

# Dispersal patterns in a harvested willow ptarmigan population

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## Summary

1. Harvest management requires knowledge of whether the harvest is sustainable as a result of compensatory mechanisms, such as dispersal. The effect of recreational harvesting on dispersal patterns in willow ptarmigan *Lagopus lagopus* was assessed over four hunting seasons in central Norway.
2. A two-parameter Weibull model was fitted to the observed absolute dispersal distance data using maximum likelihood methods. Estimates of the scale and shape parameters for the dispersal probability distribution were calculated, describing the distribution of observed willow ptarmigan dispersal distances. From the parameter estimates of the dispersal model we estimated the standard deviation of the dispersal displacement relevant for population genetic and spatial population dynamic models.
3. The effect of harvesting on dispersal patterns was examined by testing for differences in the scale and shape parameters of dispersal distance distributions in areas with and without harvest. No effect of harvesting was found, either in adults or juveniles.
4. Breeding dispersal of adult birds was estimated as a dispersal probability distribution with scale parameter  $a = 402$  m and shape parameter  $b = 2.01$ , corresponding to a dispersal standard deviation of  $\sigma = 284$  m. The dispersal probability distribution of adults was not significantly different from a bivariate normal distribution.
5. Natal dispersal had a dispersal probability distribution with scale parameter  $a = 4206$  m and shape parameter  $b = 1.16$ , corresponding to a dispersal standard deviation  $\sigma = 3728$  m. The dispersal probability distribution of juveniles was not significantly different from an exponential distribution.
6. *Synthesis and applications.* Reduction of the population density of willow ptarmigan through harvesting at moderate densities does not seem to affect the dispersal distances. Thus, if there is little or no difference in the dispersal probability distribution in harvested and non-harvested areas there will be only weak or no compensation for the harvest, given that natural mortality and reproduction is the same in both areas. Thus, erroneously assuming compensation of harvest by immigration into a local population can lead to overharvest.

**Key-words:** hunting, *Lagopus lagopus*, spatial scale, Weibull model, wildlife management

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## Introduction

Dispersal patterns and factors affecting dispersal are important in several fields of ecology, including applied

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areas such as conservation and management (Ruckelhaus, Hartway & Kareiva 1997, 1999; Ferriere *et al.* 2000; Walters 2000). Dispersal is a biological process with impact on population genetics as well as population dynamics (Slatkin 1985; Stenseth & Lidicker 1992; Clobert *et al.* 2001). How dispersal patterns between populations relate to variations in local population

densities is likely to have important consequences for their population dynamics (Lande, Engen & Sæther 1999). Empirical studies show no clear relationship between dispersal and population density, as density-independent, positively density-dependent and negatively density-dependent dispersal have been documented (referenced in Sæther, Engen & Lande 1999). There have been many theoretical analyses of dispersal (reviewed in Clobert *et al.* 2001), yet its ecological and evolutionary significance remain poorly understood because of a paucity of unbiased empirical data (Walters 2000).

Recreational harvesting (hunting) can cause both behavioural disturbance (Madsen & Fox 1995) and density reduction in a population (Solberg *et al.* 1999; Pedersen *et al.* 2004), which in turn may affect dispersal patterns. In the management of harvested populations, the movement of animals between harvested areas and surrounding areas (e.g. non-harvested refuges) is important for evaluating the impact of harvesting and the sustainability of harvesting (Novaro, Redford & Bodmer 2000). As harvesting effort can be spatially heterogeneous even within harvested units (Brøseth & Pedersen 2000), knowledge of the spatial component of dispersal patterns in continuous populations is needed when developing biologically realistic harvest models (McCullough 1996; Jonzén, Lundberg & Gårdmark 2001).

