Measuring Dispersal in Conservation Biology: Lessons from Studies in Grouse

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Abstract

Knowledge of dispersal behavior and ability is an important factor in conservation biology. When assessing habitat quality and continuity it is important to know how far a species generally disperses. This study compiled dispersal averages between sexes across nine of the total 17 species of grouse (Tetraoninae) through a systematic survey of published literature on the subject. The resulting compilation table was used to make intra and inter-species comparisons of dispersal distances. The results of intra-specific comparisons, taken in accordance with the background information provided in the respective studies, shed light on generally universal barriers to dispersal by comparing habitat qualities with dispersal distances across multiple studies of a single species. Inter-specific comparisons revealed general sex-biases favoring further female dispersal which highlighted the importance of accounting for dispersal behaviors such as inter-lek movement of females when planning habitat continuity requirements in park reserves. A comparison of the emerging field of genetic estimation methodology with radio-tracking methods suggests that this field may provide an accurate and broader representation of dispersal within an entire population.

Introduction

Importance of dispersal studies

As human development continues to diminish and fragment natural landscapes, the study of dispersal ability in species has become increasingly important in conservation efforts. Dispersal studies are important in understanding and estimating the future viability of a species in relation to human development (Montadert & Léonard, 2006). It is important to set constraints within which humans can continue to operate without causing species extinction through land-use change. To know these limits, developers require knowledge of species' habitat requirements and largely – their dispersal abilities. As populations become more and more fragmented, they become more prone to inbreeding and eventual extinction due to lack of gene flow between populations. These effects compounded with habitat loss in fragmentation leads to a general loss in biodiversity (Wilcox, 1985). To help avoid this loss, fragmentation should be kept within limits in which species of conservation concern can still disperse between populations.

Dispersal studies are also important in metapopulation studies. Metapopulations are dynamically fluctuating populations, which exists in a balance of localized colonization and extinction across patches of suitable land in a fragmented habitat. In metapopulations, a species may not survive locally, but will instead persist regionally within the fragmented habitat. Dispersal of individuals gives rise to new local populations while other populations are simultaneously outcompeted or driven to extinction by factors such as poor patch habitat quality. As dispersal plays a key role in the continuity and persistence of metapopulation dynamics, it is important to assess how increased heterogeneity (i.e. further fragmentation) impacts metapopulation persistence by altering dispersal ability in a species (Brachet *et al*., 1999). Knowledge of a species' dispersal ability can be used when limited resources require a narrowed conservation focus; for example, an assessment of what land to focus preservation efforts on based on how easily it can be reached, how much continuity there is between populations across the habitat, and how much gene flow there will be. Further, knowledge of dispersal distances and behaviors is relevant in determining how large a reserve must be to protect a species. Species which require a large amount of land to migrate between lekking grounds, for example, would require a large and continuous habitat reserve. Studies of dispersal across various habitat qualities and continuities are important in determining what poses the greatest challenges to natural dispersal and what minimum quality of land must be upheld in order to conserve a species.

Background on grouse dispersal

Grouse (Tetraoninae) present an excellent generalized model for studying dispersal in birds. The current wealth of information already published on Grouse behavior and dispersal provides a solid base on the subject and allows for more specialized and diverse studies to be conducted in the future. Furthermore, grouse is an excellent model to study bird dispersal in general because grouse represent all three mating systems- lekking, polygyny, monogamy (Caizergues, 2002). The physical characteristics of grouse also allow for accurate results in tracking and timing of dispersal because their large body size allows for grouse to be fitted with relatively accurate long-life radio transmitters (Caizergues, 2002).

Certain generalities can be drawn from previous publications about factors which influence grouse dispersal and dispersal behaviors. Many species of grouse migrate twice a year, going between summer and winter grounds (Connelly *et al*., 1988; Caizergues, 2002). Dispersal also occurs in grouse as juveniles migrate from nest-site to brood break-up site (Montadert & Léonard, 2006). This natal dispersal is thought to be as important a factor in population viability as birth and death rates in species where adults have a sedentary lifestyle (Montadert & Léonard, 2006). This is the case in certain grouse species, such as Black Grouse, in which adults of one or both sexes have relatively sedentary lifestyles, and where natal dispersal becomes the primary source for gene flow between populations. Natal movements in grouse can be categorized into either exploratory behavior or long-distance dispersal. In exploratory behavior, juveniles wander randomly in the vicinity of their nest-site, without a set destination. This is evolutionarily advantageous because it allows individuals to familiarize themselves with a greater area than their nest and adult range; an adaptation which can prove beneficial in the event of a lack of resources, mating partners, other habitat disturbances within their home range (Montadert & Léonard, 2006). Long distance dispersal is a direct movement to a new range without prior exploratory wanderings. Long distance dispersal benefits regional genetic diversity as it allows for the introduction of new genes from external sites.

