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SURVIVAL AND REPRODUCTION OF DISPERSING BLUE GROUSE[1]

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Abstract. Dispersal in a declining population of Blue Grouse (*Dendragapus obscurus*) was studied over four years on Hardwicke Island, British Columbia, Canada, by radio-tracking 66 individuals and reobserving or recapturing 126 banded individuals. On a 464-ha main study area, numbers of territorial males decreased from 152 to 94, breeding females from 276 to 113, and young grouse alive in late summer from 847 to 224 during the period of study. Despite this, dispersal distances did not vary between years and bore no clear relationship with adult densities in spring or density of juveniles in the previous fall. Rates of survival and reproduction for *long-dispersers* (grouse moving greater than the median dispersal distance) and *short dispersers* (grouse moving less than the median dispersal distance) were similar. Similar results were noted for grouse that left the study area (*dispersers*) and those that remained on the study area (*non-dispersers*). Overall, there was little evidence that dispersers fared poorly or that dispersal was greatly influenced by population density.

Key words: Dispersal; Blue Grouse; Dendragapus obscurus; *population density; reproduction; survival; British Columbia.*

INTRODUCTION

Dispersal, the movement between place of birth and place of breeding, or where an animal settled and would have bred had it not died (Howard 1960), has important implications for limitation or regulation of populations (Lidicker 1975, Watson and Moss 1979, Tamarin 1983). Hypothetically, as population density increases, social interactions may become more intense causing increased rates of emigration with dispersers having relatively poor survival and reproductive success (Christian 1970, Lidicker 1975, Krebs 1978, Moss et al. 1982, Tamarin 1983). As a consequence, population growth can be limited by increased dispersal at higher densities and the relatively low fitness of dispersing animals.

Despite these arguments, there seems to be little published evidence that dispersal is greatly influenced by population density. In a critical review of dispersal in small mammals, Gaines and McClenaghan (1980:189) wrote: "In species for which adequate demographic data are available, dispersal is clearly a density-independent phenomenon," a conclusion reached also by Stenseth (1983). Although Greenwood and Harvey (1982), in their review on dispersal in birds, suggested that the effects of density on dispersal were well established, I have been able to find little evidence that this is so from the literature. Most such evidence is based on disappearance of animals from particular study areas, and many authors have equated disappearance with dispersal despite the fact that dead animals are usually difficult to find and disappearance may represent in situ mortality (Gaines and McClenaghan 1980).

The idea that dispersers fare poorly stems especially from the work of Errington (1946, 1963) who suggested that young, wandering muskrats (*Ondatra zibethica*) were particularly susceptible to predation. Various workers have implied that this is true also in other species, but supporting data are scarce. For small mammals, Gaines and McClenaghan (1980:190) observed: "As far as we know, with the exception of some anecdotal information, there are no data on survival and reproduction of individuals after they leave a resident population." Similarly, Greenwood and Harvey (1982) noted that the life-history consequences of avian dispersal are largely unknown.

As part of a population study of Blue Grouse (*Dendragapus obscurus*), on Hardwicke Island, British Columbia, a large number of juveniles were equipped with radio transmitters in late summer and fall, 1979 to 1982. I was able to follow many of these grouse to their eventual fate and to distinguish between death and dispersal. For females, I was able to determine reproductive success. Supplementary data on other juveniles (which were banded or wing-tagged but not radio-marked) were collected also. In this report, I analyze distances moved by male and female grouse, evaluate the effects of changing population density on dispersal distance, and consider the relative survival and reproductive success of short- and long-distance dispersers.

STUDY AREA AND METHODS

The study area, Hardwicke Island (50°28′N, 125°50′W), lies between Vancouver Island and the mainland of British Columbia, Canada.

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The area of the island is 77 km^2; 464 ha comprise the main study area for Blue Grouse research. Roughly 25% of the island and over 90% of the main study area has been logged during the past 20 years. These "clearcuts" support the highest densities of Blue Grouse during the breeding season whereas other successional stages, from 21 years to over 250 years in age, support only sparse densities (Niederleitner 1982).

