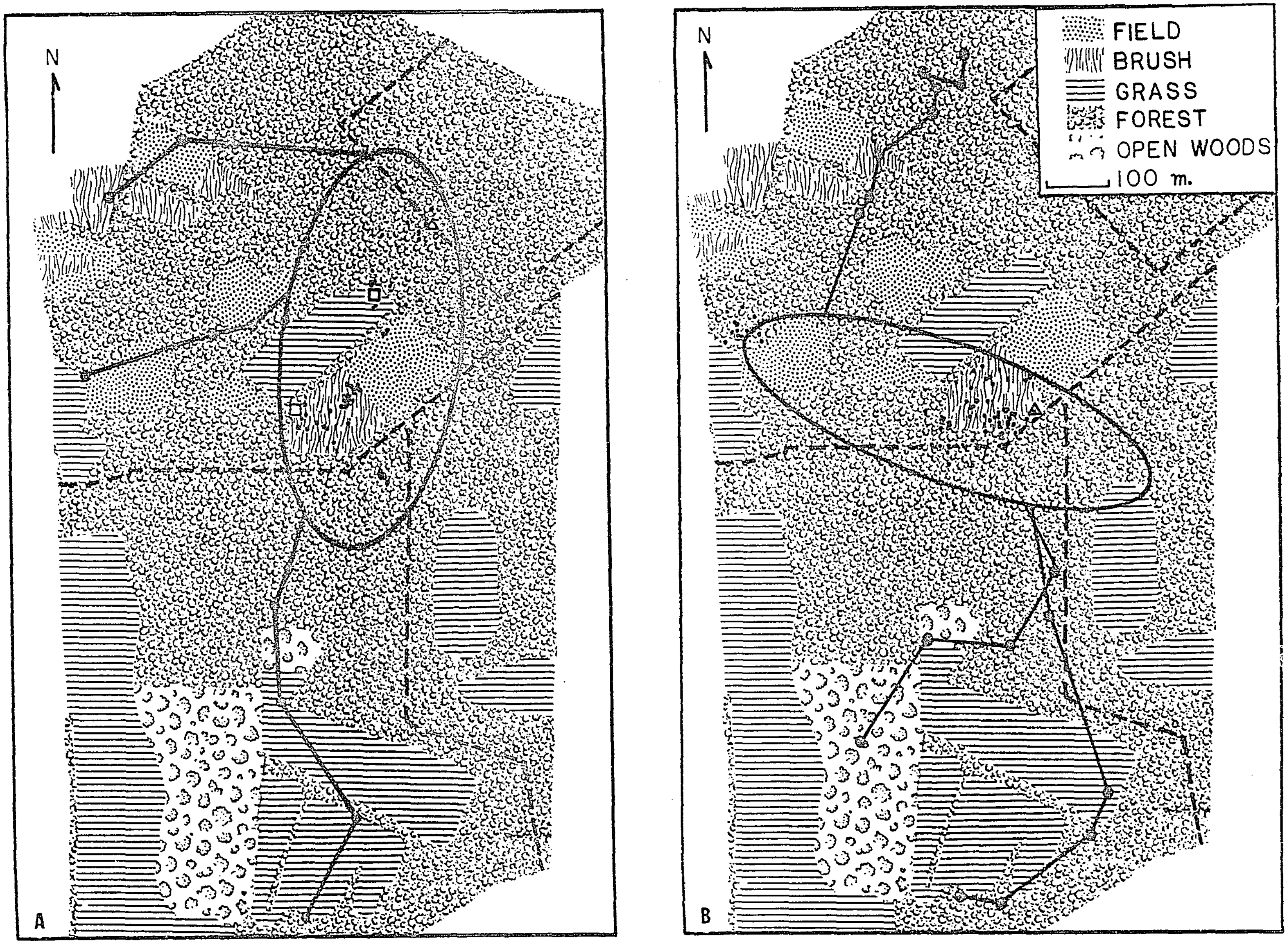

N
A
N
FIELD
BRUSH
GRASS
FOREST
OPEN WOODS
100 m.
B

Figure 7: Basic data. Dots show observation points, Squares show nesting sites, triangles show hibernation sites, ellipse shows 95% bivariate normal home range, heavy lines show routes of homing.

A: Animal #47. B: animal #59

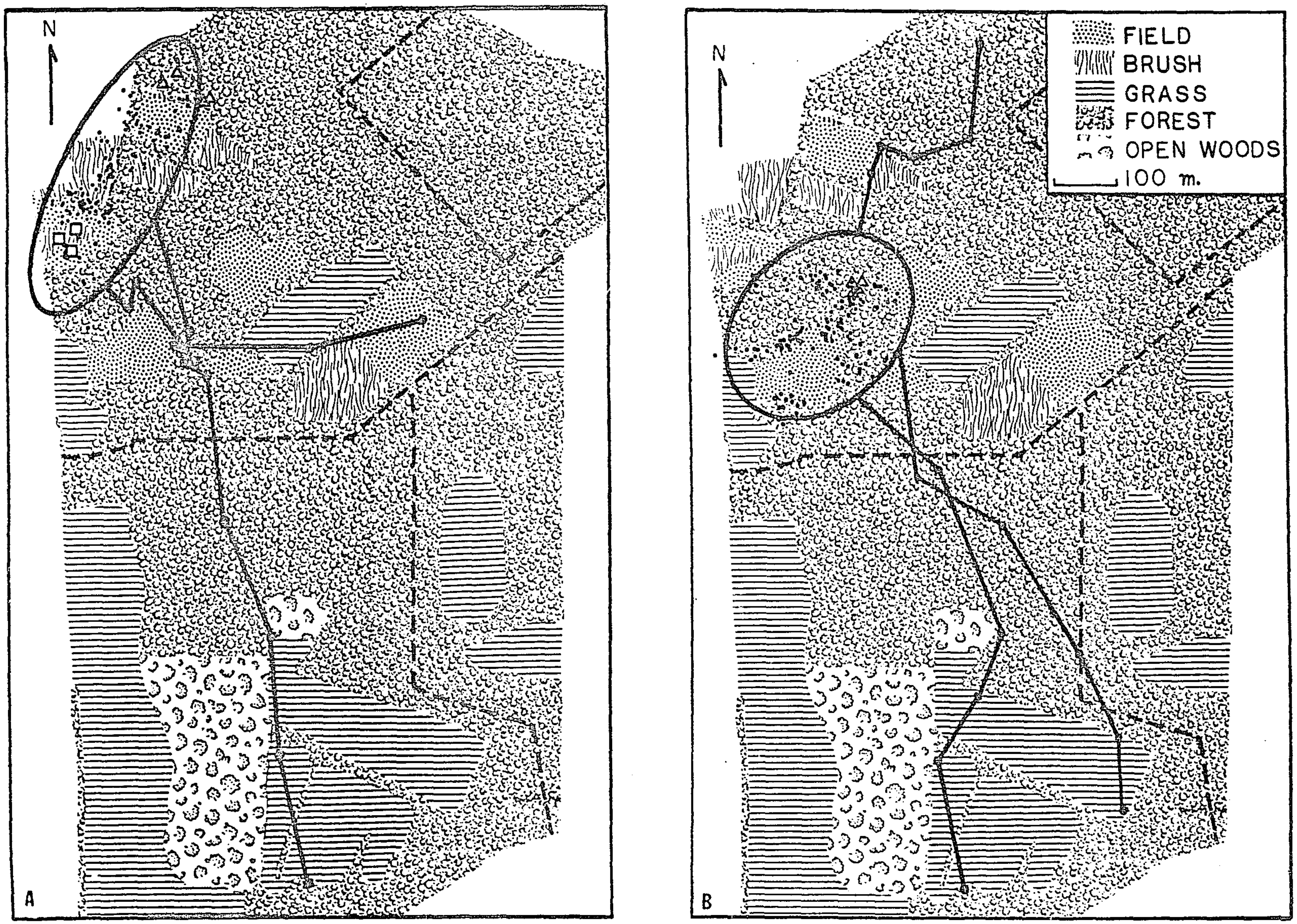

N
A
N
FIELD
BRUSH
GRASS
FOREST
OPEN WOODS
100 m.
B

Figure 8: Basic data. Dots show observation points, Squares show nesting sites, triangles show hibernation sites, ellipse shows 95% bivariate normal home range, heavy lines show routes of homing.

A: Animal #92. B: animal #106

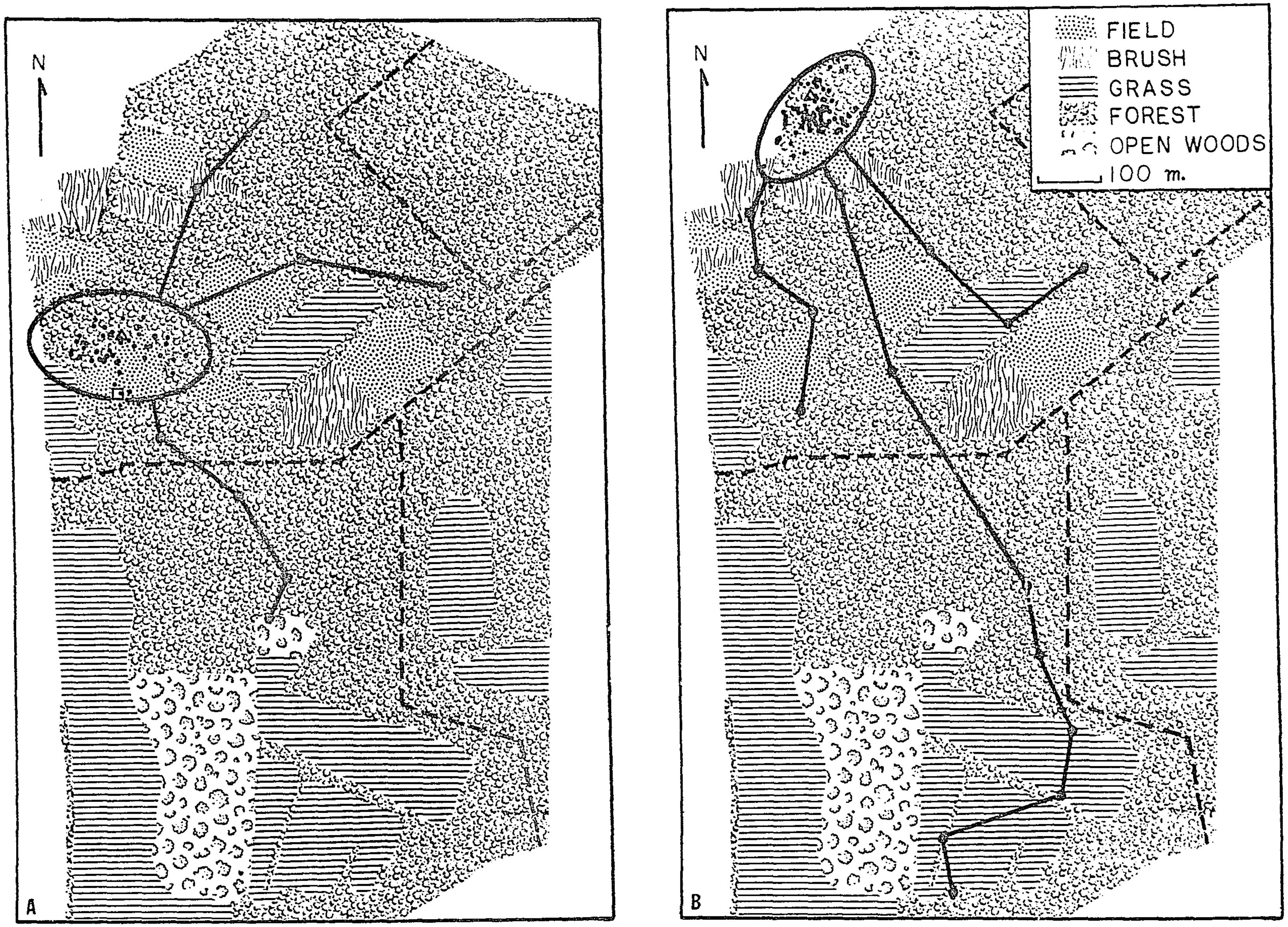

N
A
N
B
FIELD
BRUSH
GRASS
FOREST
OPEN WOODS
100 m.

Figure 9: Basic data. Dots show observation points, Squares show nesting sites, triangles show hibernation sites, ellipse shows 95% bivariate normal home range, heavy lines show routes of homing.