Methods

Literature Review

The primary research for this project was conducted through a literature review of published studies on grouse dispersal. The focus of this review was to compile data on dispersal distances reported in these publications and to determine what the most common methodology was in measuring this dispersal. Scientific articles included in this review were identified via literature searches of scientific journal databases such as ScienceDirect, Web of Science, and JSTOR. Search criteria used were either "natal dispersal in grouse", "grouse dispersal", or "gene flow in grouse". These searches were chosen to present diversity in results from natal dispersal to adult dispersal and to present papers with molecular methods for estimating dispersal to compliment the many studies which use radio-tracking methods.

Measuring of grouse dispersal

While not performed in practice during this study, field methodology is an important aspect to be included in this report as it is a key component in studies on grouse dispersal. The current most common method for measuring dispersal in grouse is radio-tracking. In radio-tracking, individuals must be captured and then fitted with necklace radio transmitters. Capture methods range from setting traps to actively going out and spotlighting grouse at night, then capturing individuals or entire broods with nets. Once fitted with transmitters, grouse movement is monitored by periodically checking individual's positions with signal receiving antennae in field excursions. As this method is time intensive and can only cover a relatively small sample size due to limited resources, it may soon be replaced by the above-described genetic estimation methods. The field portion of these genetic methods simply involves collecting tissue, scat, and feather samples from the desired study area and then extracting DNA from these samples to work with in the lab.

DNA sequencing & PCR

In addition to the literature survey, the project included a practical portion to become familiarized with the lab techniques involved in measuring dispersal within a population; i.e., DNA sequencing and PCR. There were no sets of tissue samples collected available for running a complete test of dispersal, so each step in the process was conducted instead through various ongoing projects in the lab, across multiple DNA sets. The general procedure for genetically measuring dispersal in a population involves DNA extraction from collected tissue samples, followed by PCR and Megabace genotyping of microsatellites. To run PCR, extracted DNA samples were first prepared with a master mix, primers, Q-Solution, DNA, and distilled water to dilute the samples appropriately. Master mixes are designed specifically according to what the experiment is testing and what primers will be used. The design generally follows a recipe for varied amounts of H_2O, buffer, forward and reverses primers, Dndps, and Taq-polymerase. In the specific data used for sequencing, a multiplex PCR was run using TUT1 and TUT3 primers. TUT primers are commonly used in research on grouse because they were originally cloned in capercaillie, which are closely related (Segelbacher *et al*., 2000). After the master mix is prepared, a solution of master mix, Q-solution, primer mix, and distilled water is mixed with specific amounts of each according to the experiment design. This solution is vortex mixed and then a specific amount, 9µl for example, is added to every well in a plate. A different DNA sample is then added to each well at a predetermined amount, 1µl for example. The plate is then covered with air-tight film and centrifuged before running the PCR to ensure no mixing between wells during the heating process of PCR. PCR runs throughout this project were run on preset programs created by each respective primary researcher. After the PCR, samples are stored in a freezer until they are sequenced with Megabace. To prepare for Megabace, the PCR products must first be diluted with ladder marker and distilled water. During the Megabace run, instructions for each step are given as a readout on the machine's screen. It is important to have coating solution tubes, matrix tubes, distilled water, and two linear polyacrylamide (LPA) buffer plates (at least enough for three uses) ready for use before beginning the Megabace since many steps have a time limit and must be performed without delay.

Results & Conclusion

For this project, a total of 18 publications were selected for inclusion in the data compilation. The publications included data on dispersal distances and behaviors of nine species of grouse. Black grouse, hazel grouse, sage grouse, and willow grouse were the most commonly covered species in the reviewed publications. Of the papers reported, only two used genetic methodology in measuring dispersal; the rest used telemetry. The data collected in this review (with one exception) supports the pattern commonly observed in bird species, where dispersal is greater in females than in males. Adult female dispersal across all species averaged 5.69 km, with hazel grouse having the lowest at 1.05 km and sage grouse dispersing the furthest with 11.51 km. Adult male dispersal ranged from 0.96 km in white-tailed ptarmigans to 11.3 km in sage grouse and averaged 3.99 km. Juvenile female dispersal ranged from 0.34 km in willow grouse to 11.85 km in sage grouse and averaged 4.35 km across all species. Juvenile male dispersal ranged from 0.34 km in willow grouse to 11.15 km in sage grouse and averaged 2.33 km.

