



Population Ecology

Seasonal Movements and Dispersal Patterns: Implications for Recruitment and Management of Willow Ptarmigan (*Lagopus lagopus*)

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ABSTRACT We investigated the general patterns of movements in willow ptarmigan (*Lagopus lagopus*) populations. We analyzed data from 300 radiocollared willow ptarmigan from 3 study areas in the Swedish mountain range, and from 2 previous studies of recoveries of wing-tagged chicks from 3 areas in southern Norway. We found that 80% of juvenile females dispersed more than 5 km from their natal area, whereas only 25% of juvenile males established a summer range more than 5 km from the area where they were caught as chicks. Mean dispersal distances of juvenile females were 3 times longer (10.4 km) than those of juvenile males (2.4 km). Movement differences within sexes were not associated with apparent female breeding success or ptarmigan density in the natal area, and adult females migrated between wintering areas used as juveniles and their first breeding site. We found no differences in dispersal distances between the Norwegian and Swedish populations. Movements of adult and juvenile females during spring were similar in all respects. At scales of more than 5 km, the movements of juveniles and adult females play a role in redistributing birds within landscape units, and represent important inter-population movements. The results of this study explain the apparent contradiction between non-compensatory mortality based on data from radio-marked ptarmigan, and the almost complete compensation based on annual counts. Estimating the extent of immigration into areas with high local mortality is difficult because of predation or harvest under conditions of high, fixed emigration and immigration dependent on local conditions. This represents a problem if dispersal distances include areas that are considerably larger than the size of the study area. © 2014 The Wildlife Society.

KEY WORDS dispersal, *Lagopus lagopus*, management, movement, ptarmigan, recruitment.

The importance of long-distance seasonal migration to increase fitness is well recognized (Alerstam et al. 2003, Berger 2004, Trakhtenbrot et al. 2005), but many non-migratory species also adapt to seasonal changes by shorter movements, typically between the same non-overlapping summer and winter ranges (Myserud 1999, Yáber and Rabenold 2002). The majority of bird species show strong breeding-site fidelity (Andersson 1980), and exchange between subpopulations is driven by dispersal that is defined as a 1-way movement away from a social group or home range (Nathan et al. 2003, Trakhtenbrot et al. 2005). These movements are often sex-biased, which as a consequence reduces the risk of inbreeding (Clarce et al. 1997, Guillaume and Perrin 2009). In vertebrate populations, most dispersal occurs prior to the first breeding attempt (natal dispersal), whereas dispersal after first breeding (breeding dispersal) is

less common (Greenwood and Harvey 1982, Cockburn 1992).

Dispersal can affect the population dynamics of neighboring subpopulations. Dias (1996) concluded that sink habitats can make up a large part of the total population area if the surplus in the source habitat is large and the deficit in the sink area is small. Even a population in apparent equilibrium across a wide range of habitats is probably best described as a network of subpopulations with unbalanced natality and mortality rates (Hanski and Gilpin 1997). Subpopulations with excess natality compensate for subpopulations with excess mortality through dispersal (Pulliam 1988), and the particular subpopulations demonstrating excess natality or mortality can shift between years. Dispersal will rescue isolated subpopulations from extinction, especially when demographic rates are uncorrelated among subpopulations (Stacey and Tapper 1992).

An understanding of dispersal and seasonal movements is important for management and conservation (Boyce et al. 1999). This information helps to define the spatial extent and isolation of a population, and indicates the

Received: 12 December 2012; Accepted: 10 October 2013
Published: 13 February 2014

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biologically relevant size of a conservation area (Schaub et al. 2010). It can also be used to estimate the optimal size of buffer areas in terms of harvest management (McCullough 1996, Willebrand and Hörnell 2001), and improve the interpretation of monitoring data (Brawn and Robinson 1996). Data based on specific individuals is needed to differentiate between dispersal and mortality, and the use of telemetry may be the only option when recoveries of passive tags are rare (e.g., Abadi et al. 2010).

