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ABSTRACT

Natal dispersal distances are difficult to measure, yet important for estimating the genetic structure and demographic connectedness of natural populations. Here we provide estimates of the distributions of male and female natal dispersal distances from a long-term study of Spruce Grouse (*Falcipennis canadensis* (L., 1758)) in southwestern Alberta, Canada, based on individuals marked as brood chicks and re-observed as adults during subsequent breeding seasons. The mean distance dispersed by females (2.33 km) was twice that of males (1.13 km), and both dispersal distributions were leptokurtic. Given estimates of population density and survivorship, we estimated the genetic effective neighborhood size of this population as approximately 541 individuals. We computed equivalent estimates for two additional long-term studies of this species, based on data available in the literature; mean natal dispersal distances, averaged across sexes, ranged from 1.73 km to 2.73 km for the three populations; effective deme sizes ranged from 541 to 890. Consequently, three widespread populations of Spruce Grouse yielded roughly similar estimates of demographic and genetic structure.

keywords: dispersal, effective population size, *Falcipennis canadensis*, kurtosis, Spruce Grouse

Introduction

Natal dispersal, the distance moved by an individual organism between the site where it is born and where it breeds as an adult, is an important parameter in determining the demographic and social structure of populations, as well as their genetic connectedness (Greenwood and Harvey 1982; Johnson and Gaines 1990; Stenseth and Lidicker 1992; Hedrick 2000; Caswell 2001). However, direct measurement of natal dispersal is difficult because it requires the re-observation of significant numbers of individuals many months, and often years, after they were first marked. Only from intensive, multiyear studies is it possible to obtain useful direct data for the estimation of this parameter.

An additional obstacle in estimating the magnitude of dispersal is a bias introduced by the inability to distinguish between the death of individuals and their emigration as long-distance dispersers (Barrowclough 1978). That is, if previously marked individuals are searched for over a finite study area, then individuals that disperse out of the study site will not be observed; often they will be presumed deceased for demographic purposes, and will result in an underestimate of overall dispersal. This underestimate can be alleviated, or possibly eliminated, using radio-tracking of tagged juveniles (e.g., Koenig et al. 1996), but this represents an expensive proposition, often involving surveys with aircraft or with the aid of satellites.

Grouse are a charismatic and economically important family of birds (Johnsgard 1983) and, as a consequence, have frequently been the subject of intensive, long-term field studies. Nevertheless, in a survey of mating systems, philopatry, and dispersal in birds and mammals (Greenwood 1980), no data for any member of the family were available. That absence is particularly significant because grouse possess some of the

most interesting mating systems found in birds (Wiley 1974; Wittenberger 1978). For example, the lek-based mating system in some species often results in a dramatic skew in reproductive success (e.g., Hjorth 1970; Höglund and Alatalo 1995). Additionally, several recent studies of phylogeography have suggested that at least some species of forest grouse may be characterized by low rates of dispersal and moderate effective population sizes (e.g., Piertney et al. 1998; Segelbacher et al. 2003; Barrowclough et al. 2004). It would be useful to verify that inference with demographic data.

Here we document natal dispersal distributions for male and female Spruce Grouse (*Falcapennis canadensis* (L., 1758)) from a long-term study in southwestern Alberta. Spruce Grouse are a sexually dimorphic species of gallinaceous bird characteristic of northern boreal forests with a range across Canada and the northern U.S. (Boag and Schroeder 1992). We also estimate the genetic size of a local deme or neighborhood of those birds, and compare our results to an analysis of two prior studies of geographically distant populations of the species.

Materials and methods

This study took place near Gorge Creek in the eastern foothills of the Rocky Mountains in southwestern Alberta (fig. 1: Gorge Creek). Fieldwork was carried out over the course of two decades by many researchers and their assistants. The study area and methodology have been previously described (e.g., Herzog and Boag 1978; Keppie 1979; Schroeder and Boag 1991). At various times from 1965 through 1985, Spruce Grouse were located with pointing dogs, noosed with extendable poles, fitted with leg bands, and, in some cases, tagged with radio-transmitters (Herzog 1979). After they were initially handled,

birds were relocated by intensive searches in subsequent seasons and years. Natal and adult movements were a major focus of the Gorge Creek studies (e.g., Herzog and Boag 1978; Keppie 1979; Herzog and Keppie 1980; Schroeder 1985; Schroeder 1986; Schroeder and Boag 1988), and one of us (MAS) maintained banding and re-observation records throughout the 20 year project.

