THE NATAL DISPERSAL OF RUFFED GROUSE

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ABSTRACT.—We examined the dynamics of Ruffed Grouse (*Bonasa umbellus*) natal dispersal in central Wisconsin (1982–1985). During autumn dispersal juvenile females moved more than twice the net distance (4.82 vs. 2.14 km) at twice the rate (0.53 vs. 0.26 km/day) of juvenile males. The total distance females moved during autumn dispersal was 50% greater than males (9.56 vs. 6.36 km) even though the duration of autumn dispersal was similar for both sexes (17 vs. 21 days). A substantial percentage (29%) of birds exhibited more than one distinct movement; these individuals stopped temporarily for several days or weeks before making additional movements. The most pronounced sexual differences in habitat selection occurred during autumn dispersal when females used deciduous lowlands twice as much as males (22% vs. 10%); males were found in shrub/scrub areas more often than females (17% vs. 7%). Females appear to complete their natal dispersal in autumn as all (6 of 6) eventually nested in their wintering areas. Males may wander extensively in spring, with total movements often exceeding those observed in autumn. Most males (4 of 5) established spring ranges outside their wintering areas. *Received 6 June 1988, accepted 11 August 1988.*

IN most avian species females move greater distances than males during natal dispersal, the movement between birth site and breeding site (Gauthreaux 1978, Greenwood and Harvey 1982). The explanation for this sexual difference remains unresolved (Greenwood 1980, Shields 1983, Moore and Ali 1984). Most studies emphasize immediate postfledging movements, yet additional movement often occurs months later at the onset of the breeding season (Tompa 1962, Greenwood et al. 1979, Keppie 1979). Little information exists on other spatial and temporal characteristics of dispersal, such as rate and duration of movement, and patterns of habitat use. If sexual differences in these additional characteristics exist, they may provide an important contribution to the understanding of natal dispersal.

The existence of natal dispersal in the Ruffed Grouse (*Bonasa umbellus*) has been known for over 100 years (Bump et al. 1947), and was often referred to as autumn "crazy flight" and "spring shuffle" in the early literature. Juvenile female Ruffed Grouse generally move farther than males in autumn (Godfrey and Marshall 1969), but the rate and timing of natal dispersal are unknown.

We describe the natal dispersal of Ruffed Grouse. The specific questions were whether there were inter- and intrasexual differences in dispersal in autumn and spring, if juveniles selected breeding territories in autumn or spring, and whether habitat use during dispersal differed during summer and winter.

STUDY AREA AND METHODS

Fieldwork was conducted (June 1982–May 1985) in Marquette and Waushara counties, Wisconsin (44°02′N, 89°23′W). Forested land comprised ca. 30% of these counties, with 40% in cropland, and 30% in pasture and marsh lands (Wisconsin Department of Natural Resources 1968). Twelve public hunting areas covered about 10 km^2 of the ca. 200-km^2 study area. Ruffed Grouse were captured using lily-pad traps (Dorney and Mattison 1956) from July through October, and mirror traps (Gullion 1965) during April and May. Grouse were classified as juveniles from hatching until 31 May (mean hatch date) of the following year. Those that had completed their postjuvenile molt were distinguished from adults by calamus ratios (Rogers 1979). Broods were defined as any group of 2 or more juveniles of the same age captured together, with or without a hen.

Radiomarking and monitoring.—Radio transmitters attached to either ponchos (Amstrup 1980) or backpacks (Brander 1968) were used in 1982; ponchos were used exclusively in 1983–1985 (Small and Rusch 1985). Hand-held and vehicle-mounted antennas were used to locate grouse with transmitters. The error ellipse (Lenth 1981) associated with each location was determined under the assumption that there was an error of 2° on each side of the true bearing. Most birds were located at least once every other day in summer,