Table 1. Compiled Species Dispersal Averages (all figures listed in km; Sources are found in Appendix 1).

Species	Average Adult Female Dispersal	Range of Adult Female Dispersal	Average Adult Male Dispersal	Range of Adult Male Dispersal	Average Juvenile Female Dispersal	Range of Juvenile Female Dispersal	Average Juvenile Male Dispersal	Range of Juvenile Male Dispersal
Black Grouse (*Tetrao tetrix*)	-	-	-	-	8.65	1.79 - 12.57	1.25	<1.0 – 1.50
Blue Grouse (*Dendragapus obscures*)	-	-	-	-	1.40	n/a	0.90	n/a
Hazel Grouse (*Bonasa bonasia*)	1.05	n/a	2.65	n/a	3.14	0.22 – 6.8	2.90 *	0.85 - 29.4

Red Grouse (*Lagopus lagopus scoticus*)	-	-	-	-	1.43	0.86 – 2.0	0.42	0.34 – 0.5
Ruffed Grouse (*Bonasa umbellus*)	-	-	-	-	4.82	n/a	2.14	n/a
Sage Grouse (*Centrocercus urophasianus*)	11.51	11.3 – 11.72	11.3	n/a	11.85	2.3 – 18.9	11.15 **	3.3 – 19.4
Spruce Grouse (*Canachites canadensis*)	5.0	1.3 – 9.5	1.7	0.5 – 3.0	5.0	n/a	0.70	n/a
Willow Grouse (*Lagopus lagopus*)	8.53	3.98 – 11.4	3.33	2.60 – 3.98	0.34	n/a	0.34	n/a
White-Tailed Ptarmigan (*Lagopus leucura*)	2.38	1.25 – 3.5	0.96	0.92 – 1.0	2.52	1.03 – 4.0	1.14	1.03 – 1.25

*outlier in data from a study on German Hazel Grouse dispersal has lowered the male dispersal average when in all other cases male dispersal was greater than that of females.

**possible discrepancies in data since sex was not specified in one study, and only median distances were given in another. One study states that juvenile male dispersal averaged 2.8 km further than that of females.

Applications to land preservation

Patterns in dispersal distances between sexes can provide insight to habitat matrix quality requirements in species when presented in conjuncture with background information on mating systems. Commonly in bird species, males hold on to a resource to improve mating success while females disperse further and move from site to site to compare potential mates.   This resource which males hold on to can be a physical resource, such as access to food and a good nest, or it can be conceptual, for example a sign of fitness, such as a position in a lekking arena (Dunn & Braun, 1985). The observed greater dispersal in females than in males could suggest lek mating behavior in species where this is observed. It is important to note that this compilation of data may however present a somewhat misleading representation of total distances dispersed since many of the studies simply used a measure of the straight line from the final point to the initial point of an individual. This methodology neglects to account for the entire length of paths taken to reach the final point. In species such as sage grouse, there is no notable difference in dispersal distances between the sexes when in reality females disperse further than males as they are the primary source for gene flow by traveling between many mating sites. While there are often no direct measurements reported to show the greater dispersal in females undergone in travel from lekking site to lekking site, this sex-driven gene flow and dispersal can be inferred from sage grouse's lekking mating system and high male fidelity to lek sites (Dunn & Braun, 1985). Simply stated, if a species is known to lek, greater dispersal distances can be assumed for females even if the reported numbers are equal to that of male dispersal. As realized in this case study of sage grouse, data compiled in this literature survey must be interpreted with additional background information taken into account. The collected data has relevant application to be used in determining size allotment needed for preserving land in conservation efforts because we can see from the range in dispersal distances how far certain species will spread throughout their habitat. However, additional information on dispersal behavior is needed in order to determine what efforts should be placed on maintaining habitat continuity. If, for example, a species performs minimal exploratory dispersal and only requires habitat continuity along a specific corridor to get between winter and summer site, less continuity is needed between separate groups of summer sites and separate winter sites. If, however, there are sex-based behavioral differences, and females exercise exploratory dispersal between summer sites during mating season while males remain at their established sites, greater continuity between various seasonal sites is needed.

