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RELATIVE ABUNDANCE OF NORTHERN FLYING SQUIRRELS AND RED SQUIRRELS IN DIFFERENT FOREST TYPES, BLACK HILLS, SOUTH DAKOTA

Melissa Hough

89 Brook Road
Cochecton, NY 12726
Melhough18@hotmail.com

and

Charles Dieter

Department of Natural Resource Management
South Dakota State University
Northern Plains Biostress, Room 139B
Brookings, SD 57007
Charles.Dieter@sdstate.edu

ABSTRACT—Northern flying squirrels (*Glaucomys sabrinus*) and red squirrels (*Tamiasciurus hudsonicus*) in the Black Hills National Forest (BHNF) of South Dakota represent isolated populations. Because data on both species in the region are limited, and because the northern flying squirrel in South Dakota and the Black Hills National Forest has species of concern status, we trapped throughout BHNF to determine relative abundance in different forest types for both populations. For northern flying squirrels, capture rate was higher in the northern and western hills compared to the southern and eastern hills, whereas for red squirrels, capture rate was higher in the western hills, followed by the southern and eastern hills. The northern hills are classified as mesic coniferous forest transitioning to a dry coniferous forest in the southern hills. In addition, the northern hills is characterized by a mixed coniferous-deciduous forest, whereas the southern and eastern hills are characterized by even-aged managed coniferous stands. Understanding the abundance of these two isolated squirrel populations in the different forest types of the BHNF is important in intensively managed forests, because management decisions can impact isolated populations.

Key Words: Black Hills National Forest, *Glaucomys sabrinus*, northern flying squirrel, red squirrel, small mammal, *Tamiasciurus hudsonicus*

INTRODUCTION

In the Black Hill National Forest (BHNF) of western South Dakota, disjunct and isolated populations of both the northern flying squirrel (*Glaucomys sabrinus bangsi* [Rhoads]; King 1951; Wells-Gosling and Heaney 1984) and red squirrel (*Tamiasciurus hudsonicus dakotensis*; Turner 1974) occur and coexist. Due to the limited abundance, isolation from source populations (Kiesow 2008), and changes to forest structure due to forest management practices, northern flying squirrels in the BHNF are considered a species of concern (USDA Forest Service 2005; South Dakota Department of Game, Fish, and Parks 2006). Disjunct populations of northern flying squirrels at the southern edge of their range have not been well studied (Weigl 2007). Northern flying squirrels are mycophagous and play an important role in dispersing mycorrhizal fungal spores (Carey et al. 1999; Loeb et al. 2000; Pyare and Longland 2001; Vernes 2004). Flying squirrels are part of a squirrel-fungus-tree mutualism that may help maintain forest ecosystems such as those in BHNF (Weigl 2007).

The population of red squirrels (*Tamiasciurus hudsonicus dakotensis*; Turner 1974) in the Black Hills is isolated, and there are no previous studies on red squirrels there. Red squirrels may be considered a keystone species because of their larderhoarding behavior (Pearson and Ruggiero 2003). Middens produced by red squirrels serve as a storage area for seeds and add structure to managed

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and even-aged forests, and decaying matter in the middens provides nutrient stores (Koprowski 2005).

Northern flying squirrels and red squirrels coexist throughout most of their range; however, northern flying squirrels are nocturnal (Wells-Gosling and Heaney 1984) and red squirrels diurnal (Steele 1998). The two squirrel species are sympatric and depend on mature coniferous forests for nest sites and food resources, such as fungi and seeds. However, currently no data exist on distribution and abundance of northern flying squirrels or red squirrels throughout BHNF and across their range within forest stands dominated by ponderosa pine (*Pinus ponderosa*: 83% [USDA Forest Service 2005]) and intensively managed for timber. Studying BHNF populations is important for both species because there is a threat to disjunct squirrel populations, which may be impacted by human activities such as clear-cutting, development, or any activity destroying extensive tracts of habitat (Koprowski 2005; Weigl 2007). Our objectives were to use live trapping to determine relative abundance of northern flying squirrel and red squirrel populations in different forest types in the BHNF. All methods were approved by South Dakota State University Institutional Animal Care and Use Committee (04-A021).