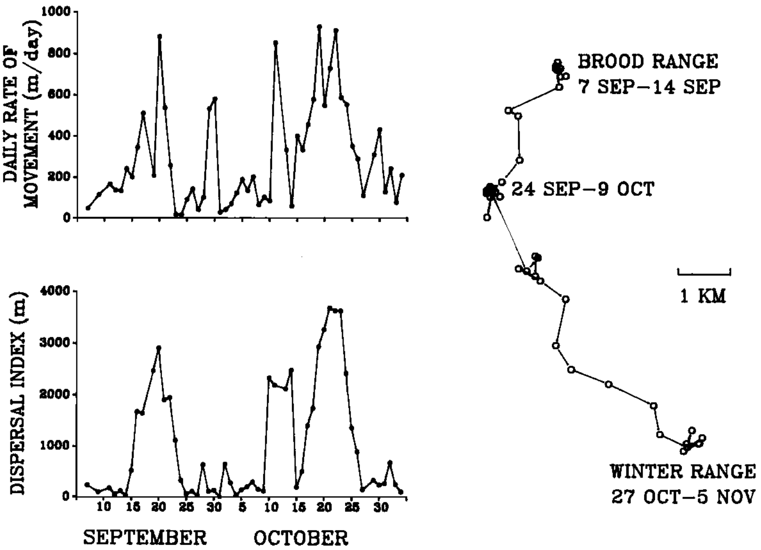

Fig. 1. Estimated natal dispersal route of a juvenile female Ruffed Grouse from 7 September to 5 November 1984 with a comparison of daily rate of movement and dispersal index (see text) to determine approximate time of dispersal.

daily in autumn and spring dispersal periods, and 2–4 times weekly in winter.

Ranges of juveniles in summer were analyzed for the periods of capture through 10 days prior to autumn dispersal (brood range), and of the 10 days before autumn dispersal (break-up range). Brood size and break-up ranges were estimated by a 90% harmonic isopleth (Dixon and Chapman 1980) based on locations of all brood members. Mean distance between brood members for each of the 10 days before and after the initiation of their autumn dispersal was calculated to ascertain the time of brood break-up. The sizes of other ranges were determined from all locations of an individual within a designated period. The center of each range was estimated from the arithmetic center of the isopleth.

Ranges and movements of adults were calculated seasonally: spring (1 March–31 May), summer (1 June–31 August), autumn (1 September–30 November), and winter (1 December–28 February).

Characteristics of dispersal.—The most common methods used to identify dispersal are an increased rate of movement and movements beyond a critical distance. These criteria were inadequate to identify dispersal of Ruffed Grouse in this study because an increased rate of movement did not necessarily represent movement away from a previously used area, and the rate of movement and straight-line movement varied greatly among individuals. We therefore developed a movement index that identified dispersal from one range to another. This index equals the linear distance between the first and last locations of a set of 5 consecutive daily locations; the index value is assigned to the middle (third) day. As an example, we plotted locations of a juvenile grouse during autumn dispersal through time (Fig. 1). The index depicts distinct movement periods. The rate of movement showed similar trends to dispersal but was more variable.

To determine the change in the index that indicated the initiation of a dispersal period, we examined the seasonal patterns of the index, in 50-m intervals, of juveniles in their brood range and of adults (Fig. 2). The distributions of the 2 age groups were similar ($\chi^2 = 17.7$, $P = 0.28$) with 90% of all movements <400 m. But, the index of juveniles after 10 September was substantially greater (Fig. 2). We decided that indices >350 m on at least 2 consecutive days indicated a dispersal period. This criterion is supported by the mean daily movement within Ruffed Grouse brood ranges of 377 m reported by Godfrey (1975). If 300 m was used as a criterion, "dispersal" periods would have occurred within the brood period; if 400 m was used, juveniles that moved away slowly from their brood range would not be recognized as dispersing birds.

Termination of dispersal was highly variable. Some birds stopped with no additional movement; others stopped temporarily for several days or weeks, and then made additional movements. We arbitrarily defined the termination of a dispersal period as a decrease in the index to <350 m on 5 consecutive locations. We allowed for >1 distinct dispersal period for an individual bird. Autumn dispersal was then defined as the dispersal period(s) which occurred from the summer (natal) range to winter range; spring dispersal as those from winter to spring (breeding) range.

Net distance and direction of autumn and spring

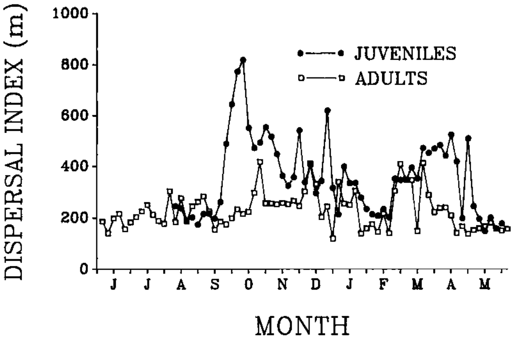

Fig. 2. Dispersal index for juvenile and adult Ruffed Grouse (1982-1985).