General methods used in the study of Blue Grouse populations have been described by Zwickel and Bendell (1967a) and Zwickel (1982). Adults, yearlings, and large juveniles are captured with noosing poles (Zwickel and Bendell 1967b) and color-banded for future identification. Smaller chicks (<4 weeks old) are usually caught by hand and marked with numbered, patagial wing tags. A minimum estimate of adult and yearling female numbers is the number of different females identified on the study area annually. Usually about 80% of the adult males on the study area are color-banded and their territories, plus those of unbanded or unidentified individuals, are plotted on maps to determine total numbers of territorial males. Production of young (the number of juveniles present on the study area in late summer) is calculated by multiplying the number of females seen with broods by average brood size for August. During late summer and fall, juvenile Blue Grouse were equipped with radio transmitters mounted as backpack units similar to those described by Brander (1968). Radio packages weighed from 2 to 6% of the body weight of juveniles and had little obvious effect on survival, reproduction, or movements of grouse (Hines and Zwickel 1985). Numbers of grouse radio-marked were 60 in 1979, 97 in 1980, 78 in 1981, and 58 in 1982, for a total of 293. Mortality of young grouse was high, and only 24 males and 42 females provided information on dispersal. Sample sizes available for different analyses vary somewhat because of radio failure or deaths of radio-tagged grouse after dispersal had been completed.

Data on dispersal came from: i) grouse that were wing-tagged or leg-banded as juveniles and later recaptured or reobserved as yearlings or adults, and ii) grouse that were equipped with radios as juveniles. Dispersal distance was defined as the straight-line distance between location of birth and location of settlement as a yearling. Actual location of birth was known for only a small proportion of all grouse that hatched on the study area and, for most juveniles, I used earliest location in summer as an approximation of site of birth. This was thought to be valid because, during June and July when most juveniles were first captured, broods were found an average distance of 320 SE = 29 m from their place of hatch (based on 115 sightings of 48 females whose nest location was known). Nest site, if known, was used as place of breeding for yearling females. For males, and for females for which no nest was found, mean location during spring (before 15 June) was used to estimate site of breeding.

For analytical purposes, I defined *long-dispersers* as animals moving more than the median dispersal distance and *short-dispersers* as those moving less than the median distance. Non-radio-marked individuals that dispersed long distances and left the study area were not apt to be found by normal census procedures, and the median dispersal distance for this group is likely underestimated. Median dispersal distance, as determined for radio-marked grouse, was therefore used to separate long-dispersers from short-dispersers among non-radio-tagged birds.

All Blue Grouse disperse to some degree, but to make the data more directly comparable to other studies where dispersal is viewed as a black-and-white process (i.e., animals either disperse or do not disperse), the following analysis was undertaken. *Dispersers* were defined as those individuals settling off the main study area and *non-dispersers* were those groups that settled on the main study area. The data were then examined to determine if dispersal influenced survival or reproductive success. Grouse marked off the main study area were omitted from this analysis.

Evidence of nesting was used as an indicator of reproduction for radio-marked females. Survival during the reproductive period (1 April to 15 June) was also compared for long-dispersers and short-dispersers. I considered non-radio-marked females to have bred if they were seen with a brood or if they had a brood patch (an indicator of incubation). Survival during spring could not be evaluated for non-radio-marked grouse.

Data on dispersal distances were tested for normality using a Kolmogorov-Smirnov test for goodness-of-fit and transformed via logarithms if the distribution was not normal. The normalized data were tested with a two-way ANOVA to see if dispersal distances differed significantly between sexes or among years. Survival rates and indicators of reproductive success were compared using Fisher's exact test when sample sizes were less than 50, or χ^2 contingency tables when sample sizes were larger.