METHODS

Study Area

This study was conducted in the Black Hills National Forest, located in western South Dakota (43°26'20"-44°32'7" N, 104°4'36"-103°13'9" W) (Fig. 1). The BHNF is a unique ecosystem that consists of forest surrounded by Great Plains grasslands (Froiland 1990). The ponderosa pine—dominated hills extend 900–1200 m above the surrounding Great Plains prairie. The Black Hills were formed by mountain uplift, extend 200 km north to south and 100 km east to west, and encompass 486,000 ha. Their elevation range is approximately 1,200 to 2,207 m, with the forested region extending to 2,102 m (Froiland 1990).

The southern Black Hills has a warmer (9.3°C) and drier (45–51 cm/yr) annual climate than the northern portion of the range (7.2°C and 61–66 cm/yr; Shepperd and Battaglia 2002). Ponderosa pine is found throughout the BHNF and is the most abundant tree species, dominating 83% of the landscape (USDA Forest Service 2005). In the central to southern hills, quaking aspen (*Populus tremuloides*) and paper birch (*Betula papyrifera*) are interspersed with pine in the bottomlands and along water sources; spruce occurs sporadically and is commonly found along streams; and there is little to no understory.

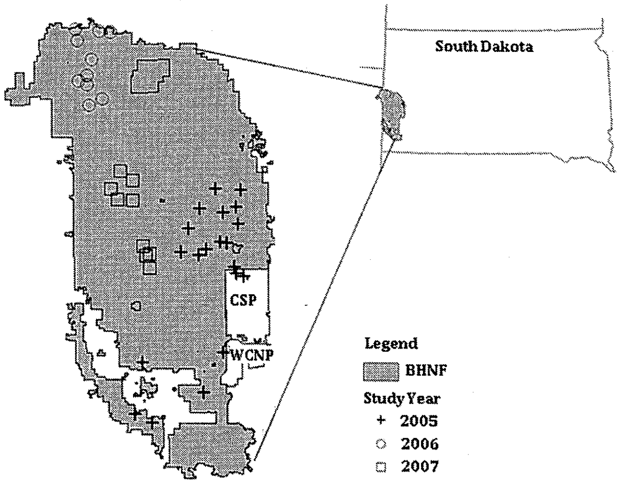

Figure 1. Location of trap sites for northern flying squirrels and red squirrels in the southern (2005), northern (2006), and western (2007) portions of the Black Hills National Forest, South Dakota (May–August, 2005–2007). Custer State Park (CSP) and Wind Cave National Park (WCNP) are located in the southeast portion of the Black Hills region.

In the northern hills, white spruce (*Picea glauca*) is more abundant, comprising 2% of the vegetation (USDA Forest Service 2005). The northern hills has an understory component, primarily bur oak (*Quercus macrocarpa*), but may also include American elm (*Ulmus americana*), green ash (*Fraxinus pennsylvanica*), box elder (*Acer negundo*), and eastern hophornbeam (*Ostrya virginiana*) (Hoffman and Alexander 1987). Quaking aspen and paper birch dominate moister environments, particularly in disturbed areas, of the central to northern BHNF (Hoffman and Alexander 1987).

Trapping

From May through August 2005, we trapped both squirrel species along established transects throughout the southern to southeastern BHNF (Fig. 1). Ten Tomahawk live traps (Model 201: 40 × 13 × 13 cm, Tomahawk Live Trap Co., Tomahawk, WI) were placed 50 m apart; this distance ensures at least four traps were in each northern flying squirrel's home range (Hough and Dieter 2009a) and three traps were in each red squirrel's home range (Kiesow 2008). This distance also accounts for home range overlap between squirrels (Carey et al. 1991). Trap placement was alternated between the ground at the base of a tree and on a branch of a tree, secured at a height of 1 to 2 m. We covered traps with ground litter and bark and baited each with oil-packed tuna or a mixture of peanut butter, oatmeal, and bacon grease.