A: Animal #124. B: animal #132

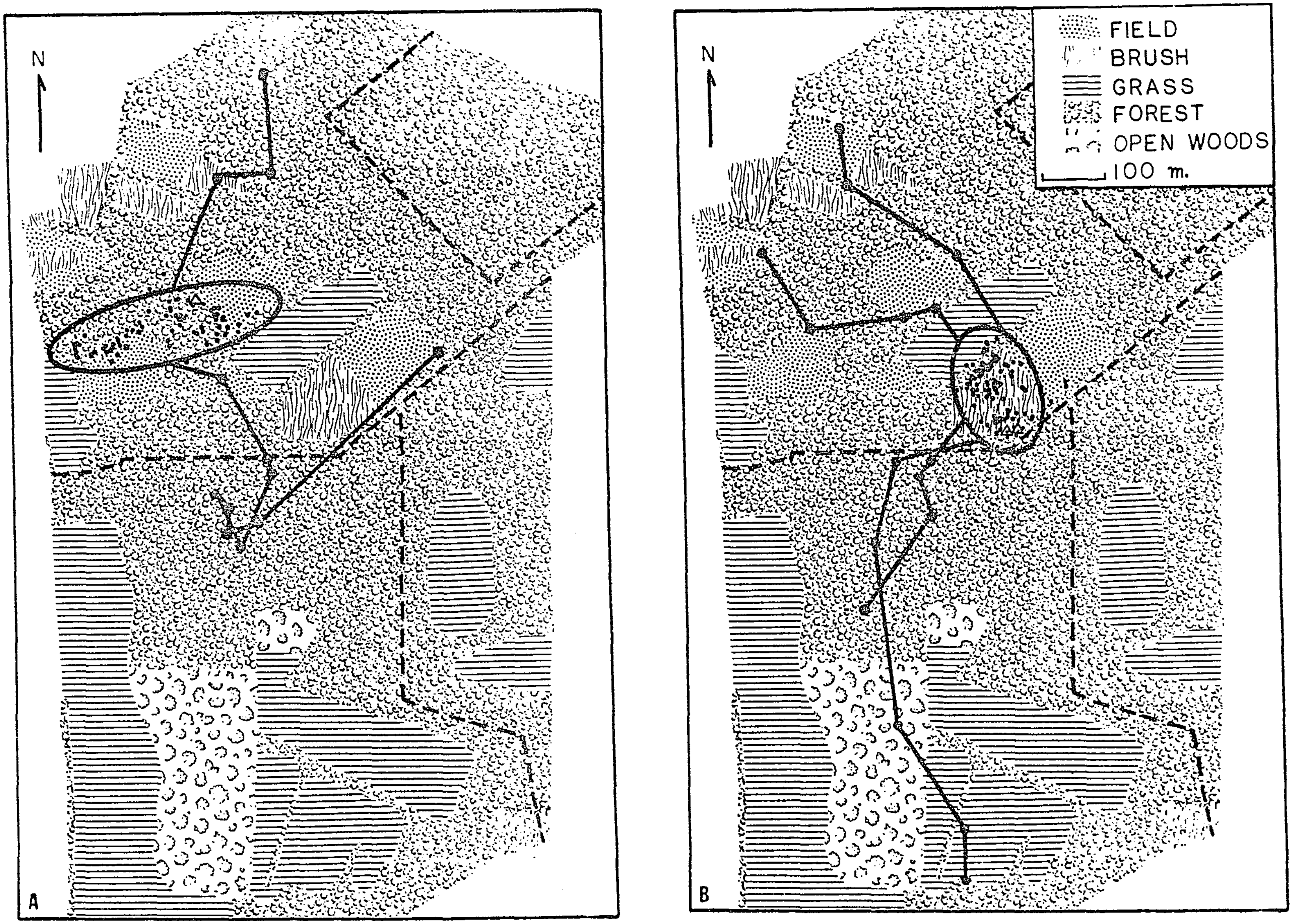

N
A
N
B
FIELD
BRUSH
GRASS
FOREST
OPEN WOODS
100 m.

Figure 10: Basic data. Dots show observation points, Squares show nesting sites, triangles show hibernation sites, ellipse shows 95% bivariate normal home range, heavy lines show routes of homing.

A: Animal #147. B: animal #154

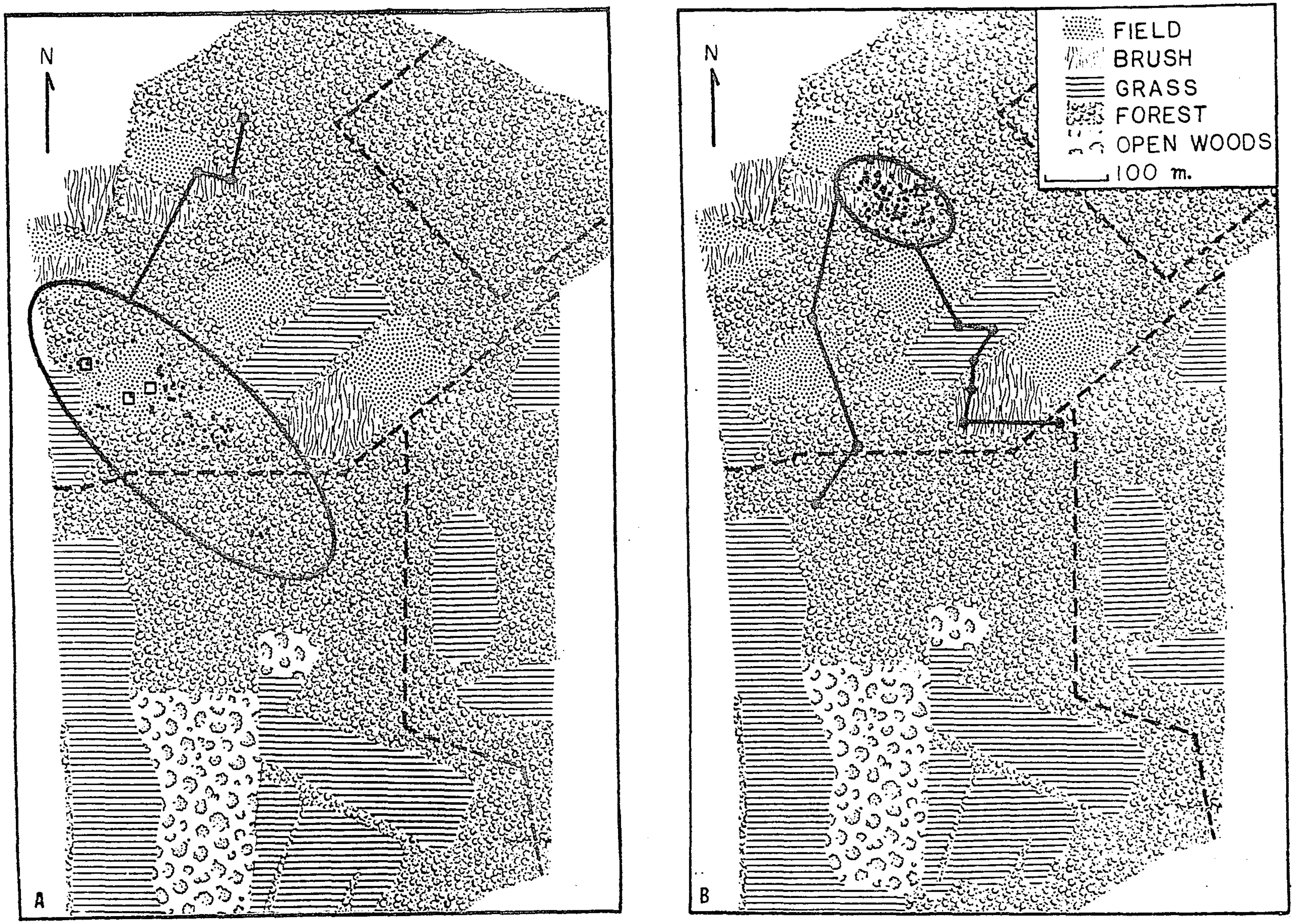

N
N
FIELD
BRUSH
GRASS
FOREST
OPEN WOODS
100 m.
A
B

Figure 11: Basic data. Dots show observation points, Squares show nesting sites, triangles show hibernation sites, ellipse shows 95% bivariate normal home range, heavy lines show routes of homing.

A: Animal #161. B: animal #167


N
A
N
FIELD
BRUSH
GRASS
FOREST
OPEN WOODS
100 m.
B

Figure 12: Basic data. Dots show observation points, Squares show nesting sites, triangles show hibernation sites, ellipse shows 95% bivariate normal home range, heavy lines show routes of homing.
A: Animal # 170. B: animal #237

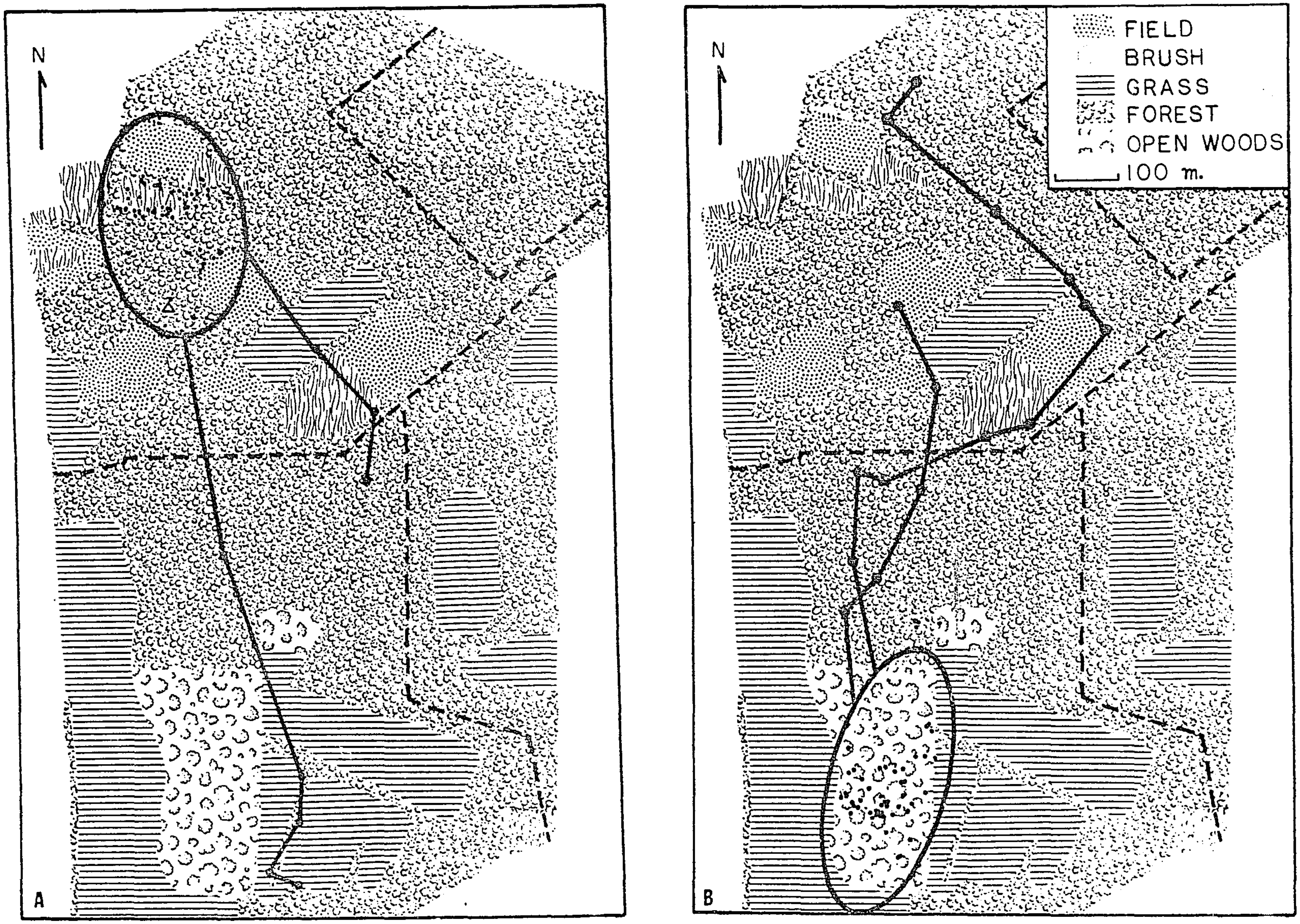

N
A
N
FIELD
BRUSH
GRASS
FOREST
OPEN WOODS
100 m.
B

Figure 13: Basic data. Dots show observation points, Squares show nesting sites, triangles show hibernation sites, ellipse shows 95% bivariate normal home range.
A: Animal #70. B: animal #72
C: animal #76. D: animal #91.