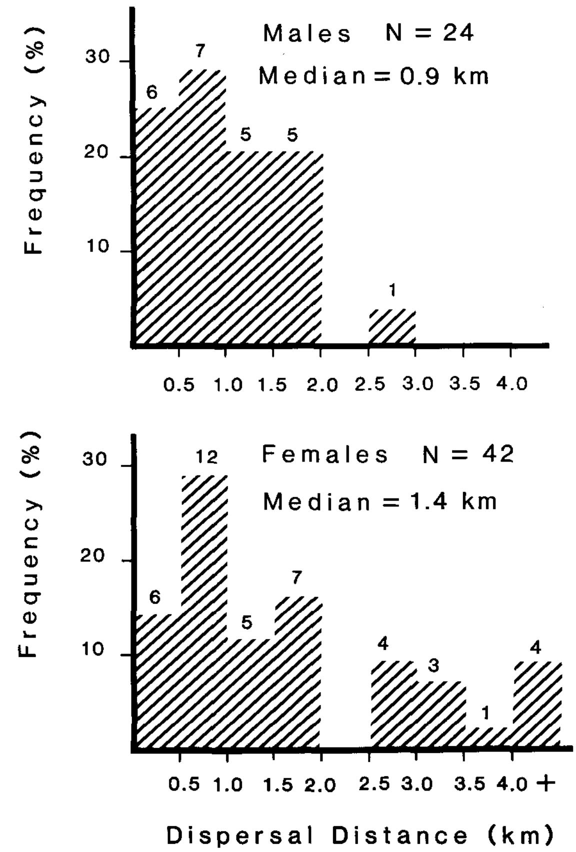

FIGURE 1. Frequency distribution of dispersal distances for radio-marked Blue Grouse, 1979–1983. Sample sizes are indicated above the histogram.

TABLE 1. Dispersal distances (km) of radio-equipped and non-radio-equipped Blue Grouse on Hardwicke Island, British Columbia, 1979–1983.

Year	Radio-equipped grouse					
	Males			Females		
	Median	n	Range	Median	n	Range
1979–1980	1.4	6	0.9–2.6	1.5	7	0.3–10.8
1980–1981	0.9	7	0.3–1.8	1.3	9	0.3–3.3
1981–1982	0.9	6	0.2–1.9	1.1	18	0.4–11.0
1982–1983	0.7	5	0.5–1.7	2.2	8	0.3–5.7
All years	0.9	24	0.2–2.6	1.4	42	0.3–11.0
	Non-radio-equipped grouse					
1979–1980	0.7	18	0.2–1.7	1.0	29	0.2–2.7
1980–1981	0.8	14	0.3–2.1	1.0	27	0.1–2.2
1981–1982	0.8	19	0.1–1.4	1.3	12	0.1–2.4
1982–1983	0.5	5	0.1–1.1	1.1	2	0.8–1.4
All years	0.7	56	0.1–2.1	1.1	70	0.1–2.7

RESULTS

DISPERSAL DISTANCES

After log-transformation to normalize the data, a two-way ANOVA showed that dispersal distances differed between sexes ($P = 0.01$) but not among years ($P = 0.44$, Table 1). Subsequently, I pooled the data for all four years and obtained a median dispersal distance of 0.9 km for males and 1.4 km for females (Fig. 1).

For leg-banded or wing-tagged individuals that were not equipped with radios, data were normally distributed without transformation. A two-way ANOVA indicated no significant differences among years ($P = 0.49$) although there was a significant difference between sexes ($P = 0.02$, Table 1). The distribution of dispersal distances was similar for radio-marked and non-radio-marked birds (Fig. 2) but distances for females in the latter group were shorter than for those in the former group (Mann-Whitney U-test, $P = 0.03$). This was likely an artifact of sampling procedures as few non-radioed animals that dispersed beyond the boundary of the study area were found by census crews. Although the trend was in the same direction, the two samples of males did not differ significantly ($P = 0.11$), possibly because of small sample sizes in the radio-marked group.

