Studies on Home Range

Relevance of Home Range Concepts to Game Biology

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Introductory speech

Introduction

The purpose of this paper is to consider new developments in the concepts of home range and territory with a view toward their relevance to management of wildlife populations. Several review papers have adequately summarized the history of these concepts (Sanderson 1966, Brown 1966, Brown and Orians 1970).

Historically, the idea of home range developed from data which indicated that an animal normally lives (when one excludes migrations and erratic wanderings) in a rather specified area throughout its lifetime. Data of this type were usually collected from mark-recapture studies or by direct observation. More recently, radio tracking techniques have provided much more comprehensive data on how animals use space.

One of the first problems in the analysis of such data was to develop methodology for measurement of home range size. It was observed early that home range size generally increased with the number of observations or the length of time an animal was observed. Thus, methods have been proposed (Odum and Kuenzler 1955, Tester and Siniff 1965, Heezen and Tester 1967) to provide guidelines to determine the sample size needed for estimates of home range size. Once such determinations have been made there are many methods which may be used to define the amount of space occupied. An early but still widely used technique, generally referred to as the minimum area method, consists of the connection of outer points of a set of locations (Mohr 1947). Mathematical models developed to measure space occupied by an animal include the circular normal model proposed by Calhoun and Casby (1958) and a more general model based on an elliptical shape considered by Jenrich and Turner (1969), and further modified by Koeppel et al. (1973). These models result in an area estimate, and sometimes a variance statement. The form developed by Koeppel et al. (1973) includes parameters which take into account home range size, shape, and orientation in space. While newer models are including more than one characteristic, it would seem that we should strive for models where estimated parameters include the major variables affecting home range. Furthermore, if the concept is to be useful for comparisons within and among species, the model must allow for statistical testing of differences among these parameters.

Similar suggestions were made by McNab (1963) and Schoener (1971) who indicated that the home range concept is closely tied to energy requirements of the particular species. They further suggest that factors such as food density, food selectivity and metabolic rate are important variables in the determination of the home range characteristics. Since it is clear that food can be highly variable in space and time, it is likely
that home range size and shape will also vary according to this important parameter.

There are many other factors which one can visualize as influencing home range. In following paragraphs, we consider examples of these factors and also review some data which indicate their importance in the concept of home range.

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**Factors influencing home range**

Recent studies indicate that an animal’s home range is influenced by habitat, season of the year, and by social interaction with individuals of the same species and sometimes of different species. The importance of each of these factors will be considered in general terms and examples from our field studies will be used to show how these factors may operate under natural conditions.

Habitat can affect an animal’s home range in several ways. Each species needs food and cover to fulfill its life history requirements. Habitat satisfying each of these requirements must occur within the range of mobility of the species. When the location of an animal is known continuously, one can determine the specific kind of habitat used for each of its activities, and although many habitat types may occur within a home range the animal may utilize only a few of these. The term ‘habitat preference’ has frequently been used in reference to this type of situation.

Studies on habitat preference of moose (*Alces alces*) (Berg and Phillips 1973) in northwestern Minnesota revealed that this species had a marked preference for certain habitat types such as mixed willow (*Salix* spp.) greater than 10 ft. tall and avoided other types such as marsh (Fig. 1). Selection of this nature can be documented by relating the amount of time that an animal spends in a given habitat type to the proportion of this habitat available within the home range.

Habitat can also affect the determination of boundaries of the home range. Animals often indicate an awareness of natural features such as roads, lakes, or rivers. While they are able to cross or go around such features in the environment, they often establish boundaries of their home range at these locations. For example, Sargeant (1972) found that red fox (*Vulpes vulpes*) on the Cedar Creek Natural History Area in east-central Minnesota located boundaries of family group territories along natural features of the environment (Fig. 2).

The time factor, or seasonality, while not affecting home range *per se*, must be taken into consideration in any evaluation of how animals use space. Habitat requirements during the breeding season may be quite different from those during the non-breeding season, and seasonal changes in weather may necessitate use of different types of cover. Some species escape the rigors of extreme weather by migrating. For these, space utilization must be considered in terms of a summer home range and a winter home range with a connecting migratory corridor.

It is obvious that description of home range should include the time factor if the description is to be biologically meaningful. In earlier studies based on recapture or observation of marked animals, the time factor has been frequently ignored because of the difficulty of obtaining sufficient data. However, reports from recent studies using telemetry indicate that biologists are well aware of the importance of the time factor.

The response of white-tailed deer (*Odocoileus virginianus*) to seasonal change in central North America has been reported by Rongstad and Tester (1969). The size of the home range of an adult male increased from 269 acres in late winter to 3,600 acres in early spring, undoubtedly because of the rapid disappearance of the winter accumulation of snow (Fig. 3).

Another example illustrating the importance of considering time in the measurement of home range relates to the process of maturation of young animals and how they establish their home range during the first few weeks of life. Rongstad and Tester
(1971) found that the size of the home range of young snowshoe hares (*Lepus americanus*) increased from week to week during the first eight weeks of life and then remained relatively constant (Fig. 4). They interpreted these data as showing that the young hare established its "adult" home range by the time it reached the age of about eight weeks.

