A Dynamic Test of Spatial Independence Among Bighorn Sheep

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Abstract

The spatial interactions of marked study animals are often of interest in studies of wildlife ecology. All forms of resource selection analysis assume that marked individuals move and select resources independently, and this is often violated when animals are social or territorial. For this paper we deal with relocation data collected from a gregarious species, bighorn sheep (*Ovis canadensis*), and wish to assess the spatial independence of marked animals. Many commonly used methods for quantifying spatial interactions do not include the spatial and temporal details of simultaneous relocation data. In their place, we used a modified nearest-neighbor method and data from three small herds of bighorn sheep in western Montana to test for independence among marked animals. Results suggested that marked ewes within each study area were not selecting habitat independently of one another. Consideration of spatial independence can be important in a *posteriori* analysis and interpretation of data, as well a *priori* consideration of necessary sample sizes.

Key words: bighorn sheep, habitat selection, overlap, *Ovis canadensis*, resource selection, spatial independence

Introduction

The spatial interactions of marked study animals are often of interest in studies of wildlife ecology. In particular, resource selection analyses require that study animals represent independent samples of space use. Animals that attract or avoid each other can violate this assumption, and thus lead to inflated sample sizes and biased results. While *a posteriori* assessment of sampling independence is encouraged, this issue should also be raised during *a priori* study planning. Given the often significant costs of capturing and monitoring many animals in an area, the *a priori* consideration of spatial independence might avoid a frustrating *a posteriori* discovery that 20 sampled animals are in fact acting as one.

Spatial independence is demanded across all forms of resource selection analysis. A variety of analytic methods are available within the broad field of resource selection, including chi-squared goodness-of-fit tests and confidence intervals (Neu et al. 1974, Byers et al. 1984), ranking methods (Johnson 1980), compositional analysis (Aebischer et al. 1993), and general linear models (Manly et al. 2002). Each of these methods has its own set of assumptions, but they all require that sampled animals select resources independently. We considered this assumption when dealing with simultaneous radio-telemetry data from a social species, bighorn sheep (*Ovis canadensis*). It was unclear if our study animals were selecting resources as a group or as individuals. Before pooling data, defining the appropriate sample unit for resource selection analyses required an assessment of spatial independence of marked individuals.

Many techniques have been used to quantify spatial independence, and they can broadly be categorized as static (Jorgensen 1968, Millspaugh et al. 2004) or dynamic (Cole 1949, Minta 1992, Millspaugh et al. 1998, Dasgupta and Alldredge 2000).

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Static analyses of spatial independence are generally a measure of shared space use (often home-range overlap) of two animals over a given study period. Dynamic methods require simultaneous relocation data and include the spatial and temporal information of each location in an analysis of independence. Simultaneous relocation data are often possible in telemetry studies with concentrated telemetry sessions, but the biologist must determine the maximum time interval between locations to consider them simultaneous.

While static analysis techniques are growing more sophisticated and studied (Millspaugh et al. 2004), we value the temporal information in simultaneous relocation data and will focus on dynamic methods for the remainder of this paper. Unfortunately, most dynamic tests are fairly simple comparisons of the number of times marked animals are observed together or apart. Cole's (1949) coefficient of association has been used sporadically in the study of bighorn sheep to coarsely assess group cohesion (Brown 1974, Elenowitz 1984, Ebert 1993) and is simply a ratio of how often two animals were observed together over the total number of times they were located. More recent tests are available (Millspaugh et al. 1998, Dasgupta and Alldredge 2000), but they reduce the spatial characteristics of radio-telemetry data into categories of "together" or "apart." This creates arbitrary cut-off values for defining how close the animals must be to be "together" and categorizes animals that are 500 m apart the same as animals 5000 m apart. It also excludes avoidance as a testable form of dependence between study animals.

In this paper, we present an alternative method for quantifying spatial independence with relocation data that has been used to detect avoidance behavior between carnivores (Keenan 1981, Major and Sherburne 1987, Arjo and Pletscher 1999). The modified nearest-neighbor technique tests dependence between two animals as a function of the distance between them, and we use it to detect dependence in radio-telemetry data from bighorn sheep. This method allows researchers to explicitly test relocation data for spatial independence before carrying out further analyses.

