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DISCUSSION PAPER

Use of Serial Dependence to Indicate Movement Decisions by Woodland Caribou in North-central British Columbia

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ABSTRACT

Methods relied primarily on using Schoener's ratio to test 11,296 VHF and 57,287 GPS telemetry relocations to distinguish serially independent segments of movements made by 216 radio-collared woodland caribou monitored from 1991 to 2006 in north-central British Columbia. Movements that caused sequentially collected relocations to become dependent were considered to be spatially and temporally different from the preceding independent set of relocations and therefore could be potentially interpreted as a decision by caribou to move to a significantly different place.

ACKNOWLEDGEMENTS

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TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

INTRODUCTION

Animal relocation data from serially-dependent datasets is problematic because the data contain redundant information that can bias home range estimates and other conclusions about animal ecology derived from relocation data. These datasets hold less information than independent datasets of equal size (Swihart and Slade 1985*b*, McNay et al. 1994, Hansteen et al 1997). Generally, increasing the time interval between animal relocations would provide more opportunity for animals to be found at random locations within their home range and therefore decreases autocorrelation among the data (Swihart and Slade 1985a, McNay et al. 1994, Hansteen et al. 1997, Schindler 2005). A test to identify serial dependency in univariate data was provided by von Neumann (1941) but relocation data are bivariate having spatial co-ordinates on both vertical and horizontal axes. Schoener (1981) developed a comparable test for bivariate data that can be used to identify temporally dependent relocations (i.e., when departure from independence occurs). Independence in relocation data is assured when the current observation is not a function of the last observation (McNay et al 1995).

Investigations that reveal patterns in the timing and location of animal movements can provide us with important biological information about use of resources. This is particularly important for species that are threatened of becoming locally extirpated, such as woodland caribou (*Rangifer tarandus caribou) (COSEWIC 2002*). Populations of woodland caribou have declined through most of their range in North America (Chowns and Gates 2004, McLoughlin et al. 2003, Wittmer et al. 2005) and successful mitigation of the decline has yet to occur. Factors leading to the decline are considered to be: (1) loss of range due to timber harvesting (Chowns and Gates 2004, Wittmer et al. 2005), mining, or development of oil and gas resources (Nelleman and Cameron 1996, Bradshaw et al. 1997, James 1999); (2) disturbance and displacement from range by humans seeking recreational opportunities (Messier et al. 2004, Seip et al. In Press), agricultural and industrial development (Chowns and Gates 2004, Dyer et al. 2001), or permanent habitation; (3) increased direct mortality resulting from excessive hunting (Johnson 1985, Seip and Cichowski 1996) or increased predation (Rettie and Messier 1998, McLoughlin et al. 2003, Wittmer et al. 2005); or (4) a combinations of these factors. Observing behaviors of caribou based on relocations of radio-collared animals has been, and will continue to be, fundamental to understanding their population decline. The objective of our study was to investigate the use of Schoener's ratio to identify disparate use of space made by woodland caribou. Outcomes from this investigation and understanding of autocorrelation in our data would presumably allow us to make biological inferences about caribou movement patterns and provide a means for weighting the importance of individual samples in subsequent use of the data.

STUDY AREA

The study area was the recovery planning area for the Wolverine, Scott, Takla and Chase caribou herds, and the management area for the Finlay caribou herd (Figure 1). The area spanned the boundary between the Northern and Southern Mountains National Ecological Areas in north-central British Columbia throughout the Rocky Mountain foothills on the east side of Williston Reservoir north to the Peace Arm and in the

Omineca Mountains on the west side of Williston Reservoir north to the Ingenika River. It also included an area north of the Williston Reservoir and east of Fort Ware (N57°30'00'', W125°24'00'') through the Rocky Mountains to Red Fern Lake. The Wolverine area was 8,443 km^2 in rolling, high-elevation foothills; the Chase area was 17,330 km^2 and situated in relatively more steep, mountainous terrain, the Takla study area was 5,000 km^2 with considerably gentler terrain than the other study areas, the Finlay area was 2,483 km^2 with a range of terrain from steep mountainous areas to the broad U-shaped Finlay River valley; and the Scott area was 5,949 km^2 with rolling foothills east of the Williston Reservoir and a relatively flat plateau west of the Williston Reservoir. Valley bottoms and mid-slopes of the areas were dominated by relatively cool and dry, or cool and moist, macroclimates of short growing seasons leading to boreal ecosystems of white and black spruce (*Picea glauca (Moench) Voss*) and *P. mariana (P.Mill) B.S.P*) (Meidinger and Pojar 1991). Large-scale and frequent wildfires were characteristic prior to fire control policy (DeLong 2002). Common in these ecosystems were large, relatively flat areas of well-drained fluvial deposits, which in combination with frequent fires gave rise to large areas of forest dominated by even-aged lodgepole pine (*Pinus contorta Dougl*). Generally, a cold moist macroclimate with long, cold winters characterized upper slopes where Engelmann spruce (*P. engelmannii Parry ex Engelm.*) and subalpine fir (*A. lasiocarpa (Hook.) Nutt*.) dominated. At the northern extent of the Chase and Finlay areas, deciduous shrubs can dominate the upper slopes. Alpine tundra prevailed above tree line (~1,600 m) throughout all areas.

