RECRUITMENT, DISPERSAL, AND DEMOGRAPHIC RESCUE IN SPATIALLY-STRUCTURED WHITE-TAILED PTARMIGAN POPULATIONS[1]

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Abstract. We studied recruitment and dispersal of White-tailed Ptarmigan (*Lagopus leucurus*) breeding in naturally fragmented alpine habitats at four study sites in Colorado from 1987–1998. Almost all recruitment for both sexes, particularly females, was of birds produced outside local populations and also external to nearby studied populations. Populations were more dependent on female recruitment than on male recruitment to sustain them, and patterns of recruitment were not correlated with local survival of adults or production of young the previous year, except at one site for females. Over 95% of recruits were yearlings. Breeding dispersal of adults, an infrequent but regular event, was also important to interpopulation connectivity. Our data for multiple populations allowed us to describe movement patterns among populations to assess consistency with conditions required for a rescue system. After widespread reproductive failure in one year, we expected all populations the next year would have low recruitment due to a reduced supply of recruits produced in the region. Recruitment was low, but impact varied among populations. We conducted an over-winter study of radio-marked offspring to determine possible influences of winter site location and relatives on recruitment patterns. Contrary to expectation, offspring remained on or near breeding sites in winter, but were not located near their mothers or siblings. Recruitment location was related to winter site location. White-tailed Ptarmigan exhibit a well developed capacity for external recruitment that allows them to persist in small populations with stochastic conditions for breeding and survival. Extensive external recruitment may be a general pattern for birds.

Key words: demographic rescue, dispersal, Lagopus leucurus, *local survival, metapopulation processes, recruitment, White-tailed Ptarmigan.*

INTRODUCTION

Periodic rescue of declining populations through recruitment from productive populations (dispersal rescue) may be an important feature of avian population biology. Dispersal rescue describes the process whereby populations that experience one or several poor years of reproduction or survival escape extinction or a population bottleneck by immigration of individuals from elsewhere in the metapopulation system (Brown

and Kodric-Brown 1977). Stacey and Taper (1992) modeled the importance of immigration rescue to persistence of small populations, and showed that external recruitment was vital to ensuring population persistence and stability. Dispersal rescue is predicted to work most effectively when neighboring populations are in close proximity, but are uncorrelated in patterns of annual production and survival (Stacey et al. 1997). If inter-patch dispersal is high, local extinction may not occur (Harrison 1991). Thus, dispersal may operate regularly to ensure local population stability; extinction may be a failed rescue process.

Studies of the patterns and mechanisms of re-

cruitment and dispersal in multiple populations allow a direct assessment of the importance of demographic connectivity among populations. Metapopulation processes may be influenced by both local and/or regional stochasticity (Hanski 1991, 1994, Hanski and Gilpin 1991, Harrison 1991). A knowledge of synchrony in populations within a region is crucial to understanding population and multi-population persistence times (Harrison and Quinn 1989, Hansson 1991).

Regardless of whether a metapopulation structure can be demonstrated for a species, investigating metapopulation processes such as dispersal and rescue, and how they interact with stochastic factors, is vital to understanding the population dynamics for species, particularly in fragmented habitats. Alpine habitats, given their naturally patchy character with regular stochastic factors, are ideal for examining rescue processes. Dispersal and other population transfer mechanisms for vagile vertebrates are poorly understood and logistically difficult to study at relevant biological and spatial scales (Martin 1998). Data are usually lacking on social interactions or movements in the post-breeding season, factors considered to be important to offspring making "decisions" regarding dispersal and recruitment. Most life history studies assume that patterns of offspring settlement show a gradual decline away from natal territories, but there are logistical and analytical problems in estimating numbers and distance of widely dispersing offspring (Koenig et al. 1996, Nichols 1996).

To examine the importance of metapopulation processes in naturally fragmented habitats, we studied four populations of White-tailed Ptarmigan (*Lagopus leucurus*) in Colorado. About 95% of both sexes spent their entire breeding life in one population, satisfying the definition of a discrete population suggested by Harrison (1991), and patches were connected by natal dispersal. Our populations showed dramatic variation in offspring production and return (local survival) of adults across years and sites (Braun et al. 1993, Hannon and Martin 1996). Reproductive failure appeared driven by climatic events and internal ecological processes such as depredation of eggs and young (Braun et al. 1993, K. Martin and K. L. Wiebe, unpubl. data). Preliminary results indicated that variation in reproductive success and survival were uncorre-

lated across sites and years, and that small populations remained stable despite stochasticity in internal population dynamics (Martin et al. 1997, K. Martin, unpubl. data). Here, we present data on origins and patterns of recruitment for four study populations that showed strong reliance on external rescue. For recruits, we present data on the relative amounts of natal (juveniles) versus breeding dispersal (breeding birds between years). Settlement patterns in relation to natal territory are given for offspring recruits in one population.

We also present data on recruitment and population size in a year following widespread reproductive failure, and compare these to recruitment patterns from all previous years when reproductive failure varied spatially across populations. Thus, with this natural experiment, we examine patterns of recruitment caused by local and regional events. We anticipated that all populations would have low recruitment in the year following regional-level failure due to a reduced supply of recruits in the region, but that populations with generally higher local survival of adults would be impacted less than populations normally requiring a high rate of rescue. We expected that one population that normally recruited a higher proportion of adult females would be buffered from this regional-level event. Finally, with a telemetry study, we examined possible social and behavioral mechanisms for natal recruitment. In one year, we followed radio-marked offspring over winter to the following spring, and examined influences of movements by mothers and siblings and winter dispersal behavior on offspring recruitment patterns.