METHODS

Study Areas

We studied Rocky Mountain bighorn sheep (*O. c. canadensis*) at three sites (Bearmouth, Garrison, and Skalkaho) in the Rocky Mountains of western Montana at elevations of ~ 1100-2000 m. The Bearmouth (N 46° 43', W 113° 27') herd occupied parts of the southern Garnet Range, 50 km east of Missoula, Montana. The Garrison (N 46° 31', W 112° 50') herd was located in the northeastern foothills of the Flint Creek Range, 100 km east of Missoula, and the Skalkaho (N 46° 10', W 113° 59') herd was in the western Sapphire Mountains, 75 km south of Missoula.

Data Collection

In March 2001, we captured and radio-collared 15 adult female Rocky Mountain bighorn sheep at three sites using a net-gun from a helicopter (Krausman et al. 1985). We attempted to capture animals from different subgroups within each herd, and finished with two (Bearmouth), seven (Garrison) and six (Skalkaho) radio-collared animals per site. Between March 2001 and August 2002 we collected 1019 locations for these 15 ewes. We allotted a minimum of 3 days between successive locations for the same animal to ensure suitable temporal independence within an individual set of locations (Swihart and Slade 1985, Swihart et al. 1988, Ebert 1993, McNay et al. 1994). We sorted locations by herd and season, so analyses were done for a given pair of ewes of the same herd during the same season. Biologically meaningful seasons were selected by finding noticeable shifts in habitat use by ewes during the transitional periods. For example, a notable shift towards rocky escape terrain marked the beginning of lambing season each spring. The lambing season lasted from early May through late July, the fall season from early August through late November, and the winter season from early December through late April. Analysis for each season required a minimum of 10 pairs of simultaneous locations (Arjo and Pletscher 1999).

The Modified Nearest-Neighbor Test

The nearest-neighbor test detects whether two animals are randomly located throughout the landscape in relation to one another. Significant results would come from animals that are closer together or further apart than would be expected from random association. It begins with a set of "simultaneous" locations for two animals over time. For our purposes, "simultaneous" meant the two animals were located on the same day, roughly within an eight-hour period. A distribution of distances is created by measuring the distance between the two animals for each pair of simultaneous locations. On a day when the two animals were located together, this distance is essentially zero.

Another distribution of distances was created by randomly pairing the same set of locations without considering time. For example, animal A's location on day 3 might be paired with animal B's location on day 12. These random pairs were selected with replacement; we used a sample size of 500 randomly selected pairs to get a distribution of 500 distances. We used the non-parametric Mann-Whitney *U* to test for differences between these 2 distributions: 1) distances between simultaneous locations of two ewes, and 2) distances between the same set of locations randomly paired with replacement. *P*-values provide a measure of statistical significance, or consistency, when testing independence but do not necessarily relate to the magnitude of the difference (Anderson et al. 2000). To consider biological significance, we also calculated the median separation distances and effect sizes (mean distance between randomly paired locations - mean distance between simultaneous locations) for each herd/season.

We applied this test to ewes from three herds with sample sizes of 2, 7, and 6 radio-collared ewes, resulting in 1, 21, and 15 possible ewe-pairs/herd, respectively. We considered the distribution and range of effect sizes and *P*-values to assess the degree of independence at the herd level.

Results

We found a lack of independence between bighorn ewes within all three herds (Table 1). Median separation distances were small, ranging from 0 to 570 m, and all effect sizes were positive, indicating that ewes were consistently closer together than random expectations. A single ewe-pair was analyzed for the Bearmouth herd; effect sizes were large, and *P*-values were low across seasons (Table 1). This suggests dependence in the movements and resource selection of these two ewes. Twenty-one combinations of ewe-pairs/season from the Garrison herd also showed large effect sizes and low significance values (Table 1); these seven radio-collared ewes evidently lacked independence in their movements. Fifteen possible combinations of ewe-pairs/season in the Skalkaho herd produced a wider range of *P*-values, though effect sizes were consistently positive (Table 1). Each ewe was dependent on at least one other ewe/season, and we found no evidence of segregation between groups of ewes. We concluded that these Skalkaho sheep lacked independence in their movements and should be analyzed as a herd instead of as individuals.

Discussion

We detected dependence among individuals in all three herds of bighorn sheep using nearest-neighbor analyses. It is inappropriate to consider data for each ewe as an independent sample of movement or habitat use. Instead of 15 independent samples of individual use, we have three independent samples of herd use.