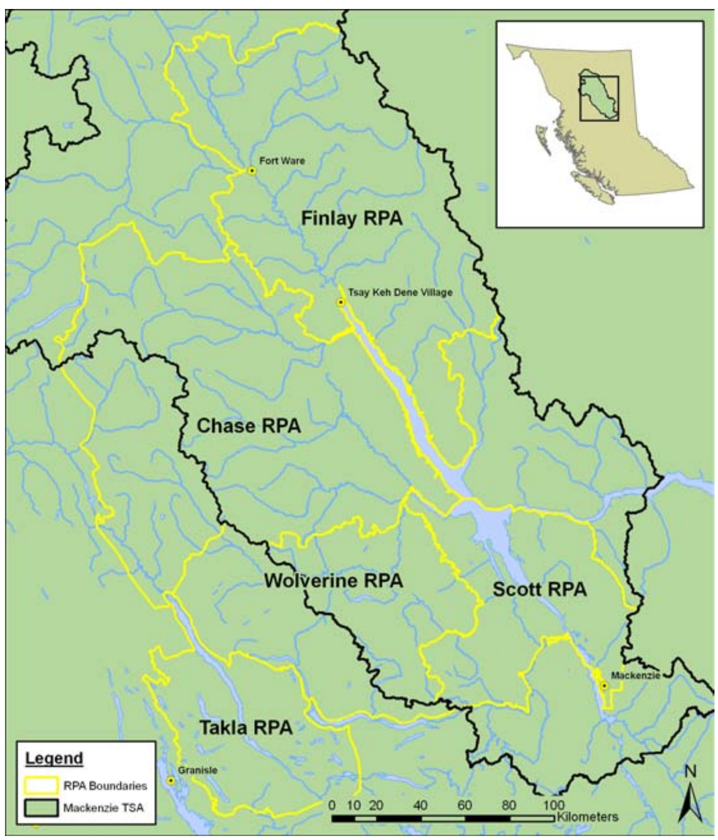

Figure 1. Geographic representation of the recovery planning area (RPA) for the Wolverine, Scott, Takla, and Chase caribou herds, and the management area for the Finlay caribou herd.

METHODS

Caribou Location Samples

We or researchers previous to us, fit caribou with Very High Frequency (VHF) radio transmitters containing mortality sensors from 1991 to 2004. Some collars also contained global positioning system (GPS) technology. Caribou relocations were usually sampled at 1-2 week intervals until the end of the study or death of the animal, given that radio contact was maintained. During the day, a Cessna 185, fixed-wing aircraft was used to facilitate sampling VHF relocations. GPS data were collected using Televilt (GPS-Simplex g01-01010, Televilt International, Lindesberg, Sweden) and Lotek (GPD 1000, Lotek Engineering, Newmarket, Ontario) GPS receivers. Animals were captured in the Finlay herd between 1999 and 2003, in the Scott herd in 2002, in the Wolverine herd from 1991 to 2004, in the Takla herd from 1996 to 1997, and in the Chase herd from 1991 to 1992 and then again from 1997 to 2003. Details of the collaring methods, deployment schedules, relocation schedules, and management of data were reported by McNay and Voller (Submitted). Relocations from radio-tagged calves of radio-collared adult, females were not included for analysis under the assumption that relocations would be redundant.