Importance of habitat continuity

Preservation of habitat continuity for dispersal is of high importance in instances in which behavior is already a limiting factor in gene flow. The high occurrence of sedentary behavior in males throughout the surveyed literature raises the concern of potential problems for maintaining genetic diversity in subpopulations within metapopulations. With random dispersal in hens, there is the risk that hens disperse to a site where there are no longer any males present, thus failing to contribute gene flow by failing to find a mate (Warren & Baines, 2002). At the edges of metapopulations, where finding males may be of concern, presence of conspecifics becomes the primary indicator of habitat quality as this indicates that potential mates will likely be present and the population will be able to locally persist. An additional potential concern with sedentary male behavior is the extremely limited male-driven gene flow between populations (Warren & Baines, 2002). While there is a loss in gene-flow associated with sedentary behavior, there are also advantages to survivorship in this behavior. Juveniles with more sedentary behavior were shown to have higher survival rates than juveniles which move greater distances during natal dispersal (Beck *et al*., 2006). This is likely due to increased vulnerability to predation and other factors of mortality during the juvenile phase. Given the varied advantages and disadvantages to sedentary behavior it is difficult to assess what the full trade-offs are between this behavior versus active dispersal. Evolution has possibly focused primarily on mating success and thus has led to sedentary behavior in males of species like sage and spruce grouse in accordance with breeding success in a lekking system.

Barriers to dispersal

Addressing the concern of where to focus efforts in land preservation becomes increasingly complex as further factors in dispersal are taken into account. Hazel grouse interestingly was the only species surveyed which had greater dispersal in adult males than in females. Juvenile dispersal in hazel grouse should have followed the same trend; however, an outlier from a study in Germany skewed the data in favor of further female dispersal despite male dispersal being greater in all other instances. Sex differences aside, hazel grouse in general are thought to be active dispersers when suitable habitat is present. The spread of hazel grouse across much of northern Eurasia supports this theory of active dispersal (Rhim & Son, 2009). This general active and far dispersal through natural habitats, as seen in Rhim & Son's (2009) study in South Korea, presents a reference point from which to compare studies in other countries to begin addressing the effects of habitat quality on dispersal. In studies where dispersal is limited or less than what was seen in the undisturbed habitat of Rhim & Son's (2009) study, the given habitat can be compared with the study area in South Korea to determine what habitat features present barriers to hazel grouse dispersal. Thus, when comparing and looking at the case studies in greater depth, limits on dispersal for hazel grouse may become apparent. The hazel grouse case studies in this survey revealed some potential barriers to dispersal which seem to be reflective of habitat quality and specifically continuity. In a comparison of studies on populations in Korea, Germany, China, France, and Sweden, dispersal distances were shortest in Sweden where the study was conducted in managed forest (Rhim & Son, 2009). Open spaces in particular appear to pose the greatest challenge to hazel grouse dispersal as grouse will move readily across large distances of less suitable habitat to find new patches for occupancy; they will not however, cross open corridors of land or farmland (Montadert & Léonard, 2006). This is potentially due to vulnerability grouse experience in open land. As grouse are not strong fliers, they are unable to simply fly away upon the approach of a predator. Farmland in particular also likely poses a barrier to grouse dispersal as these areas can be home to higher densities of generalist predators (Montadert & Léonard, 2006). Unfortunately we still cannot pinpoint open spaces as a definite barrier to dispersal, as this appears to vary according to setting. Hazel grouse tracked in the southeastern French Alps were shown to readily disperse across large open spaces such as stone fields above the timber line in order to reach the next suitable habitat patches (Montadert & Léonard, 2006). Individuals observed outside of their natural range showed similar aptitude in crossing large open spaces in order to find suitable habitat (Montadert & Léonard, 2006). Perhaps these examples suggest localized evolution in behavior where open spaces are no longer a barrier to dispersal when the benefits of finding a new habitat patch and avoiding the inbreeding effects of isolation outweigh the costs of vulnerability and increased chance of mortality while crossing open spaces.