Tetraonidae (grouse) include species distributed in the Holarctic region, where different populations of the same species may be of conservation concern or the focus of harvest management (Storch 2007). Patterns of breeding success have been well studied in many species, and are at most weakly density dependent (Steen et al. 1988, Willebrand 1992, Redpath et al. 2006). Most studies show large annual variations in breeding success, with the exception of rock ptarmigan (*Lagopus muta*) in Iceland, which maintains a large and stable population (Bergerud and Gratson 1988). Predation is the most common proximate cause of mortality of nests, chicks, and adults (Small et al. 1993, Smith and Willebrand 1999). Harvest mortality can also be substantial in hunted populations, and studies have suggested that harvest mortality may vary from total compensation to total additivity (Ellison 1991, Smith and Willebrand 1999, Sandercock et al. 2011). Some earlier studies that detected no decrease in harvested populations argued that immigration must represent an important part of the apparent compensatory response (McGowan 1975, Myrberget 1985). More recent studies have emphasized the danger of considering investigated populations as closed, and have stressed the need for a better understanding of seasonal movements and dispersal (Smith and Willebrand 1999, Devers 2005).

As in most birds, dispersal in grouse is sex-biased wherein females move longer distances than males (Schroeder 1986, Martin and Hannon 1987, Small and Rusch 1989, Warren and Baines 2002). Bröseth et al. (2005), however, found no difference in dispersal distances between juvenile male and female willow ptarmigan (*Lagopus lagopus*). The process of natal dispersal seems to occur in 2 stages: 1 phase in autumn to a wintering area and 1 in spring to a breeding area (Bergerud and Gratson 1988, Small and Rusch 1989, Warren and Baines 2002, Keppie 2004, Hannon and Martin 2006). Lebigre et al. (2008) concluded that the avoidance of inbreeding was an important factor in the sex-biased dispersal of black grouse (*Tetrao tetrix*) because females do not discriminate against relatives during mating. Familiarity with an area was shown to affect survival in ruffed grouse (*Bonasa umbellus*; Yoder and Marschall 2004), making short periods of dispersal and longer periods of site exploration an advantage. This may also explain why seasonal movements of adult female grouse appear to retrace their spring natal dispersal (Schroeder 1986). As a result, the sex ratio in winter flocks of rock ptarmigan and willow ptarmigan can show a strong sex bias (Höglund 1980, Nielsen 1996).

We examined the natal dispersal distances and seasonal movements of radiocollared and wing-tagged juvenile and

adult willow ptarmigan in Sweden and Norway. We compared adult movements between summer and winter, and evaluated the site fidelity of individuals to both summer and winter ranges in consecutive years. We investigated if juvenile willow ptarmigan demonstrated a sex bias toward females moving longer distances than males, and simulated dispersal movements of juveniles based on the estimated distribution of dispersal distances with random directions. We used the simulation results to calculate the proportion of recruitment to a population given different study area sizes.

STUDY AREA

We captured and radiotagged juvenile and adult willow ptarmigan in 3 areas in the Swedish mountain range during 3 separate time periods. These areas were located in Storulvån (hereafter site A; 63°10'N, 12°22'E) in the southern part of the central Swedish mountain range (1992–1995); Stekenjokk (site B; 65°06'N, 14°28'E) in the northern part of the central Swedish mountain range (1998–1999); and Ammarnäs (site C; 65°58'N, 16°22'E) in the Vindelfjällen mountain area in southern Lappland (1997–2000; Fig. 1). We also included data from 2 previous reports on recoveries of wing-tagged chicks in the southern mountain range. Hagen (1935) reported the recoveries from tagging in 2 areas at the southern edge of Hardangervidda, Rauland, and Tinn (site D; 60°00'N, 08°30'E) from 1928 to 1933. Olstad (1953) reported recoveries from tagging chicks in another area farther east in southern Norway, Øyer (site E; 61°20'N, 10°35'E) from 1923 to 1939 (Fig. 1). The climate in all areas is characterized by a strong continent-to-ocean gradient from southeast to northwest. The mean temperature in January varies between -12.0°C and -8.0°C and in July between 11.5°C and 12.5°C . Mean annual precipitation