The type of social system which exists for a species has a marked effect on how that species uses space. Species in which pairs or family groups are territorial during all or part of the year are likely to be more uniformly spaced in the environment than are species with overlapping home ranges. The amount of overlap in the home range has a direct relation to the density of animals that a given area can support.

Dzubin (1969) investigated spacing of waterfowl and presented evidence indicating that spacing patterns are determined
Figure 2. Home ranges of three red foxes in east-central Minnesota during May 6-June 3, 1964. The lines between fox locations connect consecutive points in travel separated by no more than a 1-hour difference in time (Sargeant 1972).

Habitat conditions and that these can change from year to year in the same area. Under certain conditions ducks will exhibit classic territorial behavior associated with a specific area; however, in years when water levels are low and fewer bodies of water exist these same species may not maintain specific territories, but will exist in a social system based on individual distance (Condor 1949) or moving territory (Dzubin 1955).

Comparison of the spacing patterns of three species of medium-size mammals living on our study area provides another interesting example of the relation of social systems and home range. Red fox family groups are highly territorial and exhibit almost no overlap between adjacent home ranges (Fig. 2, Sargeant 1972). Striped skunk (Mephitis mephitis) males show a tendency to wander over the available habitat but do not appear to exhibit any evidence of territoriality, and perhaps may not even have a well-defined home range (Houseknecht 1971). Raccoons (Procyon lotor) show no tendency towards
 territoriality, but rather have overlapping home ranges (Mech et al. 1966, Schneider et al. 1971). All three species are night-active, all utilize some of the same food resources, and all may use underground dens at certain times of the year. Although all three species are present on the same area and much interspecific overlap of home ranges occurs, we have obtained little evidence of interspecific interaction. It would appear that the types of social systems which have evolved for these species enable them to co-exist even though competition could occur with respect to space utilization, food or den sites.

The preceding discussion has indicated certain variables which influence home range characteristics. It is curious that historically the measurement of size, and to some extent shape, have drawn most of the research attention and that pattern has generally been ignored. No doubt this emphasis indicates the fact that historically home range data were derived mainly from mark-recapture information and thus pattern could not be accurately determined. However, telemetry is now providing much data on pattern and its incorporation into the home range models would seem to be an essential consideration.

Inclusion of pattern has interesting possibilities since intensity of use of specific areas no doubt reflects the distribution of food and/or cover. Hence, a home range with a very clumped pattern would indicate a few areas of high desirability to the particular resident while a dispersed pattern would indicate more uniform distribution of requirements. Such suggestions were put forth by Altmann and Altmann (1970) and Schoener (1971) who indicated that a home range may be very large but yet the resident
may use only a very small part intensively. Schoener suggested that a concept of "home variance" be considered, and that this measure could be obtained by looking at the distance from the center of gravity. However, this concept appears similar to the circular normal model proposed by Calhoun and Casby (1958) where a prime difficulty is the assumption under the model that the home range is circular in nature. In addition, the variance estimate in this model is not a true reflection of pattern.

Although shape considerations have been implied in proposed models, these have limited the form to either circular or, more recently, elliptical (Jennrich and Turner 1969, Koeppel et al. 1973). Shape is no doubt correlated with the distribution of environmental requisites, and hence variation in shape could reflect important environmental characteristics.

While such models are important in evaluation of mark-recapture data they do not provide sufficient flexibility for the analysis of home range pattern obtained from telemetry positioning. Such data indicate details of movement which are caused by the factors we have previously discussed. These details are not generally present in mark-recapture data. Thus, to make meaningful contrasts of home range characteristics within species from one region to another and also among species, a model incorporating size, shape and pattern and measures of the covariance of these parameters is a minimum that is required. Although we do not have concrete suggestions at this time as to the mathematical form such a model should take, it would seem that its development is a realistic goal.

Relevance to game biology

When information is available on the above characteristics of the home range of a species, more effective management plans for manipulating numbers can often be implemented. Examples will be given illustrating how information on home range relates to such aspects of game management as predation, harvests and habitat development.

Predation will be considered in terms of the relations between red foxes and ringnecked pheasants (Phasianus colchicus) in agricultural habitat in central North America. Red fox family groups have been shown to have permanent territories ranging in size from about one to three square miles. Size is apparently quite independent of habitat type since the studies providing these values were carried out in open, grassland type habitat as well as in densely forested areas (Sargeant 1972, Ables 1969). One can conclude that if the size of the home ranges of red foxes is not influenced by habitat type, then they probably have not changed in size in recent times.

Ringnecked pheasants, on the other hand, appear to be restricted to areas where sufficient nesting and winter cover are present. In southern Minnesota this habitat consists primarily of marshes, wooded areas, hay meadows, fields of small grain such as oats (Avena sativa) or wheat (Triticum aestivum) and weedy areas along roads and railroads. The total amount of this type of habitat has decreased markedly in recent years due to changing agricultural practices. As a result, pheasant numbers have declined and the remaining birds are concentrated in

Figure 4. Home ranges of young male snowshoe hare 229 in east-central Minnesota for various periods after its birth on July 12. Home ranges were based on accumulation of 0.1-acre squares in which the animal had been located. Numbers within the home range represent the percentage of time spent in that particular square. Squares in which the animals spent less than one percent of time were not labelled (Rongstad and Tester 1971).
those areas still having suitable cover.