Methodology analysis

Methodology plays an important role in how readily these studies can be conducted and how accurate they will be. Historically, dispersal studies methods have evolved from field observation of tagged individuals, to radio-tagging and tracking, to the new emerging methods of genetic estimation. Genetic estimation methods allow for a much larger sample size within a population than was formerly possible with radio-tracking methods (Sahlsten *et al*., 2008). However, it is important in this transition of popular methodology to ensure that the new genetic estimation methods accurately match up results with radio-tracking methods. With the extensive spread in studies covered in this survey, it is possible to compare genetic and radio-tracking results in studies on the same species and even the same geographic subgroup of a species. A study by Sahlsten *et al.* (2008) used genetic methods to estimate dispersal distances in a population of hazel grouse in northern Sweden. This study suggested an average dispersal of 900-1500m per generation, which correlated closely with the 1.2km dispersal average found by a study of 17 radio-tracked hazel grouse in Sweden and Finland (Swenson, 1991). While this correlation is high support for the accuracy in genetic estimates of dispersal, little further research has been published on genetic methods in a study of grouse dispersal, so only one additional study was cited in the survey. Corrales (2011) published a study on black grouse dispersal, using genetic estimation methods, which suggested a range of dispersals from 1.79 to 12.57km. These results fit with the 9.3 and 8.0km average dispersals in females from Warren (2002) and Caizergues (2002) respectively. However, the range is above Warren's and Caizergues' respective estimates of <1.0 and 1.5km for average male dispersal. This difference is likely due to discrepancies in local factors affecting the populations in each study since they were each conducted on different geographical subsets of black grouse across England, the French Alps, and northern Sweden. Genetic estimation methods for measuring dispersal have high potential to replace the radio-tracking methods in order to have more all-encompassing studies of greater numbers of individuals in a population, but further studies must first be conducted in order to compare the accuracy of results with those of radio-tracking methods.

Summary & future directions

With all these factors of dispersal behaviors, limitations, and comparisons of methodology in mind, a generalized consensus emerges for the parameters to be taken into account for land preservation in conservation efforts. This overarching study also shows where dispersal studies in populations of grouse can be taken next. The results of this literature survey have shown that dispersal measurements may neglect the dispersal behavior that occurs between the final and starting points recorded for individuals; barriers to dispersal appear to generally be open spaces between habitats, but these can on occasion be overcome; and that genetic estimation methods appear to coincide with results from traditional radio tracking methods. In future conservation efforts, a background on the species of concern's behavior should be taken into consideration when assessing how much continuity is required between seasonal sites; for example, by creating corridors between lekking sites to allow for female-driven gene flow between populations when males are known to lek and are mostly sedentary. Open spaces within a habitat reserve should be kept to a minimum, but further studies should still be conducted on barriers to dispersal as it is still not fully understood why these can on occasion be overcome. Further studies should also be conducted to compare results of genetic estimation methods with radio tracking results. If the genetic estimates continue to match closely with radio tracking, this method could greatly expand the scope of future dispersal studies by reducing field labor required and by including much larger sample sizes in studies of entire populations rather than just a select few individuals.

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Appendix 1

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Degree project in biology, Bachelor of science, 2012
Examensarbete i biologi 15 hp till kandidatexamen, 2012
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Table 1 Species dispersal by study (figures listed in km)

Species	Average Adult Dispersal (km)		Methods	Average Natal Dispersal (km)		Methods	Genetic Dispersal	References
Black Grouse (*Tetrao tetrix*)				8.00 : F	1.50 : M	Broods located with pointer dogs, then trapped. Chicks equipped with radio transmitters.		Caizergues, 2002
black grouse (*Tetrao tetrix*)				9.30 : F	<1.0 : M	Chicks captured and fitted with radio transmitters. Note: data not specific for males; results only stated that all males remained within 1km of their natal site.		Warren, 2002
Black Grouse (*Tetrao tetrix*)							DNA was extracted from 469 hunter-obtained wing tissue samples and was then PCR amplified to check genetic structure. The genetic neighborhood	Corrales & Höglund

							size was calculated with Nb=4$\pi D\sigma^2$, where Nb= neighborhood size, D= density, and σ^2 = axial parent-offspring dispersal rate. Axial parent-offspring distance was measured to range from 1.79 km in males to 12.57 km in females, thus supporting previous reports that female black grouse are the primary dispersing sex in the species.	
Blue Grouse (*Dendragapus obscures*)				1.40 : F	0.90 : M	Referenced from (Caizergues, 2002). All data collected with radio tracking methods. Data may be somewhat unreliable due to low sample sizes.		(Hines, 1986) via (Caizergues, 2002)
Hazel Grouse *(Bonasa bonasia*)	1.05 : F	2.65 : M	Individuals were captured after brood break-up and then radio tagged for location monitoring.	2.00 : F	4.00 : M	Individuals were captured after brood break-up and then radio tagged for location monitoring. Data for brood dispersal estimated from distance between nest-site and brood break-up site.		Montadert & Léonard, 2006
Hazel Grouse *(Bonasa*				4.8 : F China	5.7 : M China	Chicks captured with a walk-in trap and fitted		Fang & Sun, 1997

