Running Head: Variable density-dependent dispersal

Title: Variation in space and time: a long-term examination of density-dependent dispersal in a woodland rodent

Authors: Denomme-Brown[1], Simon T. (sdenommebrown@gmail.com); Cottenie[1], Karl (cottenie@uoguelph.ca); Falls[2], J. Bruce (jbruce.falls@utoronto.ca); Falls[2], E. Ann (fallseann@gmail.com); Brooks[1], Ronald J. (rjbrooks@uoguelph.ca) and Andrew G. McAdam[1] (amcadam@uoguelph.ca)

[1] University of Guelph, Dept. of Integrative Biology, 50 Stone Rd. E., Guelph, ON, Canada, N1G 2W1

[2] University of Toronto, Dept. of Zoology, Toronto, ON, Canada

Corresponding Author Information: Simon T. Denomme-Brown, sdenommebrown@gmail.com, Dept. of Integrative Biology, University of Guelph, Ontario, Canada, N1G 2W1. Phone Number: (519) 803-7993

Abstract

Dispersal is a fundamental ecological process, and population density has been observed as a driver of dispersal in various taxa. Conflicting examples of positive and negative density-dependent dispersal, however, leave little consensus regarding any general effects of density on dispersal. Deer mice (*Peromyscus maniculatus*) have exhibited both negative and positive density-dependent dispersal. Using 51-years of data on *P. maniculatus* live-trapping abundances, we examined the spatial scale of density-dependent dispersal as well as its temporal stability within this long time-series. We examined these patterns over both the entire time-series and also in ten-year shifting windows to determine whether the nature and strength of the relationship changed through time. Overall, the probability of dispersal decreased with increased local and regional population density, and the negative effect of local density on dispersal was more pronounced in years with low regional densities. Females were less likely to disperse, but female dispersal was more density-dependent than male dispersal. Additionally, the strength of negative density-dependent dispersal changed through time, from very strong in some decades to absent in others. Our study shows that the relationship between density and dispersal is not temporally static and that studies of density-dependent dispersal should consider both local and regional population densities. As well, while male-biased dispersal is often considered ubiquitous in mammals, we demonstrate that male and female dispersal may have differing levels of density-dependence. Finally, our study highlights the importance of accounting for both local and regional processes in natural systems as these types of long-term, spatially broad examinations of dispersal are crucial if spatial processes are to be represented adequately and accurately in population modelling and theory.

Keywords: Dispersal, Density-dependence, Peromyscus, Small Mammals, Spatial effects, Temporal Dynamics, Movement

Introduction

Dispersal influences fundamental ecological processes such as population growth rates and viability, genetic connectivity, and range expansions (Greenwood 1980; Nathan 2006; Holyoak et al. 2008). Dispersal is identified as one of four fundamental processes in community ecology (Vellend 2010), and a cornerstone of the metacommunity concept (Leibold et al. 2004). Yet the causes of dispersal are often poorly understood and dispersal remains difficult to measure and include in empirical studies (Koenig et al. 1996, Nathan et al. 2003, Logue et al. 2011).

Benefits of dispersal often stem from differences in conspecific densities between pre and post-dispersal settlement sites. When conspecific densities at pre-dispersal sites are greater than at post-dispersal sites (i.e. positive density-dependent dispersal), dispersing individuals may benefit from reduced competition and agonistic interactions (Murray 1967; Gaines and McClenaghan 1980; Matthysen 2005). Alternatively, negative density-dependent dispersal may be beneficial when individuals disperse to gain access to a limiting resource, or when the benefits of group living outweigh the costs of intraspecific competition (Bowler and Benton 2005).

Conflicting examples of positive and negative density-dependent dispersal (DDD) across a variety of taxa (Bowler and Benton 2005; Matthysen 2005; Rodrigues and Johnstone 2014), have left little consensus regarding general effects of density on dispersal. Matthysen (2005) concluded that both birds and mammals predominantly exhibit positive DDD. The review, however, excluded studies exhibiting temporal trends in density and seasonal variation which Matthysen (2005) acknowledged could have changed their conclusions. Contradicting effects of density on dispersal have also been found within species. DDD has been observed as both negative and positive in separate studies of the same species (Garten and Smith 1974; Rehmeier et al. 2004), or depending on when in the annual cycle density is measured (Betini et al. 2015), or simultaneously negative and positive across a patchily distributed population (Kim et al. 2009).

In particular, variable effects of density on dispersal have been reported in deer mice, *Peromyscus maniculatus*. *Peromyscus* spp. generally display male-biased dispersal (Fairbairn 1978b; Gaines and McClenaghan 1980; Rehmeier et al. 2004) and have been observed to exhibit both positive (Garten and Smith 1974; Fairbairn 1978b; Anderson and Meikle 2010) and negative DDD (Rehmeier et al. 2004; Wojan et al. 2017). These variable effects of density on dispersal suggest that temporal and spatial variation in population densities could feasibly influence the strength of density dependence in a system. Therefore, as others have proposed (e.g. Matthysen 2005), DDD must be examined using long time-series, while accounting for spatial and temporal variation in population densities. In this study, we examined the frequency and extent of dispersal by wild *P. maniculatus*, using monitoring data spanning 50 years from traplines distributed across nearly 17km of temperate forest. These data allowed us to examine dispersal patterns at large temporal and spatial scales and investigate how the strength of DDD was affected by both temporal and spatial variation in population densities.

Methods

Data Collection

Deer mice were live-trapped in Algonquin Provincial Park (APP), Ontario, Canada from 1960 - 2015. Trapping initially occurred on 10 traplines, with lines added and removed intermittently throughout the study such that the same 17 lines were trapped consistently from 1995 – 2015. Lines consisted of 10 trapping stations set along transects at 10m intervals. Early in the study, most lines had one trap at each station, but by 1979 all lines had two traps per station in an attempt to avoid trap saturation, for a total of 20 traps per line. Sherman-style live traps were used exclusively until 2013, when one Longworth trap (Natural Heritage Book Society, Totnes, Devon) replaced one Sherman at each station. Traps were baited with peanut butter and rolled oats until 1991. After 1991, water-soaked sunflower seeds were used as bait. Freeze-killed

mealworms (*Tenebrio molitor*) were added to half the traps from 2013 - 2015 as a bait supplement. Use of Longworth traps and mealworms were aimed at decreasing mortality in shrew (*Soricidae*) species (Do et al. 2013; Shonfield et al. 2013). Distances between lines ranged from 0.115 - 16.9km. Lines were located in forested habitats with different dominant trees including sugar maple (*Acer saccharum*), white pine (*Pinus strobus*), white spruce (*Picea glauca*), black spruce (*Picea mariana*), trembling aspen (*Populus tremuloides*), and red pine (*Pinus resinosa*).

Each year, trapping was conducted on three consecutive nights either once or twice a month from May through September, for a maximum of 10 three-night trapping sessions per year. Traps were set just before dusk and checked after dawn. When captured, deer mice were weighed, sexed, aged and assessed for reproductive condition. Before release, animals were fitted with uniquely coded ear tags for individual identification upon recapture.