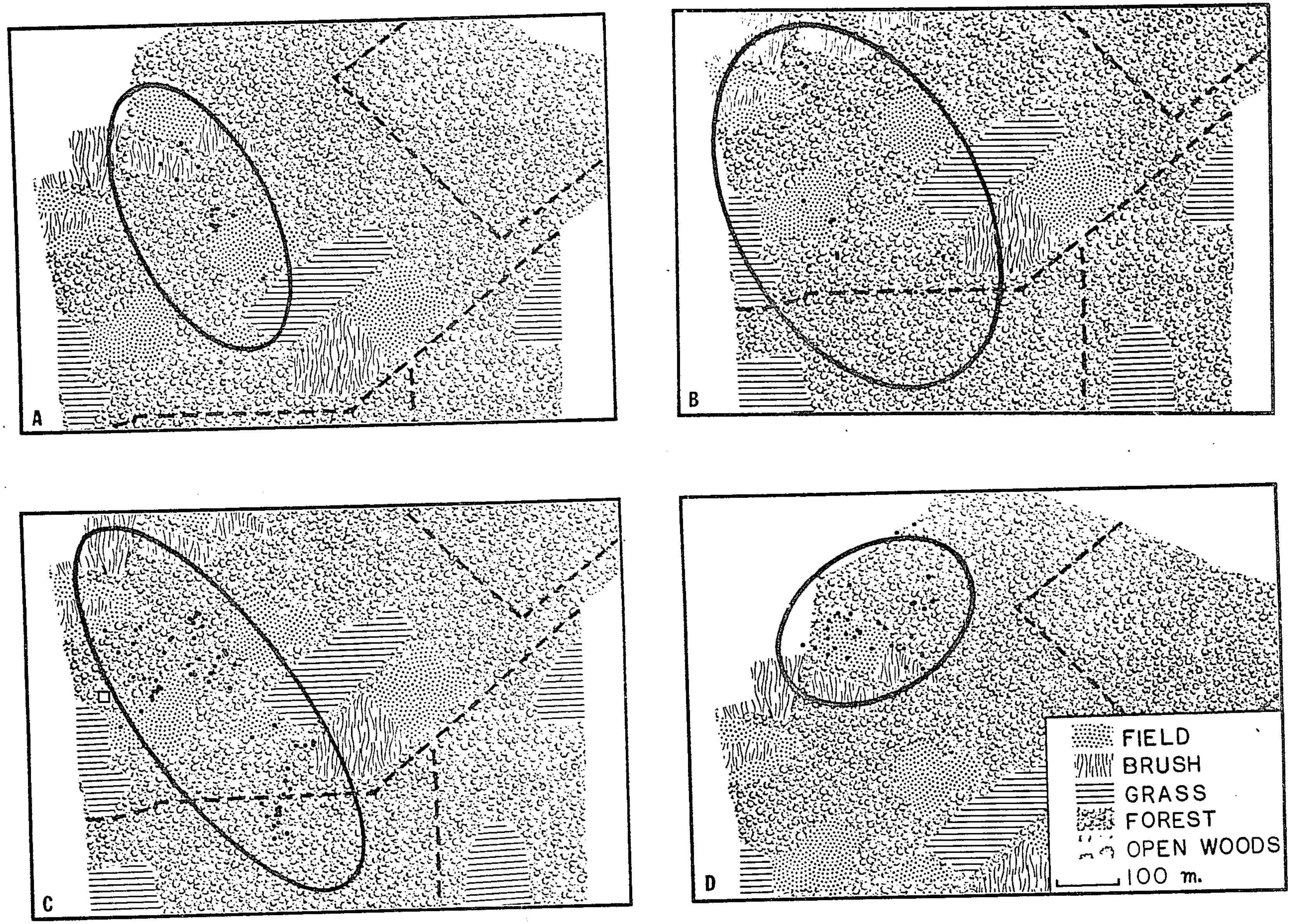

A
B
C
D
FIELD
BRUSH
GRASS
FOREST
OPEN WOODS
100 m.

Figure 14: Basic data. Dots show observation points, Squares show nesting sites, triangles show hibernation sites, ellipse shows 95% bivariate normal home range.

A: Animal #104. B: animal #122

C: animal #155. D: animal #M12.

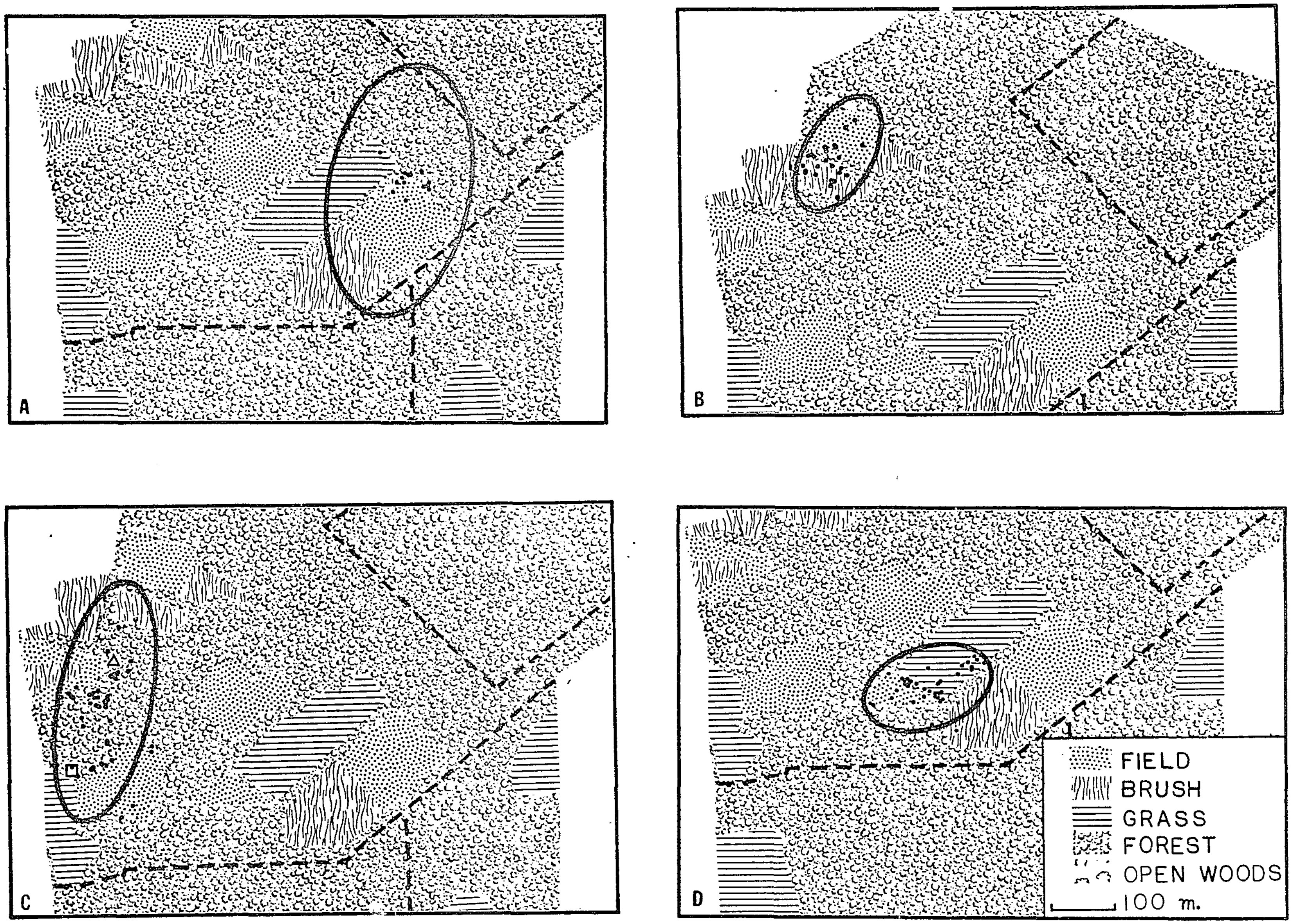

A
B
C
D
FIELD
BRUSH
GRASS
FOREST
OPEN WOODS
100 m.

Figure 15: Basic data. Dots show observation points, Squares show nesting sites, triangles show hibernation sites, ellipse shows 95% bivariate normal home range, heavy lines show routes of homing.

A: Animal #M14. B: animal #M01
C: animal #230.

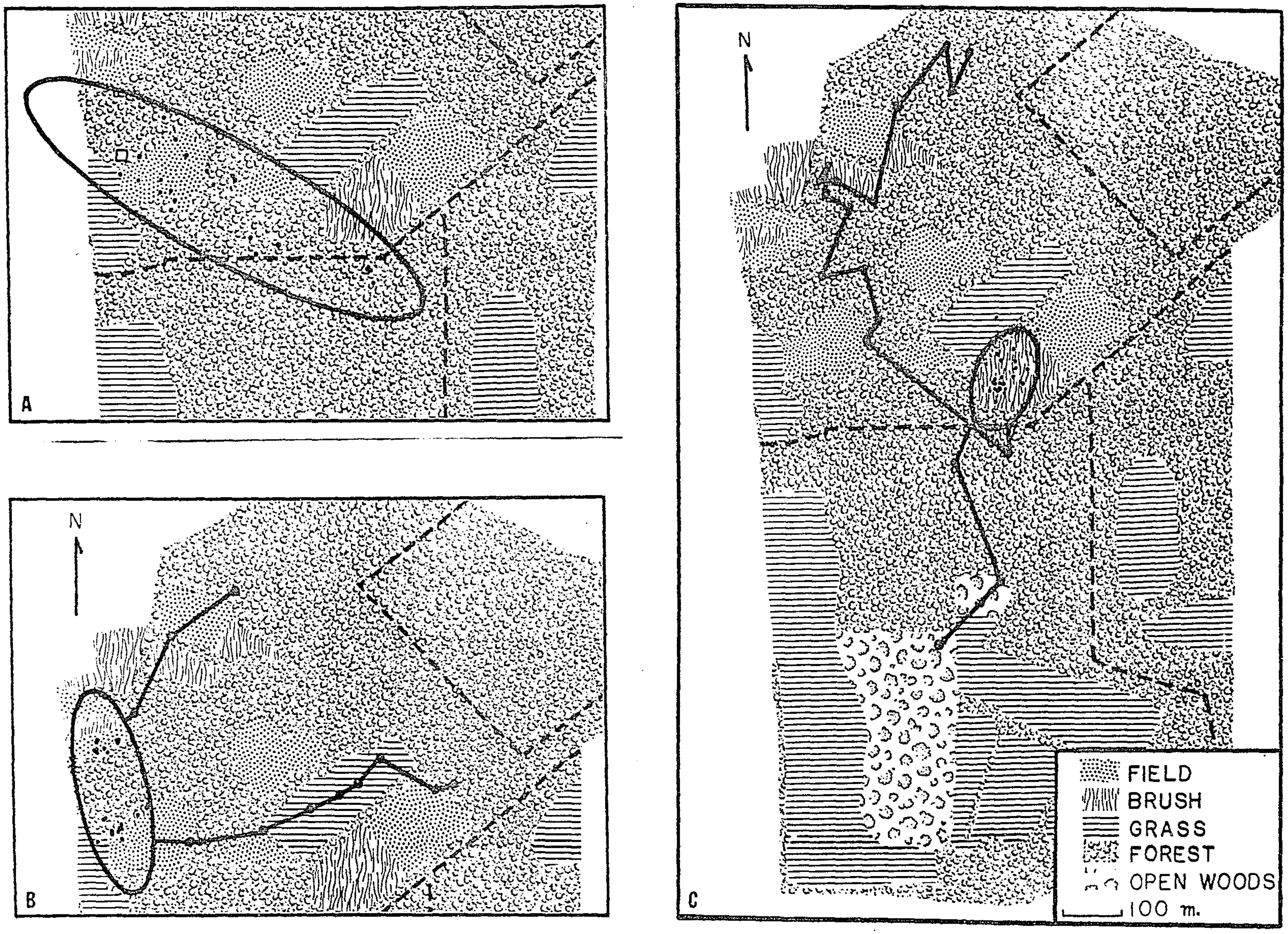
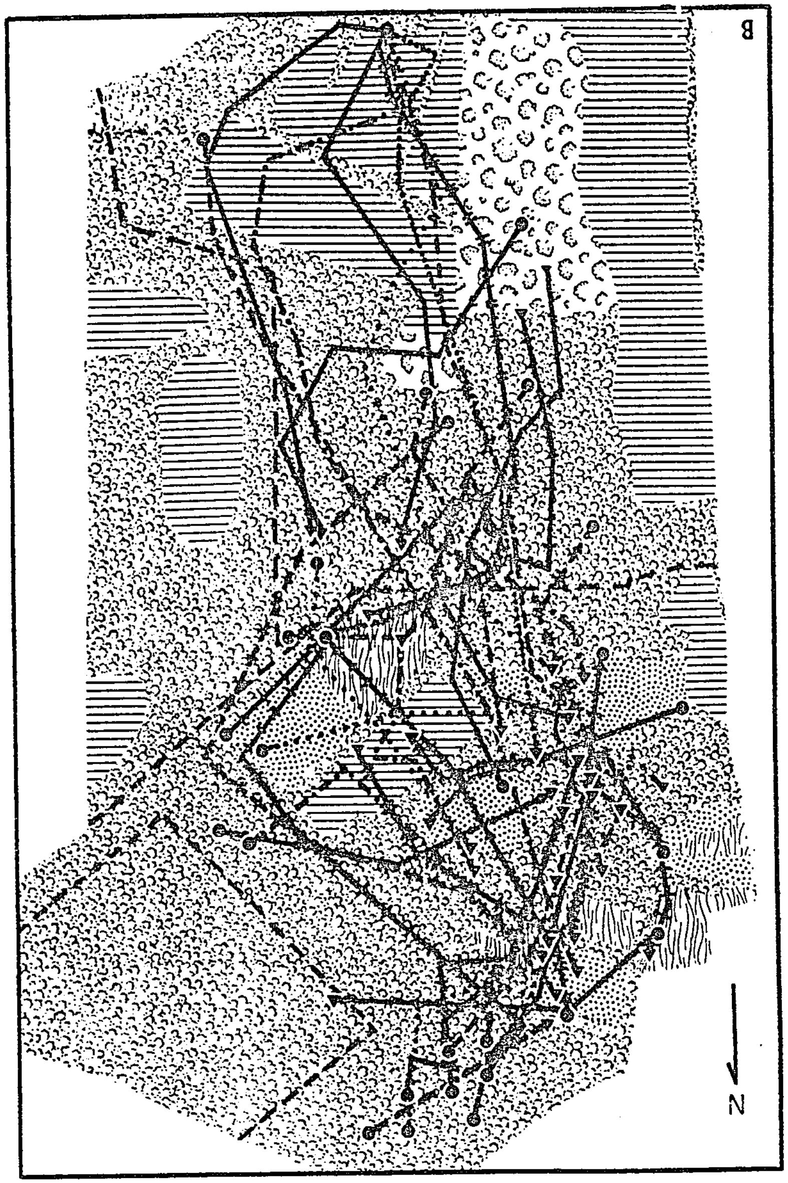