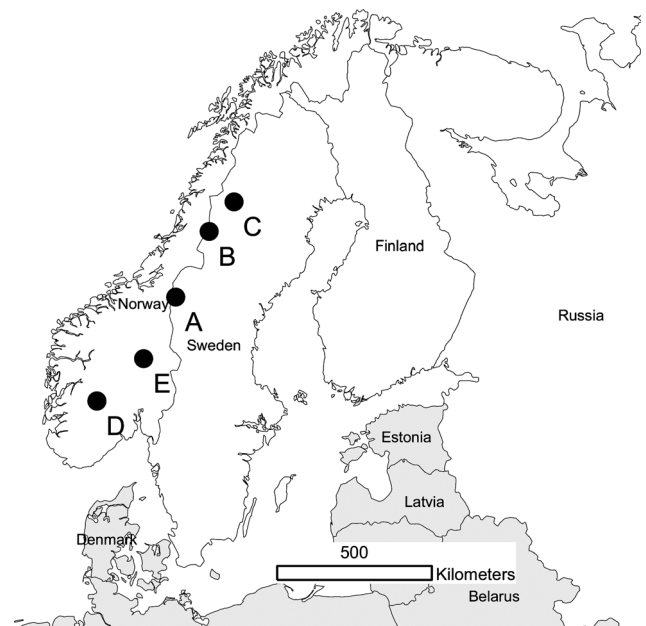


Figure 1. The locations of the 5 study areas in which dispersal and movement data on willow ptarmigan were collected: Storulvån (A), Stekenjokk (B), and Ammarnäs (C) in Sweden, and Rauland, Tinn (D), and Øyer (E) in Norway.

along the gradient ranges from 500 to 1,000 mm, half of which falls as snow..

METHODS

At our study sites in Sweden, we captured willow ptarmigan prior to brood break-up in late July and August using pointing dogs and hand-held nets (Smith and Willebrand 1999). We fitted captured birds with pataginal wing tags and a 10-g necklace radio transmitter if they weighed >300 g. At Storulvån (site A), we sexed juveniles using DNA probes (Smith 1997; 50 juveniles). In the other areas, (site B: 18 juveniles, site C: 13 juveniles) we determined sex by observation, flushing, recapture, or recovery of shot birds later in the year. In total, we acquired distance data for 102, 30, and 60 willow ptarmigan in sites A, B, and C, respectively.

In winter and early spring, we caught willow ptarmigan using walk-in traps or by spotlighting and netting from snowmobiles. We determined the age of the birds (adult [≥ 1 year] or juvenile [≤ 1 year]) by their pigmentation (Bergerud et al. 1963) and visual inspection of the tips of primaries 9 and 10, in which juveniles show more wear than adults. We used individuals aged as juveniles (<1 year) to study annual dispersal. We radiotagged all birds caught during the winter. All trapping and handling of birds was conducted according to the Swedish Animal Welfare Act. We located ptarmigans with radiocollars by triangulation using hand-held Yagi antennae; the majority of fixes obtained were within 2 km of the bird. We accepted only bearings with a difference in angle larger than 45° and recapture events based on the fixes showed that the bird was within a radius of 200 m. We conducted tracking by foot, snowmobile, or aircraft, to a maximum distance of 40 km from the point of original capture. We attempted to locate birds visually as soon as possible following dispersal, and were able to search for birds within 1 week after dispersal in most cases. However, this was not always possible, especially for site C, from which birds often crossed the Norwegian border and could not be tracked from the air or by snowmobile.

We tracked birds caught as juveniles prior to brood break-up daily in site A from August to October and March to May, and at least once a week in June, July, and November. We recorded all positions during daylight hours. We monitored birds at longer intervals between mid-December and mid-January because of poor weather and reduced access to the study area. Olsson et al. (1996) found that capture and hunting caused no significant disturbance of ptarmigan during autumn, and tracking activity did not induce long-distance movements.