Dispersal Detection

Dispersal was defined to occur when an individual deer mouse was captured on multiple traplines within a single trapping season. Movements occurring between years were excluded as the biological drivers of inter-year dispersals likely differed from those occurring within a trapping season. Additionally, few mice survive the winter in APP, and thus there were relatively few potential dispersers over this period. Movements between lines were considered dispersal events as the distance between the closest traplines (115m) was greater than the diameter of a typical deer mouse home range (Harestad and Bunnel 1979). Distances between traplines were calculated as straight-line distance between the first trap station on each line.

Although these data were collected in a consistent manner, any errors in data collection or transfer to digital records could mistakenly appear as dispersal events (e.g. incorrect tag or trapline numbers were recorded). While the error rate is likely low, the compounding of even a

low rate of error over more than 50 years of data could skew our estimates of dispersal. To minimize the frequency of such errors we used a strict criterion to identify dispersal events. To be considered a dispersing individual, an individual mouse must have been captured on multiple, consecutive occasions on one line either preceded, or followed by at least one capture on another line. We assumed that the mouse in question was either trapped while moving towards a trapline where it subsequently settled, or was trapped while dispersing from a trapline and either continued on or died. To meet this criterion, a mouse must have been captured on a minimum of three occasions within a year. Accordingly, all model analyses and calculations of dispersal frequencies discussed hereafter were performed on a dataset of mice caught three or more times in a year. Additionally, we avoided including mis-read tags by ensuring that dispersing animals had consistent records of individual traits such as sex and size. Individuals that moved to a new line and then returned immediately to their initial line were also excluded as this likely indicated a misread tag. Finally, changes in methodology and some loss of data necessitated the exclusion of five years of data from the dataset (1987-1991).

Density Measures

We calculated three measures of density and converted each from raw capture totals to captures per hundred trap-nights to account for variation in trapping effort both between years and among traplines. The first measurement was raw local trapline density (hereafter termed raw density), measured as the number of captures per hundred trap-nights at each trapline in each year. The second density measure was an average regional trapline density, calculated annually as the mean number of captures per hundred trap-nights across all traplines in APP in that year. Finally, we calculated local density for each trapline in each year by subtracting the regional density in a year from the raw density on each line that same year. This measure allowed us to include local densities and regional densities within the same models.

It should be noted that the density estimates we used do not account for spatial or temporal variation in capture probability. While spatially explicit mark-recapture techniques (SECR) represent a powerful set of statistical tools to account for these issues (Royle et al. 2013), they were inappropriate for our long-term data for several reasons. First, Bayesian SECR models are inappropriate for trapping data that are derived from single-catch traps such as those used in our study (Gerber and Parmenter 2015). Second, when using frequentist SECR models the multi-catch estimator can only be used if density is relatively constant over survey regions (Distiller and Borchers 2015), and this was not the case in our data (see Results). Finally, the single-catch estimator developed by Distiller and Borchers (2015), which allows for frequentist SECR analysis using single catch traps, requires times for all captures which were not available for our historical data. We discuss this issue further below.

Data Analysis

To assess how a deer mouse's propensity to disperse was affected by sex and population density at different spatial scales, we fitted eight separate Generalized Linear Mixed Effects Models (GLMM; binomial family, logit link) associated with local and regional population densities as well as sex of the individual mouse. They were 1) Biological Null Model (BN), 2) Sex Model (SX), 3) Local Density Model (LD), 4) Regional Density Model (RGD), 5) Raw Density Model (RWD), 6) Local and Regional Density Model (LRD), 7) Density Interaction Model (DI), 8) Density and Sex Interaction Model (DSI) (see Table 1). All eight models used the binary response variable of whether an individual mouse dispersed or not and included the fixed effect of distance (in meters) from the trapline where the mouse was initially caught to the next closest trapline. This effect was included to account for the non-uniform spatial distribution of traplines and whether differences in movement among lines were due primarily to spatial effects on the probability of detecting a dispersal event (i.e. dispersal is more likely to be detected

between nearby traplines). We used the natural log of the raw distance in kilometers (km) to correct a significant non-linearity in the relationship between this variable and the probability of dispersal. In all models, local density and regional density were converted to z-scores ($z = x - \bar{x}/\sigma$) based on the mean and standard deviation of all observations across years and lines.

We used the Akaike Information Criterion (AIC) to assess relative support for the eight models (Burnham and Anderson 2007), which included various combinations of sex, and raw, local and regional density as fixed effects (Table 1). We calculated AIC values for each model and performed model comparisons using ΔAIC (Δ_i) values (Table 1). Akaike Weights (ω_i) were calculated to examine the conditional probabilities of each model (Table 1). All models contained the same random effects, with initial trapline of capture and year of capture included to capture spatial and temporal variation in dispersal propensity. Likelihood ratio tests (LRT) were used to assess the significance of the year and trapline random effects in each of the 8 candidate models. Models were assessed for overdispersion and collinearity of variables and met model assumptions. Statistical analyses were performed in R (Version 3.5; R Core Team 2018), including the glmer function with a bobyqa optimizer in the lme4 package (Bates et al. 2015).

In addition to the model analysis described above, we performed a number of *post hoc* analyses. When first visualizing the relationship between regional density and movement frequency (Figure 1a) there appeared to be a marked change in the relationship between the two variables for portions of the time-series, particularly over a 9-year period from 2002-2010. To examine this, we ran the RWD model on a shifting ten-year window through the time-series. The RWD model was used because it was the simplest model with moderate support based on AIC comparisons. More complex models would not fit these data given the smaller sample size provided in 10-year windows of the time-series (Figure 1b).

The second set of *post hoc* analyses assessed how robust our results were to changes in trapping protocols during this long-term study (e.g. number of traps per station, change in bait, and trap types), that occurred at distinct points in our study (1979, 1991 and 2013 respectively). For this we ran our best model on subsets of our dataset from before, between and after these protocol changes occurred.

Results

Population Densities and Frequency of Movement

Over the 51 years included in this study, there were 3408 instances where a mouse was caught at least three times in a year. Of these 3408 possible dispersers, 4.5% (n = 154) dispersed between traplines. The proportion of the population that dispersed fluctuated between years ($\bar{x} \pm$ SE = 0.053 ± 0.008 mice dispersing in the population, n = 51 years), with no dispersal detected in some years and a maximum of 28% of the population dispersing between lines in 1964 (Figure 1). The population sex ratio was slightly skewed, with males comprising 53.4% of individuals in the dataset ($X^2 = 7.9$, df = 1, $P < 0.01$). This male skew was more pronounced among dispersing individuals, with 65.6% of dispersing mice being male ($X^2 = 7.7$, df = 1, $P < 0.01$). Overall, males were more likely to disperse (5.5%) than females (3.3%; Fisher Exact Test: P = 0.002).

Distances travelled by dispersing individuals ranged from 115m to 11.4 km ($\bar{x} \pm$ SE = 1.57 ± 0.18 km, n = 154) (Figure 2). There was no difference in dispersal distance between the sexes (t = 1.1, df = 95.7, p-value = 0.28) (Figure 2). Only 52.6% (n = 81) of dispersals were to the next most closely situated trapline (Figure 2). There were two traplines located only 115m apart, but dispersal between these traplines represented only 20.1% (n = 31) of all movements.