A
B
N
C
N
FIELD
BRUSH
GRASS
FOREST
OPEN WOODS
100 m.

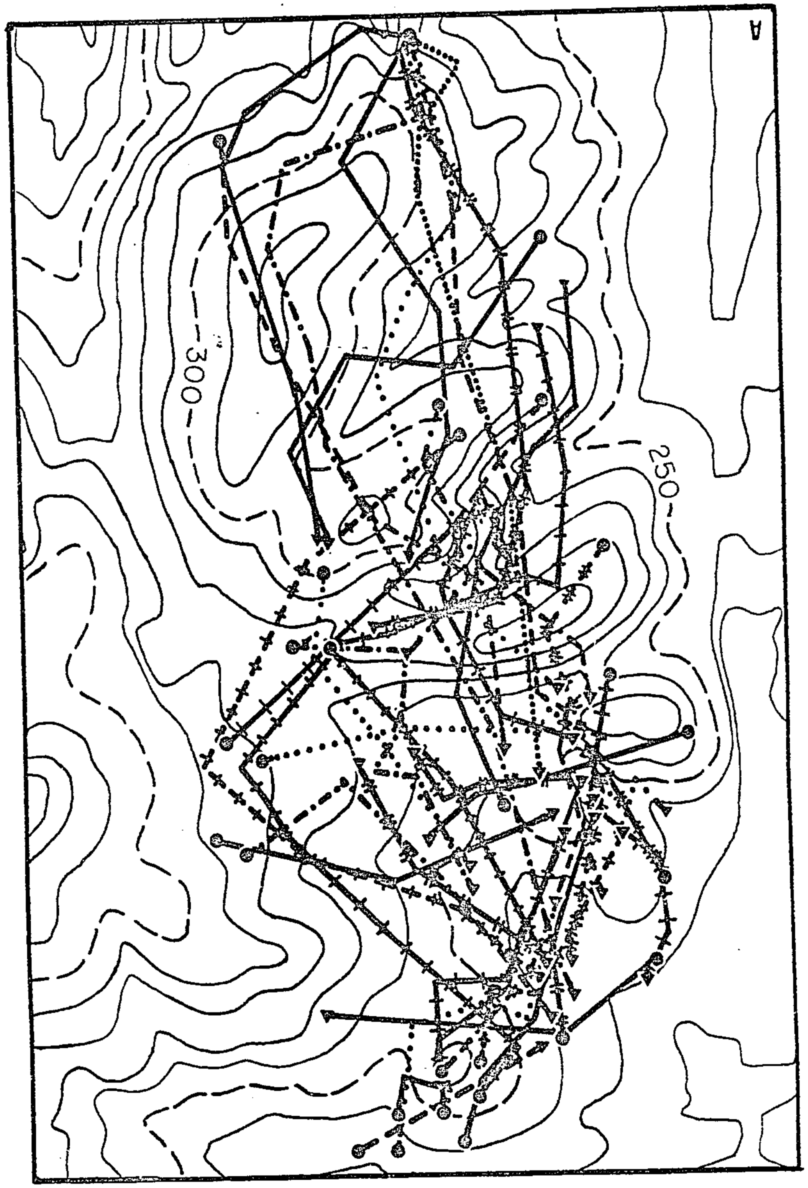
Figure 16: Homing tracks for all turtles. A plotted on contour map. B plotted on vegetation map.

Circles show release site.

Triangles show entry into 95% ellipse.

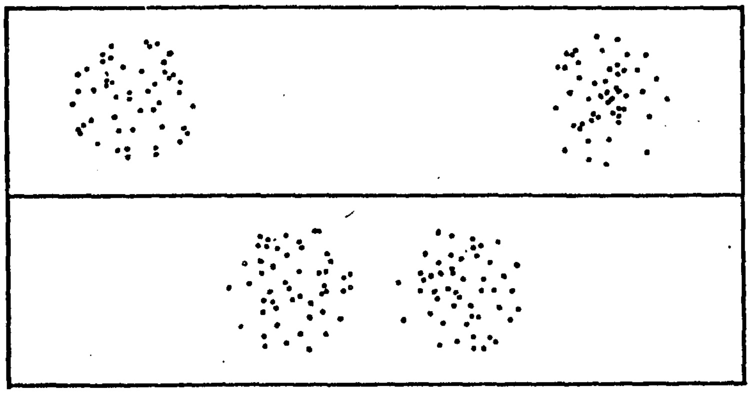


B

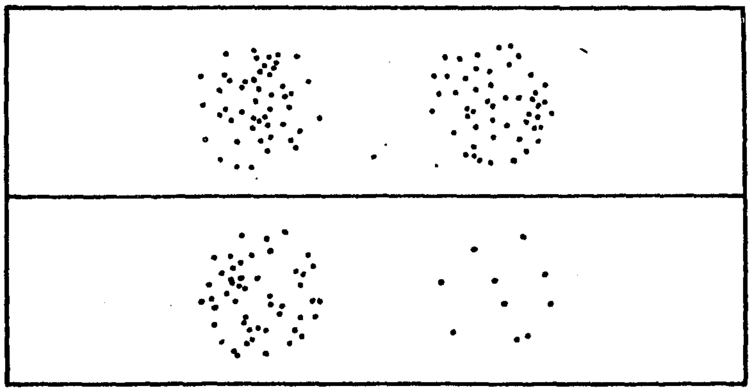


A

Figure 17: Hypothetical home ranges. A: Different distances between patches. B: Different intensity of use of patches.



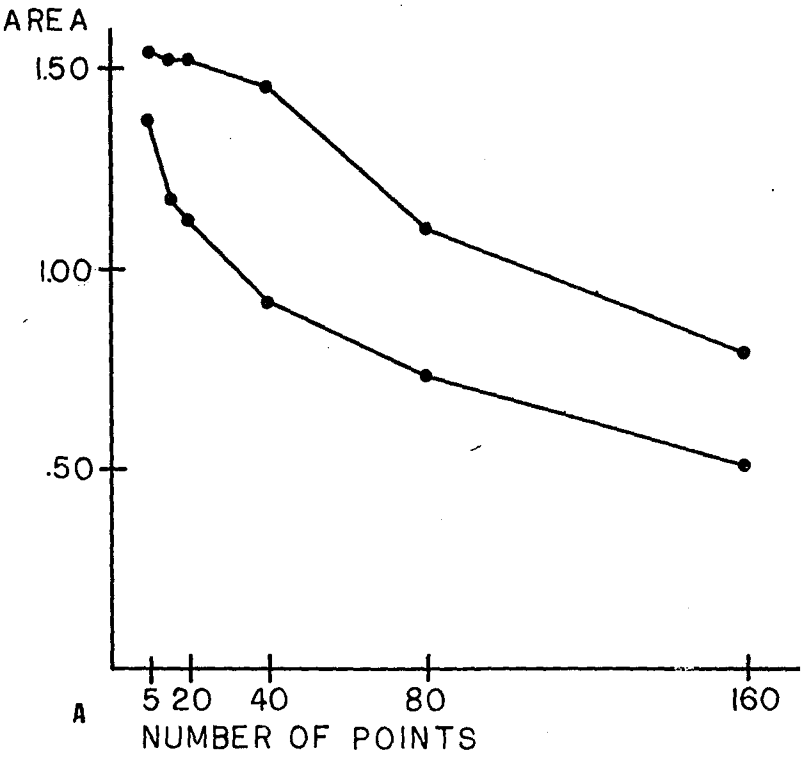
A



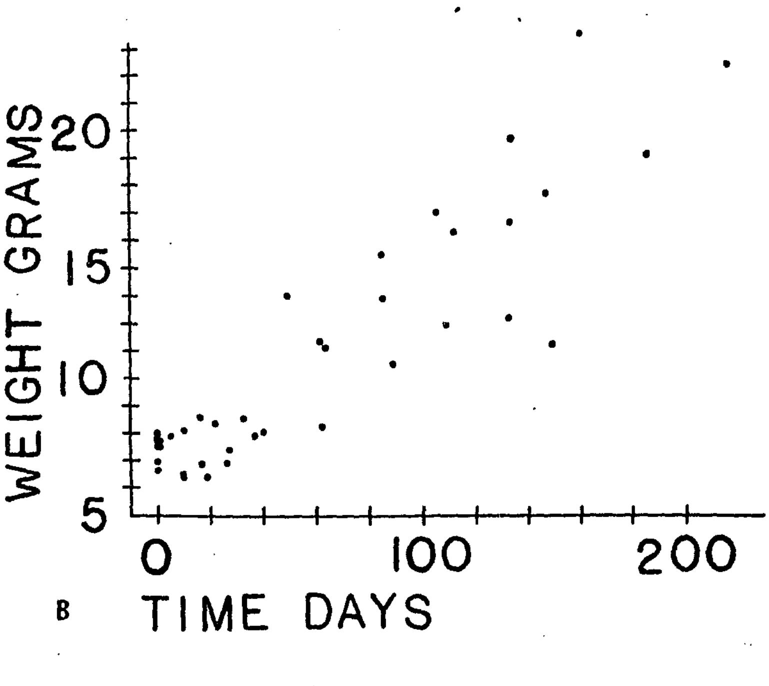
B

Figure 18A: Effective home ranges at 5-160 points for animals #47 (upper trace) and #59 (lower trace).

Figure 18B: Weight vs. age for hatchlings.