From May through August 2006 and 2007, we trapped both squirrel species along established transects throughout the northern and western BHNF, respectively (Fig. 1). We placed all traps in trees, because during 2005 more squirrels of both species were captured in tree traps than ground traps. We alternated 10 single-door Tomahawk live traps and 10 double-door Havahart live traps (Model 1025: 45.7 × 12.7 × 12.7 cm, Woodstream Corporation, Lititz, PA). All traps were baited with a mixture of peanut butter, oatmeal, and bacon grease. During all years, we set traps for at least 14 trap nights and checked them each morning.

Captures

Each individual squirrel was weighed and classified as an adult (>100 g for northern flying squirrels and >200 g for red squirrels) or juvenile. We determined the sex and reproductive condition of adults by examining the condition of male scrotums and female teats (Godin 1960). We inserted a passive integrated transponder (PIT) tag (Biomark, Boise, ID) subcutaneously into each squirrel using a 12-gauge sterile syringe implanter. Each PIT tag microchip had a unique number for identifying individual squirrels to monitor recaptures.

Statistical Analysis

Statistical analyses were conducted using JMP IN 4.0 (SAS Institute Inc., Cary, NC) using an $\alpha = 0.05$. Shapiro-Wilk's test was used to test all variables for normality. Because assumptions of normality and heterogeneity were not always met, we performed nonparametric tests. Sex ratios for adults were determined for each squirrel species and ratios were compared to a 1:1 ratio with likelihood ratio $\square^2$. We tested for differences in trapping success between years using chi-square analysis.

RESULTS

In the southern and southeastern hills (2005 study year), we captured 34 northern flying squirrels with 13 recaptures in 3,489 trap nights, for a trapping success of 1.4% (Table 1). In the northern hills, we captured 97 northern flying squirrels with 80 recaptures in 4,220 trap nights, for a trapping success of 4.2%. In the western hills, we captured 35 northern flying squirrels with 38 recaptures in 2,624 trap nights, for a trapping success of 2.8%. Overall, the trapping success was 2.9%. Capture rate was higher in the northern hills than in the southern hills ($\square^2 = 59.38$, $P = <0.0001$). There was no difference in capture rate between the northern and western hills ($\square^2 = 0.065$, $P = 0.80$) when comparing capture rates for the same trapping months (May and June). Capture rate was higher in the western hills than in the southern hills ($\square^2 = 38.07$, $P = <0.0001$) when comparing capture rates for the same trapping months (only May and June). Overall, there was an increase in trapping success as summer progressed ($\square^2 = 93.65$, $P = <0.0001$) (Fig. 2).

In the southern hills, we captured 40 red squirrels with 7 recaptures in 3,489 trap nights, for a trapping success of 1.4% (Table 1). In the northern hills, we captured 17 red squirrels with 5 recaptures in 4,220 trap nights, for a trapping success of 0.5%. In the western hills, we captured 82 red squirrels with 12 recaptures in 2,624 trap nights, for a trapping success of 3.6%. Overall, the trapping success was 1.6%. Capture rate was higher in the southern hills than in the northern hills ($\square^2 = 92.21$, $P = <0.0001$). Capture rate was higher in the western hills than in the southern hills ($\square^2 = 26.90$, $P = <0.0001$) and northern hills ($\square^2 = 103.08$, $P = <0.0001$) when comparing capture rates for the same trapping months (only May and June). Overall, trapping success during June was two times higher than trapping success during May, July, and August ($\square^2 = 15.20$, $P = 0.002$) for red squirrels (Fig. 2). When years were combined, the sex ratio for adult northern flying squirrels was not different from 1:1, but we caught more male adult red squirrels than females (Table 2).