Willow ptarmigan *Lagopus lagopus* L. is a monogamous, territorial, medium-sized grouse (0.5–0.6 kg) that is popular as a game bird. The species has a circumpolar distribution, inhabiting mainly heather moor, treeless tundra and subalpine habitats of North America and the northern parts of Eurasia (Johnsgard 1983). Willow ptarmigan populations exhibit major annual fluctuations in numbers, with large spatiotemporal variations in density of the breeding and autumn population (Jenkins, Watson & Miller 1963, 1967; Myrberget 1988; Hudson 1992; Lindström 1994; Steen & Erikstad 1996; Aanes *et al.* 2002). Males defend a relatively small (2–12 ha), exclusive breeding territory, the size of which decreases with increasing spring population density (Pedersen, Steen & Andersen 1983; Pedersen 1984). At the end of June, when the 8–12 eggs hatch and the adults start to move around with their chicks, the territory defence system breaks down. The brood-rearing area overlaps the breeding territory (Andersen, Pedersen & Steen 1986; Hudson 1992) but is usually larger and overlaps with neighbouring birds. Dispersal of juveniles from their natal area occurs in late autumn (October–November), at the same time as males start to occupy a territory for the next breeding season (Pedersen, Steen & Andersen 1983).

Harvest management requires knowledge of whether the harvest is sustainable as a result of compensatory mechanisms, such as dispersal (Ellison 1991; Smith & Willebrand 1999; Willebrand & Hörnell 2001; Pedersen *et al.* 2004). In this study we examined the effects of an experimental harvest on the dispersal patterns of a willow ptarmigan population subject to recreational

hunting in central Norway. We used a two-parameter Weibull model fitted to the observed absolute dispersal distance data to examine dispersal patterns (Tufto, Engen & Hindar 1997). This method estimates parameters such as dispersal standard deviations and shape parameters relevant to theoretical models of population synchrony (Lande, Engen & Sæther 1999), gene frequency clines (Slatkin 1973) and the spread of advantageous genes (Fisher 1937; Kot, Lewis & Driessche 1996). Estimates of these dispersal parameters is also relevant when developing biologically realistic harvest models, and they can be used for testing hypotheses about the effect of local density reductions through harvesting.

## Methods

### STUDY AREA

The study was conducted in a 130-km<sup>2</sup> area in the municipalities of Meråker and Selbu in central Norway (63°10'–63°20'N, 11°30'–11°45'E), from 1996 to 2000. The sub- and low alpine habitat of the study area is dominated by scattered mountain birch *Betula pubescens* Ehrh. woodland intersected with some drier areas and bogs. The shrub layer is dominated by dwarf birch *Betula nana* L., juniper *Juniperus communis* L. and some *Salix* spp., whereas in the field layer heather species (*Vaccinium myrtillus* L., *Empetrum nigrum* L., *Vaccinium uliginosum* L. and *Arctostaphylos uva-ursi* L.), sedges (*Carex* spp.) and grasses are most common. At higher altitudes the vegetation mainly consists of dwarf birch heath and moraine ridges with lichens and sedges. Most of the area is below the timberline, which occurs at 600–800 m a.s.l. Generally snow covers the ground from late October to May.

### HARVEST REGIMES AND POPULATION ESTIMATES

The willow ptarmigan population in the study area was surveyed each year by line transect distance sampling with pointing dogs (Buckland *et al.* 1993; Burnham & Anderson 1998). A total of about 240 km of line transects was surveyed during mid-August to estimate population density in the study area prior to harvesting (Pedersen *et al.* 1999, 2004).

The study area was divided into five administrative hunting units, each of 20–30 km<sup>2</sup>. Harvest regimes with no harvest or a prescribed harvest level were applied randomly to the five hunting area units in the study area. Recreational hunters that rented the hunting area units were given a quota (seasonal bag limit) based on the autumn population estimate and the prescribed harvest regime. In harvested units the average bag was 26% (range 11–48%) of the autumn population estimate. The average autumn density of non-harvested areas was 22.0 birds km<sup>-2</sup> (range 18.9–25.1 birds km<sup>-2</sup>), while the average density of harvested areas after

harvesting was 16·4 birds km<sup>-2</sup> (range 11·4–27·5 birds km<sup>-2</sup>). The surrounding area, to 30 km from the study area border, was similar to the habitat of the study area and subject to unregulated harvesting from recreational hunters (Pedersen *et al.* 1999, 2004; Brøseth & Pedersen 2000).