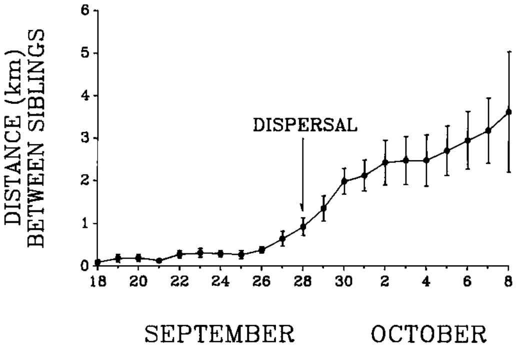

Fig. 3. Estimated mean daily distance between broodmates (n = 6 broods) surrounding their mean date of initiation of autumn dispersal.

dispersal were calculated from centers of summer and winter ranges or winter and spring ranges, respectively. Total autumn and spring dispersal distances were estimated by the sum of the distances between consecutive locations during each period. Rate of movement (km/day) was estimated by dividing net distance by the number of days separating consecutive locations within the dispersal period.

Habitat analyses.—Lowland habitats were categorized as: marsh, shrub/scrub, or deciduous forest, according to the Wisconsin wetland inventory survey of 1978. We classified upland habitat as closed canopy oak forest, open canopy oak forest, pine plantation, cropland (including open grassland), or fencerow (a strip of trees or shrubs <30-m wide with >0.4 ha of cropland on both sides). Each habitat was sampled using the point-quarter method (Cottam and Curtis 1956) to provide a general description of vegetation structure and composition (Appendix).

We recorded the habitat in which birds were located when error ellipses ≤0.3 ha. Habitat availability (Marcum and Loftsgaarden 1980) on the study area was estimated from 1,798 randomly selected 0.4-ha blocks. Use was compared to availability (Neu et al. 1974).

RESULTS

We radiomarked 44, 51, and 49 juvenile Ruffed Grouse, and 24, 22, and 5 adults in summer and autumn of 1982-1984. Radiotracking terminated in December 1982 due to transmitter failures but continued through the winter and into the breeding season in 1983-1984 and 1984-1985.

Brood break-up.—Brood members separated gradually prior to fall dispersal (Fig. 3). This suggests that a progressive deterioration of social bonds among siblings preceded dispersal. Although juveniles became increasingly independent, the size of brood ranges and break-up ranges did not differ (Paired t-test, $t = 0.075$, $P = 0.5$). Variation in size of break-up ranges was large. The break-up range of 1 brood, for example, was over twice the size of its brood range (28 vs. 73 ha), whereas brood and break-up ranges were similar for 2 other broods. In addition, although some brood members were >1 km apart before autumn dispersal, other siblings began moving together.

Autumn dispersal.—The autumn dispersal of juvenile grouse occurred primarily from late September to mid-October (Fig. 4). We considered 3 minor dispersal movements in December and January as shifts in winter range and did not include them in analyses of autumn dispersal. Only birds captured prior to 10 September and monitored through the end of November were included in the dispersal analyses, because birds captured after 10 September may have already begun to disperse.

Characteristics of autumn dispersal were recorded for 10 (77%) of 13 males and 14 (93%) of 15 females (Table 1). Average age of males and females at initiation of dispersal was similar

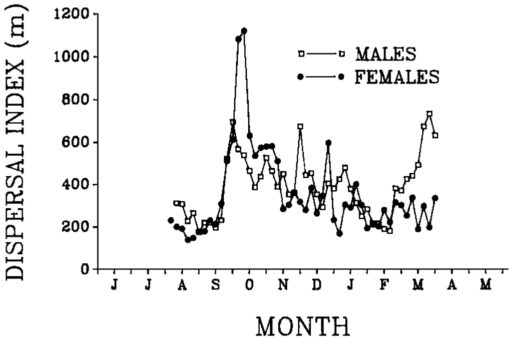

Fig. 4. Dispersal index for female and male juvenile Ruffed Grouse (1982-1985).