METHODS

STUDY AREAS

We studied four populations of White-tailed Ptarmigan breeding in naturally fragmented high alpine habitats in the Colorado Rocky Mountains (39°34-40'N, 105°35-53'W) from 1986 to 1998 (Fig. 1). The life history and breeding biology of White-tailed Ptarmigan are detailed in Braun and Rogers (1971) and Braun et al. (1976, 1993). Each of the four study areas comprised individual mountain patches separated from the other areas by distances of 1–20 km, and in some directions by areas of unsuitable ptarmigan breeding habitat (forest, wetland, willow *Salix* spp. shrub). The Mt. Evans (ME) study area was
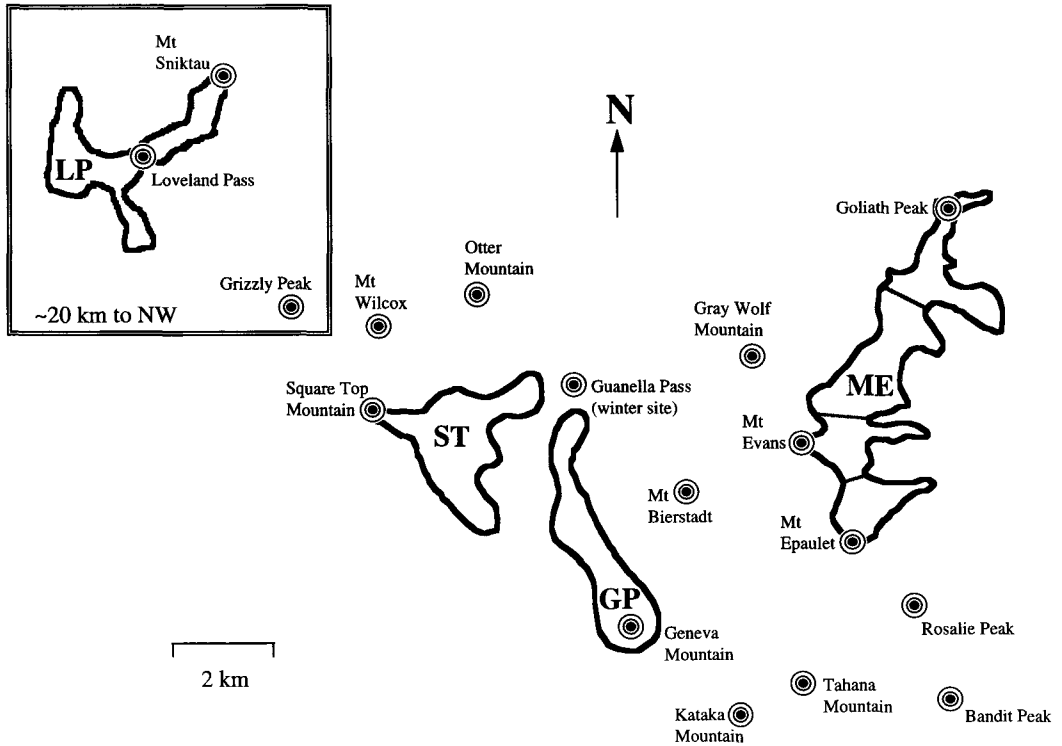
FIGURE 1. Study sites for White-tailed Ptarmigan in Colorado, including Guanella Pass winter site and adjacent mountains that were surveyed less intensively in late summer. ME—Mt. Evans, GP—Guanella Pass, ST—Square Tops, and LP—Loveland Pass. The shaded lines on ME study area indicate the four major drainages used to evaluate philopatry of internal recruits.

13.2 km² in size, and from 1987 to 1996 annual spring population sizes ranged from 26 to 67 birds (Fig. 1, Table 1). Guanella Pass (GP), 6–7 km from ME, comprised about 2.8 km², and from 1987 to 1996 (excluding 1988), populations varied from 6 to 20 birds. Square Tops (ST) was 1–2 km from GP and 8–11 km from ME. Square Tops was 4.75 km² and during 1992 to 1996 spring populations varied from 13 to 21 birds. Loveland Pass (LP), about 2.7 km², was about 20 km west of ST. Population sizes ranged from 12 to 31 birds in 1987, 1989–1992, and 1994. We also visited 12 mountains adjacent to our study sites in late summer, and captured and marked the ptarmigan adults and chicks we encountered. Although sampling of populations on adjacent mountains was limited, it allowed an opportunity to measure dispersal and recruitment between our studied populations and adjacent sites in the region. The number of years of data reported vary for different aspects of the study. We present less detail for LP because data

were missing for some years including 1995, the year of regional failure. In 1997 and 1998, we conducted less intensive censusing on ME and ST, and present data only for our over-winter study of radio-marked birds.

FIELD PROCEDURES

Field methods and data collection protocols were identical for all study sites from 1987 to 1996, and are described in Artiss and Martin (1995). In spring, pairs and single birds were located using playbacks of male territorial calls or with dogs, and captured using noose poles, noose carpets, or nets. We did not capture females until they had spent several days with a particular male on a territory and the pair bond appeared stable. We affixed necklace design radio transmitters (3.4 g, Holohil Ltd., Carp, Ontario, Canada) on all females and some males to facilitate relocation and to monitor mating status and breeding success. Birds were classified as yearlings (< 1 year old) or adults (> 1 year)

based on the amount of pigmentation on primaries 8 and 9 (Braun and Rogers 1971). All study populations contained a high proportion of known-age marked birds, with the exception of the first study years for GP and LP (1987) and ST (1992). For about 95% of 196 females monitored, we obtained data on nesting success and number of fledglings (young $\geq$ 25 days old) produced in a season. For all 369 chicks reported here, natal population was determined because chicks were individually banded or wing-tagged before brood breakup in late summer; in most cases natal territory could be assigned. From 1989 to 1993, about 74% of 117 chicks were marked with small numbered aluminum patagial tags within a few days of hatch. Loss of patagial tags was low for ptarmigan (Hannon et al. 1990, K. Martin, unpubl. data).