#### FIELD TECHNIQUES AND DISPERSAL DISTANCES

Adult willow ptarmigan were captured during March and April by using a spotlight and net from snowmobiles. Juvenile birds from broods (1–2 months age) were captured in August using pointing dogs and hand-held nets (Skinner, Snow & Payne 1998). Birds were classified as adults or juveniles according to the amount of pigmentation on the three outermost primaries (Bergerud, Peters & McGrath 1963). During the study a total of 248 birds was captured and fitted with a neck-lace radio transmitter and a unique numbered ring. Of the captured birds, 73% were juvenile. We located radio-tagged birds by triangulation at a distance of 50–100 m, and recorded positions with hand-held, non-differentially corrected 12-channel GPS receivers (Pedersen *et al.* 1999; Brøseth & Pedersen 2000). During the breeding season searches with fixed-wing aircraft were conducted to detect signals from long-distance dispersing birds. We searched up to 30 km from the study area border. This search width was about three times longer than the maximum dispersal distance recorded in this study. As we were interested in the effect of harvest on dispersal we only considered willow ptarmigan that survived to establish a breeding territory the next spring. Because of high natural mortality (40–60%) and the large proportion of the population that was harvested each year (up to 48%; Pedersen *et al.* 1999, 2004), only 32 adults and 27 juveniles met our requirements.

Dispersal distances ( $r$ ) in adults (later referred to as breeding dispersal and defined as the subsequent movement between reproduction sites; Greenwood 1980; Greenwood & Harvey 1982) were calculated as the distance between successive nest sites of individual birds. If the exact nest site position was unknown we used the arithmetic mean centre of the locations recorded during the breeding and brood-rearing period as an estimate of the nest site. Dispersal distances ( $r$ ) of juveniles (later referred to as natal dispersal and defined as the dispersal from the site of birth to that of first reproduction or potential reproduction; Greenwood 1980; Greenwood & Harvey 1982) were calculated as the distance between the arithmetic mean centre of the radio-locations recorded during the brood-rearing period (August) and the nest site for individual birds the next spring.

The process of dispersal consists of three inter-dependent stages: emigration from a site, transience and immigration to a new site (Ims & Hjermann 2001). In this study we only took into account the effect of the

conditions at the emigration stage in the dispersal process.

Many studies report spatial measures of dispersal based on simple descriptive statistics, such as the median or mean, applied directly to the observed dispersal distances. However, the relevant measure of dispersal in theory of genetic differentiation as a result of local genetic drift, local adaptations and in spatial population dynamic models is the standard deviation of the dispersal displacements in the  $x$  and  $y$  directions (Fisher 1937; Malécot 1969; Slatkin 1973; Lande, Engen & Sæther 1999). Also, the dispersal displacements constitute a frequency distribution of distances with specific shape and scale parameters. The shape parameter describes the form of the dispersal distance distribution (e.g. bivariate normal distribution or exponential distribution) and the scale parameter gives the spatial scale of the dispersal distances (e.g. metres or kilometres).

#### DISPERSAL MODEL

Assuming that the full bivariate distribution of dispersal displacements is symmetric around the origin, we estimated the standard deviation of the dispersal displacements ( $\sigma$ ) by first numerically fitting a two-parameter Weibull model with probability density:

$$f(r) = (b/a)(r/a)^{b-1} \exp(-(r/a)^b) \quad \text{eqn 1}$$

to the observed absolute distances ( $r$ ) by maximum likelihood (Larsen & Marx 2001), where  $a$  is the scale parameter and  $b$  the shape parameter of the dispersal probability distribution. In general, decreasing  $b$  corresponds with increasing the degree of leptokurtosis, i.e. more probability is concentrated at both long and short distances.