We divided the year into 2 periods: summer (May–Aug) and winter (Dec–Mar), when long distance movements were rare. Olstad (1953) found that seasonal movements could begin in September and became common later in October, when recoveries from >3 km were recorded. Movements from summer to winter are termed autumn movements and movements from winter to summer are termed spring movements. Using all the positions within autumn movements and spring movements, we calculated the sum of

distances from each position to all the other positions. The position with the minimum sum of distances was defined as the most central position, and the distance between these central positions in different seasons was used in the analysis. Each individual willow ptarmigan could potentially contribute to 7 distances; as juveniles they could provide data on seasonal movements (autumn and spring) and complete natal dispersal (summer to summer), as adults they could potentially provide data on seasonal movements (autumn and spring), and site fidelity to winter and summer ranges in consecutive years. A few adults provided more than 1 distance for a single type of movement, in which case we used the average of the distances. Individuals that had moved considerable distances could not be checked on a regular basis, and we included willow ptarmigan with only 1 position in a season in 71 of the total 473 distances calculated.

The datasets from Norway included willow ptarmigan chicks that were located with pointing dogs before they were able to fly long distances, and captured by net or hand. The chicks were marked with wing-tags or leg bands, depending on body size. A bounty was paid for all marked willow ptarmigan returned to Statens Viltundersøkelse and most birds were sent in as whole birds, thus making it possible to determine the sex. Indeed, from 248 tagged willow ptarmigan chicks, 59 of 76 recoveries were whole birds (Hagen 1935). In the other study, 302 recoveries were reported from 533 tagged willow ptarmigan (Olstad 1953). Most recoveries were of complete birds shot in the autumn of the year in which they were tagged. Distances between tagging and recovery were determined from maps or by direct estimates in the field when the distance was short. From Hagen and Olstad's datasets, we extracted data on seasonal movements for 97 juvenile willow ptarmigan recovered in the subsequent winter hunting (Dec–Mar) and complete dispersal distances for 29 birds recovered during the hunting season during the next September.

Statistical Inference and Simulations

Because the estimated distances were larger than 0 and skewed to the right, we regressed the log(variance) to the log(mean) of the age, sex, and site variables. This transformation resulted in a slope of almost 2 (slope = 1.98, $P < 0.001$, $R^2 = 0.90$), which according to Taylor's Power law suggests a gamma distribution (Crawley 2002). We used generalized linear models with gamma errors and the log link function to test for effects of sex, season, and site on movement. We analyzed adults and juveniles separately and allowed for all 2-way interactions. We removed interaction terms if they were not significant. We pooled the 3 Swedish sites and the 2 Norwegian sites when they did not significantly differ at the $\alpha = 0.05$ level. We used the function `glm.diag.plot` in the package `boot` (Canty and Ripley 2012) for model evaluation.

To explore how local recruitment was affected by the size of a study area, given the distribution of complete dispersal distances, we modified the code according to Bolker (2008:330) and assumed that dispersal distances followed a gamma distribution. We used a hierarchical model, and

assumed that the estimated distances contained a normally distributed measurement error. We estimated the shape and scale parameters separately for males and females using JAGS (Plummer 2003) and Gibbs sampling. We used non-informative priors for the parameters. We used 3 chains of 50,000 iterations with a burn-in of 1,000 and a thinning rate of 3. For all estimated parameters, $\hat{R} < 1.001$. We calculated the overlap between the distributions of the shape (male: 1.42, female: 1.59) and scale (male: 0.60, female: 0.16) parameters of the posterior distribution and found the overlap to be 0.384 and 0.005 for shape and scale, respectively. We created a uniform landscape of 40,000 km² where broods were randomly distributed at a density of 10 broods/km² with 1 male and female chick recruited successfully into the breeding population the next spring. Each chick could go in any random direction at a distance drawn from the sex-specific gamma distribution. We then calculated the proportions of male and female recruits to the local population for areas of different sizes (10–470 km²) placed at the center of the landscape. We repeated this procedure for the upper and lower 95% confidence intervals of the scale parameter to investigate the uncertainty in the predictions. The shape parameter showed a large overlap between the sexes in the posterior distribution and we only used the mean values in the simulation.