Over the study, all birds located were captured and individually color-marked. We relocated White-tailed Ptarmigan individuals throughout the breeding season to determine survival, mating status, and reproductive success. Return of birds that bred in a previous year to their original study population, an estimate of local survival, was determined by thorough checks of all the study areas and adjacent sites throughout the summer to encounter banded birds that had dispersed. Preliminary mark-recapture analyses indicated that we located about 95% of birds resident on study areas, and thus our data on "returns" closely approximate local survival (K. Martin, unpubl. data). Banding records and age classes of birds were used to classify birds as returns or recruits. Birds were classified as "returns" if they were banded and known to have resided on that study area in a previous year. A small number of adults changed sites between years (i.e., breeding dispersal), and if birds dispersed great distances from the study areas they were unlikely to be detected (Wiebe and Martin 1997). Birds were classified as "recruits" when first observed on a study area, either as marked or unmarked yearlings (i.e., first time breeder) or as individually-marked adults that were observed previously on other areas. Recruits were classified as internal (produced in that study population), local (produced in another study population or from an adjacent mountain), or external (produced outside our studied populations).

We conducted a telemetry study of juvenile movements to assess patterns and spatial scale of dispersal for offspring produced in our populations. In 1997, we radio-marked chicks and brood hens in late summer. Eighteen of 21 radios had 1 year battery life (wt = 5.8 g; about 1.5% of ptarmigan post-breeding body mass; three had mortality sensors), and radios on three brood hens had 4 month battery life. We recorded signal locations for radio-marked birds using fixed-wing aircraft during four winter flights (24 November 1997, and 6 January, 16 March, and 28 April 1998) and one summer flight (11 June 1998). We flew over ME, ST, GP, and LP several times and then censused all suitable alpine habitat around the study areas extending up to a distance of 100 km to locate dispersed birds. We recorded locations, directions, and distances of offspring from their natal territories. In summer 1998, we did ground checks of radio-marked offspring to ascertain survival, sex, and breeding status.

DATA ANALYSIS

Mean values are presented with $\pm$ SE. Statistical significance is reported for two-tailed tests ($P <$ 0.05) using ANOVA, and log likelihood chi-square tests, with G-tests when sample sizes were small. Spearman rank correlations (r_s) were done to examine synchrony of recruitment patterns with chick production in the previous year and patterns of local survival. Given unequal populations sizes and different years of study for sites, we do not report global correlations for all populations.

RESULTS

PATTERNS OF RECRUITMENT WITHIN AND AMONG POPULATIONS

Over all study sites, we marked 369 ptarmigan chicks (156 chicks leg-banded and 213 wing-tagged) from which we could measure patterns of recruitment and dispersal from 1987 to 1996. From 1987 to 1996, we monitored local survival and reproductive success for 292 female-years (196 individual females). New recruits accounted for about 50% of resident breeding females over the study, with proportions ranging from 0 to 100% across years and study populations (Table 1). ME had the lowest average proportion of recruits (45.2%) among populations, and GP the highest with an average of 69.2% of females in the population consisting of recruits. ME, the largest population, had the lowest annual variation in proportion of recruits (30–63.6%) among

TABLE 1. Number of female and male White-tailed Ptarmigan recruited and returned to four study populations, and origin of recruits in relation to population size and chick production in Colorado. Population size is the sum of returned birds plus recruits.

	Chicks produced previous year	Females							Males						
		Population size	Return	Recruit	Internal recruit	Local recruit	External recruit	% external recruits	Population size	Return	Recruit	Internal recruit	Local recruit	External recruit	% external recruits
Mt. Evans															
1987	11	21	13	8	1	0	7	88	20	14	6	1	0	5	83
1988	14	22	8	14	0	0	14	100	25	13	12	2	0	10	83
1989	29	35	17	18	1	0	17	94	32	25	7	4	0	3	43
1990	45	30	21	9	2	0	7	78	33	25	8	4	0	4	50
1991	31	26	14	12	0	0	12	100	21	13	8	5	0	3	38
1992	12	17	8	9	1	0	8	89	18	8	10	2	0	8	80
1993	23	14	6	8	0	0	8	100	12	7	5	1	0	4	80
1994	14	16	8	8	0	0	8	100	18	9	9	0	0	9	100
1995	10	21	14	7	0	0	7	100	22	15	7	1	1	5	71
1996	13	15	10	5	0	0	5	100	20	13	7	0	0	7	100
Guanella Pass															
1990	1	4	1	3	0	0	3	100	10	6	4	0	0	4	100
1991	5	6	0	6	0	0	6	100	8	6	2	0	0	2	100
1992	1	7	3	4	0	0	4	100	10	7	3	0	0	3	100
1993	7	7	1	6	0	1	5	83	9	8	1	0	0	1	100
1994	0	5	5	0	0	0	0	—	8	7	1	0	0	1	100
1995	3	8	2	6	0	0	6	100	10	6	4	0	0	4	100
1996	0	2	0	2	0	1	1	50	3	3	0	0	0	0	—
Square Tops															
1993	11	5	1	4	0	0	4	100	8	7	1	0	0	1	100
1994	5	7	3	4	0	0	4	100	14	12	2	0	0	2	100
1995	10	6	4	2	0	1	1	50	11	11	0	0	0	0	—
1996	3	5	2	3	0	0	3	100	10	7	3	0	0	3	100
Loveland Pass															
1990	14	5	4	1	0	0	1	100	8	6	2	0	0	2	100
1991	4	4	1	3	0	0	3	100	9	8	1	0	0	1	100
1992	0	4	0	4	0	0	4	100	8	5	3	0	0	3	100

TABLE 2. Recruitment and age of recruits in three study populations of White-tailed Ptarmigan in Colorado in 1996 after harsh environmental conditions in 1995, versus all previous years.