Analytical techniques

The methods we followed were similar to Swihart and Slade (1985a) and McNay et al. (1994), where we iteratively resampled data to construct 6 data subsets characterized by increasing time intervals between relocations. The 6 intervals we attempted to create in the subsampled data were: ≥2-hour, ≥4-hour, ≥1-day, ≥1-week, ≥3-week, and ≥5-week. Because of the nature in which caribou travel we constructed individual data strings for each animal, segregated by relocations >45 days apart. Only data strings that included more than three observations were retained for analysis. We calculated the critical value of Schoener's ratio for each animal data string using methods suggested by Swihart and Slade (1985a,b) to test the null hypothesis that caribou relocations were independent. We chose α = 0.25 (Swihart and Slade 1986, McNay et al. 1994).

We assessed normality (P = 0.05) of the distance between locations by using a Kolmogrov-Smirnov test (D).

We used logistic regression with maximum likelihood estimation to model the probability of a relocation being dependent. Probability of a dependent relocation (P_{dr}) took the form:

$$P_{dr} = \frac{\exp(\beta_0 + \beta_1 x_1 + \beta_2 x_2 + ... + \beta_n x_n)}{1 + \exp(\beta_0 + \beta_1 x_1 + \beta_2 x_2 + ... + \beta_n x_n)}\text{; where}$$

$ß_0$ was the regression intercept and $ß_1 … ß_n$ were coefficients for independent variables $x_1 … x_n$. We used the Akaike's Information Criterion with small-sample bias adjustment (AICc), output from Proc Logistic (SAS Institute Inc., Cary, North Carolina), to help identify a suite of parsimonious models that explained our data best among the possible combinations of variables (Burnham and Anderson 2002).

RESULTS

We obtained 11,296 vhf and 57,287 GPS relocations from 216 individual caribou observed from 1991 to 2006. The mean time between locations in each data subset was: 47.1 hours (SE = 0.5, N = 63,255) in the ≥2-hour, 56.9 hours (SE = 0.6, N = 52,412) in the ≥6-hour, 5.0 days (120.2 hours, SE = 1.1, N = 24,790) in the ≥1-day, 1.9 weeks (320.6 hours, SE = 2.1, N = 9,236) in the ≥1- week, 4.0 weeks (665.7 hours, SE = 2.7, N = 4,199) in the ≥3-week, and 6 weeks (1008.9 hours, SE = 4.1, N = 2429) in the ≥5-week. The average number of data strings per animal in each of the data subsets was 2.72 (SE = 0.15) in the ≥2-hour, 2.71 (SE = 0.15) in the ≥6-hour, 2.72 (SE = 0.15) in the ≥1-day, 2.67 (SE = 0.15) in the ≥1- week, 2.49 (SE = 0.13) in the ≥3-week, and 1.99 (SE = 0.11) in the ≥5-week.

Independence of Relocation Observations

We rejected the hypothesis of independence (P < 0.25) for most (>50%) animal data strings regardless of the time interval between relocations (Figure 2). Increasing the time interval between relocations did not increase the number of independent animal relocation data strings for the ≥2-hour, ≥6-hour and ≥1-day time interval classes. Increasing the time interval to ≥5 weeks resulted in a modest increase in the number of independent animal strings (~31% of animal strings tested) (Figure 2). The number of relocations and gender both contributed to the probability of a data string becoming serially dependent (

Table 1).

Distance Between Relocations

The average distance between relocations increased as the time interval between locations increased (Figure 3). Distance between relocations was not distributed normally. Generally, the degree of normality decreased as the time interval increased for the ≥2-hour (N = 62,708, D = 0.374, P = <0.0100), ≥6-hour (N = 51,867, D = 0.364, P = <0.0100), ≥1-day (N = 24,246, D = 0.312, P = <0.0100), ≥1-week (N = 8705, D = 0.225, P = <0.0100), ≥3 week (N = 3746, D = 0.194, P = <0.0100), and ≥5-week (N = 2098, D = 0.177, P = <0.0100) time interval classes. In all data subsets, there was relatively fewer large locations with most of the data falling within a range of 0.3 to 13 km.

Chronological plots of Schoener's Ratio (1981) and distance between relocations (Figure 4) demonstrated that large movements could cause a lack of independence in the data subset. However, subsequent movements did not affect the overall conclusion of serial dependence within the data subset.

Table 1. Logistic regression model estimating the probability of dependency in data.