The density of deer mice in APP fluctuated over an order of magnitude during this study, with yearly regional population densities ranging from 1.9 to 27.8 captures per hundred trap nights ($\bar{x} \pm$ SE = 11.15 ± 0.81 captures per hundred trap-nights, n = 51 years) (Figure 1a). Local

densities also varied, with the average range in local population densities among traplines within years ($\bar{x} \pm SE = 19.37 \pm 1.22$ captures per hundred trap-nights, n = 51 years) approaching the aforementioned range in regional densities among years. In particular, 9 of 51 years exhibited a greater range in density among lines within a year than the range in regional density across the 51 years, with a maximum range of 47.2 captures per hundred trap-nights in 2001.

Dispersal Models

The model that had the lowest AIC score of the eight fitted models was the DSI model which included the fixed effects of both regional and local density, sex, and interactions between both local density and regional density, and local density and sex (Table 2). In the DSI model, the probability of dispersal decreased with increasing distance to nearest trapline ($\beta \pm SE = -1.16 \pm 0.17$, $Z = -7.0$, $P < 0.0001$), increased regional density ($\beta \pm SE = -0.57 \pm 0.15$, $Z = -3.9$, $P < 0.0001$), and increased local density ($\beta \pm SE = -0.087 \pm 0.025$, Z -3.45, $P = 0.0006$). The significant positive interaction between local and regional densities ($\beta \pm SE = 0.031 \pm 0.014$, $Z = 2.23$, $P = 0.026$) indicated that in years of low regional density, local densities had a stronger negative effect on the probability of dispersal (Figure 3a). For example, three of the five years displaying the highest proportions of dispersers in the study were 1964 (0.286), 1962 (0.192) and 1976 (0.150), which represented three of the 11 lowest density years within the study.

The DSI model also included sex as a significant predictor of dispersal, with males dispersing more frequently than females ($\beta \pm SE = 0.38 \pm 0.19$, $Z = 2.04$, $P = 0.04$) (Figure 3b). However, the interaction between local density and sex was marginally significant ($\beta \pm SE = 0.057 \pm 0.029$, $Z = 2.0$, $P = 0.051$), suggesting that while males disperse more than females, females were more sensitive to local density than males and were more likely to disperse when densities were low (Figure 3b). Year was a significant random effect in this model (LRT,

Deviance = 1098.3, X^2_1= 9.8, P = 0.0017) whereas initial line of capture was not (LRT, Deviance = 1106.7, X^2_1 = 1.5, P = 0.23). Overall, the DSI model explained 12.56% of the deviance.

There was also strong support for the density interaction model (DI) ($\Delta_i < 2$), which was identical to the DSI model except it did not include an interaction between local density and sex. All effects in this model were in the same direction as in the DSI model and the DI model explained 12.26% of the overall deviance. Considerably less support was seen for models that did not contain the interaction between local and regional densities, with all these models demonstrating either moderate ($\Delta_i < 7$) or no support ($\Delta i > 10$) (Table 1).

Despite evidence of negative DDD overall, visual inspection of the time series of density and dispersal probability (Figure 1a) suggested temporal changes in the strength of density-dependent dispersal. When running the RWD model on the shifting 10-year window through the time series, the effect of raw density on dispersal probability never became positive. The effect size did approach zero, however, and the negative relationship between raw density and dispersal probability was significant for only 14 of 32 ten-year windows in the analysis (Figure 1b). Finally, when running the DSI model on our data before and after each change in trapping methodology, there were no changes in the direction of effects for all explanatory variables save one. The exception was the effect of sex on dispersal, which was reversed prior to the initial bait change, but the effect was not significant.

Discussion

Probability of Dispersal

Overall, deer mice in APP exhibited negative DDD, with a lower probability of dispersal under high-density conditions, regardless of the scale at which density was measured. Multiple explanations have been proposed to explain negative DDD. Attraction to conspecifics (Danielson and Gaines 1987; Stamps 1991), range constriction in the face of high densities

255 (Stickel 1960; Taitt 1981) and exclusionary behavior towards immigrants in periods of high
256 density (i.e. "social fences"; Hestbeck 1982) have all been proposed as possible mechanisms. If
257 trap saturation had occurred within our system it could mimic a natural social fence, denying
258 immigrants access to traps in densely populated lines and biasing our results towards the
259 appearance of negative DDD. This seems unlikely, however, as densities on even the most
260 highly populated traplines fell well short of saturation of available traps (i.e. average captures per
261 100 trap-nights in APP across all lines throughout this study was 22.62 with SE = 0.42 and a
262 standard deviation of 10.66, while the highest capture rate on any line in any year of the study
263 was 73.81 captures per 100 trap-nights). Additionally, there was no obvious change in the
264 direction of density-dependence before and after the traps per station were doubled in 1979.
265 While the result of negative DDD runs counter to generalizations of positive DDD in
266 mammals (Matthysen 2005), previously reported relationships between dispersal and density in
267 *Peromyscus* spp. have been inconsistent. Positive DDD has been observed in *P. maniculatus*
268 (Fairbairn, 1978a), *P. polionotus* (Garten and Smith 1974), and genetic estimates show that *P.*
269 *leucopus* is more likely to disperse from high density habitat patches (Anderson and Meikle
270 2010). In contrast, evidence of negative DDD has been found in both *P. maniculatus* (Rehmeier
271 et al. 2004) and *P. boylii* (Wojan et al. 2015). The spatial and temporal breadth of our study may
272 elucidate why studies on *Peromyscus* spp., and other dispersing organisms, often yield divergent
273 results. For while deer mice in our study consistently exhibited negative DDD, the strength with
274 which density affected dispersal varied temporally, spatially and between males and females.
275 The relationship between density and dispersal varied throughout our time-series. This
276 variation is evident upon examining the time-series of regional density and movement frequency
277 on the same axis (Figure 1a), particularly in the 9-year period from 2002-2010 which visually
278 suggests a possible positive relationship. The effect of raw density on dispersal probability in the

RWD model was never positive in any 10-year window along the time-series, however, the effect size approached zero in the 1990's before becoming increasingly negative (Figure 1b). Also, the majority of the 10-year windows examined (n = 18) did not exhibit a significant relationship between density and dispersal. Few studies investigating DDD have been performed using long-term data (Matthysen 2005), despite the fact that inferences drawn from short-term studies can differ drastically from those generated by long-term research (Kratz et al. 2003), and that effects of some ecological processes become more pronounced over time (Cardinale et al. 2007). Our data highlight the importance of long-term time-series to drawing accurate conclusions regarding the density-dispersal relationship, as an unfortunately timed relatively long-term study (i.e. 10 years) would not detect the negative effect of density on dispersal that exists in this system.

In addition to varying temporally, the strength with which local density affected dispersal was also mediated by regional densities. This positive interaction between the regional and local density effects on dispersal indicates that the negative effect of local density on dispersal is greater in years of low regional density and muted in years of high regional density (Figure 3b). This suggests that local population density can be an important driver of dispersal in this system, but only when examined in concert with regional density. Low local densities that increase the probability of dispersal are only noteworthy in years when population densities across the APP system are also low. This relationship between local and regional densities as interacting drivers of dispersal has not been shown previously to our knowledge. It is important to highlight that when examining dispersal, local population densities must be considered within the context of their accompanying regional densities, as many existing studies provide only densities for localized sites of emigration (Matthysen 2005), which based on our findings may lead to spurious results if context is not provided in the form of associated regional densities. As well,

the few large datasets that have been used to examine DDD fail to differentiate between spatial and temporal variation in densities (Matthysen, 2005, but see Pasinelli and Walters 2002; Catchpole et al. 2004) despite the fact both temporal variation and interactions between densities at multiple spatial scales affect dispersal.