	1996			Previous years			
	Population size	Recruits			Recruits[a]		
	size n	n	% adult	Population size mean ± SE	Mean ± SE	n	% adult
Females							
Mt. Evans	15	5	20	22.1 ± 1.7	10.2 ± 1.1	93	2.2
Guanella Pass	2	2	0	6.2 ± 0.6	4.2 ± 1.0	25	4.0
Square Tops	5	3	67	6.3 ± 0.5	3.3 ± 0.7	10	50.0
Males							
Mt. Evans	20	7	57	22.2 ± 2.2	8.0 ± 0.7	72	2.8
Guanella Pass	4	0	—	9.2 ± 0.4	2.5 ± 0.6	15	13.3
Square Tops	10	3	67	10.3 ± 1.8	1.0 ± 0.6	3	0.0

[a] Recruitment from previous years includes: ME—1987 to 1995; GP—1990 to 1995; ST—1993 to 1995.

breeding females. Smaller populations had higher annual variation in their dependence on recruits, with GP showing extremes of 0 to 100% recruits. Numbers of female recruits in a given year were not correlated with number of returning females (local survival) for ME (r_s = 0.24, P = 0.51, n = 10 years) or GP (r_s = −0.28, P = 0.54, n = 7 years). Numbers of female recruits in study populations were correlated with chick production in the previous year at GP (r_s = 0.94, P = 0.001, n = 7 years), but not at ME (r_s = 0.59, P = 0.07, n = 10 years).

From 1987 to 1996, we monitored local survival and reproductive success for 347 male-years (168 males, includes paired and unpaired males). Recruits comprised only 30.6% of male populations, a significantly lower proportion than females (G_1 = 25.1, P < 0.001). Proportions of male recruits varied across study populations from 14% at ST to 35.8% at ME (Table 1). Thus, males showed the opposite pattern of dependence on recruitment to females, with the larger population (ME) showing the highest proportion of recruitment. As for females, the number of male recruits in a given year was not correlated with numbers of returning males (local survival) at ME (r_s = −0.4, P = 0.69, n = 10 years) or at GP (r_s = −0.05, P = 0.92, n = 7 years). Also, numbers of male recruits to study populations were not correlated with the previous years' chick production at ME (r_s = 0.12, P = 0.73, n = 10 years), nor at GP (r_s = 0.28, P = 0.55, n = 7 years).

In general, 95% of ptarmigan of both sexes newly recruiting to populations were first time breeders (yearlings, Table 2). ST was an exception as 50% of females recruiting there were observed first as adults (> 1 year old).

Despite working on four populations, three in close proximity, only 29 marked offspring (8 females and 21 males) recruited to our study sites between 1987 and 1996 (Fig. 2). Numbers of known-origin recruits varied from none to six annually (Table 1). We were able to determine the origin of only 8 (5.9%) of 137 female ptarmigan recruits to our populations from 1987 to 1996 (Table 1, Fig. 2). Seven of eight female recruits of known origin were yearlings. Only 5 of 98 females recruiting to Mt. Evans were produced on that site, and none was known to have originated from the other study populations or adjacent mountains (Table 1). Two of 27 recruits to GP were produced on other study sites (Fig. 2, ME, ST). We observed local recruitment of females (connectivity) between all three proximate populations (ME, GP, and ST), but none with Loveland Pass (Fig. 1). Likewise for males, the majority of recruits came from outside our studied populations. However, male natal philopatry was higher than females as 21.4% of male recruits were internal recruits (Fig. 2; males vs. females: G_1 = 15.0, P < 0.001). At ME, 25% of 77 male recruits were produced there, and there was 1 local recruit from ST (Fig. 2). With our less intensive population data, we encountered none of our marked offspring among the 26 birds captured and banded (14 males, 12 females) on adjacent mountains, and none of 18 chicks tagged or banded on adjacent mountains recruited to our study sites. Also, we recorded no marked offspring among 33 ptar-
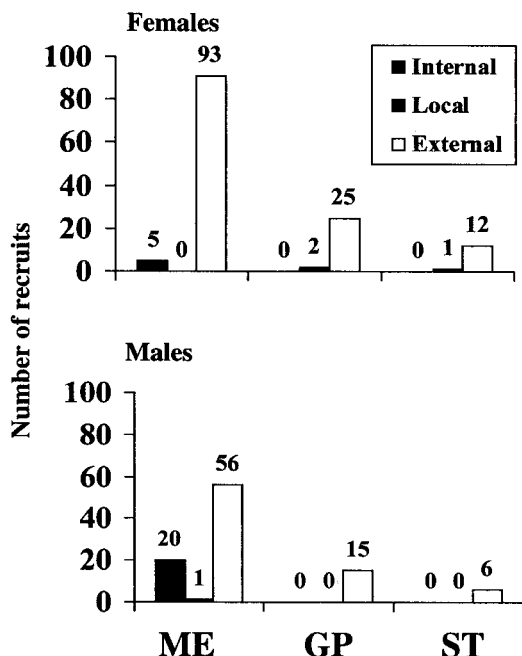
FIGURE 2. Origin of birds recruiting to three White-tailed Ptarmigan populations in Colorado. Study site abbreviations as in Figure 1. Years of study varied with site; ME: 1987–1996, GP: 1990–1996, ST: 1993–1996. Internal represents a recruit produced in that population, local recruits were produced in another study population, and external recruits came from outside the studied populations. Numbers above bars indicate sample size for recruits.

migan banded as either spring or fall migrants on our study sites.