Having fitted this model the standard deviation of dispersal distances was given by:

$$\sigma = a \sqrt{\frac{1}{2} \Gamma(1 + 2/b)} \quad \text{eqn 2}$$

(Tufto, Engen & Hindar 1997, equations 8 and A.1). Standard errors of the parameter estimates were then estimated by parametric bootstrapping (Efron & Tibshirani 1993).

The Weibull model was appropriate for examination of dispersal patterns in the willow ptarmigan population for two reasons. First, the model estimates dispersal standard deviations. Secondly, different values of the shape parameter in the Weibull model correspond with special cases of underlying dispersal processes (Tufto, Engen & Hindar 1997) that result in well-known dispersal distance distributions (see below). Incorrect assumptions about the shape parameter can lead to large bias in estimation of dispersal standard deviation (Tufto *et al.* 2005). The advantage of this model is that the shape of the distribution as well as the standard deviation of dispersal distances can be estimated. These parameters are important in a number of theoretical

spatial models, including Slatkin (1985), Kot, Lewis & Driessche (1996) and Lande, Engen & Sæther (1999).

#### TEST OF HYPOTHESES

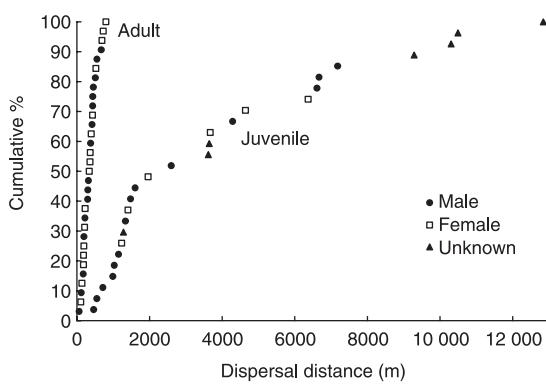
The effects of harvesting and possible differences between age and sex classes were tested for in the distribution of dispersal displacements. We tested the hypothesis of uniform shape and scale parameters of the Weibull model in the population against the alternative hypothesis of subgroup-specific parameters. The test was based on the change in two times the log likelihood, which was approximately or asymptotically  $\chi^2$  distributed with degrees of freedom equal to the change in the number of parameters (Stuart, Ord & Arnold 1998).

The Weibull model includes two models frequently used in the dispersal literature as special cases. For  $b = 1$  it is equivalent to the exponential model, and for  $b = 2$  it corresponds with a bivariate normal distribution for the dispersal displacements in the  $x$  and  $y$  directions (Tufto, Engen & Hindar 1997). We therefore tested the hypotheses of  $b = 1$  and  $b = 2$  against the fitted Weibull model from the observed dispersal distances in the population. The test was based on the change in two times the log likelihood, which was approximately  $\chi^2$  distributed.

#### Results

Dispersal patterns were clearly different between the two age groups. There was a significant difference in both the scale ( $\chi^2 = 75$ , d.f. = 1,  $P < 0.001$ ) and shape ( $\chi^2 = 7.1$ , d.f. = 1,  $P = 0.008$ ) parameters between adult and juvenile birds when comparing the dispersal probability distributions. In juvenile birds the observed mean dispersal distance was 3978 m (median = 2598 m,  $n = 27$ ), whereas in adult birds the observed mean dispersal distance was only 355 m (median = 351 m,  $n = 32$ ; Fig. 1).

