

ANIMAL MOVEMENTS AND CAPTURE-RECAPTURE DATA

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ABSTRACT

In studying animal movements the capture-recapture method is often used to measure dispersal rate or home range size. The recapture locations are often treated as if they are normally distributed. Several models which have been proposed to describe animal movement are considered here, including Brownian motion and the Ornstein-Uhlenbeck process. While these models predict normal distributions of animal locations at particular times, the distribution of recapture locations will not be normal if the animals enter the traps at random times. This fact may help to explain certain experimental observations.

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INTRODUCTION

When animal movements are studied by capture-recapture methods the data on recapture locations are sometimes analyzed as if the locations where the animals are recaptured have a bivariate normal distribution (Dobzhansky and Wright 1943, 1947; Calhoun and Casby 1958; Jennrich and Turner 1969). One mechanism suggested (Andrewartha and Birch 1954) to produce such a bivariate normal distribution for dispersing animals is random movement (or Brownian motion) of the animals.

A model which has been proposed for movements of animals with home ranges is the Ornstein-Uhlenbeck process (Dunn and Gipson 1977). Like Brownian motion, the Ornstein-Uhlenbeck (OU) process describes a kind of random movement, but in the OU process there is a force back toward the center and this force increases linearly as the distance from the center increases.

If animal movements are accurately described by Brownian motion or the OU process, then the locations of animals at a given time will have a normal distribution. If, however, animals can actually enter the traps at various times, then the distribution of the locations where animals are trapped will not be a single normal distribution but

will be a mixture of normal distributions.

The cases of animal dispersal and of home range use will be discussed.

Dispersal. In their studies of dispersal distance Dobzhansky and Wright (1943,1947) released a number of genetically marked Drosophila and for several days they counted the number of flies recaptured in each of a number of traps arranged in the shape of a cross with the release point at the center of the cross.

According to Dobzhansky and Wright (1943, p. 320): "The simplest hypothesis with respect to the dispersion is that the distribution on any day is a radially symmetric bivariate normal one except as modified by local conditions." The observed distribution was not normal. There were too many flies trapped near the release point and far from the release point and too few trapped at intermediate distances. That is, the distribution was leptokurtic: the kurtosis (the ratio of the fourth central moment to the squared variance) was too great. For a normal distribution the kurtosis is 3 and for most experiments the kurtosis observed by Dobzhansky and Wright was four or more and was particularly high on the first day.

Home ranges. In many studies on home range in small mammals the animals are captured, marked, released and recaptured. The locations at which they are recaptured are used to determine the home range. Hayne (1949) suggested that the animals might not use their home range

uniformly and suggested what was later called a "utilization distribution" by VanWinkle (1975). Calhoun and Casby (1958) suggested that a bivariate normal distribution be used to represent a home range. They considered a circular home range, while Jennrich and Turner (1969) suggested that the home range might have an elliptical shape.

In her work on Peromyscus Myton (1974) demonstrated that capture-recapture data may show too many captures near the center of the home range or far from the center and too few at intermediate distances. She offered her data as evidence that the bivariate normal assumption may be wrong.

This paper shows that if animals forage at random this need not be reflected in a bivariate normal distribution of recapture locations. Different random mechanisms may be used to model animal movements and different models generally produce different distributions of recapture locations. Thus recapture locations may be used not only to estimate dispersal rate or home range size, but also to understand the movements themselves.

CAPTURE-RECAPTURE DATA AND THE ASSUMPTION OF NORMALITY

It is convenient if the locations where animals are captured or recaptured are normally distributed because then well-established statistical theory may be used. For animals

dispersing from a release point the rate of dispersal is of interest. If dispersal is random and uniform in all directions and the animals are trapped at the same time, then the recapture locations will be normally distributed and the dispersal rate may be identified with the variance of the resulting normal distribution. If the recapture locations have a radially symmetric bivariate normal distribution then there is only one parameter to worry about, the variance. Unfortunately, their data suggested to Dobzhansky and Wright that the normality assumption was wrong, that the distribution of recapture locations was leptokurtic. They suggested that non-normality was due to environmental heterogeneity and to variability between individual flies. Dobzhansky et al. (1979) have considered a more general diffusion model and suggest that flies move at different rates in different habitats. This conclusion is implicit in the earlier work of Dobzhansky and Wright.

Calhoun and Casby (1958) suggested a radially symmetric (circular) bivariate normal distribution for recapture data for animals with home ranges. If the recapture data accurately represent the pattern of use of the home range then the home range area will be proportional to the variance of the distribution of recapture locations.

