Dispersal patterns in a harvested willow ptarmigan population

HENRIK BRØSETH,* JARLE TUFTO,† HANS CHR. PEDERSEN,* HARALD STEEN‡ and LEIF KASTDALEN‡
*Norwegian Institute for Nature Research, N-7485 Trondheim, Norway; †Department of Mathematical Sciences, Norwegian University of Science and Technology, N-7491 Trondheim, Norway; and ‡Department of Biology, University of Oslo, N-0316 Oslo, Norway

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


Introduction

Dispersal patterns and factors affecting dispersal are important in several fields of ecology, including applied 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...
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 param-
eters such as dispersal standard deviations and shape
parameters relevant to theoretical models of population
synchrony (Lande, Engen & Sæther 1999), gene fre-
cquency clines (Slatkin 1973) and the spread of advan-
tageous 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-km² 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 pubes-
cens* 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

The study area was divided into five administrative
hunting units, each of 20–30 km². 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 esti-
mate. The average autumn density of non-harvested
areas was 22.0 birds km⁻² (range 18.9–25.1 birds km⁻²),
while the average density of harvested areas after

---

Dispersal in willow ptarmigan

Dispersal in willow ptarmigan (Lagopus lagopus) is a critical aspect of their life cycle, particularly for juvenile birds. In this study, we only took into account the effect of the immigration to a new site (Ims & Hjermann 2001). In the next spring, we used the arithmetic mean centre of the locations recorded during the brood-rearing period (August) and the nest site for individual birds as an estimate of the nest site. Dispersal distances ($r$) were calculated as the distance between successive nest sites of individual birds. If the exact nest site position was unknown, the distance between the arithmetic mean centre of the locations recorded during the breeding and brood-rearing period was given by:

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

(eqn 2)

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:

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

(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:

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

(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

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 (\( \chi^2 = 75, \text{d.f.} = 1, P < 0.001 \)) and shape (\( \chi^2 = 7.1, \text{d.f.} = 1, P = 0.008 \)) 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 (\( \chi^2 = 0.37, \text{d.f.} = 1, P = 0.54 \)) or the shape (\( \chi^2 = 0.52, \text{d.f.} = 1, P = 0.47 \)) parameters was found between males and females. For adult breeding dispersal, the parameters of the Weibull model were estimated to \( a = 402 \pm 37 \text{ m and } b = 2.01 \pm 0.30 \) (Fig. 2a), corresponding with a dispersal standard deviation of \( \sigma = 284 \pm 25 \text{ m.} \) The breeding dispersal distance distribution was not significantly different from a bivariate normal distribution (\( b = 2, \chi^2 = 0.01, \text{d.f.} = 1, P = 0.92 \)). However, the hypothesis of an exponential distribution of the dispersal distances (\( b = 1 \)) could be rejected for adult birds (\( \chi^2 = 18.4, \text{d.f.} = 1, P < 0.001 \)).

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

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 (\( \chi^2 = 2.98, \text{d.f.} = 1, P = 0.08 \)) and shape (\( \chi^2 = 1.04, \text{d.f.} = 1, P = 0.31 \)) parameters was found between birds from harvested [median 297 m, 95% confidence interval (CI) 

![Fig. 1](image1.png)

![Fig. 2](image2.png)

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 km$^{-2}$ in all years, whereas in the present study the pre-harvest density in most years was < 30 birds 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 & Roskaft 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 & Roskaft 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 $b = 0.65$ (Nurminiemi 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 (α) and dispersal standard deviations (σ) 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-hunted 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.

**Acknowledgements**

The Norwegian Directorate for Nature Management, the Norwegian Research Council’s programme ‘Use and management of wildlands’ and the Norwegian Institute for Nature Research provided financial support to this study. We are indebted to many people who contributed to this project in different ways. We especially thank I. Rimul, O. Rimul and S. L. Svartaas for their effort in capturing and tracking willow ptarmigan. Rolf A. Ins, John Atle Kållås, Steve Rushton, Bernt-Erik Sæther and three anonymous referees made valuable comments on earlier drafts that greatly improved the manuscript. John D. C. Linnell improved the English.

**References**


Dispersal in willow ptarmigan


Received 19 December 2003; final copy received 26 January 2005

Editor: Steve Rushton