TABLE 1. Temporal and spatial characteristics ($\bar{x} \pm$ SE) of autumn dispersal of juvenile Ruffed Grouse in central Wisconsin (1982–1985).

Characteristics of dispersal	Female ($n = 14$)	Male ($n = 10$)	t	P
Net distance[a] (km)	4.82 ± 0.87	2.14 ± 0.38	2.48	0.02
Total distance[b] (km)	9.56 ± 1.13	6.36 ± 1.40	1.79	0.09
Duration (days)	17.2 ± 4.16	21.9 ± 7.06	0.61	0.55
Rate (km/day)	0.53 ± 0.10	0.26 ± 0.07	2.14	0.04
Straightness index[c]	0.54 ± 0.08	0.43 ± 0.09	0.86	0.40
No. of discrete movements	1.21 ± 0.11	1.70 ± 0.34	1.56	0.13
Age at initiation (days)	124.3 ± 2.80	120.2 ± 2.32	1.06	0.30
Date of initiation	4 Oct ± 4	25 Sep ± 2	1.54	0.14

[a] Distance between center of brood range and center of winter range.
[b] Length of dispersal path.
[c] Batschelet (1981: 33).

while mean date of initiation of dispersal was nearly 9 days earlier for males than females. This difference may not represent an actual sexual difference, but a difference between broods, since radiomarked females occurred in only 3 of the broods that dispersed latest. Stepwise linear regression of juvenile age and daily high and low temperatures vs. dispersal date indicated that age was an important explanatory variable ($r^2 = 0.38$), but temperature was not.

Net dispersal distance of females was more than twice that of males while total distance moved was only about 50% greater than males (Table 1). Females moved at twice the rate of males. The percentage of birds that exhibited >1 distinct move within the autumn dispersal period was substantial (29%). Males exhibited >1 distinct move more often than females. Five (71%) of seven birds captured after 10 September that made >1 move were males. Directions of dispersal by both females and males did not differ from random ($P = 0.30$) (Rayleigh test; Batschelet 1981: 54).

Spring dispersal.—Among 11 juveniles followed through 1 May (initiation of egg laying), spring dispersal was recorded in 2 of 6 females and 4 of 5 males. The male that did not disperse in spring had not dispersed during the previous autumn and established a breeding territory on its brood range. The remaining 4 males had dispersed in autumn, but their brood ranges were unknown. Mean net dispersal distance in spring by these 4 males was only 0.86 km, yet their mean total distance was 10.38 km, indicating substantial wandering in spring dispersal. Two of these males continued to disperse for over a month before settling into a spring range. Both females that dispersed in spring nested within 0.3 km of their winter range. Total distances moved by these 2 females were 2.23 and 3.52 km, made in 5- and 6-day periods. Five of six females nested successfully, including one renest.

The net distance moved from known brood range to breeding range was recorded for only 2 males (0.79 and 0.08 km) and 2 females (2.62 and 3.36 km).

Juvenile habitat selection.—Habitat selection was highest by both sexes in summer when lowland habitats received 67% of total use but comprised only 16% of total available cover (Table 2). All upland habitats, except closed oak, were used less often than expected.

Habitat selection in autumn dispersal was substantially less. A significant difference between the sexes, however, was observed in the use of lowland habitats. Females preferred deciduous lowlands, whereas males preferred shrub/scrub lowlands (Table 2).

Habitat use in winter was similar to that during autumn dispersal and most birds remained in the uplands and deciduous lowlands. Shrub/scrub was preferred by females but not males. Open oak was preferred by both sexes; and although use of pine was highest in winter, it remained below the expected level.

DISCUSSION

The distance juveniles move from their birth site to their breeding site is critical in understanding population structure and gene flow (Lidicker 1975, Shields 1983). Explanations of sexual differences in natal dispersal distance have led to much debate (Dobson and Jones 1985), and demonstrated the need for more detailed analyses of dispersal (Cunningham 1986, Pusey 1987). The series of spatial and temporal

TABLE 2. Percentage of habitat use by juvenile Ruffed Grouse in central Wisconsin (1982-1985).