If the distribution of recapture locations is bivariate normal, but not necessarily circular, then it is necessary to estimate three parameters, the variances in the East-West

direction and North-South direction and the covariance between the East-West locations and the North-South locations. Jennrich and Turner (1969) have considered this case and they suggest $6\sqrt{\det A}$ as a measure of the area of the home range. Here $\det A$ is the determinant of the covariance matrix.

If the recapture data is bivariate normal then it is preferable to estimate home range size using normal theory and a method such as Jennrich and Turner's instead of using the older methods such as "included area", which is the area of the convex area formed by joining the outermost recapture locations for a given animal. The home range size estimate obtained using the "included area" depends on the sample size and tends to increase as sample size increases. If recapture data is normally distributed then area estimates based on variances and covariances will be more precise than those based on "included area".

If recapture data is not normally distributed estimates of area based on variances and covariances may still be used, and in many cases the estimates will be more precise than those obtained by using "included area", but the interpretation of the estimates will no longer be so nice.

If the area of the home range is used uniformly, as seems to have been believed before Hayne's work (see Hayne 1949), and as is predicted by models by Cody (1971) and Ryke (1978), then the "included area will give a more

precise estimate of home range area than will Jenrich and Turner's method which is based on the assumption of normality.

In this paper a number of models of animal movement will be considered. The pattern of movement will determine the proportion of time spent at each part of an animal's range and will also determine the proportion of time the animal is captured at each part of its range.

While most of the models considered predict that the location of an uncaptured animal will have a normal distribution at any given time, it is not true that the locations where animals are recaptured will have a normal distribution. This is because animals will not all be caught at the same time. Thus the location of recaptures will have a distribution which is a mixture of normals. This idea is explored further below.

It is the movement of animals that is of interest, but I will treat the animal as a mathematical point, which I will refer to as a particle. This particle will be assumed to move according to mathematical rules and will be stopped or "caught" at a random time which will be independent of its movement. When I speak of the distribution of recapture locations I refer to the distribution of locations where my "particles" are "caught". In most of the models considered movement takes place in two dimensions but it is treated as if it is the result of two independent

one-dimensional processes. I only consider one-dimensional processes.

Brownian motion is considered as a model for movement of animals dispersing from a release point. For animals with home ranges two types of processes are considered, those with attraction toward a center, like the Ornstein-Uhlenbeck process or the Brownian bridge, and those where a boundary is respected, as in the models considered by Cody (1971) and Ryke (1978). The pattern of home range use (and as a consequence, the distribution of recapture locations) is strongly influenced by whether the movements are governed by attraction toward a center of avoidance of a boundary.

DISPERSAL AND BROWNIAN MOTION

In their experiments on the dispersal of Drosophila Dobzhansky and Wright (1943, 1947) considered the hypothesis that the distance moved by flies on a given day would have a radially symmetric bivariate normal distribution. Such a distribution would arise if the animal movements were random as suggested by Andrewartha and Birch (1954, p 94).

The mathematical version of random movement is known as Brownian motion or the Wiener process (see Karlin 1966 for a good discussion of Brownian motion). Since I am interested in the pattern of movements rather than the actual distances moved I will consider Standard Brownian motion, where the variance of the distance moved in unit

time is one. At time t , the location of the Brownian motion particle will have probability density

$$(1) \quad f(x,t) = \frac{1}{\sqrt{2\pi t}} \exp(-x^2/2t).$$

Notice that the variance of the location equals t , the time the particle has been moving. As time increases the particle tends to be further from the origin.

While the location of the Brownian motion particle has a normal distribution with mean 0 and variance t at a particular time t , if the particle is observed at random times, the observed locations will not be normal but will be a mixture of normals. This idea of looking at the Brownian motion particle at random times corresponds to trapping a dispersing animal at a random time. In fact, animals captured in capture-recapture experiments do not all enter the traps at the time the traps are examined but rather, they enter the traps at some time during the trapping interval.

In order to study the effect on the distribution of recapture locations of the fact that animals enter the traps at different times within the trapping interval a simple mathematical model is used. The animal movements are represented by Brownian motion and the time at which the Brownian motion particle is observed is assumed to be random, having either: a) a uniform, or b) a truncated exponential distribution over the trapping interval.

Calculations are done here assuming that capture time is distributed over the entire interval from release of the animals until the traps are examined. This assumption is probably more realistic in studies of home ranges than in dispersal studies but it is made for definiteness. If traps are set out at some time after the animals are released and examined shortly after they are set out then the animals recaptured will be caught at essentially the same time and my argument does not apply.