Several potential mechanisms could cause this interaction between local and regional densities and their effect on dispersal. Deer mice populations in APP are closely tied to maple seed crops, with mouse populations peaking after seed masting events (Falls et al. 2007). *Peromyscus* spp. will also move based on both habitat quality and population density (Morris and Diffendorfer 2004). It may be that individuals select habitat and disperse to high quality, maple-rich areas when possible; but in years of high regional densities, local densities in high-quality habitats become high enough to prevent such immigration. Such a process would strike a balance between traditional dispersal hypotheses predicting positive DDD in the face of increased competition (Greenwood 1980), and ideas of conspecific attraction (Stamps 1991) and habitat selection. This type of balance between competition and facilitation amongst conspecifics has been observed previously in a colony of blue-footed booby (*Sula nebouxii*), where simultaneous positive and negative DDD was thought to result from the costs of competition and the advantages of increased mating choice options (Kim et al. 2009).

It may be that mate availability plays a role in dispersal in the APP system because the strength of density-dependence also differed between males and females. Males dispersed more often than females, which is consistent with findings of male-biased dispersal in both *Peromyscus* spp. (Fairbairn 1978a; Goundie and Vessey 1986; Rehmeier et al. 2004; Mabry 2014), and other mammals (Greenwood 1980; Dobson 1982; Mabry et al. 2013). However, we also found evidence that dispersal in females was more sensitive to changes in local density than in males, such that females dispersed more frequently than males when local densities were very

low. Examples of sex-biased dispersal switching from male-bias to female-bias within a system are rare (but see Pérez-González and Carranza 2009), but could have important implications for understanding the role of mating strategies in dispersal. The predominance of male-biased dispersal in mammals (and female-biased dispersal in birds) has long been attributed to mating systems, although the simplicity of this relationship has been questioned (Mabry et al. 2013). If males disperse to track females and females rely on available resources for reproduction (Emlen and Oring 1977), then at exceedingly low densities the lack of available mates may outweigh the benefits of familiar surroundings, resulting in a spike in female dispersal. Alternatively, if densities are associated with food availability, then low densities may indicate low food availability, which would affect dispersal in females more strongly than in males due to their reliance on resources for reproduction (Emlen and Oring 1977). Such differences between male and female dispersal sensitivity to local population density mean that spatial variation in density could potentially affect sex ratios, which could in turn affect population density.

As mentioned previously, our density measures did not account for variation in capture probabilities. While we have described the practical reasons for not being able to utilize SECR methods, we recognize that this is not an ideal. However, the lack of trap saturation on any of our lines throughout the study, the fact that frequency of recapture of individuals within this study ($\bar{x} \pm SE = 2.63 \pm 0.07$) did not decrease with increased regional annual densities (linear regression; $\beta \pm SE = 0.012 \pm 0.01$, $t = 1.09$, $P = 0.28$), and the fact that the density-dispersal relationships in our models were not altered by the changes in trapping methodologies that occurred throughout this study all speak to the robustness of our findings.

Frequency and Distance of Dispersal

In general, deer mice in APP dispersed as often as expected based on existing literature, but over much greater distances than anticipated. Rehmeier et al. (2004) reported that over a 10-

351 year period 4% of deer mice in a tallgrass prairie undertook long-distance dispersals (LDDs,
352 >125m); Bowman et al. (2001b) similarly reported 4.2% of deer mice demonstrating LDD
353 (>100m) in mixed-wood forest. Based on these papers, our dispersals (>115m) can be classified
354 as LDDs and the yearly mean frequency of LDD by deer mice in APP of 4.5% was remarkably
355 similar to these other frequencies reported in the literature. However, these absolute frequencies
356 of dispersal should be interpreted with some caution as mark-recapture studies have limited
357 ability to detect dispersal. The majority of studies monitoring small mammal populations utilize
358 trapping grids of insufficient size to detect LDDs (< 2ha, from Bowman et al. 2001a).
359 Comparisons with radio tracking data and genetic estimates of dispersal have shown that such
360 trapping practices combined with mark-recapture methods underestimate dispersal distances
361 (Koenig et al. 1996). Unfortunately, expanding trapping grids to detect greater dispersal
362 distances is often impractical, as increasing the maximum straight-line distance across a grid
363 requires an exponential increase in area and monitoring effort. Our study provides an alternative
364 approach by instead monitoring dispersal using many smaller trapping transects. This reduced
365 our ability to detect individual dispersal events, however, this was overcome through extensive
366 temporal replication. So, while our raw rates of detected dispersals are surely downwardly
367 biased, our measurement of dispersal across 3408 individuals, 17 traplines and 51 years allowed
368 us to assess the effects of large-scale processes on the probability and extent of dispersal.
369 The spatial extent of dispersal within our system exceeded previous reports for this
370 species. Of 154 dispersal events we observed, 13% (n =20) exceeded the previous maximum
371 long-distance movement reported for *P. maniculatus* (4287 ± 10m, in Wood and McKinney
372 2015). The maximum dispersal distance of 11.3km in this study represents a 164% increase on
373 that previous reported maximum. As well, we detected more frequent movements of great
374 distances than previous studies. For instance, 3.3% of potentially dispersing mice in APP

375 dispersed over 200m compared to 1% of mice dispersing beyond this same distance in previous
376 studies (Brant 1962; Groves and Keller 1986). We also observed 2.8% and 2.1% of mice
377 dispersing beyond 300m and 500m respectively, while roughly 1% of populations travelled these
378 distances in previous studies (Diffendorfer et al. 1999; Rehmeier et al. 2004). This indicates that
379 the tail of the dispersal distance distribution of this species has previously been underestimated.

380 Dispersal distances tend to follow a leptokurtic distribution, with many individuals
381 dispersing short distances and few individuals exhibiting LDD. Understanding the rate and
382 extent of LDDs is particularly important as the spread of a species in a landscape is determined
383 largely by the frequency and extent of LDD, as represented in the tail of the species' distribution
384 of dispersal distances (Kot et al. 1996; Levin et al. 2003; Green and Figuerola 2005). However,
385 tails of dispersal distance distributions are notoriously difficult to quantify (Koenig et al. 1996),
386 which has led to LDD in deer mice being generally reported with little detail or as anecdotal
387 observations (Jung et al. 2005; Wood and McKinney 2015). Our results suggest that LDD by
388 deer mice is more common than reports in the literature would suggest, reinforcing claims that
389 relatively small scale mark-recapture techniques used to monitor many species fail to accurately
390 capture LDD (Koenig et al. 1996). Our results, however, indicate mark-recapture studies can
391 detect dispersal between distant locations, provided the temporal extent of the study is sufficient.