From the band/re-observation data, we tabulated those instances in which an individual, banded as a chick or dependent juvenile in a brood hen's flock, was later re-observed as an adult, presumably breeding individual, during a subsequent breeding season. These marked adults were classified as to sex by plumage, and the distance moved from their initial site of banding to the position of their eventual re-observation, as long as the observation was during the breeding season (16 May to 31 July), was treated as their natal dispersal distance. These individual distances were then tabulated as a distribution, by sex.

We attempted to investigate the magnitude of potential sampling bias in our estimates of natal dispersal using the procedure outlined by Barrowclough (1978). We computed the probability of detecting dispersal events of various distance classes if the Gorge Creek study area had been a homogeneous circular patch of habitat with an area identical to that of the actual study site. We divided the observed number of dispersers in each class by the detection probability for the class to obtain a better estimate of the dispersal distribution, corrected for possible unobserved long-distance movements. We computed the median dispersal distance for this corrected distribution, and compared it to our observed median dispersal distance.

We compared the male and female natal dispersal distributions using a Kolmogorov-Smirnov two-sample test. We computed the mean and median absolute distances dispersed for the male and female distributions, along with their bootstrap 95% confidence intervals (1000 pseudo-replicates).

Dispersal distributions, like all statistical distributions, can be characterized by their moments. The first moment, the mean, is the center of the distribution; the second, variance, describes the width, or scale, of the distribution; the third, skewness, informs us of its symmetry, or lack thereof; and the fourth moment, kurtosis, carries information about the shape of the distribution. Although dispersal distances are usually presented as frequencies of individuals moving various distance classes, the actual movements occur in two-dimensional space and possess both magnitude and direction. In the canonical presentations, only the absolute magnitude is provided (e.g., fig. 2); however, individual movements, in homogeneous habitat, are expected to be radially symmetric with no directional bias. For that case, all the odd moments of the distribution are expected to be zero; that is, dispersal events in any one direction are balanced by those in the opposite direction. Thus, although the mean absolute distance moved is a positive quantity, the mean of the actual dispersal distribution is zero. Likewise, the third moment, skewness, is also expected to be zero. Consequently, for gene flow purposes, the appropriate second moment of the underlying distribution, variance, is usually estimated as the root-mean-square dispersal distance (σ), not corrected for the mean of the absolute values (Wright 1969). Similarly, we estimated kurtosis of the male and female dispersal distributions by assuming radial symmetry and computing the g_2 statistic (Sokal and Rohlf 1981) assuming all the odd moments were zero. As is traditional, we subtracted 3.0 from the

appropriate ratio of the fourth to the second moment so that a normal distribution would have an expected value of zero.

We estimated the neighborhood size (Wright 1969) of a local Spruce Grouse population as the number of adult individuals in a circle of radius 2σ (Lande and Barrowclough 1987; Barton 1992). That is, $N=4\pi\rho\sigma^2$, where ρ is the local population density of the birds. We estimated this density using data reported by Keppie (1979).

We estimated the genetic effective size of a Spruce Grouse neighborhood by estimating the ratio of effective size to census size using the approach of Barrowclough (1980) and Barrowclough and Rockwell (1993): we assumed that the population was approximately stable in size, had a one-to-one sex ratio, and had lifetime variance in offspring number principally governed by variation in adult survivorship. We assumed that survivorship had a geometric distribution, that is, that adult year-to-year survival had an approximate constant probability, i.e., a type-II life table (Deevey 1947; Ricklefs 1972). We estimated the year-to-year survival of adult Spruce Grouse using data reported by Keppie (1979).

To help assay the generality of our results, we computed equivalent dispersal and genetics statistics for two additional populations of Spruce Grouse, using data available in the literature. Robinson (1980) studied a small population of Spruce Grouse, over a period of five years, on an area of approximately 6.5 km² on the Upper Peninsula of Michigan (fig. 1: Yellow Dog). He reported male and female natal dispersal distances, the approximate census size, and adult year-to-year survivorship. His dispersal and density data were based on intensive searches; only a few radio transmitters were used.

Robinson (1980) presented his dispersal and density data in units of miles; we have converted them to kilometers.