DISCUSSION

Distribution

The highest trapping success for northern flying squirrels (4.2%) occurred in the northern hills. The northern BHNF is classified as mesic coniferous forest (Marriott et al. 1999), which typically supports higher population densities of northern flying squirrels than xeric forest (Lehmkuhl et al. 2006; Hough 2008). Gabel et al. (2006) found that 90% of the contents of northern flying squirrel feces collected from captured squirrels in the northern BHNF were fungal spores. Hypogeous fungi fruiting bodies require moist, nutrient-rich and cool environments to grow (Pyare and Longland 2001). An increase in moisture results in an increase in fungal community diversity (Carey and Johnson 1995) and abundance (Luoma et al. 1991). In a related study, northern flying squirrels in BHNF were positively associated with higher precipitation and closer distances to streams (relative to availability) (Hough and Dieter 2009b).

Trapping success for red squirrels was low in the

TABLE 1.
NUMBER OF CAPTURES AND TRAPPING SUCCESS RATES FOR NORTHERN FLYING SQUIRRELS AND RED SQUIRRELS IN THE BLACK HILLS, MAY–AUGUST, 2005–2007

		Northern flying squirrels		Red squirrels	
Study area and year	**Total trap nights**	**Captures (n)**	**Trapping success (%)**	**Captures (n)**	**Trapping success (%)**
Southern Black Hills, 2005					
May	1,009	2	0.20	9	0.89
June	1,430	14	0.98	24	1.68
July	700	12	1.71	14	2.00
August	350	19	5.43	0	0.00
Total	3,489	47	1.35	47	1.35
Northern Black Hills, 2006					
May	870	23	2.64	1	0.11
June	1,420	38	2.68	1	0.07
July	600	35	5.83	0	0.00
August	1,330	81	6.09	20	1.50
Total	4,220	177	4.19	22	0.52
Western Black Hills, 2007					
May	1,374	11	0.80	30	2.18
June	1,250	62	4.96	64	5.12
Total	2,624	73	2.78	94	3.58
Total	**10,333**	**297**	**2.87**	**163**	**1.58**

northern hills and higher in the western and southern hills. Red squirrels rely heavily on conifer seeds (Kemp and Keith 1970; Rusch and Reeder 1978; Kiesow 2008) and are adapted to drier environments, conditions found in the western and southern hills. Kiesow (2008) determined 94.5% of stomach content from red squirrels captured in BHNF consisted of pine seeds.

The northern hills is characterized by well-developed forest understory, more snags and coarse woody debris, and a mixed coniferous-deciduous forest, whereas the southern and eastern hills are characterized by even-aged managed coniferous stands with little to no understory or ground cover (Marriott et al. 1999). Red squirrels are associated with coniferous forests, as the resources they required, including food and shelter, are provided by conifers (Kemp and Keith 1970). Northern flying squirrel abundance has been linked to increased understory cover (Smith et al. 2004), snags, and down, dead, decaying wood (Carey et al. 1999). Understory provides increased foraging opportunities by providing cover from predators (Carey 1995; Carey et al. 1999; Pyare and Longland 2002), and some understory species may provide food for northern flying squirrels (Smith et al. 2004). Snags provide nesting locations for northern flying squirrels. Down woody debris provides cover, travel paths, burrow sites, and a substrate for northern flying squirrel food such as fungi and lichen (Maser et al. 1985; Carey and Johnson 1995).

Northern flying squirrel trapping success was higher in the northern hills and western hills than the southern-southeastern hills. Juvenile recruitment for northern flying squirrels was earlier in the northern and western hills than in the southern hills. In the southern hills, the first juvenile was captured in August, whereas in the northern hills the first juvenile was captured on July 4 and in the western hills on June 20. After the first juvenile capture, juveniles were regularly captured throughout the rest of the summer. In both study areas, trapping success increased as the summer progressed, but there was a marked increase during the months of juvenile recruitment.