392 Our evidence of greater frequencies of LDD in this species has important ecological
393 implications as species with "fat-tailed" dispersal distributions are thought to exhibit more rapid
394 spread throughout landscapes (Kot et al. 1996). Dispersal distance distributions can influence
395 persistence in the face of climate change (Schloss et al. 2012) and the spread of zoonotic diseases
396 (Mundt et al. 2009), such as Hantavirus and Lyme disease for which *Peromyscus* spp. are vectors
397 (Meerburg et al. 2009; Gaitan and Millien 2016). This is particularly worthy of attention as small
398 mammal populations in this region are already responding to climate change (Myers et al. 2009).

We have demonstrated that deer mice exhibit negative DDD that is more pronounced during periods of low regional densities and that female dispersal is more sensitive to these changes in density than that of males. We also have demonstrated that the relationship between density and dispersal is not static but rather varies conspicuously over large time scales. These results show that long-term field studies are beneficial to the examination of ecological processes such dispersal, as smaller scale projects are likely to miss or potentially misrepresent the broader signal entirely. As well, our findings suggest that while local population densities are important, their influence on dispersal can be affected by broader regional population densities. As such, future studies should account for both local and regional densities when testing for DDD. Additionally, we have shown that well-established phenomena such as mammalian male-biased dispersal may also be density-dependent. These results together suggest that the conflicting relationships between density and dispersal in the literature may result from broader context-dependence in DDD. Finally, our results add to a previously modest body of empirical literature examining LDD. We have demonstrated that deer mice dispersal of greater than 100m is not uncommon and that LDD occurs more frequently, and to greater extents, than previously thought. This reinforces that dispersal distributions estimated from short-term mark recapture studies may be drastically underestimated, which is potentially important for future conservation.

Acknowledgements

We would like to acknowledge countless individuals who collected these data. Thank you to the Algonquin Wildlife Research Station for logistical support. This work was supported through funding from the National Science and Engineering Research Council of Canada and the Ontario Ministry of Natural Resources. We dedicate this work to the memory of our colleague Dr. Leslie Rye who said it best: “I can’t believe I am getting paid to work in Algonquin!”

References

Anderson, C. S., and D. B. Meikle. 2010. Genetic estimates of immigration and emigration rates in relation to population density and forest patch area in Peromyscus leucopus. Conservation Genetics 11:1593–1605.

Bates, D., M. Maechler, B. Bolker, and S. Walker. 2015. Fitting Linear Mixed-Effects Models Using lme4. Journal of Statistical Software 67:1–48.

Betini, G. S., A. Pardy, C. K. Griswold, and D. R. Norris. 2015. The role of seasonality and non-lethal carry-over effects on density-dependent dispersal. Ecosphere 6:art272.

Bowler, D. E., and T. G. Benton. 2005. Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. Biological reviews of the Cambridge Philosophical Society 80:205–225.

Bowman, J., C. V. Corkum, and G. J. Forbes. 2001a. Spatial Scales of Trapping in Small-mammal Research. The Canadian Field-Naturalist 115:472–475.

Bowman, J., G. Forbes, and T. Dilworth. 2001b. Distances moved by small woodland rodents within large trapping grids. Canadian Field-Naturalist 115:64-67.

Burnham, K.P. and D.R. Anderson. 2007. Model Selection and Inference: A Practical Information-Theoretic Approach (2nd edition) New York, NY: Springer.

Brant, D. H. 1962. Measures of the Movements and Population Densities of Small Rodents. University of California Publications in Zoology 62:105–184.

Cardinale, B. J., J. P. Wright, M. W. Cadotte, I. T. Carroll, A. Hector, D. S. Srivastava, M. Loreau, and J. J. Weis. 2007. Impacts of plant diversity on biomass production increase through time because of species complementarity. Proceedings of the National Academy of

Sciences 104:18123–18128.

Catchpole, E. A., Y. Fan, B. J. T. Morgan, T. N. Coulson, and T. H. Clutton-Brock. 2004. Sexual dimorphism, survival and dispersal in red deer. Journal of Agricultural, Biological and Environmental Statistics 9:1–26.

Danielson, B. J., and M. S. Gaines. 1987. The influences of Conspecific and Heterospecific Residents on Colonization. Ecology 68:1778–1784.

Diffendorfer, J. E., M. S. Gaines, and R. D. Holt. 1999. Patterns and impacts of movements at different scales in small mammals. Pages 63–88 in G. W. Barrett and J. D. Peles, editors. Landscape ecology of small mammals. Springer-Verlag, New York.

Distiller, G., and D. L. Borchers. 2015. A spatially explicit capture-recapture estimator for single-catch traps. Ecology and Evolution 21:5074-5087.

Do, R., J. Shonfield, and A.G. McAdam. 2013. Reducing accidental shrew mortality associated with small-mammal livetrapping II: a field experiment with bait supplementation. Journal of Mammalogy 94:754-760.

Dobson. 1982. Competition for Mates and Predominant Juvenile Male Dispersal in Mammals. Animal Behaviour 30:1183–1192.

Emlen, S. T., and L. W. Oring. 1977. Ecology, Sexual Selection and the Evolution of Mating Systems. Science 197:215–223.

Fairbairn, D. J. 1978a. Dispersal of Deer Mice. Oecologia 193:171–193.

Fairbairn, D. J. 1978b. Behaviour of dispersing deer mice (Peromyscus maniculatus). Behavioral Ecology and Sociobiology 3:265–282.

Falls, J. B., E. A. Falls, and J. M. Fryxell. 2007. Fluctuations of Deer Mice in Ontario in Relation to Seed Crops. Ecological Monographs 77:19–32.

Gaines, M. S., and L. R. McClenaghan. 1980. Dispersal in Small Mammals. Annual Review of Ecology and Systematics 11:163–196.

Gaitan, J., and V. Millien. 2016. Stress level, parasite load, and movement pattern in a small-mammal reservoir host for Lyme disease. Canadian Journal of Zoology 94:565–573.

Garten, C. T., and M. H. Smith. 1974. Movement By Oldfield Mice and Population Regulation. Acta Theriologica 19:513–514.

Gerber, B.D., and R.R. Parmenter. 2015. Spatial capture-recapture model performance with known small-mammal densities. Ecological Applications 25:695-705.

Goundie, T. R., and S. H. Vessey. 1986. Survival and Dispersal of Young White-Footed Mice Born in Nest Boxes. Journal of Mammalogy 67:53–60.

Green, A. J., and J. Figuerola. 2005. Recent advances in the study of long-distance dispersal of aquatic invertebrates via birds. Diversity and Distributions 11:149–156.

Greenwood, P. J. 1980. Mating systems, philopatry and dispersal in birds and mammals. Animal Behaviour 28:1140–1162.

Groves, C. R., and B. L. Keller. 1986. Ecological characteristics of small mammals on a radioactive waste disposal area in southeastern Idaho. American Midland Naturalist 46:404–410.

Harestad, A. S., and F. L. Bunnel. 1979. Home Range and Body weight -- A Reevaluation. Ecology 60:389–402.

Hestbeck, J. B. 1982. Population Regulation of Cyclic mammals: The Social Fence Hypothesis. Oikos 39:157–163.

Holyoak, M., R. Casagrandi, R. Nathan, E. Revilla, and O. Spiegel. 2008. Trends and missing parts in the study of movement ecology. Proceedings of the National Academy of Sciences of the United States of America 105:19060–19065.