Harrison (2001) studied Spruce Grouse movement and survivorship over a period of three years on a large area in east-central British Columbia (fig. 1: Bowron). He used radio-telemetry and fixed-wing aerial surveys to relocate Spruce Grouse tagged as part of a study of the effect of habitat fragmentation treatment on survival and movement. Among the data he reported were maximum natal dispersal distances (not classified by sex), population density, and adult year-to-year survivorship.

We compared the dispersal distributions from the three studies using pairwise Kolmogorov-Smirnov two-sample tests; because the dispersal data from the Bowron study were not classified by sex, we pooled the male and female distributions for the comparisons of Gorge Creek and Yellow Dog with Bowron.

Results

The observed distributions of natal dispersal distances for male and female Spruce Grouse on the Gorge Creek study site are shown in figure 2. The vast majority of males dispersed a distance of less than 2.5 km (median=1.03 km), but the females had a less truncated distribution (median=1.84 km); the two distributions differed significantly ($P<0.01$). The parameter of interest for genetic purposes, the root-mean-square dispersal distance (e.g., Endler 1977), was estimated as 1.51 km for males and 3.19 km for females, with a harmonic mean of 2.05 km (Table 1, 2). The bootstrap 95% confidence intervals for σ were 1.17–1.86 km for males and 2.25–4.24 km for females. Our estimates of kurtosis, 4.85 for males and 3.64 for females, indicate the two distributions were

substantially leptokurtic, that is, they had greater density under the peak and under the tails than found in, for example, a normal distribution—which has an expected kurtosis of zero.

We computed the probabilities of dispersal detection for 0.25 km distance intervals, assuming the 5.2 km² study site had been circular with a radius of 1.3 km. When corrected for the sampling bias due to a finite searched area, the median dispersal distance for males increased from 1.0 km to approximately 2.2 km; for females, it increased from 1.8 km to 2.4 km.

Keppie (1979) recorded between 77 and 107 adults in a surveyed area of 5.2 km² over a period of four years; we computed the harmonic mean of those four densities and obtained an overall density estimate of 17.8 km⁻² for adult Spruce Grouse at Gorge Creek. Keppie (1979) also reported adult year-to-year survivorship of 0.80 for males and 0.66 for females; we averaged these estimates to obtain an overall value. Using these results, we computed a neighborhood census size of 935.4 Spruce Grouse for Gorge Creek. The survivorship data resulted in an estimate of the genetic effective size of a local population of 540.7 (Table 2).

The sample sizes of observed dispersing individuals for the Yellow Dog study of Robinson (1980) were substantially smaller than for the Gorge Creek site. The natal dispersal distributions for the two sexes (Fig. 2) differed significantly ($P < 0.05$). Our estimates of the dispersal statistics are presented in Table 1. The estimates of the mean and median distances dispersed by females exceeded those of males. However, the estimates of σ for the two sexes were quite similar; this was because one male dispersed substantially further than all the others. The distribution for males was leptokurtic, but

that of females was actually platykurtic (-1.11) and flatter than a normal distribution. Consistent with that result, its appearance was somewhat flat with distance (Fig. 2), but was based on only 14 individuals. Robinson (1980) estimated an average total of 44 adults on an overall area of 6.5 km², for a density of 6.80 km⁻²; he estimated adult year-to-year survivorship of 0.50 for males and 0.45 for females. Consequently, we estimated an effective local neighborhood size of 890.2 adults (Table 2).

The distribution of dispersal distances for the Bowron study (Harrison 2001) is shown in figure 2. The median distance dispersed was approximately 1.00 km, σ was 3.01 km, and the distribution was leptokurtic (Table 1). However, the estimate of kurtosis should be treated with caution; it was based on a combination of the two sexes that, based on the results for both Gorge Creek and Yellow Dog, probably had different underlying distributions. Harrison (2001) reported a spring breeding density (averaged over treatments) of 10.15 km⁻², and an adult year-to-year survivorship (averaged over treatments) of 0.58; hence, our estimate of effective neighborhood size was 731.4 (Table 2).

We used Kolmogorov-Smirnov tests to examine whether the observed dispersal distributions varied among study sites. Because the Bowron results did not segregate birds by sex, we combined the male and female distributions for the other two sites for these comparisons. The two studies with the largest sample sizes, Gorge Creek and Bowron, did not differ ($P > 0.05$). However, the distribution for the smaller, Yellow Dog, site differed statistically from those of both of the larger studies, with greater density in the tail.