	Intercept	Function	Estimate	Standard Error	Chi-Square	P
2-hour time interval						
	Intercept	Dependent		Reference		
		Independent	-0.7549	0.3599	4.40	0.0360
Locations per animal string		Dependent		Reference		
		Independent	0.3523	0.0588	35.87	<.0001
Gender	Male	Dependent		Reference		
		Independent		Reference		
	Female	Dependent		Reference		
		Independent	-0.4675	0.1944	35.87	0.0162
6-hour time interval						
	Intercept	Dependent		Reference		
		Independent	-0.7347	0.3658	4.03	0.446
Locations per animal string		Dependent		Reference		
		Independent	0.3577	0.0598	35.84	<.0001
Gender	Male	Dependent		Reference		
		Independent		Reference		
	Female	Dependent		Reference		
		Independent	-0.5239	0.2017	6.75	0.0094
1-day time interval						
	Intercept	Dependent		Reference		
		Independent	-0.6823	0.3616	3.56	0.0591
Locations per animal string		Dependent		Reference		
		Independent	0.3527	0.0591	35.67	<.0001
Gender	Male	Dependent		Reference		
		Independent		Reference		
	Female	Dependent		Reference		
		Independent	-0.5175	0.2015	6.59	0.0102
1-week time interval						
	Intercept	Dependent		Reference		
		Independent	-0.9525	0.3107	9.40	0.0022
Locations per animal string		Dependent		Reference		
		Independent	0.3435	0.0490	49.14	<.0001
Gender	Male	Dependent		Reference		
		Independent		Reference		
	Female	Dependent		Reference		

		Independent	-0.2426	0.1652	2.16	0.1421

3-week time interval						
	Intercept	Dependent		Reference		
		Independent	-0.9029	0.2767	10.65	0.0011
Locations per animal string		Dependent		Reference		
		Independent	0.3007	0.0454	43.88	<.0001
Gender	Male	Dependent		Reference		
		Independent		Reference		
	Female	Dependent		Reference		
		Independent	-0.0762	0.1357	0.32	0.5746
5-week time interval						
	Intercept	Dependent		Reference		
		Independent	-0.0395	0.2651	0.02	0.8817
Locations per animal string		Dependent		Reference		
		Independent	0.1586	0.0405	15.33	<.0001
Gender	Male	Dependent		Reference		
		Independent		Reference		
	Female	Dependent		Reference		
		Independent	-0.3088	0.1522	4.12	0.0424