Habitat	Available[a]	Summer brood	Dispersal		Winter	
			Female	Male	Female	Male
Upland						
Open oak	0.14	0.08*[b]	0.22	0.26	0.26*	0.33*
Closed oak	0.21	0.18	0.29	0.26	0.24	0.24
Pine	0.08	0.01*	0.04	0.05	0.06	0.05
Fencerow	0.07	0.01*	0.03	0.02*	0.08	0.01*
Cropland	0.34	0.05*	0.12*	0.11*	0.09*	0.06*
Lowland						
Marsh	0.04	0.02*	0.01	0.03	0.01*	0.05
Shrub/Scrub	0.04	0.16*	0.07	0.17*	0.09*	0.06
Deciduous	0.08	0.49*	0.22*	0.10	0.17*	0.26*
n	1,798	881	103	117	611	508

[a] Expected estimates after Marcum and Loftsgaarden (1980).

[b] Use significantly (* = $P < 0.05$) greater or less than expected (Neu et al. 1974), indicating preference or avoidance of a particular habitat type.

events which constitute the final natal dispersal distance have received little attention, yet may prove important in understanding the effects of dispersal on population structure and gene flow.

Distinct sexual differences exist in both autumn and spring dispersal among juvenile Ruffed Grouse. Due to the high mortality rate of juvenile grouse from the brood period to the following breeding season, however, it is difficult to monitor individual birds throughout both dispersal periods. Therefore, our discussion will emphasize the two distinct phases, autumn and spring, of Ruffed Grouse natal dispersal.

Females are the predominant disperser of most avian species, and the median dispersal distance is usually the only parameter compared between the different sex and age classes. Although the most distinct sexual difference in autumn dispersal of Ruffed Grouse was net distance moved, we found substantial sexual differences in three additional characteristics. The rate at which females moved was slightly more than twice that of males, the total distance moved by females was 50% greater than males, and males selected shrub/scrub lowlands while females selected deciduous lowlands. In addition, extensive spatial and temporal "wandering" was exhibited only by males, not females, during spring dispersal. It appears from these sexual differences that dispersal of Ruffed Grouse is more complex than a simple random spacing behavior.

Ruffed Grouse exhibit a promiscuous mating system where males attempt to attract females by securing a territory and females have the option of choosing among males, thus avoiding the high costs of establishing a territory (Emlen and Oring 1977). It has not been shown that female Ruffed Grouse establish and defend territories like other species of grouse (Nugent and Boag 1982). Gullion's (1967) observation of juvenile males "testing" numerous logs in autumn suggest they are searching for vacant territories. Our observations of a juvenile female within 5 m of a male in full display on the seventh day of her autumn dispersal and on two of the next three days suggest juvenile females may be searching for potential mates during autumn dispersal. If the costs, including time, of establishing and defending a territory by juvenile males are higher than those experienced by females trying to locate territorial males, females may be able to move through new areas faster than males, and to move greater distances (both total and net) than males. This could allow females to traverse more adult male territories to select potential mates. Female sage grouse (*Centrocercus urophasianus*) select males after visiting several leks (Dunn and Braun 1985), and it is this female wandering rather than male fidelity to natal areas that caused greater female dispersal. Since it appears as though mortality is not unusually high for dispersing Ruffed Grouse (Small 1985), the costs of rapidly moving through areas may not be as high as thought previously.

The difference in habitat use between the sexes during autumn dispersal was the most pronounced sexual difference in habitat use we recorded. Juvenile females used deciduous lowlands twice as often as juvenile males (22% vs. 10%), whereas juvenile males were found in shrub/scrub areas more often than females (17% vs. 7%). Whether or not the differential use of habitat during dispersal is related to selection of potential mates, vacant territories, suitable nesting areas, or other factors is unknown, and will remain difficult to determine.