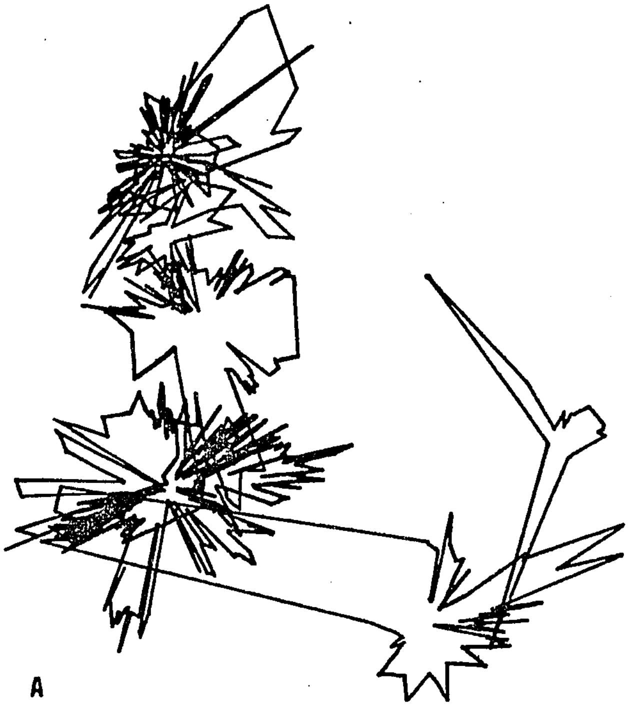

AREA
1.50
1.00
.50
5 20 40 80 160
NUMBER OF POINTS

A


WEIGHT GRAMS
20
15
10
5
0
100
200
TIME DAYS

B

Figure 19: A--Minimum polygon home ranges of males.
B--Minimum polygon home ranges of females.



A

B

Figure 20: Home ranges by months. A=April, M=May, J=June Y=July, A=August, S=September, O=October. Left figure shows 95% bivariate normal range, right figure shows 95% confidence regions for the centers of gravity.

A and B: animal #34

C and D: animal #47

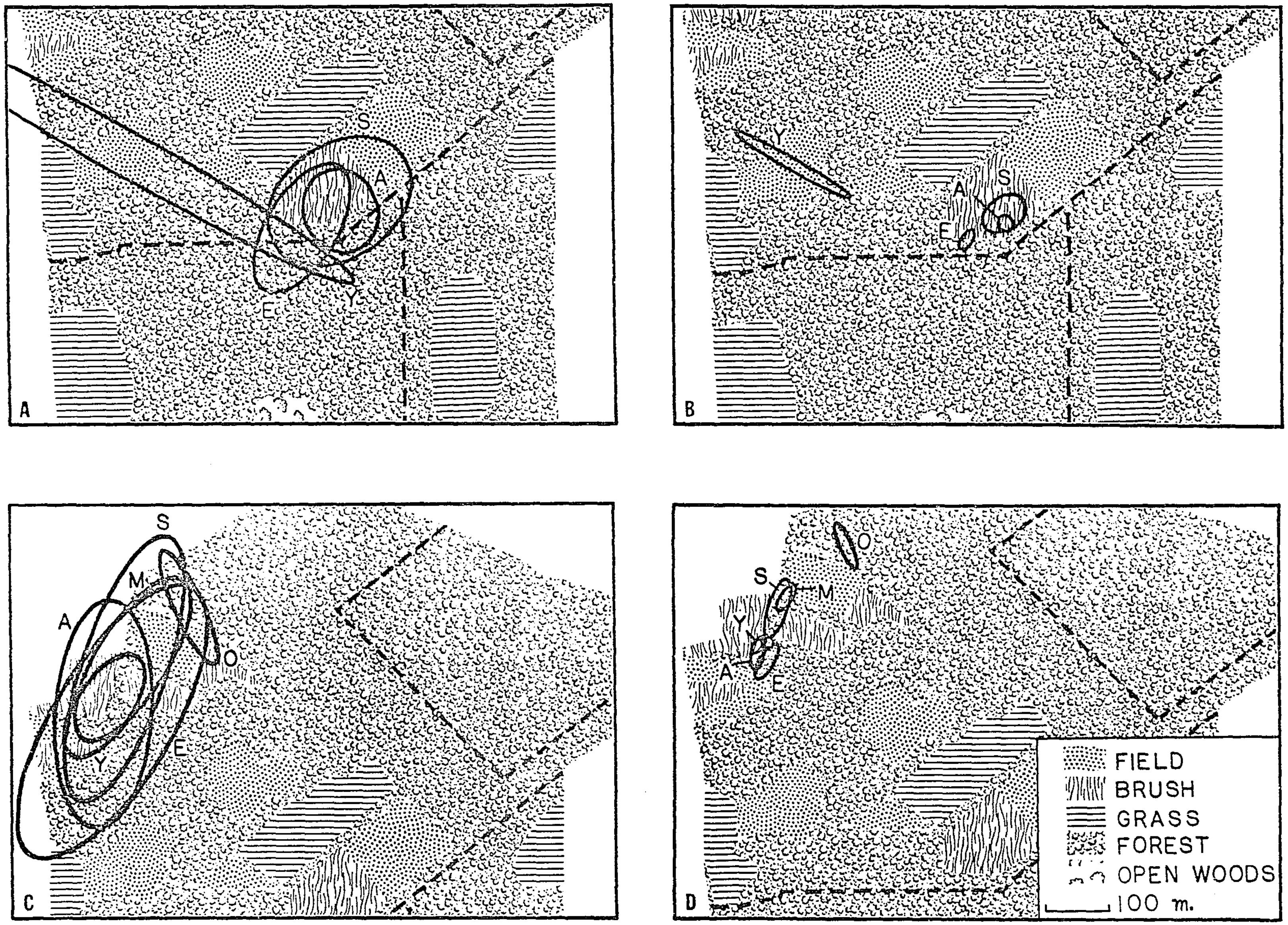

A
S
A
E
Y
B
Y
A
S
E
C
S
M
A
O
E
Y
D
O
S
M
Y
A
E
FIELD
BRUSH
GRASS
FOREST
OPEN WOODS
100 m.

Figure 21: Home ranges by months. A=April, M=May, J=June Y=July, A=August, S=September, O=October. Left figure shows 95% bivariate normal range, right figure shows 95% confidence regions for the centers of gravity.

A and B: animal #59

C and D: animal #76

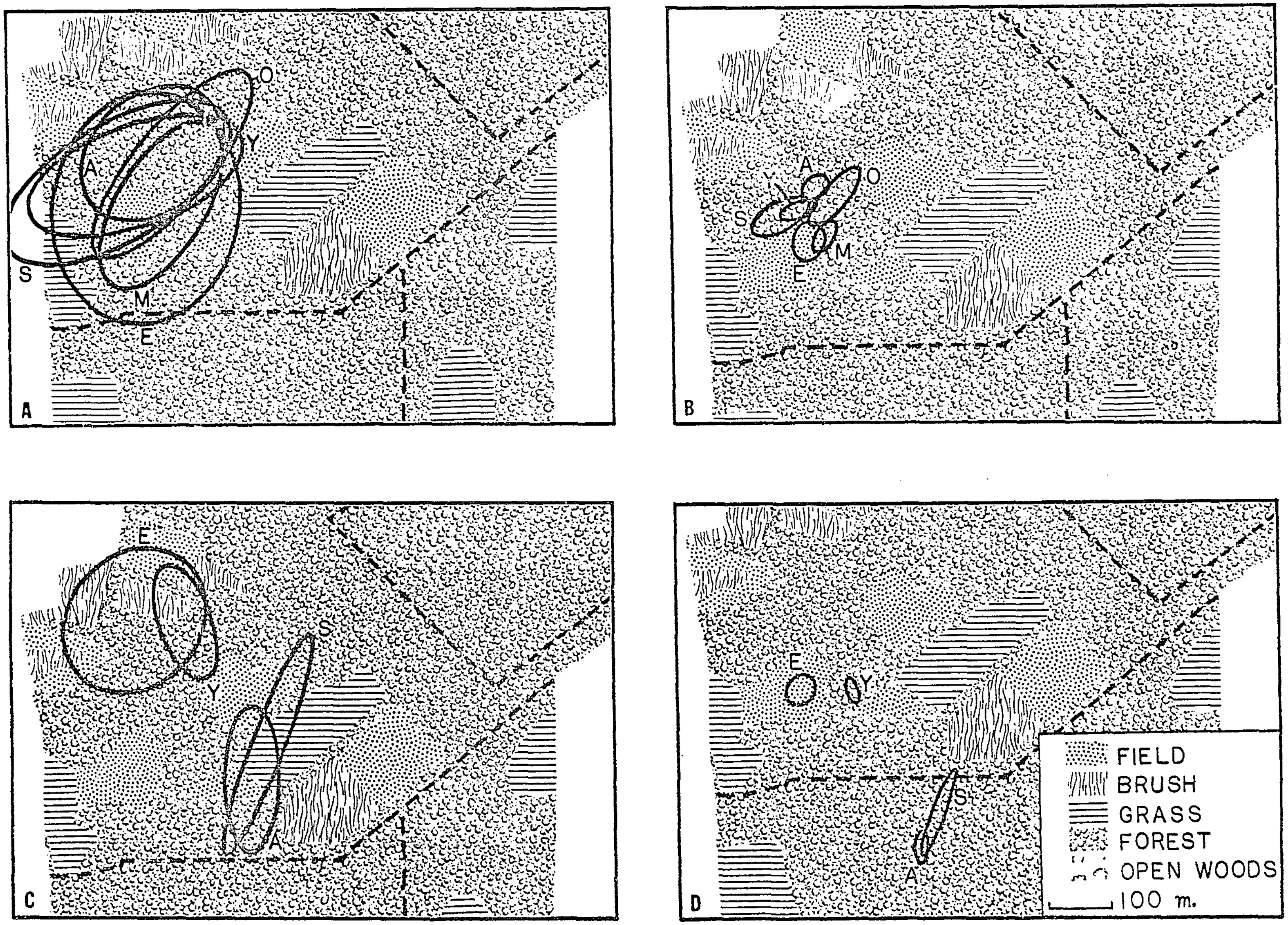

A
O
Y
A
S
M
E
B
A
Y
O
S
M
E
C
E
Y
S
A
D
E
Y
S
A
FIELD
BRUSH
GRASS
FOREST
OPEN WOODS
100 m.

Figure 22: Home ranges by months. A=April, M=May, J=June Y=July, A=August, S=September, O=October. Left figure shows 95% bivariate normal range, right figure shows 95% confidence regions for the centers of gravity.

A and B: animal #92
C and D: animal #106

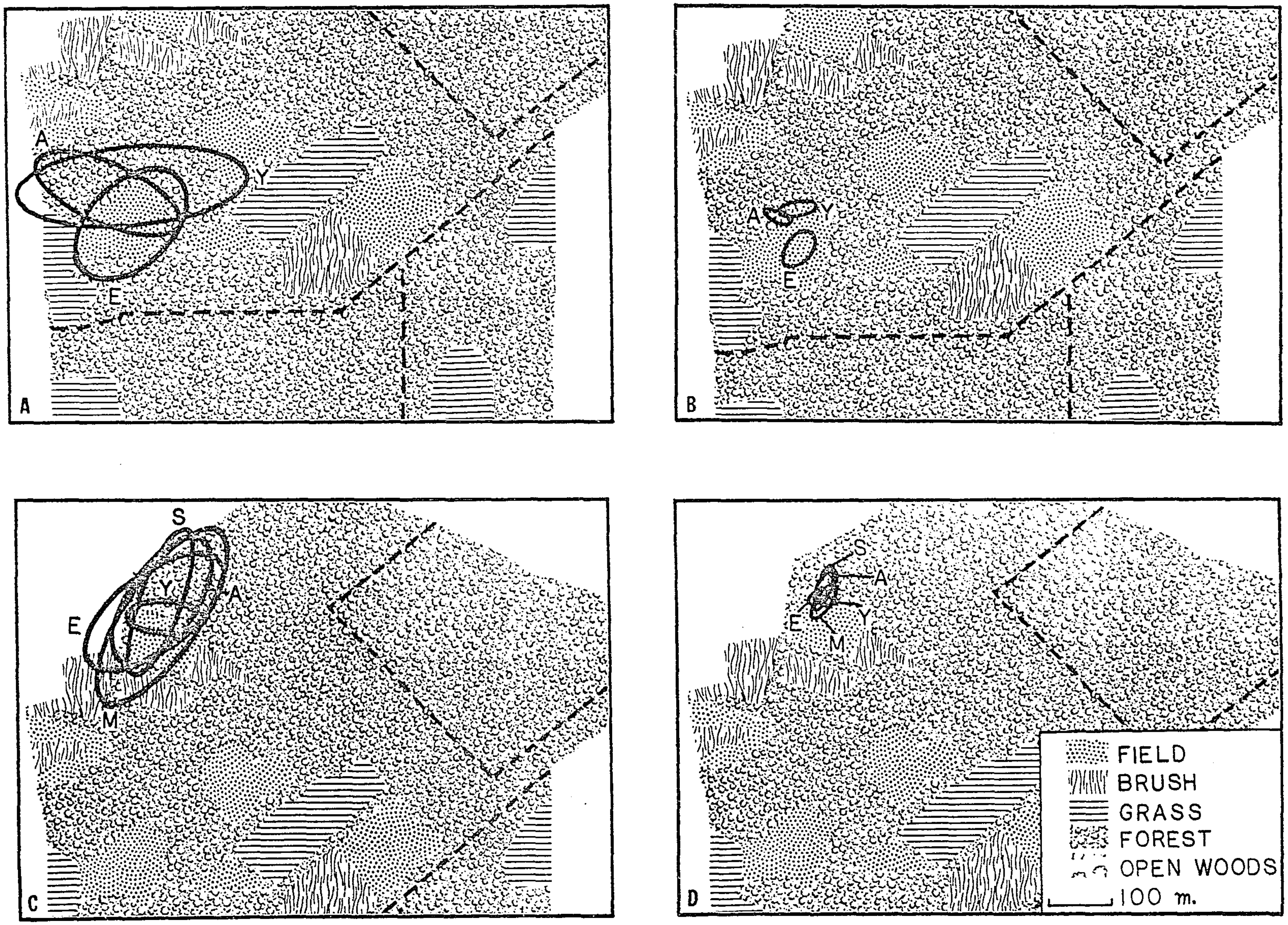

A
A
Y
E
B
A
Y
E
C
S
Y
A
E
M
D
S
A
E
Y
M
FIELD
BRUSH
GRASS
FOREST
OPEN WOODS
100 m.