Jung, T., K. O'Donovan, and T. Powell. 2005. Long-distance movement of a dispersing Deer Mouse, Peromyscus maniculatus, in the boreal forest. Canadian Field-Naturalist 119:451–452.

Kim, S. Y., R. Torres, and H. Drummond. 2009. Simultaneous positive and negative density-dependent dispersal in a colonial bird species. Ecology 90:230–239.

Koenig, W., D. Van Vuren, and P. N. Hooge. 1996. Detectability, philopatry and the distribution of dispersal distances in vertebrates. Trends in Ecology & Evolution 11:514–517.

Kot, M., M. A. Lewis, and P. Van Den Driessche. 1996. Dispersal Data and the Spread of Invading Organisms. Ecology 77:2027–2042.

Kratz, T. K., L. A. Deegan, M. E. Harmon, and W. K. Lauenroth. 2003. Ecological Variability in Space and Time: Insights Gained from the US LTER Program. BioScience 53:57–67.

Leibold, M. a., M. Holyoak, N. Mouquet, P. Amarasekare, J. M. Chase, M. F. Hoopes, R. D. Holt, J. B. Shurin, R. Law, D. Tilman, M. Loreau, and a. Gonzalez. 2004. The metacommunity concept: a framework for multi-scale community ecology. Ecology Letters 7:601–613.

Levin, S. A., H. C. Muller-Landau, R. Nathan, and J. Chave. 2003. The ecology and evolution of seed dispersal: a theoretical perspective. Annual review of Ecology, Evolution, and

Systematics 34:575–604.

Logue, J. B., N. Mouquet, H. Peter, and H. Hillebrand. 2011. Empirical approaches to metacommunities: a review and comparison with theory. Trends in ecology & evolution 26:482–91.

Mabry, K. E. 2014. Effects of sex and population density on dispersal and spatial genetic structure in brush mice. Journal of Mammalogy 95:981–991.

Mabry, K. E., E. L. Shelley, K. E. Davis, D. T. Blumstein, and D. H. van Vuren. 2013. Social Mating System and Sex-Biased Dispersal in Mammals and Birds: A Phylogenetic Analysis. PLoS ONE 8:1–9.

Matthysen, E. 2005. Density-dependent dispersal in birds and mammals. Ecography 28:403–416.

Meerburg, B. G., G. R. Singleton, and A. Kijlstra. 2009. Rodent-borne diseases and their risks for public health. Page Critical Reviews in Microbiology.

Morris, D. W., and J. E. Diffendorfer. 2004. Reciprocating dispersal by habitat-selecting white-footed mice. Oikos 107:549–558.

Mundt, C. C., K. E. Sackett, L. D. Wallace, C. Cowger, and J. P. Dudley. 2009. Long-distance dispersal and accelerating waves of disease: empirical relationships. The American Naturalist 173:456–466.

Murray, B. G. J. 1967. Dispersal in Vertebrates. Ecology 48:975–978.

Myers, P., B. L. Lundrigan, S. M. G. Hoffman, A. P. Haraminac, and S.H. Seto. 2009. Climate-induced changes in small mammal communities of the Northern Great Lakes Region. Global Change Biology 15:1434-1445.

Nathan, R. 2006. Long-Distance Dispersal of Plants. Science 313:786–788.

Nathan, R., G. Perry, J. T. Cronin, A. E. Strand, and M. L. Cain. 2003. Methods for estimating long-distance dispersal. Oikos 103:261–273.

Pasinelli, G., and J. R. Walters. 2002. Social and environmental factors affect natal dispersal and philopatry of male Red-cockaded Woodpeckers. Ecology 83:2229–2239.

Pérez-González, J., and J. Carranza. 2009. Female-biased dispersal under conditions of low male mating competition in a polygynous mammal. Molecular Ecology 18:4617–4630.

Rehmeier, R. L., G. A. Kaufman, and D. W. Kaufman. 2004. Long-Distance Movements of the Deer Mouse in Tallgrass Prairie. Journal of Mammalogy 85:562–568.

Rodrigues, A. M. M., and R. A. Johnstone. 2014. Evolution of positive and negative density-dependent dispersal. Proceedings of the Royal Society B: Biological Sciences 281:20141226–20141226.

Royle, J. A., R. B. Chandler, R. Sollmann, and B. Gardner. 2013. Spatial capture-recapture. Academic Press.

Schloss, C. A., T. A. Nuñez, and J. J. Lawler. 2012. Dispersal will limit ability of mammals to track climate change in the Western Hemisphere. Proceedings of the National Academy of Sciences of the United States of America 109:8606–8611.

Shonfield, J., R. Do, R. J. Brooks, and A.G. McAdam. 2013. Reduc King accidental shrew mortality associated with small-mammal livetrapping I: an inter- and intrastudy analysis. Journal of Mammalogy 94: 745-753.

Stamps, J. A. 1991. The effects of conspecifics on habitat selection in teritorial species. Behavioral Ecology and Sociobiology 28:29–36.

Stickel, L. F. 1960. Perommyscus Ranges at High and Low Population Densities. Journal of Mammalogy 41:433–441.

Taitt, M. J. 1981. The Effect of Extra Food on Small Rodent Populations: I. Deermice (Peromyscus maniculatus). Journal of Animal Ecology 50:111–124.

Vellend, M. 2010. Conceptual synthesis in community ecology. The Quarterly review of biology 85:183–206.

Wojan, C.M., Knapp, S.M., and K.E. Mabry. 2015. Spatial variation in population density affects dispersal behavior in brush mice. Ecology 96:1661-1669.

Wood, C. M., and S. T. McKinney. 2015. Record Long-distance Movement of a Deer Mouse, Peromyscus maniculatus, in a New England Montane Boreal Forest. Canadian Field Naturalist 129:10–11.

Table 1: Eight generalized linear mixed effects models (binomial response, logit link) fitted to the data for predicting the probability of an individual deer mouse dispersing

Model	K	AIC	ΔAIC	LogLik	AIC ω	Rank
Density and sex interaction model (DSI): ~ Local Density + Regional Density† + Sex‡ + Closest Distance¶ + Local Density:Sex + Local Density:Regional Density	9	1115.16	0	-548.57	0.582	1
Density interaction model (DI): ~ Local Density + Regional Density + Sex + Closest Distance + Local Density:Regional Density	8	1116.92	1.764	-550.46	0.241	2
Raw density model (RWD): ~ Raw Density + Sex + Closest Distance	6	1118.64	3.482	-553.32	0.102	3
Local and regional density model (LRD) ~ Local Density + Regional Density + Sex + Closest Distance	7	1119.39	4.228	-552.69	0.070	4
Regional density model (RGD): ~ Regional Density + Sex + Closest Distance	6	1125.34	10.182	-556.67	0.004	5
Local density model (LD): ~ Local Density + Sex + Closest Distance	6	1128.20	13.044	-558.10	<0.001	6
Sex model (SX): ~ Sex + Closest Distance	5	1134.55	19.397	-562.28	<0.001	7
Biological null model (BN): ~ Closest Distance	4	1140.68	25.518	-566.34	<0.001	8