INFLUENCE OF POPULATION DENSITY ON DISPERSAL

The number of territorial males on the main study area was 152 in 1980, 140 in 1981, 123 in 1982, and 94 in 1983. Numbers of banded adult plus yearling females were 276, 208, 162, and 113 in these years. Production of young decreased steadily from an estimated 847 in 1979 to 612 in 1980, 354 in 1981, and 224 in 1982. To determine if changes in population density had any influence on dispersal, I used a regression analysis with dispersal distances (for each individual) as dependent variables and densities of adult males, adult females or juveniles (in the previous fall) as independent variables. Samples of radio-marked or non-radio-marked grouse were considered separately in this analysis. For both samples, dispersal distances of yearling females were not correlated with density of females in spring (for radio-tagged females, $r = 0.02$, $n = 42$, $P = 0.91$; for non-radioed females, $r = -0.08$, $n = 70$, $P = 0.51$) or density of juveniles in the previous fall (for radio-tagged females, $r = 0.02$, $n = 42$, $P = 0.90$; for non-radioed females, $r = -0.08$, $n = 70$, $P = 0.48$). Radio-marked males appeared to disperse shorter distances in years of low adult density ($r = 0.38$, $n = 24$, $P = 0.07$) or following years of low production of juveniles ($r = 0.40$, $n = 24$, $P = 0.05$). This relationship did not hold for the sample of non-radio-marked males as there was little correlation between dispersal distance and density of adult males ($r = 0.14$, $n =$

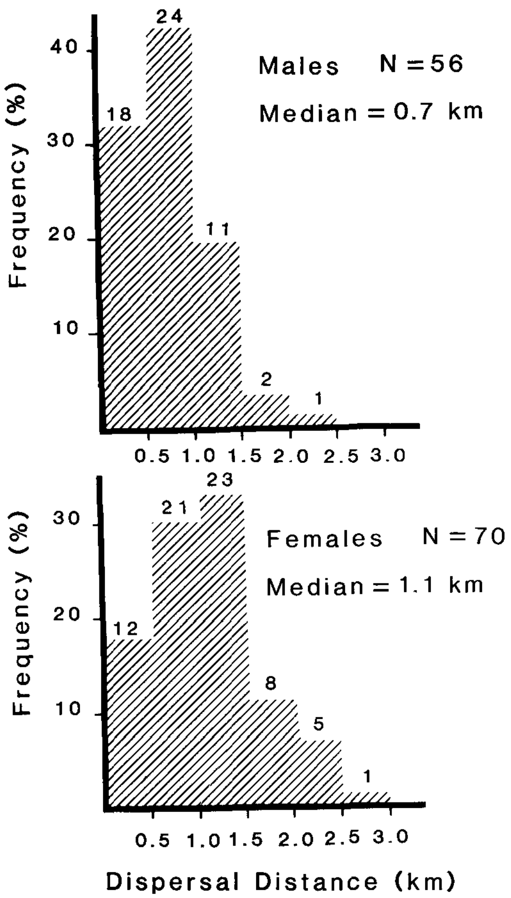

FIGURE 2. Frequency distribution of dispersal distances for non-radio-marked Blue Grouse, 1979–1983. Sample sizes are indicated above the histogram.

56, $P = 0.30$) or density of juveniles ($r = 0.11$, $n = 56$, $P = 0.44$).

One might argue that although median dispersal distances were relatively constant among years, the proportion of grouse appearing varied annually. The proportion of grouse dispersing long distances was 10 of 13 in 1979–80, 7 of 16 in 1980–81, 10 of 24 in 1981–82, and 6 of 13 in 1982–83 (samples of males and females were pooled because of small sample sizes). The proportion of grouse dispersing longer distances did not vary among years (χ^2 contingency table, $P = 0.19$).

SURVIVAL AND REPRODUCTION OF LONG- AND SHORT-DISTANCE DISPERSERS

Among the radio-marked grouse, long-dispersers of both sexes survived as well as short-dispersers during spring (Table 2). Reproductive success of females also seemed equivalent between groups as the proportion of females alive on 1 April that eventually nested and the proportion of females that survived the reproductive period and nested, were similar for both samples (Table 2, $P > 0.10$ in all instances).