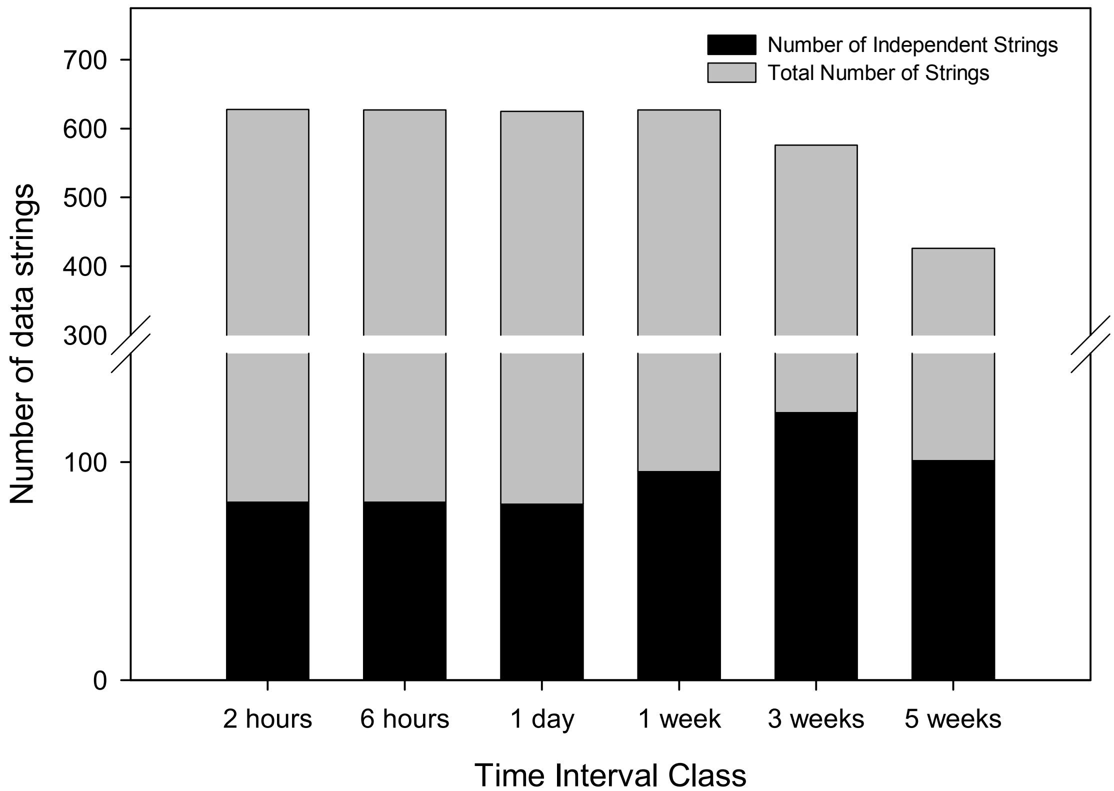

Figure 2. Total number of independent animal strings in each of the time interval classes (2-hour, 6-hour, 1-day, 1-week, 3-week, and 5-week). The area shaded in grey denotes the total number of animal strings sampled. The area shaded in black denotes the total number of independent animal strings identified by Schoener's Ratio.

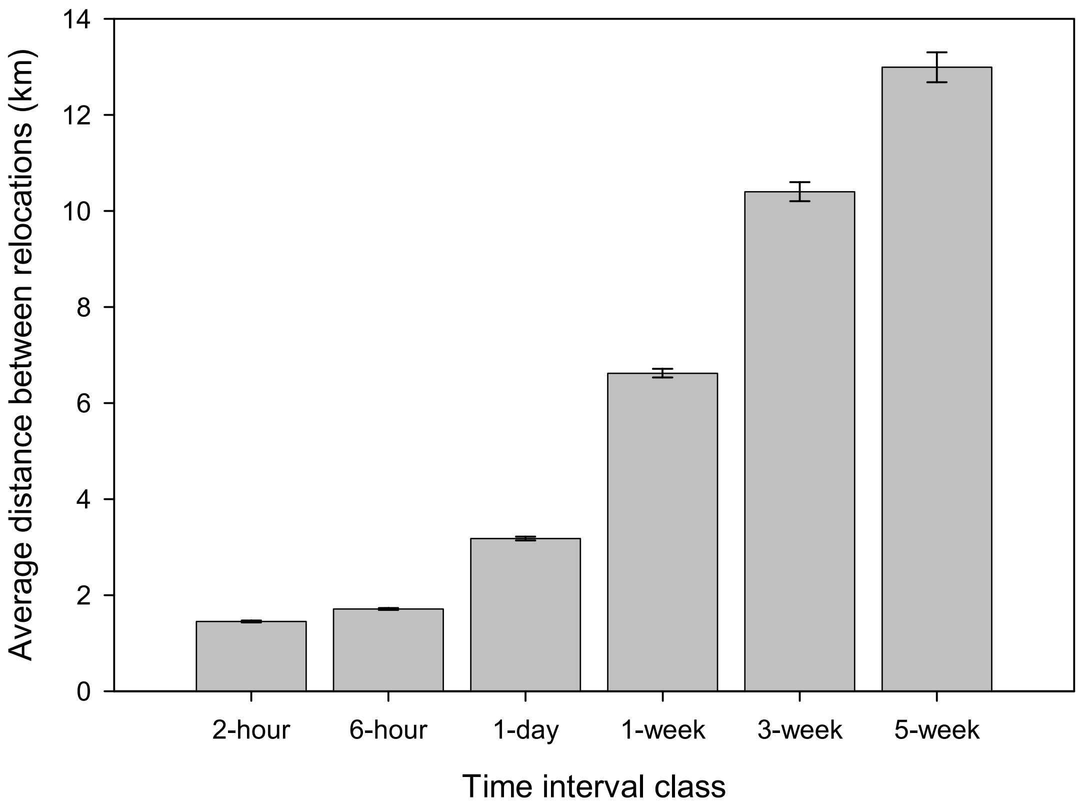

Figure 3. Average (histogram) and standard error (bars) of distance between relocations of radio-collared woodland caribou taken from data subsets created for 6 time interval classes (≥2-hour, ≥6-hour, ≥1-day, ≥1-week, ≥3-week, and ≥5-week).