Alway and Boag (1979) and Greenwood et al. (1979) contend that natal dispersal is not complete in autumn but rather in spring, when territorial behavior is at its peak. This may be true only for juvenile male Ruffed Grouse, as four of five established spring ranges outside their wintering areas. Jamieson (1983) observed a similar pattern in yearling male Blue Grouse (*Dendragapus obscurus*). Young male Ruffed Grouse may be trying to secure "persistent" sites, as recorded for young male Blue Grouse (Jamieson and Zwickel 1983), because the two juveniles which did not drum were in areas which contained vacant logs that had been used in previous years. Marshall (1965) observed a juvenile drumming on a log the day after the resident adult was killed; the juvenile had previously visited other logs without drumming. Spring dispersal of juvenile females appeared to represent a search for drumming males as all females eventually nested in their wintering area; hence, females may complete their natal dispersal in autumn. These observations, plus the 100% nesting success observed in this study and others (Brander 1967, Maxson 1978), suggest that competition among males for potential breeding territories is higher than among females for nesting areas. This may cause the extensive spring movements by juvenile males.

Intensive observation of grouse throughout autumn and spring dispersal and detections of interactions between and among the sexes are now necessary to isolate possible causes of the numerous spatial and temporal differences we observed in the natal dispersal of Ruffed Grouse.

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APPENDIX. Density (no./ha) of trees, shrubs (all woody species except tree species >1-m tall), and saplings (tree species <1.5 cm dbh) in the 5 major habitats used by Ruffed Grouse in central Wisconsin (1982–1985).

	Open Oak			Closed Oak			Pine	Shrub/scrub			Deciduous		
Species	Tree	Shrub	Sapling	Tree	Shrub	Sapling	Tree	Tree	Shrub	Sapling	Tree	Shrub	Sapling
Larix laricina	—	—	—	—	—	—	—	49	—	30	22	—	—
Quercus rubra	279	—	4,473	255	—	7,524	—	—	—	—	10	—	2,286
Pinus sylvestris	15	—	324	—	—	—	—	—	—	—	—	—	—
Quercus alba	47	—	2,268	96	—	1,525	—	—	—	—	17	—	1,211
Betula papyrifera	—	—	—	—	—	408	—	7	—	—	225	—	—
Acer rubrum	—	—	—	17	—	914	—	22	—	183	237	—	2,688
Quercus ellipsoidalis	—	—	—	20	—	—	—	—	—	—	—	—	—
Pinus strobus	40	—	324	37	—	1,730	—	—	—	—	—	—	—
Prunus serotina	15	—	195	2	—	2,950	—	15	—	183	22	—	1,075
Prunus virginiana	—	—	—	—	—	1,018	—	—	—	—	—	—	—
Ostrya virginiana	—	—	—	—	—	203	—	—	—	59	22	—	3,496
Pinus resinosa	5	—	—	—	—	—	3,682	—	—	—	—	—	—
Fraxinus nigra	—	—	—	—	—	—	—	7	—	91	138	—	6,859
Populus tremuloides	—	—	—	5	—	—	—	15	—	—	15	—	941
Tilia americana	—	—	—	—	—	—	—	—	—	—	5	198	—
Populus deltoides	—	—	—	—	—	—	—	—	—	304	—	—	—
Pinus banksiana	—	—	—	5	—	—	—	—	—	—	—	—	—
Corylus cornuta	—	91	—	—	59,526	—	—	—	—	—	—	7,109	—
Cornus spp.	—	—	—	—	2,587	—	—	—	1,483	—	—	2,370	—
Rubus spp.	—	—	—	—	5,177	—	—	—	—	—	—	—	—
Viburnum spp.	—	—	—	—	1,942	—	—	—	—	—	—	—	—
Ilex verticillata	—	—	—	—	—	—	—	—	2,634	—	—	9,086	1,075
Alnus rugosa	—	—	—	—	—	—	—	—	7,905	—	—	6,321	—
Salix sp.	—	—	—	—	1,295	—	—	—	660	—	—	—	—
Toxicodendron vernix	—	—	—	—	—	—	—	—	166	—	—	988	—
Amelanchier arborea	—	—	—	—	1,942	—	—	—	—	—	—	791	—
Lonicera spp.	—	7	—	—	—	—	—	—	—	—	—	—	—
Vaccinium spp.	—	—	—	—	13,588	—	—	—	—	—	—	1,777	—
Ilex spp.	—	—	—	—	—	—	—	—	—	—	—	197	—
Total	401	98	7,584	437	86,057	16,272	3,682	115	12,848	850	713	28,837	19,631
S.E.	105	59	1,864	87	21,263	2,379	—	16	3,125	102	93	3,375	2,007