Settlement patterns of internal recruits were expected to be highest close to natal territories with a gradual decline as one moves away. ME was naturally divided from north to south into four major drainages (Fig. 1); 15 of 18 male internal recruits settled in the same drainage as their natal territory, and the remaining 3 settled in an adjacent region. In contrast, one of three female internal recruits at ME settled close to her natal territory and the other two settled in the most distant section from their natal site. Thus, male offspring returned close to their natal territory or they did not return, and female offspring settled away from natal territories.

BREEDING DISPERSAL

We observed movements between populations after natal dispersal events, both within season and between years. In four of seven years, we

observed late spring dispersal where females that settled on our study sites for one to several weeks, deserted their mate and territory, and dispersed to other mountains. In 1990, this phenomenon occurred at a higher rate and on all study sites. In 1990, females paired normally, and then between 17 May and 6 June, 17% of 42 radio-marked females dispersed to sites 10–30+ km. The mean date of clutch initiation for 1990 was 10 June $\pm$ 0.7 for 31 females remaining on study sites. Nine (64.3%) of 14 dispersing females (populations and years pooled) were yearlings compared to the study average of 46.9% yearling breeding females (1987 to 1996, $n = 307$ female-years, $G_1 = 1.6$, $P = 0.2$). In two cases, females deserted mates and territories three weeks and four weeks after settling, and moved 3–4 km to breed on adjacent mountains. They made these movements 5 days and 1–2 days, respectively, before initiating egg laying. All females attempted breeding in their new location and their overall reproductive success of 2.6 chicks female^{-1} ($n = 8$ females) was above average for our studied populations (1.04 $\pm$ 0.1 chicks female^{-1}, $n = 159$ female-years). Dispersal of females, even when just before laying, also did not appear to decrease survival. One of nine spring-dispersing females located at the end of the season was found dead, comparable with the 12% mortality rate during the breeding season for females in our study populations (Braun et al. 1993).

The proportion of unbanded adults recruiting to our populations was a measure of breeding dispersal between years because all females attempt breeding in their yearling year, and most birds previously resident in our populations were banded. About 6.2% of 128 females recruiting to our populations were adults and thus represented breeding dispersal (Table 2). For the above data, we excluded birds on edges of study sites where we might have missed recruits from previous years. We have direct observations of breeding dispersal for four females (2.6%) out of 155 between-year observations on our sites. Two females moved from GP to elsewhere, one after two years of breeding there. Only one male moved between study sites, recruiting to ST as a yearling and moving one year later to ME where he remained for four years. Thus, breeding dispersal was infrequent, but occurred regularly, and was more common among females than males.

PATTERNS OF RECRUITMENT AFTER A REGIONAL FAILURE IN REPRODUCTION

Unseasonally late and protracted snowstorms through May, June, and early July 1995 resulted in the latest breeding season in our 12-year study. Weather records from Mt. Evans showed that snowmelt in 1995 was the latest since ptarmigan studies began in 1966 (C. E. Braun, unpubl. data). In 1995, we observed high reproductive failure in all populations with only 16% of 32 females raising chicks in 1995 compared to about 50% of 164 females in previous years ($G_1 = 14.2$, $P < 0.001$). Mean chick production of 0.4 ± 0.2 chicks female^{-1} ($n = 32$ females) in 1995 was the lowest observed during the study, and less than half that of previous years (mean = 1.0 ± 0.1 chicks female^{-1}, $F_{1,158} = 3.6$, $P = 0.05$, K. Martin and K. L. Wiebe, unpubl. data). In 1995, only one of seven radio-marked females that left the study areas in spring and bred on adjacent mountains successfully raised chicks, suggesting that breeding success in 1995 also was low off the study areas. However, overwinter survival of adults was not affected by the harsh 1995 season. Local survival was not reduced after the 1995 breeding season for either sex; 41% of 32 females returned to the study sites in 1996 compared to a return rate of 43% of 265 female-years in previous years, and 53.5% of 43 males returned in 1996 compared to 65% of 204 male-years in earlier years (1996 vs. previous years: females: $G_1 = 0.09$; males: $G_1 = 2.0$, $P = 0.15$).

We used the harsh year of 1995 as an opportunity to assess the possibility of a regional dispersal rescue system, and expected that overall recruitment rates should be much reduced in 1996 following the widespread reproductive failure in 1995. As expected, female population sizes declined at two sites in 1996 (29% at ME and 75% at GP) from 1995 levels and for males by 70% at GP (Table 1). The number of female recruits was lower than in any other year at ME and lower than in all other years but one at GP (Table 1). Male recruitment in 1996 did not show the sharp declines observed in females, but over half the recruits in 1996 were adults in contrast to under 3% in other years (Tables 1 and 2; adult male recruits: 96 vs. previous years: $G_1 = 25.0$, $P < 0.001$). In 1996, 20% of female recruits were adults compared to an average of 6.3% in other years (Table 2, $G_1 = 0.95$). Over the study, GP depended heavily on recruits

(mostly yearlings) to maintain its population of six to eight pairs (Table 1). In 1996, GP showed the most dramatic population decline from 1995 as both local survival and recruitment were the lowest observed in the study for both sexes (Table 1). ST was the only population to maintain its density in 1996; it did so by maintaining its normal rate of return and recruitment for both females and males (Tables 1 and 2).