bonasia)				6.8 : F Germany 0.22 : F Sweden	0.85 : M Germany 1.4 : M Sweden	with a transmitter. Broods were then radio tracked to gather dispersal data. Note, data may be unreliable due to small sample size. Note, data for Germany and Sweden referenced from other reports.		Additional data referenced from: Swenson, 1991 & Kämpfer-Lauenstein, 1995
Hazel Grouse *(Bonasa bonasia*)							Using the formula, $NS=4\pi D\sigma^2$, where D = population density, NS = neighborhood size, and σ = axial distance between related individuals. The data need for this formula can be found by genotyping microsatellite loci from tissue samples collected. Results suggest a dispersal of roughly 900-1500m per generation.	Höglund, Sahlsten, & Thörngren, 2008
Hazel grouse (*Bonasa bonasia*)				1.894 : F	2.525 : M	1-2 month old juveniles were captured with nets and radio-marked. The population was then radio monitored three times per week over the duration of the		Rhim & Son, 2009

						experiment.		
Red Grouse (*Lagopus lagopus scoticus*)				2.00 : F	<0.5 : M	Referenced from (Caizergues, 2002). All data collected with radio tracking methods. Data may be somewhat unreliable due to low sample sizes.		(Hudson, 1992) via (Caizergues, 2002)
Red Grouse (*Lagopus lagopus scoticus*)				0.861 : F	0.343 : M	146 juveniles were caught using a spotlighting method and a net. Individuals were radio-marked and then tracked. Data compiled from multiple years.		Warren & Baines, 2007
Ruffed Grouse (*Bonasa umbellus*)				4.82 : F (net) 9.56 : F (total)	2.14 : M (net) 6.36 : M (total)	Juveniles captured with lily-pad traps and equipped with radio transmitters. Individuals then tracked with hand-held or vehicle-mounted signal receiver antennae. Note, only data from autumn dispersal used.		Small & Rusch, 1989
Sage Grouse (*Centrocercus urophasianus*)				Juvenile male dispersal ranged from 3.3 to 19.4km while female ranged from 2.3 to 18.9km. Male dispersal averaged 2.8km further than that		Individuals were captured in traps and through spotlighting techniques. The juveniles were then aged and sexed and fitted with radio transmitters which were used to monitor their movements during the experiment. Two		Beck et al., 2006

				of females.		brood groups were tracked at two separate sights.		
Sage Grouse (*Centrocercus urophasianus*)	Data only provided for females. Average maximum summer dispersal: 9.74 +/- 7.7 km, Winter: 13.7 +/- 9.3km.		Individuals were captured, fitted with radio transmitters, and translocated to a new site where they were monitored for survival, dispersal and adaption to the new area. Birds were monitored through observation and telemetry.					Baxter et al., 2008
Sage Grouse (*Centrocercus urophasianus*)	Sex not specified in the averages. Average of 11.3km from summer to winter range.		Individuals were captured and tagged and radio-marked. Locations of radio-marked individuals were observed 1-4 times per month by antenna monitoring from a light aircraft.	Sex not specified in the averages. Average of 14.9km from summer to winter range.		Individuals were captured and tagged and radio-marked. Locations of radio-marked individuals were observed 1-4 times per month by antenna monitoring from a light aircraft.		Connelly et al., 1988
Sage Grouse (*Centrocercus urophasianus*)				8.80 : F (median)	7.40 : M (median)	Birds captured (with a variety of methods) and banded. Individuals then tracked through field observation. Data		Dunn & Braun, 1985