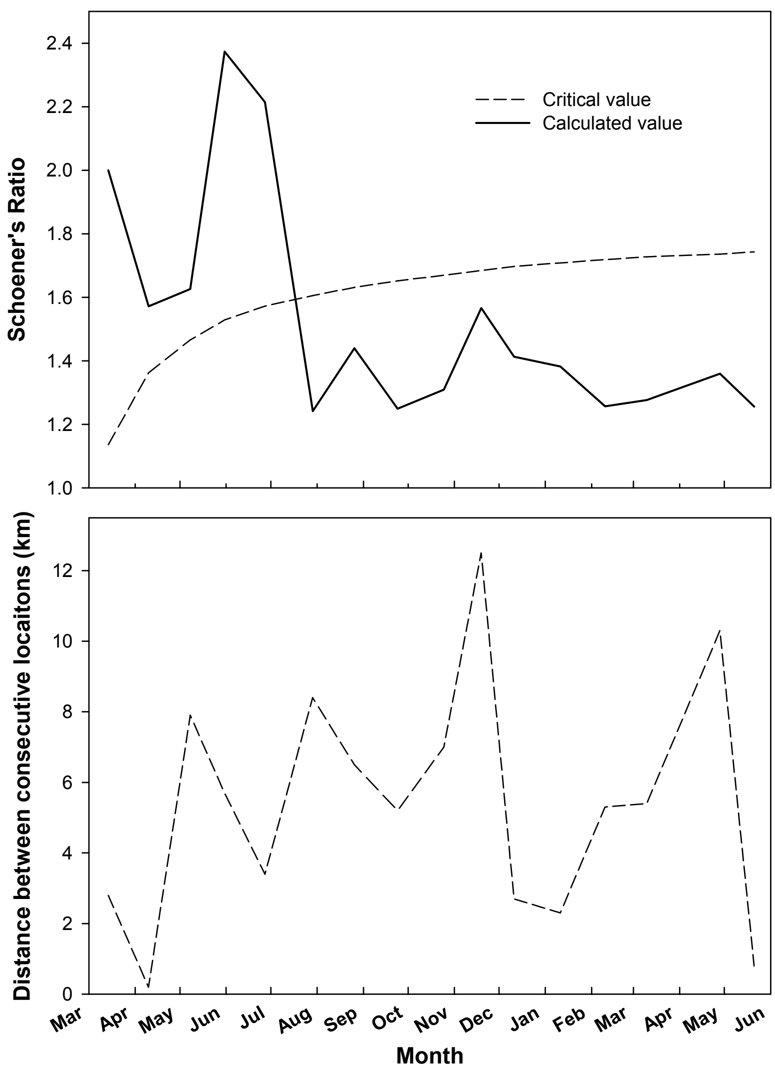

Figure 4. Chronological plot of Schoener's Ratio (1981) calculations (top) and distance between locations (bottom) for one individual animal string (CF220T1), from the 3-week time interval class. Location data was collected approximately once a month from 1996 – 1997. Critical value is the Schoener's Ratio test statistic.

DISCUSSION

The majority of our observations of the use of space by woodland caribou contained relocations that were serially dependent or auto-correlated which we took to imply temporally disparate use of space. As time interval increased between relocations, so did the percent of independent samples in our datasets but even with ≥5 weeks between samples, we could not guarantee independence. These results were similar to those found on black-tailed deer (McNay et al. 1994). Reducing the number of relocations beyond this is likely too excessive for data with skewed distributions (McNay 1994), leaving biological inferences about caribou movement patterns difficult. Johnson et al. (2002) reported that small-scale, intra-patch (foraging areas) movements by woodland caribou were highly correlated. Therefore if we were to choose ≥5 weeks as a sampling interval for independent relocations, the result would lead to a mean distance between locations of ~12 km and an inability to ask questions about foraging movements. Because animal movements are based on the behavior of the species, it is nearly impossible to achieve normality in animal location data without losing important biological information (McNay et al. 1994). Therefore, as recommended by Otis and White (1999), the sampling interval should be based on specific ecological questions and sound biological knowledge of the species.

Independence of data subsets implies that the data come from a normal distribution (i.e., relatively non-disparate use of space). When this test is applied to skewed data distributions there is a potential for the data to be recognized as dependent even when independence is achieved for the majority of the data (McNay 1994). Therefore, where we expect skewed data distributions or disparate use of space, we should not expect to achieve a lack of statistical serial correlation. Identification of the movements that cause serial dependence may be useful in identifying disparate use of space compared to relatively normal or random use of space. For example, we observed a lack of independence in data to arise when large movements occurred. We expected at least some of these movements to be consistent with migration or movement between seasonally disparate ranges. However, relatively small movements may also cause a lack of independence if preceded by a series of larger movements. Both types of movements likely have biological and ecological significance and prompt us to further explore the application of Schoener's Ratio as a consistent way to identify disparate use of space.

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