Blue Grouse prefer early successional stages for breeding (Niederleitner 1982) and one might expect that long-dispersers, if they are socially subordinate, would be more apt to settle in poorer quality (older) habitats than short-dispersers. Although 6 long-dispersing females settled in more mature habitats (>20 years in age), the median age of habitats occupied by 32 long-dispersers was 10 years (range 3 to 250+) and did not differ significantly from that for short-dispersers (median = 11 years, range 3 to 20, Mann-Whitney U-test, $n = 32$, $P = 0.45$). I conclude that long-dispersers found early successional habitats as well as did short-dispersers.

I could not directly assess the proportion of non-radio-marked yearling females that bred, because their nests were difficult to find. For this group, females sighted with broods or captured females which had brood patches were considered to be breeders. Nearly equal percentages of long-dispersing (75% of 24) and short-dispersing (74% of 42) females showed signs of breeding, indicating that dispersal did not influence reproductive success (χ^2 contingency table, $P = 0.92$).

Another possible indicator of fitness is time of nesting. For a pooled sample of radio-marked and non-radio-marked grouse, mean date of hatch was similar for the broods of long- (16 June ± SE 2 days, $n = 21$) and short- (17 June ± 1 day, $n = 27$) dispersers (Mann-Whitney U-test, $P = 0.57$). I conclude that the act of dispersing a longer distance did not delay nesting in females.

A commonly used operational definition of a disperser is an animal which settles off the study area. For radio-marked grouse originating from the main study area, the survival and reproductive success of birds settling either on (non-dispersing) or off the study area (dispersing) were compared. Neither survival nor reproductive status differed between groups (Table 3).

DISCUSSION

The hypothesized role of dispersal in limiting or regulating populations rests on two important tenets: (1) population density influences dispersal, and (2) dispersers have relatively poor survival and reproductive success. The implications of my results with regard to these assumptions are now considered.

Data for both radio-tagged and non-radio-tagged grouse demonstrate that changes in population density had little effect on the distance dispersed by young females. This occurred despite the fact that spring density of female grouse on the main study area decreased by about 60% and numbers of juve-

TABLE 2. Survival through the breeding season (1 April to 15 June) and reproduction by short- and long-dispersers, 1979–1983. Sample sizes are in parentheses.

Parameter	Short-dispersers[a]	Long-dispersers[b]	P^c
Percent survival (males)	82 (11)	75 (12)	1.00
Percent survival (females)	74 (19)	75 (20)	1.00
Percent of all females nesting	68 (19)	50 (20)	0.33
Percent of females surviving breeding season that nested	93 (14)	67 (15)	0.17

[a] Grouse dispersing <0.9 km for males, <1.4 km for females.
[b] Grouse dispersing >0.9 km for males, >1.4 km for females.
[c] Fisher's exact test.

niles decreased by a factor of about four during the study. For males, the data are inconclusive. Radio-marked males apparently moved farther in years following high production of chicks and when densities of adult males were high. The sample of non-radio-marked grouse indicated no such correlation, and the overall relationship between population density and dispersal distances of males is unclear.

To my knowledge, few studies of birds have shown that dispersal is greatly influenced by population density, despite the claim of Greenwood and Harvey (1982) to the contrary. In an earlier paper (Greenwood et al. 1979), these authors reported that dispersal was inversely correlated with population density in female Great Tits (*Parus major*) while it was positively correlated with density in males. They used two criteria for measuring dispersal: distance, and number of territories dispersed. Dispersal distance was inversely correlated with population density in females and there was no significant correlation between male density and dispersal distance. They indicated a positive relationship between number of territories dispersed and population density for males only. This correlation was of borderline significance ($0.05 < P < 0.10$). If dispersal distances were constant between years, birds would necessarily move across more territories in years of high density than in years of low density. Other studies, relating dispersal in Great Tits to population density, equate disappearance of animals with dispersal (Dhondt 1971, Kluyver 1971) but such disappearing animals may have died rather than dispersed. Jenkins et al. (1964) reported that numbers of dispersing Red Grouse (*Lagopus lagopus*) were greatest in years of high population density and lowest in years of population lows. They did not show that *rates of dispersal* increased with density and my calculations, based on their Table 5, revealed no correlation between proportion of animals that dispersed and population size ($r = 0.10$, 7 df, $P = 0.80$). More recently, Watson et al. (1984) reported that spring dispersal was density dependent in Red Grouse.