Discussion

Several prior studies have documented movements and dispersal in Spruce Grouse. Ellison (1973) used color bands and radio transmitters to study a population on the Kenai Peninsula in southern Alaska. He reported home range sizes of marked birds and also documented seasonal movements of juveniles and adults; however, the distances moved by juveniles between their brooding range and breeding ranges were not reported. Similarly, Beaudette and Keppie (1992) and Keppie (2004) reported on autumn and spring movements of juveniles in populations in New Brunswick and Ontario, but did not provide distributions of distances moved. Fritz (1979, 1985) examined Spruce Grouse occupancy of fragmented habitat in the Adirondack Mountains of New York over a four-year period; he concluded that the failure of populations to recolonize small patches following local extinction was the result of low dispersal propensity, but he did not directly document dispersal distances. Whitcomb et al. (1996) documented autumn juvenile dispersal through deciduous forest in fragmented habitat on an island on the Maine coast, but the observation period did not extend to the spring breeding season. Thus, other than the three studies analyzed here, we know of no prior documentation of the observed distributions of natal dispersal distances in this species. A DNA sequencing study (Barry and Tallmon 2010) reported substantial genetic divergence between populations of Spruce Grouse on islands in the Alaskan panhandle, and modest F_{st} values among populations on the mainland; these are consistent with low to moderate dispersal propensity.

Our results indicate that the natal distances moved by female Spruce Grouse exceeded those moved by males for the largest, Gorge Creek study; this is the generally

observed pattern found in birds (Greenwood 1980). For the Yellow Dog population, the root-mean-square distance moved by males exceeded that of females, but this was largely due to a single male in the sample that moved 8 km, more than ten times the median; the median distance moved by females was more than twice that moved by males.

Although it has long been recognized that the dispersal distributions of many organisms are leptokurtic (e.g., Bateman 1950; Wright 1969), the topic has not been widely investigated in natural populations and we do not know of any prior estimates of the parameter for populations of birds. This omission is due, at least in part, to the small samples sizes often available from such studies, but also may be the result of the fashion in which the distributions have usually been presented: as a summary of absolute distances dispersed without the associated angular vectors. We have attempted to alleviate this problem by assuming radial symmetry; this ought to be reasonable for studies taking place in extensive, homogeneous two-dimensional habitat. Our estimates indicated that the natal dispersal distributions for the two Spruce Grouse populations with the largest sample sizes (Gorge Creek and Bowron) were leptokurtic. That is, the distributions generally had "fatter tails" than that of a normal distribution. This is consistent the suggestion by Schroeder and Boag (1988) that Spruce Grouse might display heterogeneous dispersal tendencies, possibly as a result of genetic predisposition.

Estimates of dispersal distances based on mark-recapture or re-observation studies are subject to underestimation due to a bias against the observation of longer distance dispersal events (Barrowclough 1978). However, this bias is reduced as the size of a study area gets larger and exceeds the range of dispersal distances; we attempted to get an estimate of the possible extent of the bias by modeling the Gorge Creek study area as a

circle. Those results indicated that the median dispersal distances might have been underestimated by on the order of 1.2 km and 0.6 km for males and females, respectively. However, there is reason to believe that extrapolation might actually represent an upper bound. During the course of the Gorge Creek study, field personnel conducted extensive surveys for marked Spruce Grouse outside of the boundaries of the primary study area and, for both males and females, recorded several dispersal events well beyond those boundaries. Radio-tracking also reduces the bias in estimating dispersal. In our case, we observed that the distribution of dispersal distances from the Bowron study, which primarily used aircraft to search for radio-tagged dispersers over a large, highly fragmented landscape, was not significantly different from that of the small, relatively homogeneous landscape associated with Gorge Creek. This suggests that the size of the Gorge Creek study site, together with the extensive surveys, were of sufficient size to ameliorate some of that potential bias. Even so, the larger number of male dispersers observed (105) compared with female dispersers observed (49) at Gorge Creek (Fig. 2) suggests that as many as half of the females may have been missed, perhaps due to relatively larger movements, lower detection probability, or both.