K = number of parameters, AIC = Akaike Information Criterion, ΔAIC = Model's AIC - the lowest AIC of any model, LogLik = log likelihood, AICω = Aikaike Weight.
Random effects in both models were year and trapline of emigration.
* density (captures/hundred trap-nights) of deer mice on the trapline an individual is initially captured on minus the regional density in that year
† density (captures/hundred trap-nights) of deer mice averaged across all traplines in a year
‡ whether an animal is male or female, male used as reference category
¶ natural log of the distance in metres from the line of an individual's initial capture to the next most closely situated line

Table 2: Summary of the statistical results from density and sex interaction model (DSI)

Fixed	β ± SE	Z	P
Closest Distance	-1.16 ± 0.17	-7.009	<0.0001
Sex (Male)	0.38 ± 0.19	2.037	0.04
Local Density	-0.087 ± 0.025	-3.449	0.0006
Regional Density	-0.57 ± 0.15	-3.858	0.0001
Local Density : Reg. Density	0.031 ± 0.014	2.232	0.03
Local Density: Sex (male)	0.057 ± 0.029	1.195	0.05
Random	∂^2	X^2_1	**P**
Year	0.316	9.818	0.002
Initial Trapline	0.0638	1.455	0.2

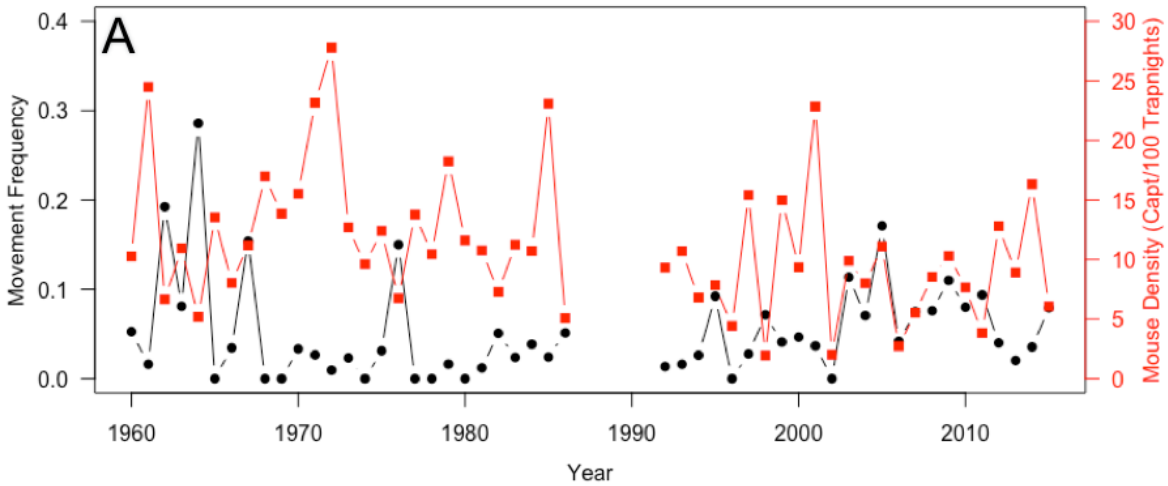
This model best fitted the observed dispersal data and had strong support based on model comparisons using AIC.
Significant effects ($P < 0.05$) are in boldface
Likelihood ratio tests were used to assess the significance of each random effect.

Figure Legends

Figure 1: Proportion of possible dispersers that in fact dispersed each year plotted alongside the density of the deer mouse (*Peromyscus maniculatus*) population in Algonquin Provincial Park Ontario Canada between 1960-2015 (A). For much of the time series density and the proportion of mice that dispersed were negatively associated. This is reflected in a negative effect of raw density on the probability of dispersing (effect size in panel B), which was measured separately for each of 32 ten-year moving windows. The magnitude of this effect of raw density on the probability of dispersing (effect size) is plotted against the midpoint of the 10-year window (B). Significant effects of raw density on the probability of dispersing are shown as triangles, whereas non-significant effects are shown as circles. Significance determined at $\alpha = 0.05$.

Figure 2: Total number of deer mice that were observed to disperse (N = 154 mice) various distances. The top panel (F) is for females while the bottom panel (M) is for males. The number of individuals that dispersed to the closest trapline is depicted by the height of the open bars, whereas those that dispersed farther than the nearest trapline are depicted by the height of the shaded bar. There was no difference in dispersal distance between the sexes ($t = 1.1$, $df = 95.73$, p-value = 0.28).

Figure 3:(A) Partial plot of the interaction between Local Density and Sex (F=Female, M = Male) from the DSI model ($\beta \pm SE = 0.057 \pm 0.029$, $Z = 1.951$, $P = 0.051$). While males are more likely to disperse, this interaction is approaching significance and suggests that female dispersal may be more sensitive to changes in local density than male dispersal. (B) Partial plot of the interaction between Regional Density and Local Density from the DSI model ($\beta \pm SE = 0.031 \pm 0.014$, $Z = 2.23$, $P = 0.026$). Regional Density is grouped by tertile. The positive interaction can be seen to make the negative density-dependent dispersal in response to local density more pronounced when regional density was low (green trend-line). When regional density was high (pink trend-line) there was no effect of local density.


A
Movement Frequency
0.4
0.3
0.2
0.1
0.0
Mouse Density (Capt/100 Trapnights)
30
25
20
15
10
5
0
1960
1970
1980
1990
2000
2010
Year

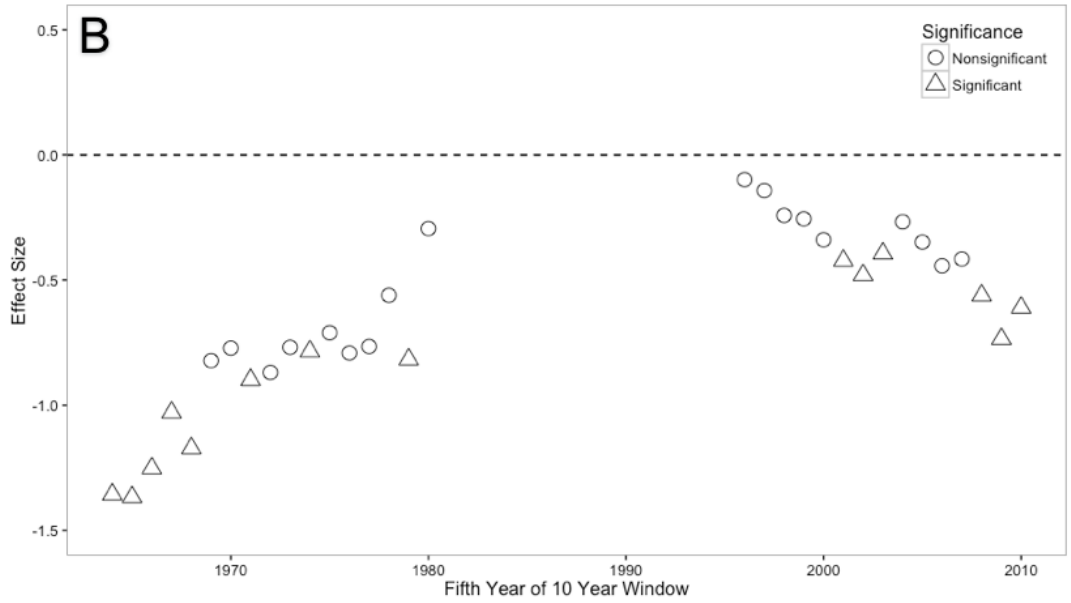

B
Significance
Nonsignificant
Significant
Effect Size
0.5
0.0
-0.5
-1.0
-1.5
1970
1980
1990
2000
2010
Fifth Year of 10 Year Window