Among adult birds no difference in either the scale ( $\chi^2 = 0.37$ , d.f. = 1,  $P = 0.54$ ) or the shape ( $\chi^2 = 0.52$ , d.f. = 1,  $P = 0.47$ ) parameters was found between

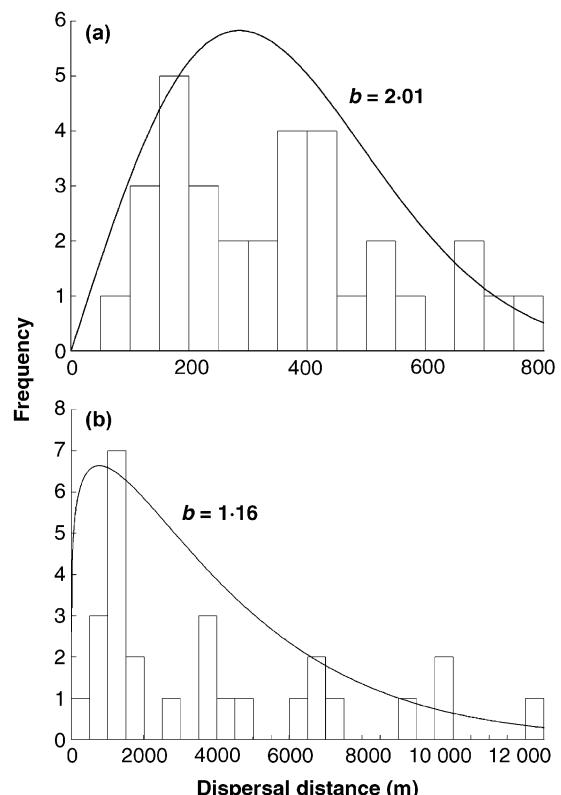


**Fig. 1.** Recorded natal and breeding dispersal distances of willow ptarmigan in continuous subalpine habitats of central Norway. Adults ( $n = 32$ ) and juveniles ( $n = 27$ ) shown as the observed cumulative distance distribution.

males and females. For adult breeding dispersal, the parameters of the Weibull model were estimated to  $a = 402 \pm 37$  m and  $b = 2.01 \pm 0.30$  (Fig. 2a), corresponding with a dispersal standard deviation of  $\sigma = 284 \pm 25$  m. The breeding dispersal distance distribution was not significantly different from a bivariate normal distribution ( $b = 2$ ,  $\chi^2 = 0.01$ , d.f. = 1,  $P = 0.92$ ). However, the hypothesis of an exponential distribution of the dispersal distances ( $b = 1$ ) could be rejected for adult birds ( $\chi^2 = 18.4$ , d.f. = 1,  $P < 0.001$ ).

In juvenile birds as well, no difference in either the scale ( $\chi^2 = 0.16$ , d.f. = 1,  $P = 0.69$ ) or shape ( $\chi^2 = 1.35$ , d.f. = 1,  $P = 0.25$ ) parameters was found between the two sexes. For juvenile natal dispersal the parameters of the Weibull model were estimated to  $a = 4206 \pm 730$  m and  $b = 1.16 \pm 0.19$  (Fig. 2b), corresponding with a dispersal standard deviation of  $\sigma = 3728 \pm 640$  m. This dispersal distance distribution was not significantly different from an exponential distribution ( $b = 1$ ,  $\chi^2 = 0.94$ , d.f. = 1,  $P = 0.33$ ) but the hypothesis of a bivariate normal distribution ( $b = 2$ ) could be rejected ( $\chi^2 = 16.9$ , d.f. = 1,  $P = 0.001$ ).

We tested for the effect of harvesting on dispersal distributions separately in the two age groups. In adult birds no statistically significant difference in the scale ( $\chi^2 = 2.98$ , d.f. = 1,  $P = 0.08$ ) and shape ( $\chi^2 = 1.04$ , d.f. = 1,  $P = 0.31$ ) parameters was found between birds from harvested [median 297 m, 95% confidence interval (CI)



**Fig. 2.** Frequency distribution of observed dispersal distances of willow ptarmigan, (a) adults and (b) juveniles, with fitted probability densities from the two-parameter Weibull model with estimated shape parameters  $b$  for the two age groups. Note the differences in values on the x-axis.