Figure 23: Home ranges by months. A=April, M=May, J=June Y=July, A=August, S=September, O=October. Left figure shows 95% bivariate normal range, right figure shows 95% confidence regions for the centers of gravity.

A and B: animal #122
C and D: animal #124

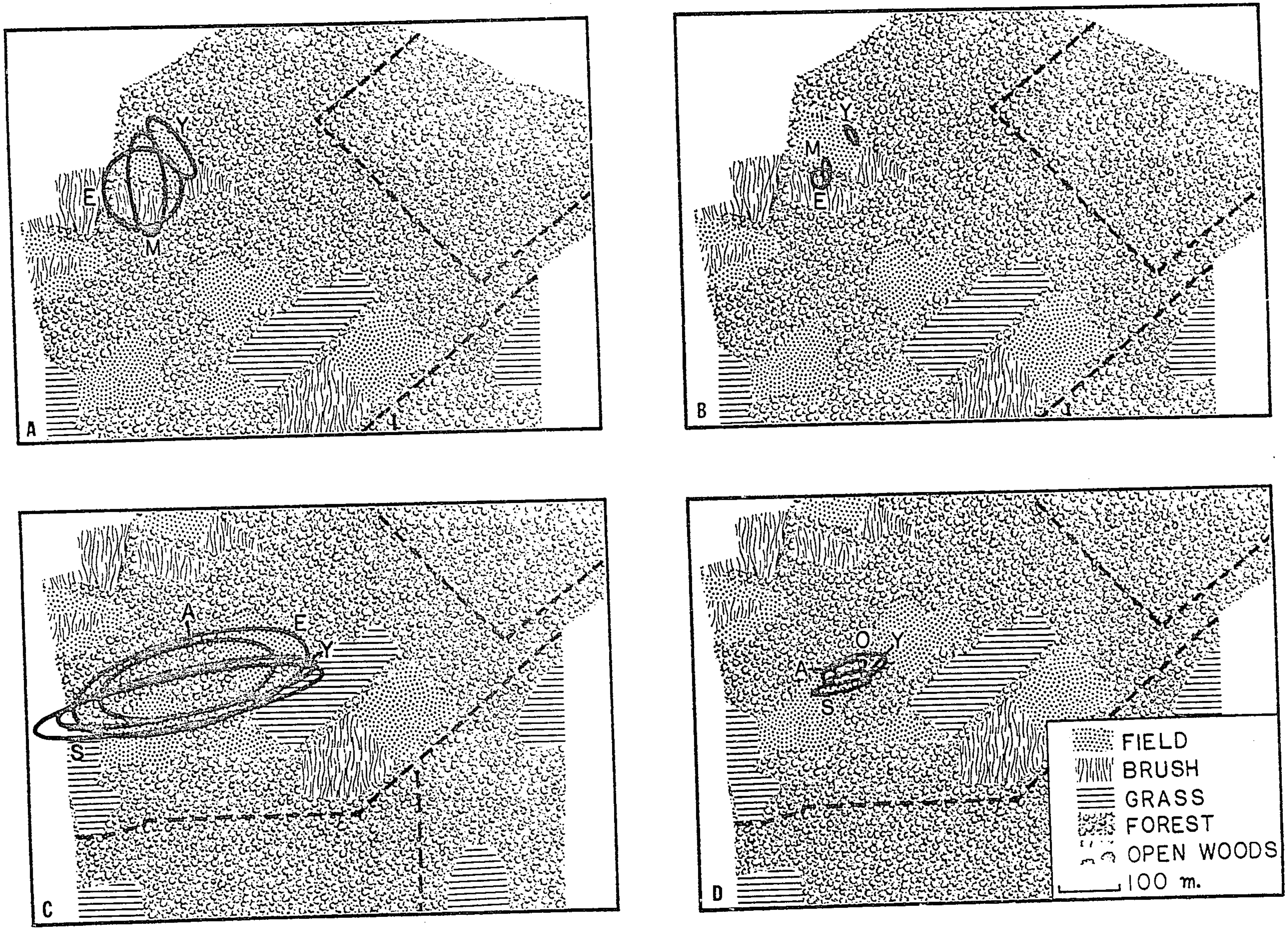

A
Y
E
M
B
Y
M
E
C
A
E
Y
S
D
O
Y
A
S
FIELD
BRUSH
GRASS
FOREST
OPEN WOODS
100 m.

Figure 24: Home ranges by months. A=April, M=May, J=June Y=July, A=August, S=September, O=October. Left figure shows 95% bivariate normal range, right figure shows 95% confidence regions for the centers of gravity.

A and B: animal #132

C and D: animal #147

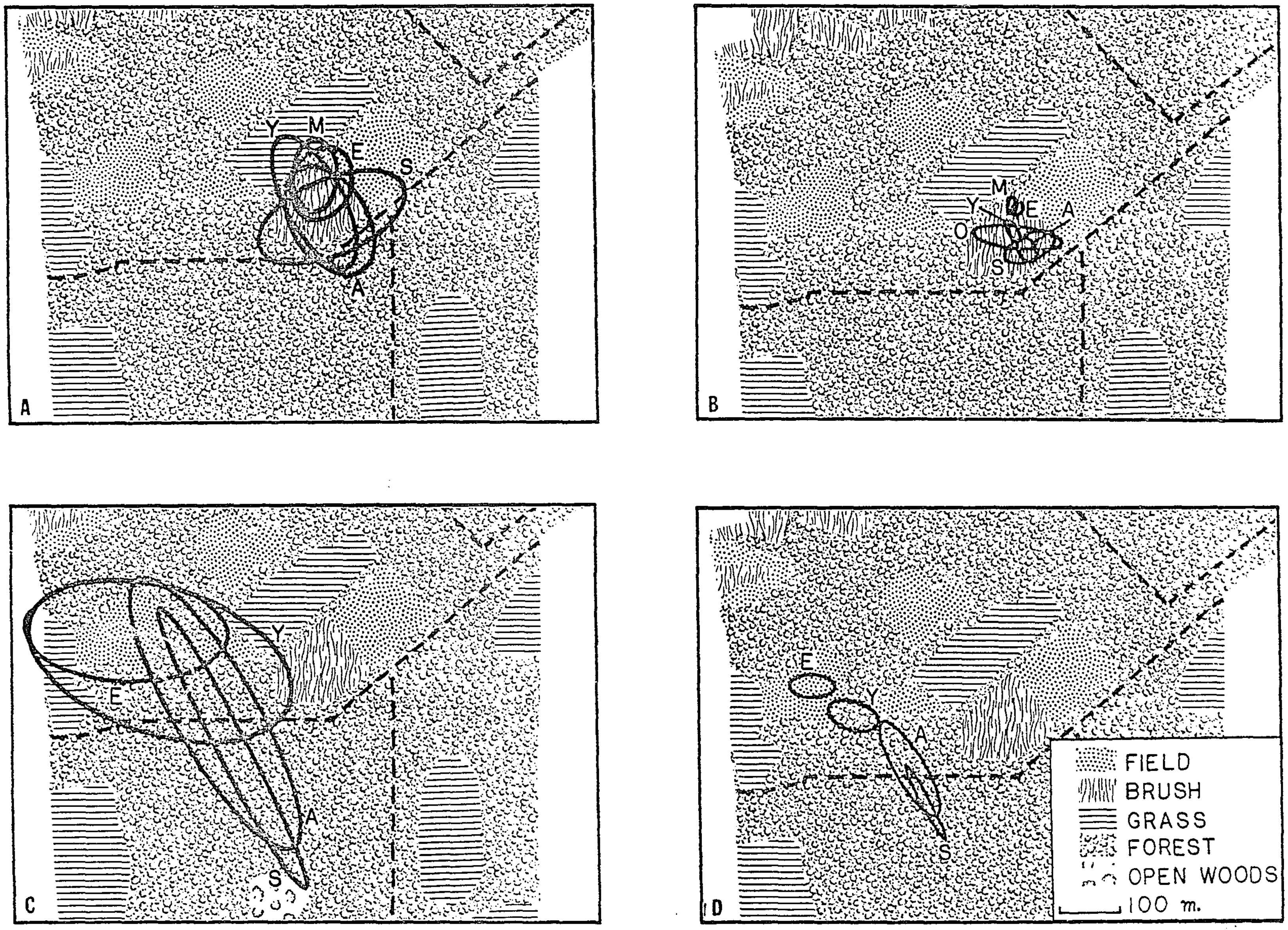

A
Y
M
E
S
A
B
M
Y
O
E
A
S
C
Y
E
A
S
D
E
Y
A
S
FIELD
BRUSH
GRASS
FOREST
OPEN WOODS
100 m.

Figure 25: Home ranges by months. A=April, M=May, J=June Y=July, A=August, S=September, O=October. Left figure shows 95% bivariate normal range, right figure shows 95% confidence regions for the centers of gravity.

A and B: animal #154
C and D: animal #155

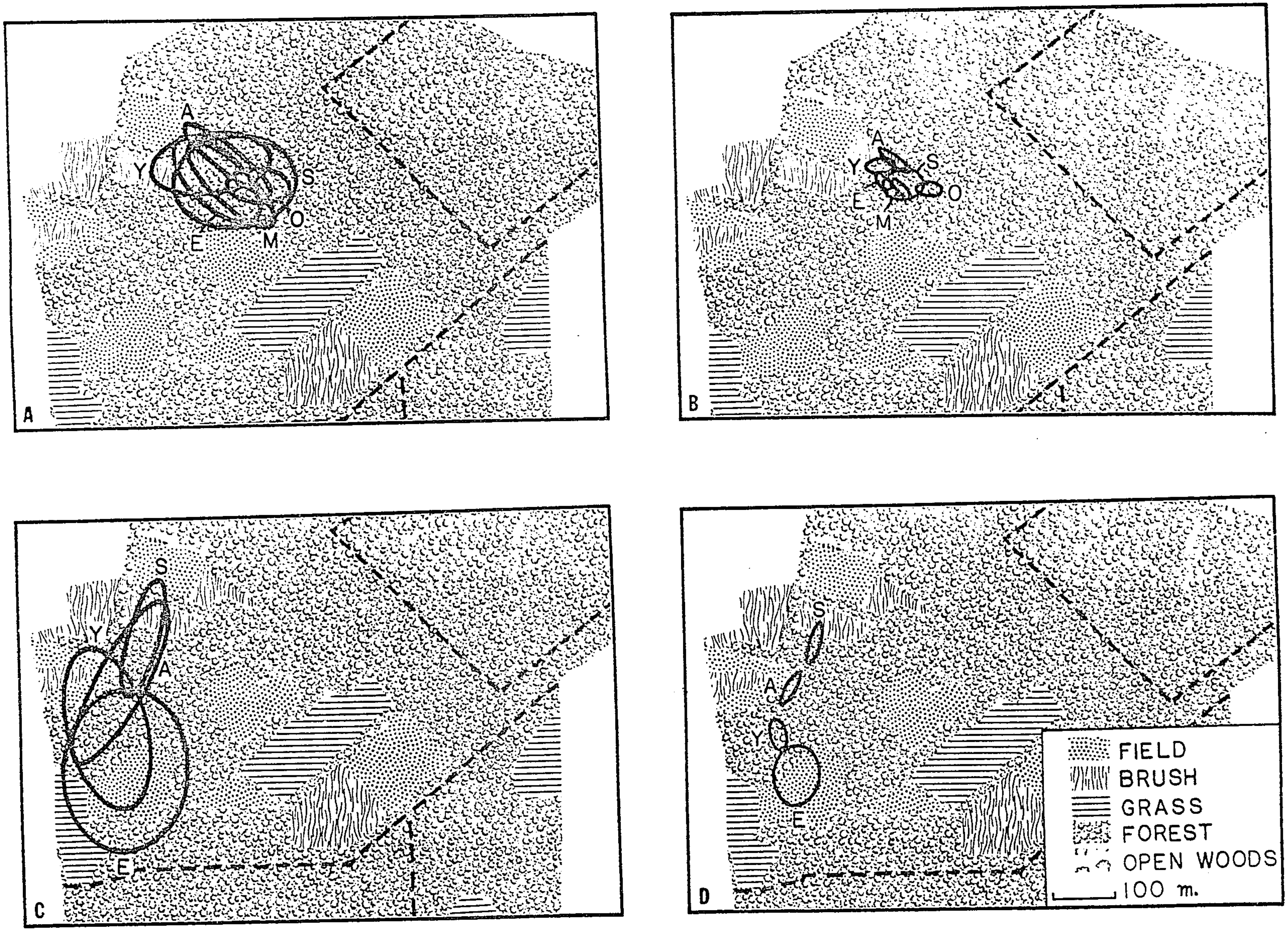

A
Y
S
O
E
M
B
A
Y
S
O
E
M
C
S
Y
A
E
D
S
A
Y
E
FIELD
BRUSH
GRASS
FOREST
OPEN WOODS
100 m.