The truncated exponential distribution of capture times corresponds to having the chance of an uncaptured animal entering a trap at any time be constant. As the number of uncaptured animals decreases the number of animals tends to decrease because there are fewer animals remaining to enter the traps. The capture rate, k , may be determined by observing the proportion of released animals recaptured. If proportion p of the animals are recaptured during an interval, then the recapture rate k is given by

$$(2) \quad e^{-k} = 1 - p.$$

A uniform distribution of capture times is similar to having an exponential distribution with a very low capture rate.

If the capture rate has a uniform distribution; that is, if

$$g(t) = 1 \text{ for } 0 \leq t \leq 1, \\ = 0 \text{ otherwise,}$$

then the distribution of capture locations will have distribution

$$(3) \quad f(x) = \int g(t) \frac{1}{\sqrt{2\pi t}} \exp(-x^2/2t) dt \\ = \int_0^1 \frac{1}{\sqrt{2\pi t}} \exp(-x^2/2t) dt.$$

If the capture times have a truncated exponential distribution; that is, if

$$g(t) = \frac{e^{-kt}}{1 - e^{-k}} \text{ for } 0 \leq t \leq 1, \\ = 0 \text{ otherwise,}$$

then the distribution of capture locations will have distribution

$$(4) \quad f(x) = \int g(t) \frac{1}{\sqrt{2\pi t}} \exp(-x^2/2t) dt \\ = \frac{1}{1 - e^{-k}} \int_0^1 \frac{1}{\sqrt{2\pi t}} \exp(-kt - x^2/2t) dt.$$

Figure 1 shows the distribution given by (3) of recapture locations when the capture time has a uniform distribution. Only positive values of x are shown in the figure because the distribution is symmetric about 0. This distribution is compared with the corresponding normal distribution with the same variance. Notice that the distribution given by (3), which is a mixture of normals, has more probability assigned to values close to the mean and far from the mean while the single normal has more probability at intermediate distances. This leptokurtic

effect is greater for distributions given by (4) resulting from capture time having a truncated exponential distribution.

Dobzhansky and Wright (1943, 1947) used kurtosis as a measure of how well their recapture data fitted the normal distribution they assumed it would have. They found that the observed kurtosis was consistently too large, generally being 4 or more, while the kurtosis for a normal distribution is 3.

When the capture time has a uniform distribution the kurtosis of the resulting recapture location distribution is 4. When the capture time has a truncated exponential distribution the kurtosis of the capture locations will be greater than 4 and is given by

$$(5) \quad K_u = \frac{6(1 - e^{-k})(1 - e^{-k} - ke^{-k} - k^2e^{-k}/2)}{(1 - e^{-k} - ke^{-k})^2}$$

where k is the capture rate.

Figure 2 shows the kurtosis of the capture location as a function of the capture rate, k . As the capture rate increases the kurtosis also increases.

If the traps are not put out until some time after the animals are released the capture times will necessarily be distributed over a shorter interval than if the traps are available to capture the animals at any time after release. When the trapping interval is shorter the kurtosis of the distribution of capture locations will be smaller

but it will still be greater than 3 and thus the distribution will still be leptokurtic.

MOVEMENTS OF ANIMALS WITH HOME RANGES: THE ORNSTEIN-UHLENBECK PROCESS AND THE BROWNIAN BRIDGE

Brownian motion may fairly accurately represent the movements of dispersing animals, but for animals with home ranges, such as most birds and mammals, movements are not unrestricted and Brownian motion is not an appropriate model.

Dunn and Gipson (1977) have suggested using the Ornstein-Uhlenbeck process as a model to describe radio-tracking data on home ranges.

The Ornstein-Uhlenbeck process (see Breiman 1968) is a diffusion process with an elastic force toward the origin. If an animal were thought to begin movement from an origin, say a nest, at some time, and move randomly but with a tendency to move back toward the origin which was proportional to the distance from the origin, then the OU process might represent the animal's movement in one direction, say east-west.

For a particle that moves according to the OU process, starting at point a (different from the "origin" toward which the animal is attracted) at time 0, the distribution of the location of the particle at time t will be normal with mean $ae^{-\alpha t}$ and variance $\rho(1 - e^{-\alpha t})$ where α is the

"relaxation" rate and β is the limiting variance. A high value of α indicates a strong force toward the origin, while a high value of β indicates a large home range. For a particle starting at the origin the mean location will be 0 at any time t .

If the movement of an animal is thought of as a realization of an OU process beginning at the origin at time 0, and if the animals are trapped at a random time which is independent of location, then the distribution of capture locations will be a mixture of normals, as was the case with Brownian motion. And as in the case of Brownian motion, the kurtosis of the distribution of the resulting capture locations will be greater than that for a single normal, which is $K_u = 3$.