243–393 m] and non-harvested areas (median 436 m, 95% CI 302–634 m). Nor was there a significant effect of harvesting between harvested (median 1477 m, 95% CI 823–5821 m) and non-harvested areas (median 2280 m, 95% CI 1100–4312 m) on the dispersal distance distribution in juvenile birds (scale,  $\chi^2 = 0.40$ , d.f. = 1,  $P = 0.53$ ; shape,  $\chi^2 = 1.53$ , d.f. = 1,  $P = 0.22$ ).

## Discussion

We found no statistically significant effect of harvesting on dispersal patterns in either adult or juvenile willow ptarmigan in this study. The apparent lack of differences in dispersal in harvested vs. non-harvested areas is interesting. Hunting reduces density locally and an earlier study on willow ptarmigan in central Norway provided evidence for density-dependent dispersal, at least in males (Rørvik, Pedersen & Steen 1998). One possible explanation for the different results from these two studies might be the absolute density in the two study populations. In the study by Rørvik, Pedersen & Steen (1998), the pre-harvest density was  $> 50$  birds  $\text{km}^{-2}$  in all years, whereas in the present study the pre-harvest density in most years was  $< 30$  birds  $\text{km}^{-2}$ . Hence in the present study density-dependent dispersal mechanisms might not have come into play. If this represents a threshold for density-dependent effects it should be considered when harvest management plans are developed, especially if they are based on non-harvested (refuge) source areas (*sensu* Pulliam 1988). An earlier study of survival of willow ptarmigan in harvested and non-harvested areas in Sweden found that immigration must have been a significant force, sustaining the population on the harvested area (Smith & Willebrand 1999). However, these immigrants did not come from the non-harvested areas immediately surrounding the harvested area (Smith & Willebrand 1999), indicating that movements at a much larger landscape scale, from source areas with high densities, may have a substantial role in maintaining local populations.

Surprisingly, we found no statistically significant difference in natal dispersal distances between males and females (Fig. 1). Most studies of birds show that natal dispersal is female-biased (Greenwood 1980; Greenwood & Harvey 1982; Clarke, Sæther & Røskift 1997) and this has been demonstrated for willow ptarmigan and other tetraonids (Schroeder 1986; Martin & Hannon 1987; Small & Rusch 1989; Giesen & Braun 1993; Smith 1997; Warren & Baines 2002). One possible explanation for the absence of any sex differences in natal dispersal is the low sample size of juvenile females ( $n = 6$ ). The low proportion of juveniles identified as females in the sample was probably not because of differences in the sex ratio within the population but because males ( $n = 14$ ) were more likely to be positively identified by their call. It is possible that seven unidentified individuals were females. However, we cannot disregard the hypothesis that the lack of difference in dispersal distance

between juvenile males and females in this population is real under the conditions studied. Furthermore, the three longest dispersing juvenile willow ptarmigan of known sex were all males (Fig. 1).

Juvenile willow ptarmigan dispersed much further than adults and the dispersal pattern was quite different between the two age groups (Fig. 1). Juvenile natal dispersal distance pattern was not significantly different from an exponential distribution. Most juveniles settled 1–2 km from their natal area, with a few individuals moving up to 10 times further (Fig. 2b). In contrast, adult dispersal distances were normally distributed around the mean, indicating that most adults have high site fidelity once they have bred (Fig. 2a). The difference in the dispersal pattern of juveniles and adults found in this study has been reported previously for willow ptarmigan and other tetraonids, as well as many non-migratory bird species (Greenwood 1980; Greenwood & Harvey 1982; Johnsgard 1983; Hudson 1992).