If dispersal of Blue Grouse is not greatly influenced by population density, perhaps it is "innate" (Howard 1960) or has a large "presaturation" component (Lidicker 1975). Several authorities have suggested that this might be the case among other birds. For example, Weise and Meyer (1979) believed that dispersal of Black-capped Chickadees (*Parus atricapillus*), which occurred mainly in late summer when aggression was low, was largely innate. Similarly, Alway and Boag (1979) found minimal aggression associated with fall movements of Spruce Grouse (*Dendragapus canadensis*), although they reported greater aggression at the time of spring dispersal. For the same species, Keppie (1979) demonstrated that although dispersal was important in determining population size, it was not density-dependent.

Although sample sizes are small, my data suggest that dispersing females were able to settle and breed as soon as short-dispersers and that the act of dispersing did not greatly influence subsequent reproduction or survival in spring. However, a potential bias arises because dispersal distance is determined by a

TABLE 3. Survival through the breeding season and reproduction by radio-tagged grouse settling on (non-dispersers) and off (dispersers) the main study area, 1979–1983. Sample sizes are in parentheses.

Parameter	Non-dispersers	Dispersers	P^a
Percent survival (males)	81 (16)	71 (7)	1.00
Percent survival (females)	74 (23)	73 (15)	1.00
Percent of all females nesting	61 (23)	53 (15)	0.74
Percent of females surviving breeding season that nested	82 (17)	73 (11)	0.65

[a] Fisher's exact test.

complex interaction of movements including fall migration to winter range, spring migration to potential breeding habitats, and, to a lesser degree, movements on breeding range (Hines 1986). As a result, I could not determine which grouse were long-dispersers and which ones were short-dispersers until they arrived on breeding range. If long-distance or short-distance dispersers suffered different rates of mortality before arriving on breeding range in spring, the effect of dispersal on survival would be estimated inaccurately. About two thirds of the over-winter mortality of radio-tagged grouse occurred before juveniles migrated in fall or after they had localized on winter range, thus most losses were not associated with the time of year when grouse moved widely, and were not directly attributable to dispersal.

Overall, my data do not support the viewpoint that dispersers fare poorly. Similar information on the fate of dispersing individuals is sparse in the literature. For Great Tits, there is some evidence that dispersers survive (Dhondt 1979, Greenwood et al. 1979) and reproduce (Greenwood et al. 1979) as well as do non-dispersers. In contrast, Jenkins et al. (1964) suggested that juvenile mortality was highest at the time of year when young Red Grouse dispersed and implied that this relationship was cause and effect. Mortality of adult grouse (which do not disperse) was also greatest at this time of year (Jenkins et al. 1963, Table 27) indicating that high mortality was not necessarily caused by dispersal.

Various authors have implicated dispersal as an important factor in limiting populations of birds and mammals (Krebs and Myers 1974, Watson and Moss 1979, Tamarin 1983). Dispersal distances for female Blue Grouse were relatively constant from year to year and had little influence on subsequent survival or reproductive success. Accordingly, it would be difficult to argue that annual variations in dispersal greatly influenced recruitment to this population.

The present study covered only a four-year period, at a time when population levels declined greatly, and results may not be representative of what would occur in increasing or more stable populations of Blue Grouse or other animals. Despite this shortcoming my data indicate that, for Blue Grouse, the act of dispersing was not necessarily a liability. Long-distance dispersers found suitable habitats, settled, and maintained high rates of reproduction and survival. Perhaps, for Blue Grouse and many other species, dispersal should be viewed as an essential feature of the life history of an individual rather than a fate suffered by doomed individuals.

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