Figure 1

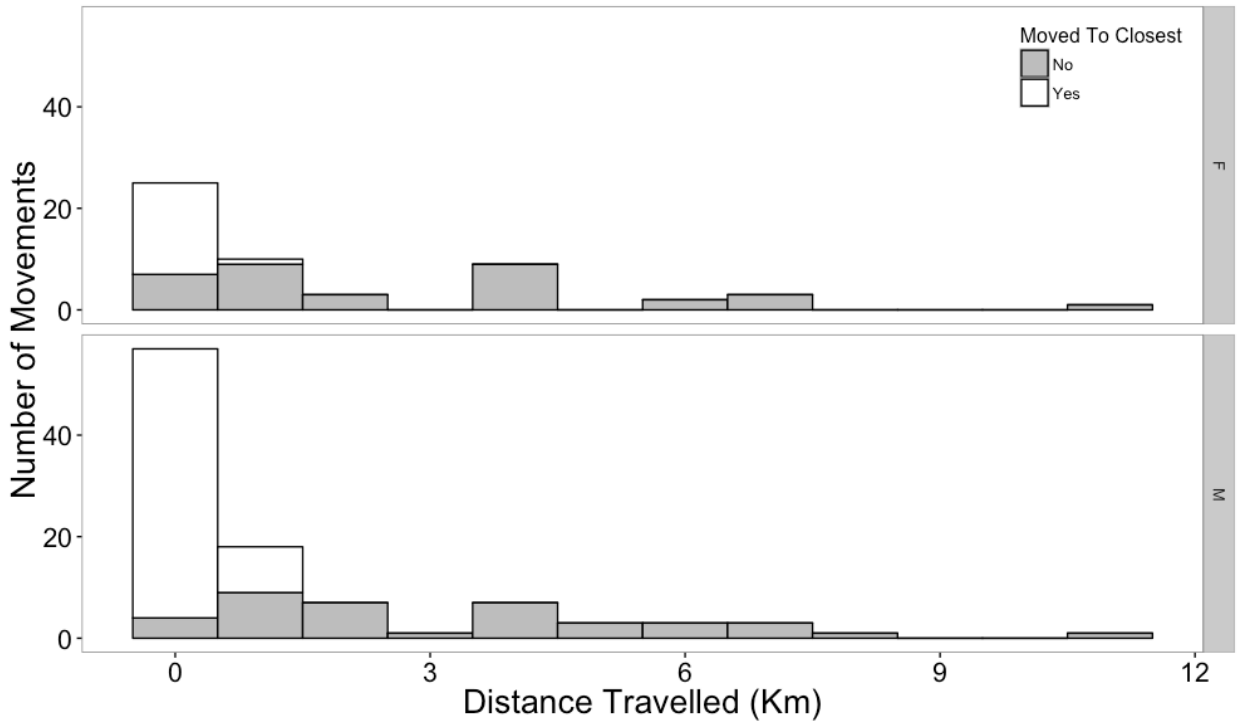

Moved To Closest
No
Yes
F
M
Number of Movements
0
20
40
0
3
6
9
12
Distance Travelled (Km)

Figure 2

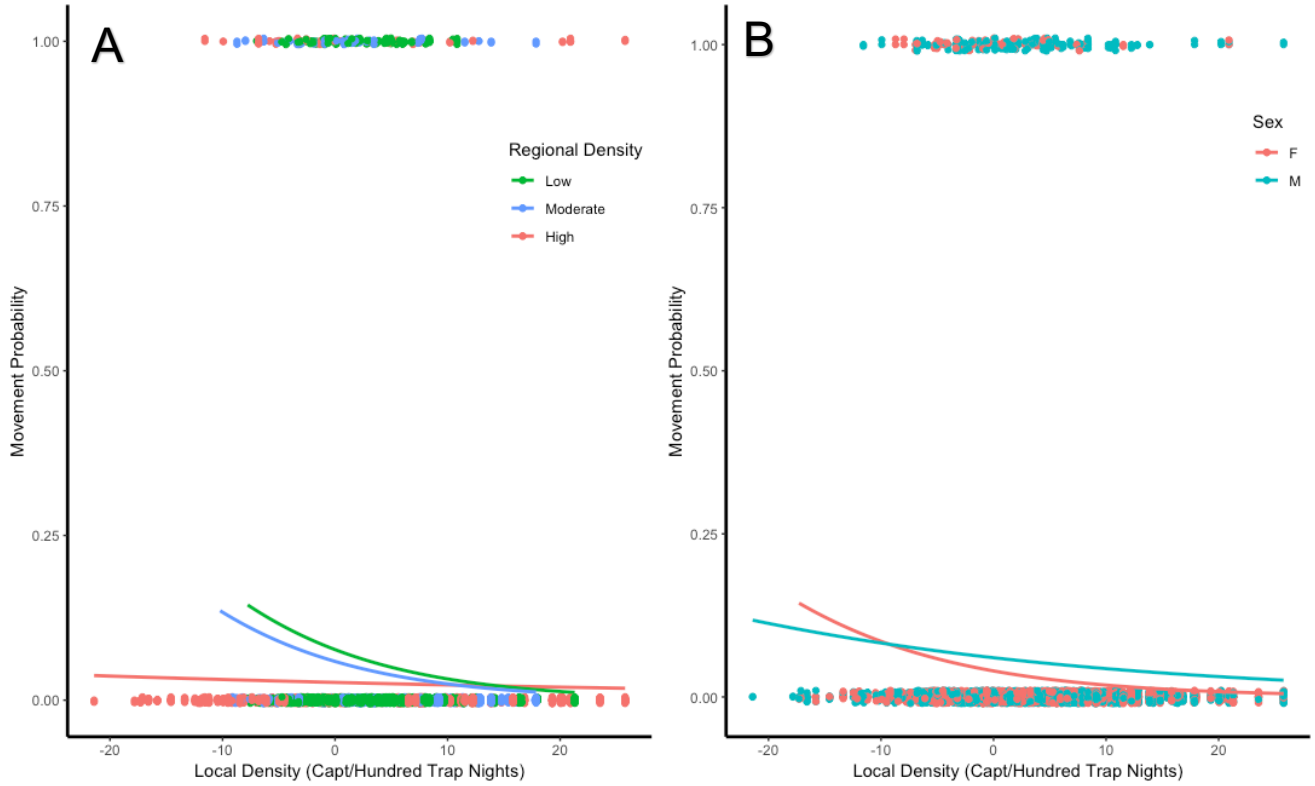

A
B
Regional Density
Low
Moderate
High
Sex
F
M
Movement Probability
1.00
0.75
0.50
0.25
0.00
-20
-10
0
10
20
Local Density (Capt/Hundred Trap Nights)

Figure 3