Figure 26: Home ranges by months. A=April, M=May, J=June Y=July, A=August, S=September, O=October. Left figure shows 95% bivariate normal range, right figure shows 95% confidence regions for the centers of gravity.

A and B: animal #170
C and D: animal #237

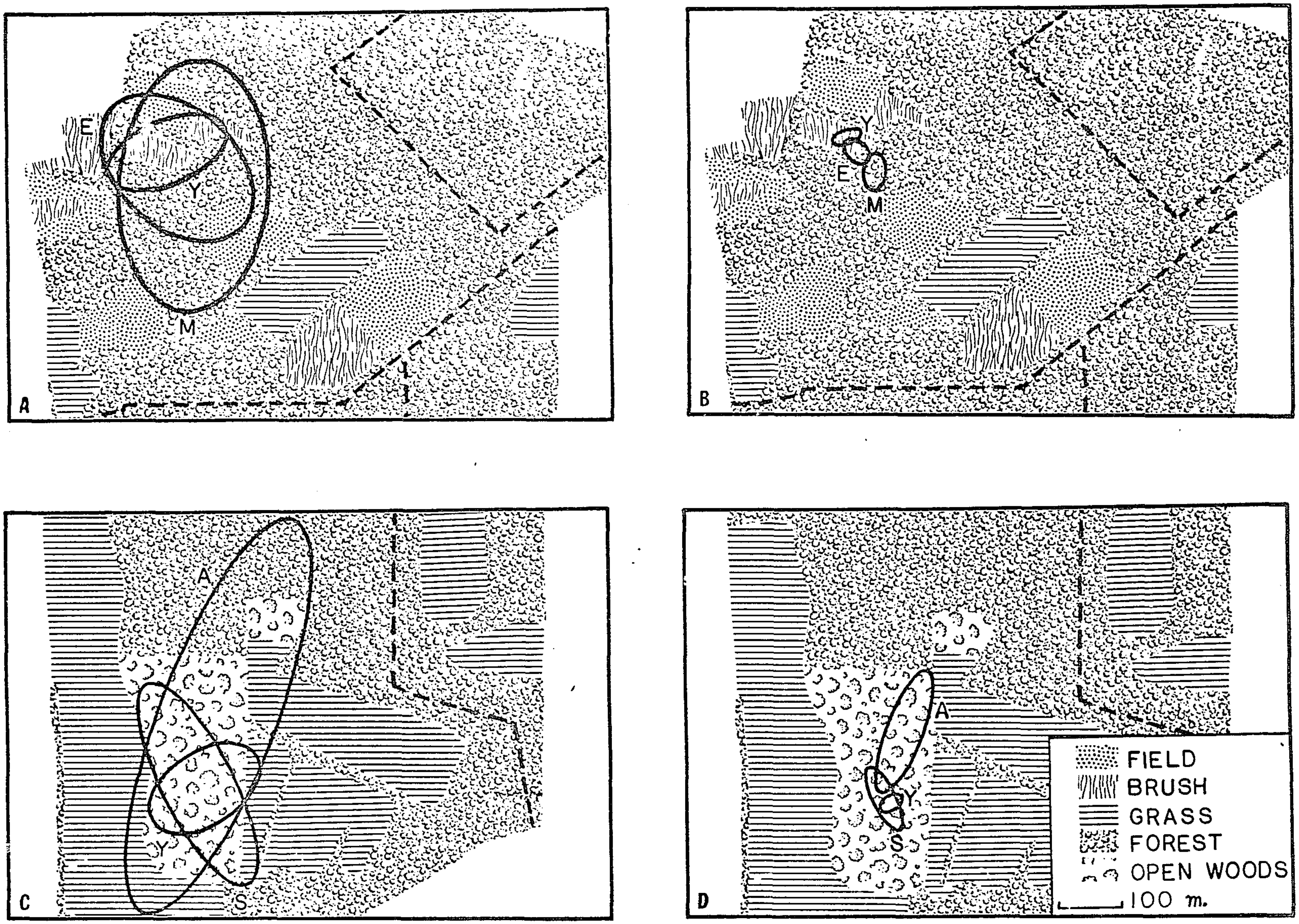
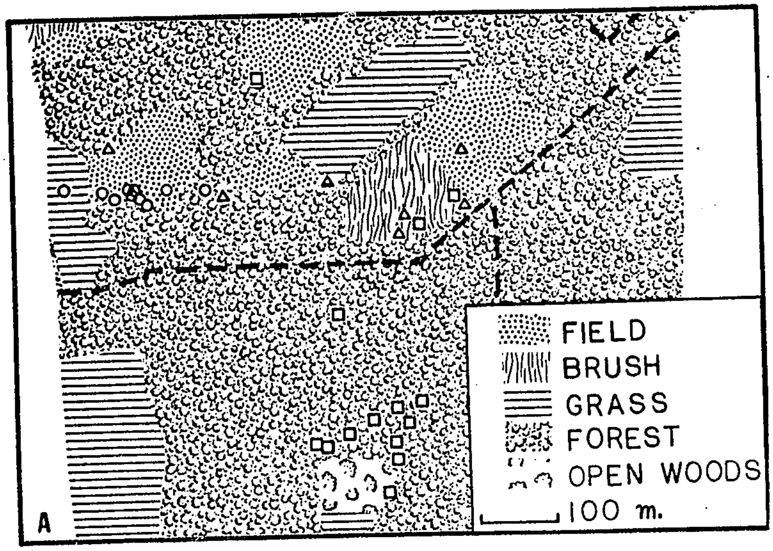
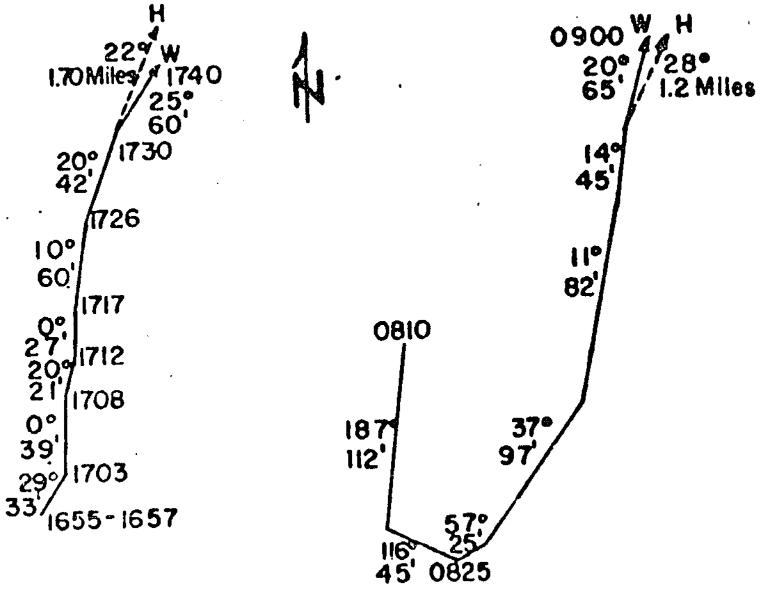

A
E
Y
M
B
E
Y
M
C
A
Y
S
D
A
Y
S
FIELD
BRUSH
GRASS
FOREST
OPEN WOODS
100 m.

Figure 27A: Data for animal #82. Triangles show recaptures from Kalbfleish station data. Circles show June telemetry data. Squares show July telemetry data.

Figure 27B: Two typical tracks from Gould (1957).





B No. 69- 22 Aug, Parade Field (P) 1655-1815

No. 14 - 24 June, Golf Course (G) 0810-0900

Figure 28: 95% confidence regions of home ranges by years.
A: animal #18. B: animal #34
C: animal #47. C: animal #59

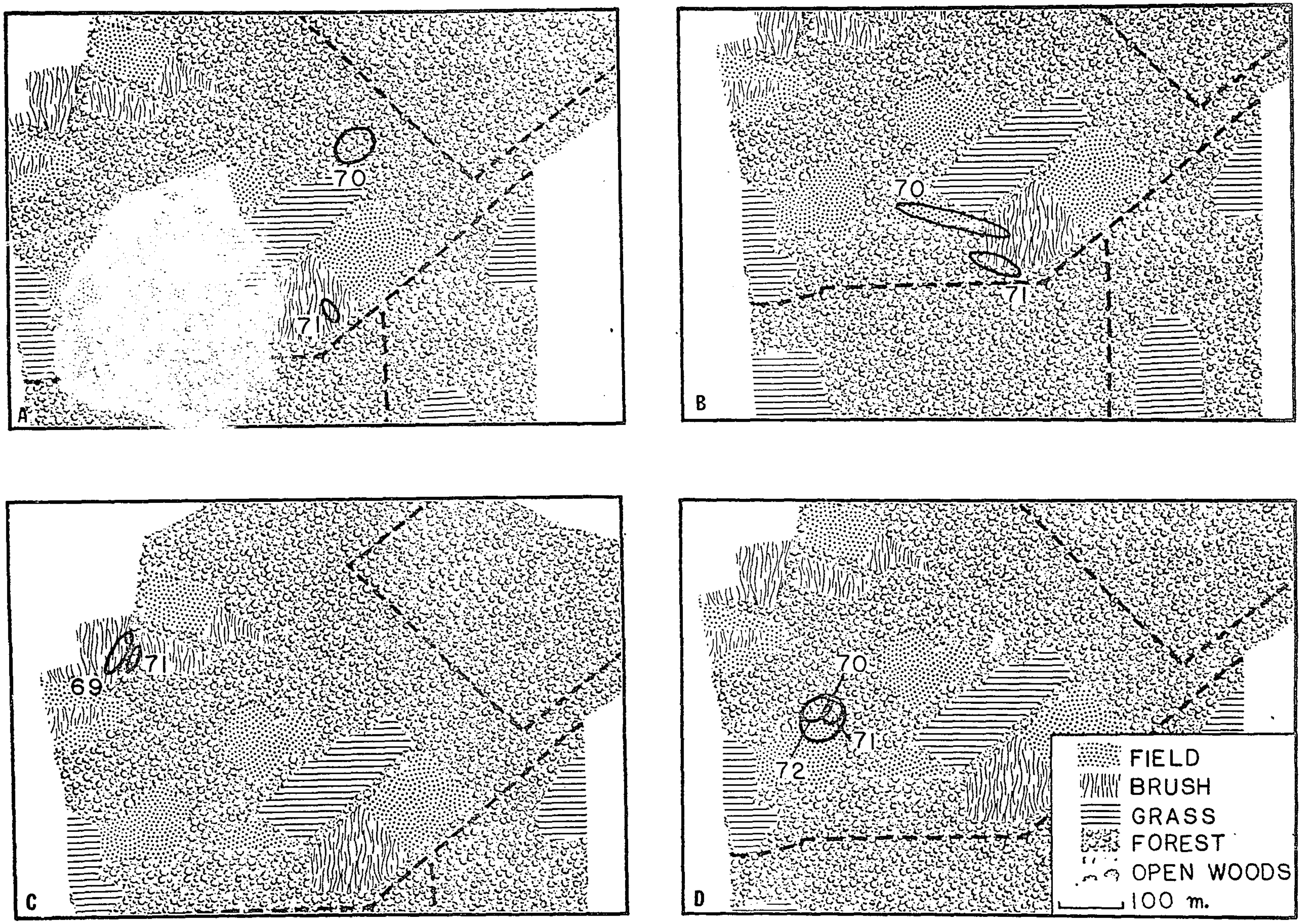

A
70
71
B
70
71
C
69
71
D
70
71
72
FIELD
BRUSH
GRASS
FOREST
OPEN WOODS
100 m.