Estimates of dispersal distances obtained from field studies of marked individuals are generally biased by the decreasing probability of detection as dispersal distances increase (Clarke, Sæther & Røskift 1997). Predicting the probability of rare long-distance dispersal events is therefore becoming increasingly important, for example in conservation and risk assessment of transgenic organisms (Higgins & Richardson 1999). Knowledge of the exact shape of the dispersal distance distribution is valuable for estimating dispersal in cases where observations are limited. The estimated value of the shape parameter  $b = 1.16$  for natal dispersal in willow ptarmigan indicates that the dispersal displacements follow a less leptokurtic distribution than in other organisms, such as wind-pollinated plants for which this shape parameter has been estimated as  $b = 0.60$  (Tufto, Engen & Hindar 1997) and  $b = 0.65$  (Nurminniemi *et al.* 1998). The exact shape of the dispersal distribution is of importance for evaluating the predictions from several theoretical models, for example for predicting the pattern of synchrony in spatially structured populations (Engen, Lande & Sæther 2002). It is interesting to note that the hypothesis of  $b = 2$ , corresponding with dispersal distances following a bivariate normal distribution, can be rejected for natal dispersal in this willow ptarmigan population. This dispersal distribution is frequently used in theoretical studies (Ruckelhaus, Hartway & Kareiva 1997; Engen, Lande & Sæther 2002).

We know of only one earlier study (Tufto *et al.* 2005) that has estimated dispersal standard deviations and shape parameters in birds. Recently, Tufto *et al.* (2005) fitted a gamma-binormal model, very similar to the Weibull model, to three species of passerines. The estimated shape parameters (termed  $\alpha$  in the gamma-binormal model) from the passerine species indicated strong to moderately leptokurtic dispersal displacements in the passerine populations, where  $\alpha$  ranged from 0.66 to 2.27 (Tufto *et al.* 2005). For comparison, it can be noted that with the gamma-binormal model the

shape ( $\alpha$ ) and dispersal standard deviations ( $\sigma$ ) for adult willow ptarmigans in this study were estimated to be  $\alpha = 202$  and  $\sigma = 284$  m, respectively. The corresponding values for juvenile willow ptarmigans with the gamma-binormal model were  $\alpha = 0.75$  and  $\sigma = 3716$  m.

Obtaining accurate information on long-distance dispersing individuals generally is a problem, sometimes causing underestimation of the tail of the dispersal probability distribution, especially in resighting and recapture studies of birds and small mammals (Koenig, Vuren & Hooge 1996). In our study we tried to reduce this possible bias in several ways. First, we used radio-tracking to follow individuals in the population. Secondly, we searched large surrounding areas up to 30 km from the study area border by fixed-wing aircraft several times each year. Thirdly, individuals that dispersed long distances should have been reported through the autumn harvesting, in which almost all suitable willow ptarmigan habitats within several hundred kilometres were covered by recreational hunters. For example, a rock ptarmigan *Lagopus mutus* captured and marked in the study area in late winter was reported shot 89 km from the capture site in autumn. Finally, in our analysis of the observed dispersal distances we applied a model-fitting procedure that estimates both scale and shape parameters of the dispersal probability distribution, as well as the dispersal standard deviation.

#### MANAGEMENT IMPLICATIONS

For non-harvested areas to act as source areas for a hunted population, dispersal movements must occur from the non-harvested to the harvested areas. Our study shows no significant difference in willow ptarmigan dispersal patterns between non-harvested and harvested areas under the conditions studied. Thus, if there is little or no difference in the dispersal probability distribution in harvested and non-harvested areas, there will be weak or no compensation for harvested birds, given that both areas have the same natural mortality and reproduction. Any evaluation of the sustainability of harvesting should therefore consider whether adjacent source areas exist from which the hunted population can be supplemented.

In this study we have shown how to estimate important dispersal parameters such as shape, scale and standard deviation of dispersal displacements. These parameters are essential when developing biologically realistic harvest models that can be used for management decisions. In addition, if the size of the management area is large enough to encompass the scale of dispersal in the population, the effect of dispersal will diminish. However, the dispersal parameters will vary greatly between species, and even between populations under different conditions.

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