We carried out all analyses and simulations using the R statistics package (R Version 2.15.2, www.r-project.org, accessed 10 Nov 2012). We used libraries R2jags (R2jags Version 0.03-8, cran.r-project.org/web/packages/R2jags/index.html, accessed 10 Nov 2012) and R2WinBUGS (R2WinBUGS Version 2.1-18, cran.r-project.org/web/packages/R2WinBUGS/index.html, accessed 10 Nov 2012) to interface R with JAGS.

RESULTS

Site Fidelity and Seasonal Movements of Adults

Females tended to move farther between consecutive summer or winter ranges ($\beta_{\text{sex(females)}} = 0.74$, $t_1 = 2.42$, $P = 0.02$). Neither site ($\beta_{\text{site(Norway)}} = 0.24$, $t_1 = 0.77$, $P = 0.43$) nor season ($\beta_{\text{season(autumn)}} = 0.24$, $t_1 = 0.80$, $P = 0.44$) affected adult movement distances between consecutive summer and winter ranges. The consecutive winter and summer ranges were on average 1.12 km apart for males and 2.06 km for females indicating strong site fidelity (Table 1). However, we observed approximately 10% of adult (breeding) dispersal. Two of 28 males moved 5.0 km and 6.0 km to new summer ranges in early spring, 3 of 33 females moved 12.0–12.4 km to new summer ranges, and 2 other females shifted their consecutive winter ranges by 10.0 km and 14.0 km.

Females moved significantly farther than males ($\beta_{\text{sex(females)}} = 1.88$, $t_1 = 9.8$, $P > 0.001$) between summer and winter ranges, but for both sexes, the distances were similar for moves from winter to summer or from summer to winter ($\beta_{\text{season(winter)}} = 0.12$, $t_1 = 0.77$, $P = 0.45$). In site B, the distances moved between seasons were farther ($\beta_{\text{site(B)}} = 1.19$, $t_1 = 5.17$, $P < 0.001$), and especially for

Table 1. Distances moved (km) of adult willow ptarmigan with radio tags in 3 different areas (A, B, and C) in Sweden. Site fidelity, distance between consecutive seasons (summer–summer, winter–winter), was similar for all 3 areas. Females always moved farther than males between summer and winter ranges and seasonal distances were longer in area B compared to A and C.

Group	Sex	Min.	25%	Mean	75%	Max.	<i>n</i>
Site fidelity	Male	0.0	0.4	1.1	1.4	6.0	42
	Female	0.0	0.3	2.1	1.6	14.0	65
Between seasons (A, C)	Male	0.1	0.3	0.8	1.2	2.3	68
	Female	0.0	0.5	5.0	4.8	33.4	68
Between seasons (B)	Male	0.1	0.8	2.5	2.8	17.3	37
	Female	0.1	1.5	7.3	8.2	24.9	56

males ($\beta_{\text{area(B):sex(females)}} = -0.82$, $t = -2.66$, $P = 0.008$). During seasonal movements, males on site B moved on average 3.3 times farther than males on sites B and C, whereas females from site B only moved 1.5 times farther than females on sites B and C (Table 1). Some individuals moved long distances between summer and winter ranges. In total, 3 of 30 males (10%) moved 6.9–17.3 km in spring, and 11 of 39 (28%) and 17 of 45 (38%) females moved 6.3–33.4 km in autumn and spring, respectively. We tracked 4 females for 2 autumn and spring movements, and they returned to the previous seasonal range, independent of the distance traveled (6.3–24.4 km). The radiocollar on the female that moved 33 km between 2 summer ranges and 1 winter range failed the second winter, but it was shot in February in the previous winter range.