Figure 29: 95% confidence regions of home ranges by years.
A: animal #106. B: animal #124
C: animal #132. C: animal #170

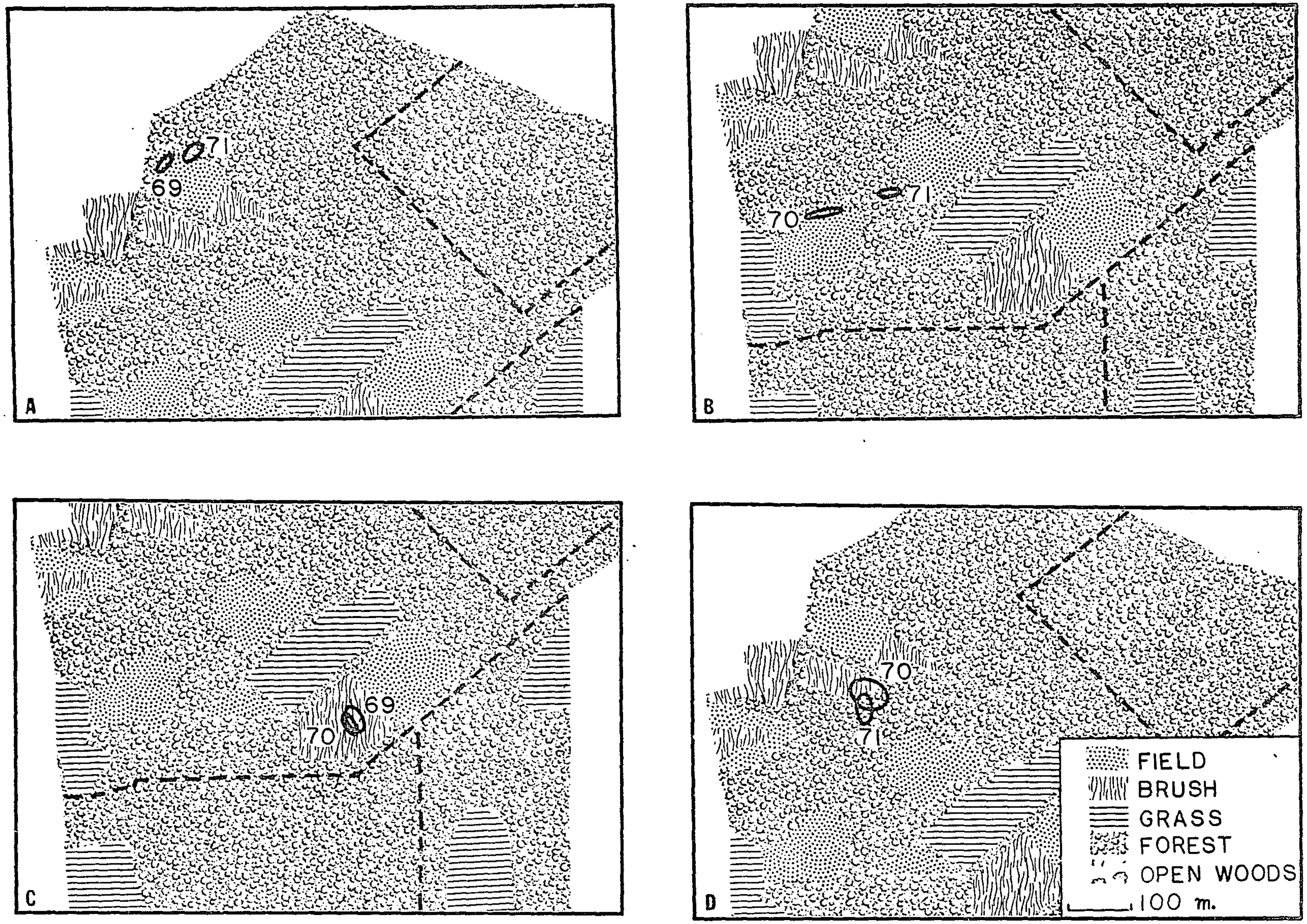

A
69
71
B
70
71
C
69
70
D
70
71
FIELD
BRUSH
GRASS
FOREST
OPEN WOODS
100 m.

Figure 30: Initial movements of hatchlings. N=nest.

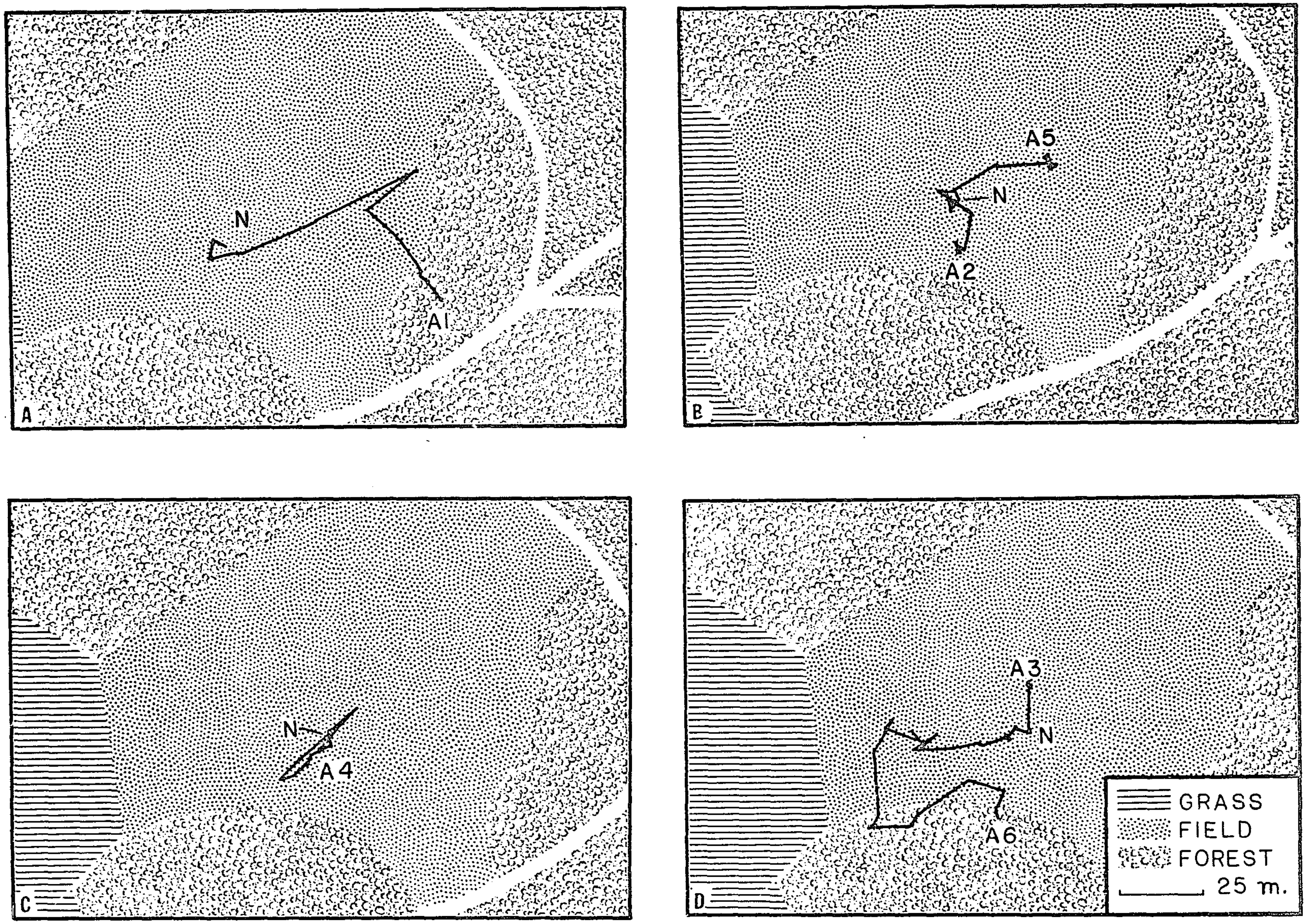
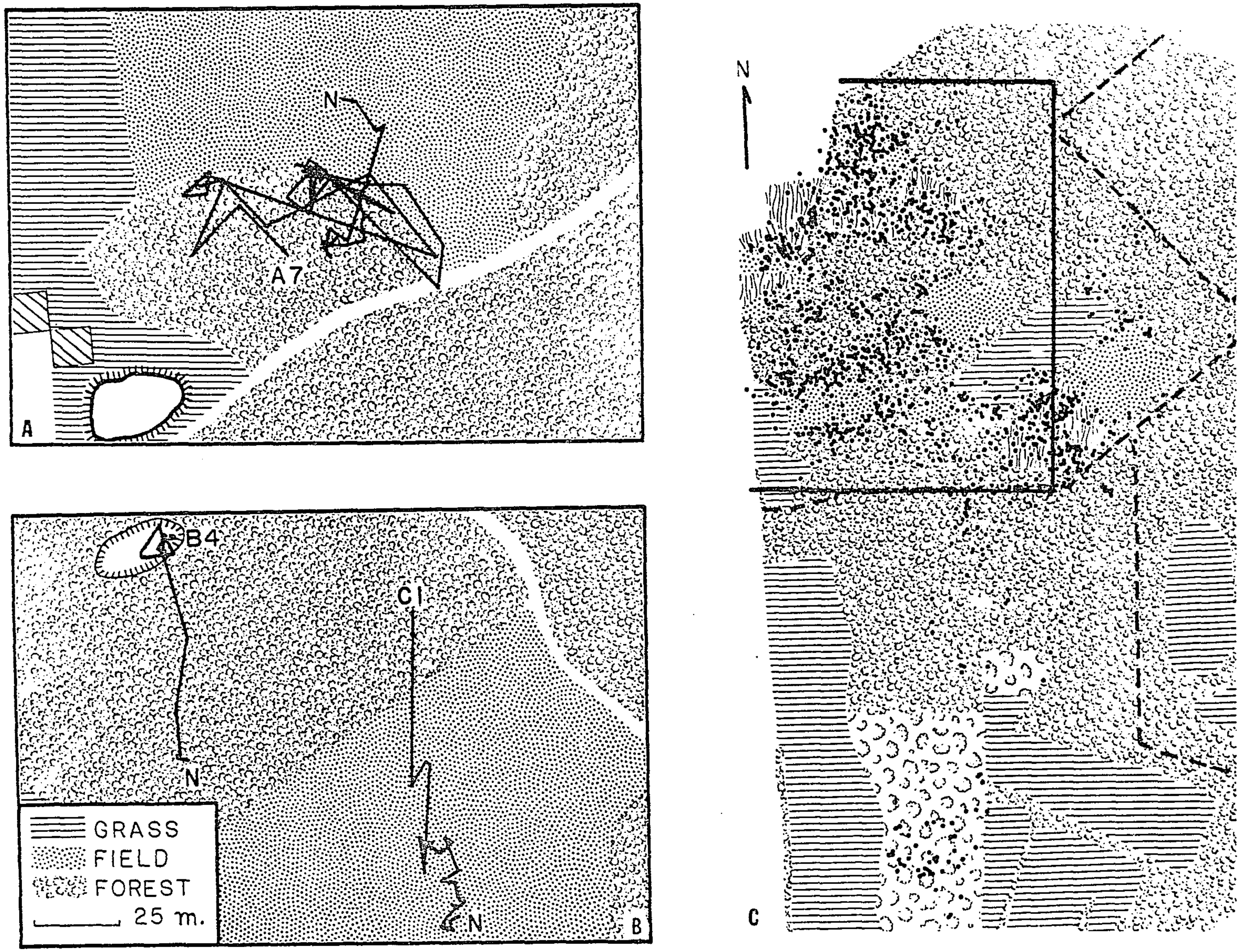

A
N
A1
B
A5
N
A2
C
N
A4
D
A3
N
A6
GRASS
FIELD
FOREST
25 m.

Figure 31A and B. Initial movements of hatchlings. N=nest.

Figure 31C: All observation points for all adult turtles.


N
A7
A
B4
C1
N
N
GRASS
FIELD
FOREST
25 m.
B
N
C