						recorded as a straight-line measurement between banding location and the known lek.		
Spruce Grouse (*Canachites canadensis*)				5.00 : F	0.70 : M	Referenced from (Caizergues, 2002). All data collected with radio tracking methods. Data may be somewhat unreliable due to low sample sizes.		(Boag and Schroeder, 1992) via (Caizergues, 2002)
Spruce Grouse (*Canachites canadensis*)	5.0 +/- 1.0 : F	1.7 +/- 0.5 : M	Birds were captured and fitted with radio transmitters. Radio-marked individuals where then tracked by their radio-signal.					Herzog & Keppie, 1980
Willow Grouse (*Lagopus lagopus*)	0.355 (sex unspecified)		Birds were captured and fitted with a necklace radio transmitter. Birds were tracked on GPS receivers.	3.978 (sex unspecified)		Birds were captured and fitted with a necklace radio transmitter. Birds were tracked on GPS receivers.		Brøseth H, 2005
Willow Grouse (*Lagopus lagopus*)	Numerical data incomplete. 25% of males dispersed further than 5km. 'Most' females dispersed		During winter months, Birds caught with walk-in traps or spotlighted and netted. Once equipped with radio transmitters, individual locations	10.2 : F	3.40 : M	Chicks located with pointing dogs, then caught before brood break-up and equipped with radio transmitters. Individual locations monitored on GPS receivers. Data recorded		Hörnell-Willebrand M, 2005

	further than males.		were monitored. Data recorded as straight-line of the maximum distance between time periods.			as straight-line of the maximum distance between time periods.		
Willow Grouse (*Lagopus lagopus*)				11.4 : F	2.60 : M	Referenced from (Caizergues, 2002). All data collected with radio tracking methods. Data may be somewhat unreliable due to low sample sizes.		(Smith, 1997) via (Caizergues, 2002)
White-Tailed Ptarmigan (*Lagopus leucurus*)	3.50 : F	1.00 : M	Used playback of recorded calls to find and brand the birds. Observed birds in the field with intensive searches and binocular observations. *Note, median dispersal distances provided in this study, not mean.	4.00 : F	1.25 : M	Located chicks with playback of tape-recorded chick distress calls and then banded individuals. Individuals recaptured and reobserved to mark locations. Data recorded as straight-line between initial site and breeding site.		Braun, 1993
White-tailed Ptarmigan (*Lagopus leucura*)	Adult Average: 1.15km; 1.25km for females, 0.92km for males (averages for each sex		Individuals were captured and fitted with a necklace radio collar which they were then tracked with. Note, populations were isolated by	Juvenile Average: 1.03km		Individuals were captured and fitted with a necklace radio collar which they were then tracked with.		Fedy et al., 2008

	includes data from juveniles and adults)	natural features, so dispersal was short and random.				

Species dispersal averages (figures reported in km)

Species	Average Adult Female Dispersal	Range of Adult Female Dispersal	Average Adult Male Dispersal	Range of Adult Male Dispersal	Average Juvenile Female Dispersal	Range of Juvenile Female Dispersal	Average Juvenile Male Dispersal	Range of Juvenile Male Dispersal
Black Grouse (*Tetrao tetrix*)	-	-	-	-	8.65	1.79 - 12.57	1.25	<1.0 – 1.50
Blue Grouse (*Dendragapus obscures*)	-	-	-	-	1.40	n/a	0.90	n/a
Hazel Grouse (*Bonasa bonasia*)	1.05	n/a	2.65	n/a	3.14	0.22 – 6.8	2.895 *	0.85 - 29.4
Red Grouse (*Lagopus lagopus scoticus*)	-	-	-	-	1.43	0.861 – 2.0	0.42	0.343 – 0.5
Ruffed Grouse (*Bonasa umbellus*)	-	-	-	-	4.82	n/a	2.14	n/a
Sage Grouse (*Centrocercus urophasianus*)	11.51	11.3 – 11.72	11.3	n/a	11.85	2.3 – 18.9	11.15 **	3.3 – 19.4
Spruce Grouse	5.0	1.3 – 9.5	1.7	0.5 – 3.0	5.0	n/a	0.70	n/a

(*Canachites canadensis*)								
Willow Grouse (*Lagopus lagopus*)	8.53	3.98 – 11.4	3.33	2.60 – 3.98	0.34	n/a	0.34	n/a
White-Tailed Ptarmigan (*Lagopus leucura*)	2.375	1.25 – 3.5	0.96	0.92 – 1.0	2.52	1.03 – 4.0	1.14	1.03 – 1.25

*outlier in data from a study on German Hazel Grouse dispersal has lowered the male dispersal average when in all other cases male dispersal was greater than that of females.

**possible discrepancies in data since sex was not specified in one study, and only median distances were given in another. One study sites that juvenile male dispersal averaged 2.8 km further than that of females.

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