The distributions of natal dispersal distances for the three studies summarized here indicate that Spruce Grouse neighborhoods were 8 to 16 km in diameter, with breeding census and genetic effective sizes on the order of hundreds of individuals. The Spruce Grouse dispersal distances were larger than those reported for several species of passerine birds (Barrowclough 1980), but the genetic sizes were actually similar in magnitude to those of the tabulated passerines, as a result of the lower population densities of the grouse. We note that, in general, the estimation of genetic size assumes

homogeneous environment; if the empirical dispersal data were for a region that included unsuitable habitat, then the actual effective size of the population would be less than the estimate, according to the proportion of poor habitat. With respect to other species of grouse, few studies have reported the distributions of natal dispersal distances; rather, a few have reported average movements of juveniles, but those have not always been to known breeding sites (e.g., Jamieson and Zwickel 1983). Martin and Hannon (1987) did report on a study of natal dispersal in Willow Ptarmigan (*Lagopus lagopus* (L., 1758)), but the reported distributions were in terms of numbers of territories, not physical distances. For another forest species, the Ruffed Grouse (*Bonasa umbellus* (L., 1766)), average autumn dispersal distances (Small and Rusch 1989) substantially exceeded the natal distances of Spruce Grouse, but actual natal dispersal, from brood site to breeding site, was not reported. For an open country species, the Greater Sage-Grouse (*Centrocercus urophasianus* (Bonaparte, 1827)), median natal dispersal distances, 7–8 km (Dunn and Braun 1985), greatly exceeded those of the Spruce Grouse; genetic data suggest sage-grouse dispersal distances may be substantially greater than 7–8 km (Davis et al. 2015). Thus, given the anecdotal data cited above from prior studies, as well as the analyses reported here, it appears that natal dispersal in Spruce Grouse is limited, female biased, and that this may be one of the more philopatric species of grouse.

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Table 1. Descriptive parameters from studies of Spruce Grouse (*Falcipennis canadensis*) at the Bowron (central British Columbia), Gorge Creek (southwestern Alberta), and Yellow Dog (Upper Peninsula of Michigan) field sites.

Parameter:	Bowron	Gorge Creek		Yellow Dog	
	Total	Male	Female	Male	Female
Study area (km ²)	4160	5.2		6.5	
Observed dispersers	62	105	49	16	14
Natal dispersal distances (km):					
Mean	2.13	1.13	2.33	2.30	3.16
Median	1.00	1.03	1.84	1.05	2.98
Root-mean-square	3.01	1.51	3.19	4.05	3.79
Kurtosis (<i>g</i> ₂)	0.72	4.85	3.64	7.27	-1.11

Table 2. Demographics and genetic structure of Spruce Grouse (*Falci pennis canadensis*) populations at Bowron (central British Columbia), Gorge Creek (southwestern Alberta), and Yellow Dog (Upper Peninsula of Michigan) study areas.

Parameter	Bowron	Gorge Creek	Yellow Dog
Adult density ρ (km^{-2})	10.15	17.80	6.80
Adult annual survivorship	0.58	0.73	0.48
Root mean square natal dispersal distance* (σ -km)	3.01	2.05	3.92
Effective population size (N_e)	731.4	540.7	890.2

*Harmonic mean of sexes.

Figure Legends.

Figure 1. Approximate locations of three long-term study sites of Spruce Grouse (*Falcapennis canadensis*) in British Columbia (Bowron), Alberta (Gorge Creek), and Michigan (Yellow Dog). Geographic range of the species is indicated by dark gray.

Figure 2. Observed natal dispersal distributions and sample sizes from studies of Spruce Grouse (*Falcapennis canadensis*) at the Bowron (central British Columbia), Gorge Creek (southwestern Alberta), and Yellow Dog (Upper Peninsula of Michigan) field sites. Dispersers were birds marked as chicks or juveniles encountered during a subsequent breeding season.

Figure 1. Approximate locations of three long-term study sites of Spruce Grouse (*Falcipennis canadensis*) in British Columbia (Bowron), Alberta (Gorge Creek), and Michigan (Yellow Dog). Geographic range of the species is indicated by dark gray.
76x57mm (300 x 300 DPI)

Figure 2. Observed natal dispersal distributions and sample sizes from studies of Spruce Grouse (*Falcapennis canadensis*) at the Bowron (central British Columbia), Gorge Creek (southwestern Alberta), and Yellow Dog (Upper Peninsula of Michigan) field sites. Dispersers were birds marked as chicks or juveniles encountered during a subsequent breeding season.
273x369mm (300 x 300 DPI)