From these data, one can hypothesize that the effectiveness of foxes as predators on pheasants may have changed markedly over the past 20-50 years because of the way in which these two species utilize space. Foxes are occupying the same size of home range as in the past, whereas pheasants are essentially living in only those few acres within the home range of a fox family group where suitable cover still exists. In the 1930's and 1940's excellent pheasant habitat existed throughout the agricultural areas in southern Minnesota and pheasants were undoubtedly distributed throughout the home range of a fox family. With a widely distributed prey, the fox would likely be a less efficient predator than with a concentrated prey, as is the case with pheasants today. Data presented by Hessler et al. (1970) indicating that conventional methods of measuring predation may greatly underestimate the importance of fox predation on pheasants lend support to the hypothesis.

This may provide a partial explanation to Errington's (1967) implication that predation has little relevance in terms of its effect on sport hunting. Many of his field investigations were conducted during the 1930's and 1940's when game cover was often abundant. However, at the present time, because of the changes in habitat resulting in concentration of the remaining pheasants, red foxes may be very efficient predators on pheasants and may well exert a considerable influence on pheasant density.

The size of a species' home range must be taken into consideration when planning a harvest, whether by shooting or trapping. For most game species, shooting pressure is widespread and the harvest is typically controlled by establishing bag limits and a specified time period during which shooting can occur. In this situation the harvest is probably distributed throughout the range of the species. However, for species whose numbers are low, the effect of harvest can be quite different.

Studies on movements of certain species of game and furbearers have shown that individuals living in a particular locality constitute a rather distinct breeding popula-
tion. Home ranges of animals living in these populations are relatively small compared to the distances between populations. Consequently, there is little mixing of animals from one population to another. Harvests, therefore, would have to be made on the basis of each breeding population with limits established as to the number or percent of each sex and age category that could be taken from a given population. If home ranges were large with respect to the distances between breeding populations one would expect mixing and rapid recolonization of areas from which a large harvest had been made. Data presented at this Congress by J. Lentfer on polar bears (Ursus maritimus) provide an example of this situation.

With the strong emphasis that has been placed on habitat management to increase populations of game species in recent years, the relationship between habitat and home range becomes extremely important. Densities of animals can be increased by creating the required mix of habitat within the area of the species' home range and densities can be reduced by removing essential elements of the habitat, such as breeding or wintering cover.

Efforts are currently being made to increase the productivity of duck populations in agricultural areas in central North America by establishing tracts of several acres to tall dense vegetative cover. Such tracts were found by Duebbert (1969) to contain high densities of duck nests. In addition, hatching success was also found to be high.

All of the species of ducks breeding in the vicinity of these tracts of dense cover were found to nest in the tract. However, mallards (Anas platyrhynchos) made up only 9% of the breeding pairs of the area but contributed 40% of the nests in the dense cover. Duebbert suggested that mallards may have come from as far away as 3 to 5 miles to nest in this preferred cover. It would appear that the size of the mallards' home range was greatly influenced by the presence of this dense cover.

Success of a program to develop nesting cover, or any other component of breeding habitat, can be determined only in terms of
its effect on productivity of the population. If nests are concentrated in a few locations, the number of ducklings utilizing nearby water areas might be extremely high. Competition for food might become severe under such conditions and mortality of ducklings could occur due to food shortage. Alternatively, hens could lead their broods overland long distances to water areas located farther away from the nesting cover. This could also result in duckling mortality due to exposure or predation (Keith 1961, Dzubin 1969). Therefore, the effects of this proposed habitat manipulation on the movement patterns and home ranges of the species present must be evaluated.

A somewhat similar situation of duck nest concentration has been reported by Duebbert (1966). He located 121 nests of gadwalls (Anas strepera) on a seven-acre island. Breeding pairs and lone drakes near the island exhibited high levels of hostility. Home ranges, however, were several hundred acres. Duebbert concluded that individual distance or moving territory was a more appropriate description of the social organization of these birds than territory based on topographic reference. Gates (1962), on a study area in Utah, reported that breeding home ranges of gadwalls overlapped, but pairs used an average of only 67 acres. It is apparent from these examples that the home range of certain species of ducks, and probably many other animals, can be altered by habitat conditions and that such changes must be evaluated prior to initiating programs of habitat manipulation.

Conclusions

Recent data on animal movements obtained by telemetry have shown that an animal's home range is influenced by habitat, season of the year, and by social interaction. These factors determine the pattern of use of the home range space. A biologically meaningful concept of home range must include measures which reflect the influence of these factors. Such measures should be an integral part of any home range model.

Game biologists must be aware of these aspects of home range when developing management programs. The examples discussed above illustrate how management related to predation, harvest and habitat manipulation are dependent upon a thorough knowledge of home range.

References