TELEMETRY STUDY OF OFFSPRING RECRUITMENT: SOCIAL FACTORS AND OVERWINTER MOVEMENTS

To examine factors affecting natal recruitment, we conducted a telemetry study of juvenile ptarmigan. In late August and September 1997, we radio-marked 6 brood females and 12 chicks on ME and 1 brood female and 2 chicks at ST (1 chick of each sex per brood where possible). On winter census flights, we obtained 52 signal locations for 19 of 21 radio-marked birds; all chicks were located ($n = 40$ locations for 14 birds) and 5 of 7 brood hens (Table 3). The two undetected brood females had 4-month radio-tags. The most unexpected result was that most birds remained near, often within 1 km of breeding sites during winter. They did not remain on their natal territories but rather moved around the area or to adjacent mountains. One ME chick moved southwest 18 km to a winter site, and a second chick was located three times during winter on or near ME, but in late April moved 20 km to the northwest. In only 1 of 52 locations was a bird from ME found on the traditional Guanella Pass winter site. Offspring did not appear to be associating with parents or siblings over winter (Table 3).

We recorded recruitment locations of radio-marked offspring by an aerial census on 11 June, followed by several ground checks between May and August 1998. Six chicks (five males) recruited to their natal populations, one female from ME recruited to GP, and five chicks dispersed 9.5–20 km from their natal territories (Table 3). We verified survival, sex, and breeding status for all internal and local recruits, but were less successful in obtaining this information for external recruits (likely predominantly females) as late spring snows hampered trips to distant mountains in June 1998. For some dispersed offspring, we determined locations from the air and assigned probable survival based on changes in signal locations during aerial checks

TABLE 3. Winter migration, dispersal, and recruitment locations and behavior during 1997–1998 for radio-marked White-tailed Ptarmigan offspring in Colorado.

Sex	n	No. locations	No. locations on study area	Close to sibling?	Close to mother?	Recruitment site[a]	Recruitment site close to winter site[b]
Male	5	18	18	0/12	1/15	5 internal	5/5
Female	2	5	3	0/5	—	1 internal 1 local	2/2
Unknown[c]	7	17	3	2/16	0/15	5 external[a]	3/5[b]
Total	14	40	24	2/33	1/30	6 internal 1 local 5 external[a]	10/12[b]

[a] External recruits dispersed 9.5–20 km to the south, southeast, southwest (n = 2 chicks), and north of their natal areas.
[b] Recruitment site data were not scored for two offspring because it is possible they were dead.
[c] Sex was unknown for offspring that were not located by ground checks.

and line of sight checks from different ground locations in June and August 1998. Despite limited censusing in 1998, 30% of 30 chicks banded in 1997 (includes radio-marked chicks) recruited to our study populations (1 local and 8 internal recruits) in 1998, the highest recruitment rate recorded in our study (annual range: 0 to 18.2%), and well above the overall recruitment rate of 7.9% for previous years (369 marked chicks, G_1 = 13.3, $P < 0.001$).

We examined whether recruitment sites might be related to winter dispersal movements. For all internal and local recruits and three of the five external recruits, recruitment sites were close to where they spent the winter (Table 3). Radio-marked offspring that dispersed had moved off the natal area by late November, and recruited close to or on the site where they were located during winter. However, for one dispersing offspring we recorded no movements over winter, but in April, it dispersed 20 km north and then settled 15 km to the south. Our data are minimal estimates of movement because it is likely that most offspring made significant movements and visited multiple areas before choosing breeding sites.

DISCUSSION

EXTERNAL RECRUITMENT AND DISPERSAL RESCUE

White-tailed Ptarmigan are suitable to study metapopulation processes such as dispersal rescue and recruitment. Both sexes are territorial and they inhabit patchy environments with small populations and exhibit high demographic and environmental stochasticity. The most remarkable feature of our study was that most recruit-

ment, particularly for females, came from outside the study populations and also from outside nearby populations. This pattern occurred in all years and applied to both sexes; external recruitment varied annually from 78 to 100% for females and from 37 to 100% for males. Another population study (1966–1989) of ptarmigan in Rocky Mountain National Park reported 77% external recruitment for females and 50% for males (Giesen and Braun 1993). It is possible that we underestimated internal recruitment as we could have missed some locally produced offspring in some years. However, we recorded the reproductive fate of over 95% of resident females in our populations, and we marked over 90% of chicks with brood females. We surely underestimated local recruitment because not all birds on adjacent mountains were marked. However, the extremely low rate of recruitment of those that were marked between the study populations is undeniable evidence that local recruitment is infrequent, and that external recruitment dominates.

Our ptarmigan breeding populations depended heavily on annual recruitment to sustain them, especially for females where about half of the population each year was comprised of new birds. Although recruitment varied dramatically over years, it was not strongly or consistently correlated with internal population dynamics. Patterns of recruitment were not correlated with local survival of either sex at the two sites with seven or more years of data. If population size was strongly influenced by local production, one would expect to see the strongest relationship between male recruitment and chick production in the previous year, given higher natal philo-

patry of males. However, the only significant correlation between recruitment and chick production in the previous year was observed for females at GP, and not for males.

Annual variation in demographic factors, especially if mediated by environmental stochasticity, has been suggested to select for increased natal and breeding dispersal distances (Stenzel et al. 1994, Paradis et al. 1999). Our ptarmigan populations showed surprising stability in population size over our study. Despite small population sizes, low densities, relatively low fecundity, and high annual variation in most population parameters, none of our studied White-tailed Ptarmigan populations have been extirpated, and probably are not threatened. Most ptarmigan populations have persisted for at least 30 years (Braun et al. 1993), and records of ptarmigan breeding on Mt. Evans extend back to 1890 (Lewis 1904).