The month with highest trapping success for both species was the month with highest juvenile recruitment. This occurred during August (6.0%) for northern flying

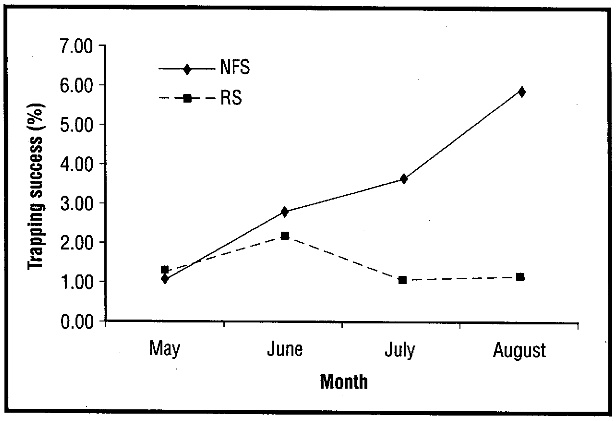

Figure 2. Comparison of trapping success for northern flying squirrels (NFS) and red squirrels (RS) during the months of May–August, 2005–2007, in the Black Hills National Forest, South Dakota.

TABLE 2.
COMPARISON OF SEX RATIOS FOR NORTHERN FLYING SQUIRRELS AND RED SQUIRRELS IN THE BLACK HILLS NATIONAL FOREST, MAY–AUGUST, 2005–2007

	Northern flying squirrel		Red squirrel	
Year	**M:F**	***P*-value***	**M:F**	***P*-value***
2005	11:17	0.26	16:13	0.58
2006	24:19	0.45	6:4	0.53
2007	21:14	0.24	25:13	0.05
Total	56:50	0.56	47:30	0.05

*All comparisons tested with Fisher's exact text ($P \leq 0.05$).

squirrels and during June (2.2%) for red squirrels. For northern flying squirrels, the increase in trapping success during July reflects the beginning of the juvenile recruitment period, and recruitment peaks during August (Fig. 2). Red squirrel capture success peaks during June, with a marked decrease in August.

Sex Ratio

Sex ratios for northern flying squirrels are not normally skewed (Smith 2007), as was found in this study (Table 2). Vernes (2004) had similar results in New Brunswick. In western Oregon, Rosenberg and Anthony (1992) found no sex ratio difference for northern flying squirrels in old-growth stands, but they found a higher proportion of females in second-growth stands. Rosenberg and Anthony (1992) also found more juveniles in second-growth stands and suggested these stands were sink habitats.

There were more male than female red squirrels trapped in the BHNF (Table 2). Vernes (2004) reported a sex ratio difference in favor of males during one year of study in New Brunswick. In other areas across their range, male and female juvenile red squirrel sex ratios were similar, but adult sex ratios increased in favor of males as age increased (Kemp and Keith 1970; Davis and Sealander 1971; Rusch and Reeder 1978). Higher capture rates for males may exist because males move around while females are caring for their young (Kemp and Keith 1970) or because of habitat conditions, as Rosenberg and Anthony (1992) suggested for northern flying squirrels.

Our results indicate that northern flying squirrels were present throughout the BHNF but were most abundant in the mesic mixed coniferous-deciduous forest in the northern hills, with well-developed forest understory and more snags and coarse, woody debris. Northern flying squirrels were also most abundant in the western hills, which is a transition from the northern hills to the southern hills. The western hills are dominated by coniferous trees with aspen and birch in the bottomlands and along water sources. In addition, there is some understory and ground cover, as these forests are not as intensively managed as the even-aged coniferous forests in the southern-southeastern hills. Juvenile recruitment was earlier in the northern and western hills, resulting in higher capture rates. Red squirrels were also present throughout the BHNF but were most abundant in the less intensively managed coniferous forests of the western hills, where there is some understory and ground cover, followed by the southern-southeastern hills, which is comprised of intensively managed even-aged coniferous stands with little to no understory or ground cover. Very few red squirrels were captured or observed in the mesic mixed coniferous-deciduous forests in the northern hills.

Understanding the abundance of these two isolated squirrel populations in the different forest types of the BHNF is important in intensively managed forests, because across their range the two squirrel species play important roles in the forests they occupy, and management decisions can impact isolated populations. The results of this study contribute to the knowledge gap for populations of northern flying squirrels at the southern portion of their range (Smith 2007; Weigl 2007), and they also provide information on red squirrels, which have not been well studied in the Black Hills National Forest.

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