Limited solutions are available when a lack of independence has been detected in a set of data. In terms of resource selection, we considered two methods of defining the sample unit. Analyses like the chi-square goodness-of-fit test (Neu et al. 1974) and general liner models (Manly et al. 2002) define the relocation as the sample unit.

Table 1. Median separation distances (m), effect sizes (m) and Mann-Whitney *U* Test probability values for modified nearest-neighbor tests of spatial independence between bighorn sheep ewes of Bearmouth ($n = 2$), Garrison ($n = 7$), and Skalkaho ($n = 6$), Montana, 2000-2001. All possible ewe-pairs within each herd were tested. Separation distance is the median distance between simultaneous locations of ewes. Effect size per ewe-pair = (mean distance between randomly paired locations – mean distance between simultaneous locations).

		Season								
		Lambing			Fall			Winter		
Site	Ewe-pairs	Median separation (m)	Median effect size (m)	*P*	Median separation (m)	Median effect size (m)	*P*	Median separation (m)	Median effect size (m)	*P*
Bearmouth	1	290	1153	<0.001	0[1]	780	0.002	570	373	<0.001
Garrison	21	150	518	<0.001 - 0.012	27	977	<0.001 - 0.003	149	852	<0.001 - 0.096
Skalkaho	15	313	622	<0.001 - 0.617	357	224	<0.001 - 0.460	472	441	<0.001 - 0.907

[1] Distance between ewes was recorded as 0 m on days when animals were located together.

In these cases, we suggest data be pooled, switching the sample unit from the locations of individuals to the location of groups. In this way, a group of five radio-collared animals in the same place would be recorded as a single location, and a single radio-collared animal in a different place would be another group location (a group of one). This approach has been used in past studies of gregarious animals like bighorn sheep (Gionfriddo and Krausman 1986, Andrew et al. 1999).

In analyses like Johnson's (1980) ranking method or compositional analysis (Aebischer et al. 1993) where the animal, and not the relocation, is the sample unit, a solution is less evident. If there are multiple social groups of dependent animals, (but the groups remain independent), then the sample unit might become the social group. This could require much data, as in the case of our three herds of bighorn sheep; we have three independent populations, and $N = 3$.

Before pooling these data, we considered the difference between statistical dependence and biological dependence (Millspaugh et al. 1998). For example, in studies of obligatory cooperative hunters, such as African hunting dogs (*Lycaon pictus*), the appropriate sample is the pack, and data from individuals within a pack should be pooled. Radio-collared elk (*Cervus elaphus*) that converge on a patch of scarce winter range may show a lack of statistical independence, when in fact, each elk made an independent choice to be there. Biologically, one might still consider each elk an independent sample (Millspaugh et al. 1998). In the case of bighorn sheep, researchers might argue that ewes congregate on steep, cliffy habitat during lambing season because it is the best habitat, not because of dependence. Each ewe may make an independent choice to be there. However, social groups are a consistent, year-round behavior of bighorn sheep (Geist 1971), and we observed a lack of independence across all seasons; this suggested both statistical and biological dependence. We do not, however, believe that bighorn data from a given site should always be pooled due to lack of independence. Festa-Bianchet (1986) found that three distinct populations of bighorn ewes used a single area during different times of the year. A test of spatial independence with such data would reveal independence between groups, and prevent the loss of information by pooling data across independent study animals.

Dasgupta and Alldredge (2000) adjusted the Neu et al. (1974) method of analysis to incorporate dependency. Unfortunately, their dependency parameter reduces spatially continuous location data into groups of "together" or "apart," and is a less sensitive test than that presented in this paper. However, their goal of accounting for dependency in resource selection analyses is a promising one. They include the degree of independence as an additional parameter in the chi-square goodness-of-fit test for resource selection. We encourage development of such a technique for more recent resource selection analyses like compositional analysis or generalized linear modeling.

Spatial independence is an important assumption in the study of resource selection by animals. When simultaneous data are collected, it is prudent to make full use of all the spatial and temporal information available in such data. We recommend the modified nearest-neighbor test as a dynamic analysis of independence between study animals. Although we have focused on *a posteriori* detection of spatial independence, this is an issue that should be considered *a priori* in future studies. Before expending great effort and resources into marking dependent animals, we encourage researchers to take into account the biology and behavior of the study species. Both *a priori* and *a posteriori* consideration of this issue will improve the reliability of results.

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