Natal Dispersal and Seasonal Movement of Young

We found that sex ($\beta_{\text{sex(female)}} = 1.45$, $t_1 = 5.40$, $P < 0.001$) affected the complete natal dispersal distances of juvenile willow ptarmigan, but we found no difference in natal dispersal distances between the old wing-tag data from southern Norway and the more recent Swedish telemetry data ($\beta_{\text{area(Sweden)}} = 0.01$, $t_1 = 0.054$, $P = 0.96$). The average distances for complete natal dispersal from brood to consecutive summer range were 2.44 km for males and 10.39 km for females (Table 2). None of the males showed a natal dispersal distance farther than 10 km, but 10 of the 21 females moved between 10.3 and 39.0 km from their brood area to their consecutive summer range.

Table 2. Complete natal dispersal and seasonal movements (km) of juvenile willow ptarmigan in Sweden (A–C) and Norway (D, E). Norwegian data were wing-tagged chicks later recovered during hunting. All Swedish ptarmigans were radio-tagged, and spring movements were only available from Sweden.

Group	Sex	Min.	25%	Mean	75%	Max.	<i>n</i>
Natal dispersal (A–D)	Male	0.1	0.9	2.4	4.0	10.0	29
	Female	0.6	4.0	10.4	14.7	39.0	21
Spring (A–C)	Male	0.1	0.9	2.8	3.2	18.1	19
	Female	0.1	1.4	7.1	10.8	24.5	38
Autumn (D, E)	Male	0.1	2.0	4.6	4.9	29.0	54
	Female	0.2	0.4	0.8	1.1	2.2	11
Autumn (A–C)	Male	1.0	7.5	12.2	17.0	30.0	43
	Female	0.1	0.8	7.1	12.6	17.5	11

Juvenile females moved farther than males in autumn ($\beta_{\text{sex(female)}} = 1.17$, $t_1 = 6.36$, $P < 0.001$), but the distances moved were farther for both sexes in the Norwegian data ($\beta_{\text{area(Sweden)}} = -1.06$, $t_1 = -4.21$, $P < 0.001$). In the Norwegian banding data, the juvenile males on average moved almost 4 km farther in autumn than juvenile males in the Swedish telemetry data. Juvenile females in the Norwegian dataset on average moved approximately 5 km farther than juvenile females in the Swedish dataset. Spring movements were only available for radiotagged willow ptarmigan in Sweden, and females moved farther than males ($\beta_{\text{sex(females)}} = 1.03$, $t_1 = 3.61$, $P < 0.001$; Table 2). Seven of 65 (11%) juvenile males moved 11.0–29.0 km in autumn, but only 1 of 19 (5%) moved farther than 10 km in spring (18.1 km). Twenty-five of 52 (48%) females moved 10.0–30.0 km in autumn, and 12 of 38 (32%) moved 10.0–25.5 km in spring.

Distribution of Dispersal Distances and Recruitment Simulation

The estimated shape parameter assuming a gamma distribution of natal dispersal distances showed a large overlap of males and females, 1.42 (0.66–2.71) and 1.59 (0.82–2.75), respectively. The scale parameter on the other hand, was different for males and females, 0.60 (0.26–1.13, 95% CI) and 0.16 (0.07–0.28, 95% CI), respectively. The difference between the posterior distributions of the scale parameter overlapped with less than 5%. The estimated distribution for male natal dispersal distance from 10,000 randomly drawn distances showed that the central 50% of distances were between 0.9 and 3.3 km, whereas the central 50% range for females was between 4.2 and 13.6 km (Fig. 2).

Fifty percent of the male recruitment occurred in an area of about 20 km², whereas 50% of the female recruitment occurred in an area of 395 km² (Fig. 3). The recruitment of