We observed the majority of our recruits of known origin (predominance of males) to settle in their natal population. However, we did not observe male offspring from ME or ST recruiting to GP, ST, or to adjacent mountains. Thus, male offspring returned close to their natal territory or they did not return, suggesting a discontinuous pattern of offspring dispersal as opposed to a steady decay with distance from natal territory. Although we observed 75 to 100% external recruitment for our populations in the earlier years of our study, we also have the puzzling result from our telemetry study that all radiomarked male offspring we located returned to their natal population in 1998. Although we followed multiple populations in reasonable proximity, our study, like most others, was not designed specifically to measure demographic exchange among sites.

The phenomenon of external recruitment has been observed in other studies. Two single-site studies of Willow Ptarmigan (*Lagopus lagopus*) showed different rates of external recruitment, one in the central Canadian Arctic had about 51% external recruitment for males and 91% for females, whereas a population in northwestern British Columbia had 89% external recruitment for males and 97% for females (Martin and Hannon 1987). The two studies differed in spatial scale and population density with the arctic study site being over twice the size of the site in British Columbia (10 vs. 4 km²) but less than half the density (5–10 vs. 20–40 pairs km⁻²,

Hannon and Martin 1996). Natal philopatry was lower in British Columbia than in the Arctic (Martin and Hannon 1987). Studying multiple connected populations provides more accurate information on general patterns and variance in recruitment that increase our understanding of spatial population structure. For example, if we had studied only the Mt. Evans population, we would have missed about 5% of marked male recruits and 37.5% of female recruits. Within the same geographic region, recruitment rates have been shown to vary widely within species in relation to patch size and proximity to other breeding populations. The proportion of external recruits entering Song Sparrow (*Melospiza melodia*) populations varied from 5% on an island that could sustain over 70 pairs, 57% on small islands close to a mainland source, to 92% on the mainland (Smith et al. 1996). Song Sparrow populations with higher rates of external recruitment were more stable, consistent with the conclusions of Paradis et al. (1999) that local synchrony increased positively with dispersal distances for 53 bird species in Britain. Although investigators tend to focus more on philopatric offspring, these usually constitute less than 50% of recruits (Greenwood 1980). Thus, extensive external recruitment is probably a general pattern for birds.

PROPENSITY FOR DISPERSAL AND COSTS OF DISPERSING

Movement between different breeding sites has been documented within and between seasons for many bird and mammal species (Greenwood 1980). Snowy Plovers (*Charadrius alexandrinus*) in California have dispersed up to 175 km to breed between seasons; these movements were not related to prior reproductive success (Stenzel et al. 1994). About 5% of females moved to another population after having completed a breeding season elsewhere (Wiebe and Martin 1997). Breeding dispersal may be uncommon but contributes significantly to interpopulation connectivity because it happens regularly in all ptarmigan populations (Hannon and Martin 1996, this study). The high proportion of adult female recruits at Square Tops likely represents a different pattern of recruitment at that site as we feel our sampling efficiency at ST was similar to other populations. Also, although uncommon, we observed late spring breeding dispersal in most years. Interestingly, the phenom-

enon of late spring dispersal in 1990 was observed also in Rocky Mountain National Park, 150 km to the northwest, where after settling for one to several weeks, 3 of 12 radio-marked female White-tailed Ptarmigan dispersed to other mountains to breed (Melcher 1992). Breeding site fidelity for yearling females appears lower than for older birds as the majority of birds dispersed before or after their first breeding attempt. Thus ptarmigan, like a number of other species, show reduced fidelity to breeding sites in their first year of breeding (Black 1996).

Data are limited on the consequences of late spring dispersal to other breeding sites, however, dispersing females appeared to experience similar reproductive success to those remaining on territories where they had previous breeding experience. Dispersal of females even in their prelaying period did not appear costly to survival. Survival of radio-marked forest and arctic grouse was not related to distance moved, and reproductive costs were not observed for birds switching territories or mates within sites (Beaudette and Keppie 1992, Hannon and Martin 1996, Smith 1997). Thus, ptarmigan females showed a propensity to disperse even after initiating breeding activities on a site, and did not incur survival or reproductive costs. Given that reproduction of White-tailed Ptarmigan shows strong age dependence, with older females raising more chicks (Martin 1995, Wiebe and Martin 1998), even a small amount of breeding dispersal could make a significant contribution to local annual production. The ability to make significant movements without incurring survival or reproductive costs is an important pre-condition to the development of a dispersal rescue system.

SPATIAL SCALE AND INFLUENCES OF OTHER LIFE HISTORY STAGES ON DISPERSAL

Data on seasonal movement patterns and distances are required to determine the spatial scale at which population exchange might occur. These exist for few species. Median dispersal and recruitment distances for chicks banded on breeding areas were 1.2 km for 126 males (up to 8 km) and 4.0 km for 40 females (up to 29 km) in earlier studies of White-tailed Ptarmigan at Rocky Mountain National Park and Mt. Evans (Giesen and Braun 1993). These distances and patterns underestimate true dispersal because they relied on relocation of banded birds away from the study areas, and the potential areas for dispersal were vast and often inaccessible. Given the spatial scales involved for most vertebrates, radio telemetry is required for survival estimation in dispersal studies (Nichols 1996). In northwestern British Columbia, Willow Ptarmigan were radio-marked on a breeding site and followed to winter sites. Females moved an average of 26–30 km (up to 88 km) and males 14–21 km (up to 90 km, Gruys 1993). Over winter, there were multiple movements between breeding and winter sites. The search area was restricted to 100 km around the breeding site and, because some birds were not located, dispersal distances reported also were conservative. Given the problems of detecting individuals that disperse the farthest, all empirical studies underestimate spatial scales of population connectivity (Koenig et al. 1996, Lambrechts et al. 1999).