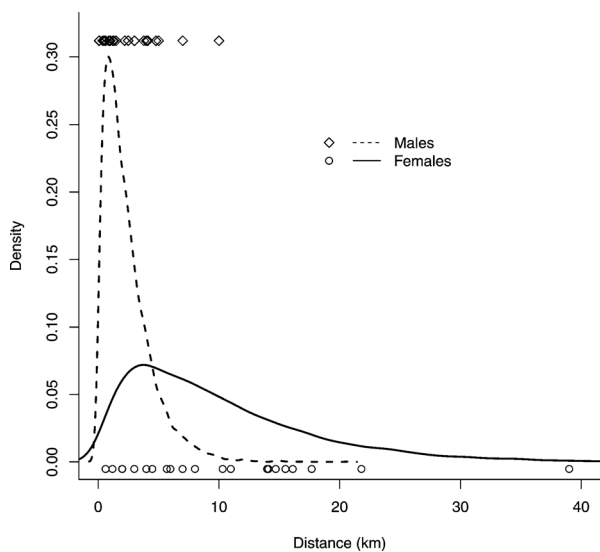


Figure 2. Estimated distribution of willow ptarmigan natal dispersal distances for females (solid) and males (dashed) in Sweden and Norway. The individual distances used to calculate the scale and shape parameter of the gamma distribution are shown at the bottom for females (circles) and at the top for males (diamonds).

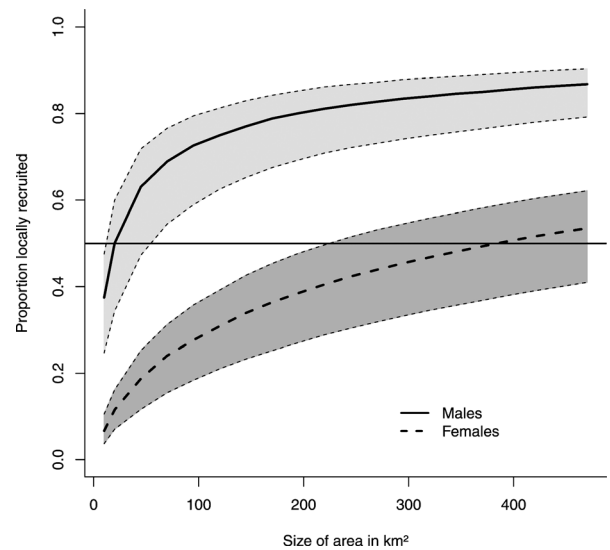


Figure 3. Proportion of young recruited from chick production the previous year in relation to the size of the area. Male willow ptarmigan (thick solid line) and female willow ptarmigan (stippled thick line) are shown separately. Distances were drawn from a gamma distribution using the estimated shape and scale parameters, assuming random dispersal directions. The gray area between the thin stippled lines shows the upper and lower standard error of the scale parameter. The horizontal line depicts the area required for 50% recruitment from within the area.

males from within the area leveled off at about 75 km², and reached 80–85% within 300–500 km².

DISCUSSION

Variations in recruitment will have large impacts on the population dynamics of willow ptarmigan because of the high (35–60%) annual adult mortality (Smith and Willebrand 1999, Sandercock et al. 2011), and the subsequent high juvenile-to-adult spring ratio in most years. Ptarmigan in all the investigated areas showed a similar natal dispersal pattern, with local recruitment of males and recruitment of females from a large surrounding area. Most willow ptarmigan research and management areas in Scandinavia are smaller than 100 km², and will thus experience a net effect of juvenile female dispersal. Areas smaller than 30 km² would also have to account for a net exchange of juvenile males with surrounding areas. We could ignore these effects if all areas had the same levels of chick production, and if the annual fluctuations were spatially correlated. However, neighboring monitoring areas showed substantial differences in terms of average chick production, and spatial correlation in breeding success was weak (Hörnell-Willebrand et al. 2006). Aanes et al. (2002) modeled the population dynamics of a local population of willow ptarmigan, and the best model resulted in unrealistically high growth rates at extremely low densities. We suggest that this could be explained by a greater than expected recruitment based on the local chick per adult ratio.

Bowler and Benton (2005) emphasized that dispersal is a poorly understood process, and concluded that it should be partitioned into 3 separate events: emigration, inter-patch movement, and immigration. They also suggested that

condition-dependent dispersal strategies would be superior to fixed strategies. Bocedi et al. (2012), however, showed that high emigration rates would be expected in unpredictable environments. We believe that the autumn movement (emigration) is a fixed strategy driven by brood break-up and birds leaving for winter habitats. In spring, males return to their brood areas and try to establish themselves close to their fathers, which is similar to the strategy seen in young male red grouse (*Lagopus lagopus scoticus*; MacColl et al. 2000) and black grouse (Warren and Baines 2002). Juvenile females do not return, but end up farther away from their brood area after the spring (inter-patch) movement. This movement is accomplished in a single step, with no apparent exploration of sites in between. As in the majority of grouse species, males disperse shorter distances than females, although the distances involved were longer in this study than those seen for most forest and plains grouse species (Schroeder 1985, 1986; Hines 1986; Small and Rusch 1989; Marjakangas and Kiviniemi 2005; Hannon and Martin 2006; Moss et al. 2006). One study deviated from this general pattern; Brøseth et al. (2005) found no differences in dispersal distances between juvenile female and male willow ptarmigan in central Norway, with average dispersal distances of <4 km, and with adults of both sexes moving 400 m less than juveniles.

Avoidance of inbreeding is likely to be the most important factor explaining the observed sex difference in dispersal; Lebigre et al. (2008) suggested that females are unable to recognize kin, and thus disperse to avoid inbreeding. Inbreeding avoidance could also be the result of male-bias dispersal, which is common in mammals but is seldom seen in birds (Mabry et al. 2013). Females in large continuous landscapes and subject to large unpredictable annual variations in breeding conditions could benefit from a fixed strategy of long inter-patch movements, but become vulnerable if fragmentation increases as a result of increased human land use. We believe that the third step, immigration, is the most condition-dependent part of the natal dispersal process, and determines the distribution on a small scale (<10 km²). We propose this conceptual model of a 3-step process as a null model representing natal dispersal in willow ptarmigan, and probably in other grouse species, and conclude that the net effects of dispersal may be more important than previously assumed.

We caution against generalizing about the pattern of movement between summer and winter ranges, because this is partly driven by the change to shrub and birch habitats at lower altitudes. Adult males move shorter distances than females and stay closer to their breeding range in winter. Most females use the same ranges in consecutive summers and winters, but females from the same summer range may go to different winter ranges and join flocks with ptarmigan from other summer ranges. Similar to ruffed grouse (Yoder and Marschall 2004), and as proposed for spruce grouse (*Falci pennis canadensis*; Schroeder 1985) and black grouse (Willebrand 1988), female willow ptarmigan probably benefit from using a winter range that they are familiar with, and thus retrace their juvenile spring movement. The

redistribution of willow ptarmigan between summer and winter will change local densities, making it difficult to use summer counts as an index of winter population size. Boyce et al. (1999) demonstrated that a failure to incorporate seasonality into population models could lead to erroneous predictions about predation and harvest mortalities, and concluded that seasonal redistribution of individuals must be accounted for.

MANAGEMENT IMPLICATIONS

Monitoring programs should consider the potential net effects of natal dispersal, and that using sampling units of different spatial scales may result in different patterns of population change. The extents of dispersals and seasonal movements will also affect the required size of protected areas; a small and isolated area of suitable habitat may be sufficient for males, but could put females at risk as they are more likely to move into unprotected surroundings. Seasonal movements can explain the apparent contradiction between non-compensatory mortality based on data from radio-marked ptarmigan, and almost complete compensation based on annual counts. The effect of immigration to compensate for high local mortality can be difficult to estimate if emigration is less dependent than immigration on local conditions and the source of immigration is considerably larger than the size of the study area. The seasonal movements of dispersal and migration will alter the distribution and change local abundances of ptarmigan. Some individuals from the local summer population will form groups consisting of individuals from other local populations in winter, especially in the case of females. This will complicate inferences from predator response and compensatory mortality, and individuals captured and marked in one season are probably not representative of the studied population in another season.

ACKNOWLEDGMENTS

We thank the technicians A. Hammarström, J.-P. Magnusson, G. Ericsson, G. Olsson, S. Edfalk, E. Edfors, and E. Ringaby, as well as the other assistants who did a great job of catching and tracking ptarmigan in the field. The study was financed by the Swedish Environmental Protection Agency and the Swedish Hunters' Association.

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Associate Editor: Daniel Twedt.