To understand linkages among spatially organized vertebrate populations, we need to examine the potential influence of seasonal movements during post-breeding life history stages, and winter environmental conditions on dispersal patterns. When White-tailed Ptarmigan complete breeding activities they abandon territories and gather in late summer flocks at higher elevations (Braun and Rogers 1971). Females with broods normally go to the closest mountain top, but males and unsuccessful females regularly move to nearby mountains (Herzog 1977, Braun et al. 1993, K. Martin, unpubl. data). In late fall, birds are thought to move to winter sites in most years (Braun et al. 1993). A study of 99 White-tailed Ptarmigan in Colorado banded on winter sites and relocated in summer reported average dispersal distances of 6.8 km for adult females, 8.5 km for yearling females, 2.5 km for adult males, and 4.0 km for yearling males (Hoffman and Braun 1975). Birds moved in all directions but in a northwest predominance, with maximum distances of 23 km for females and 10 km for males. Hoffman and Braun (1975) predicted females dispersed within an area of 40–60 km^2 to breed. Seasonal movements from breeding to post-breeding and winter sites allow individuals to assess potential habitat for recruitment, and likely facilitate dispersal decisions. There is much scope for research on starting and stopping rules to advance our understanding of dispersal behavior (Martin 1998).

Data on maximum movement distances such as provided by Sutherland et al. (2000) and on

potential dispersal barriers are required to identify the scale at which studies of multiple populations should be designed. Maximum movement distances recorded for White-tailed Ptarmigan were for two males transplanted in spring to another breeding site, that traveled 43 and 50 km, respectively, across primarily forested landscape to return to their territories (Braun et al. 1993). A successful transplantation of White-tailed Ptarmigan to Pike's Peak, an area of apparently suitable but unoccupied habitat about 60 km from the nearest occupied habitat, suggested this site exceeded normal ptarmigan dispersal distances (Hoffman and Giesen 1993; C. E. Braun, pers. observ.). Demographic exchange likely occurs between populations of White-tailed Ptarmigan within 5–10 km for males and 20–30 km for females.

We do not know whether our one-year telemetry study showing the surprising lack of migration to winter sites was representative of overwinter movements on our study sites generally. Although most of our radio-tagged birds did not leave their breeding sites over winter, there were normal numbers of birds resident on the traditional Guanella Pass winter site in 1997–1998 (K. Martin and C. E. Braun, pers. observ.). It is possible that radio-tagging altered dispersal behavior, but we also observed high local recruitment of chicks in 1998 that were not radio-tagged. In an earlier study, ptarmigan moved shorter distances in mild winters than in severe winters, and thus, weather patterns may influence the spatial scale of dispersal (Hoffman and Braun 1977). The 1997–1998 winter may have been sufficiently mild to allow exposed ridges where birds found adequate forage. Rock Ptarmigan (*Lagopus mutus*) in Iceland showed annual and regional variation in winter movements ranging from remaining on or near breeding sites to migrating up to 300 km (O. K. Nielsen, pers. comm.). Even in sedentary species like the Acorn Woodpecker (*Melanerpes formicivorus*), young birds made regular excursions from their natal area. When territorial vacancies occurred, birds settled rapidly resulting in a discontinuous pattern of recruitment (Koenig et al. 1996). The role of offspring movements in facilitating sampling of potentially suitable recruitment locations is a fascinating and important area of population connectivity research.

REGIONAL-LEVEL STOCHASTICITY

Dispersal rescue is predicted to be most advantageous to population persistence when there is little regional stochasticity affecting reproduction, and least advantageous when regional stochasticity is high and/or when it affects adult survival (Hanski 1991). We predict the heavy reliance on external recruitment we observed for White-tailed Ptarmigan would persist only if regional-level stochastic events were relatively rare (i.e., occur less frequently than the average lifespan of individuals). The extreme weather conditions in 1995 provided a type of natural experiment on consequences of regional failure on local population recruitment. Although sample sizes were small, recruitment in 1996 was lower than in previous years as expected, and we were able to predict the severity of the impact on population size among study sites. The 1995 event had a relatively short-term impact on population size given that most birds comprising 1996 populations were older and represented the most productive cohorts (Martin 1995, Wiebe and Martin 1998). By 1997, populations had recovered. White-tailed Ptarmigan are relatively invulnerable to such regional-level events, especially if these do not greatly reduce adult survival. Such regional-level catastrophes as described for 1995 are not sufficiently frequent to threaten persistence of populations, given current climatic conditions. However, climate change is expected to result in increased frequency of stochastic weather patterns (Körner 1999), providing conditions that may result in increased demographic stochasticity and synchrony in high-elevation habitats (Martin 2000).

White-tailed Ptarmigan may not fit all criteria for a traditional metapopulation structure because they do not show regular extinctions and recolonizations of populations. However, many of the principles and processes associated with metapopulations appear highly relevant to stability of ptarmigan populations. Ptarmigan exist in spatially organized populations that are linked by a well developed system of exchange, principally via natal dispersal. The exchange linking populations may not be frequent or reciprocal. Given the demographic and environmental stochasticity characteristic of this ground-nesting tetraonid, the well developed *rescue* pattern of immigration of individuals from elsewhere in the multi-population system appears responsible

for maintaining stability in White-tailed Ptarmigan populations.

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