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

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Abstract

Dispersal is a fundamental ecological process that can be affected by population density, yet studies report contrasting effects of density on propensity to disperse. Additionally, the relationship between dispersal and density is seldom examined using densities measured at different spatial scales or over extensive time-series. We used 51-years of trapping data to examine how dispersal by wild deer mice (*Peromyscus maniculatus*) was affected by changes in both local and regional population densities. 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. 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. Additionally, the strength of negative density-dependent dispersal changed through time, ranging from very strong in some decades to absent in other periods of the study. Finally, while females were less likely to disperse, female dispersal was more density-dependent than male dispersal. Our study shows that the relationship between density and dispersal is not temporally static and that investigations of density-dependent dispersal should consider both local and regional population densities.

Introduction

Dispersal is defined as movement of an individual from a place of origin to one of reproduction or from one reproductive locale to another (Greenwood 1980), and 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.

Materials and 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 initially detected when an individual deer mouse was captured on multiple traplines within a single trapping season. 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 determine whether detected movements between traplines represented 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. Instances where an animal returned to their original line of capture following a capture on a different line were not considered to be dispersal events. These could have represented nomadic wandering between lines rather than dispersal or this could have been caused by a misread tag or data entry error. Animals last caught on their initial line of capture were therefore not considered to have dispersed (n = 136).

Movements occurring between years were not considered as few mice survive the winter in APP, and thus there were relatively few potential dispersers over this period. Movements between lines were considered to be potential dispersal events as the distance between the closest traplines (115m) was greater than the diameter of home ranges for this species typically reported in the literature (Stickel 1968; Bowers and Smith; 1979; Harestad and Bunnel 1979; Van Horne 1980; Abramson et al 2006; Wood 2010). Distances between traplines were calculated as straight-line distance between the first trap station on each line. 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 converted raw capture totals to the number of captures per hundred trap-nights per year to account for variation in trapping effort both between years and among traplines. The first

114 measurement was raw local trapline density (hereafter termed raw local density. We converted
115 these raw local densities into two types of densities for the statistical analyses that determined the
116 independent effect of regional and local density on dispersal. The first density measure was the
117 average regional trapline density, calculated annually as the mean number of captures per
118 hundred trap-nights across all traplines in APP in that year (or regional density) Second, we
119 calculated relative local density (hereafter local density) for each trapline in each year by
120 subtracting the regional density in a year from the raw local density on each line that same year.
121 This local density measure thus captures the additional effect of local densities after accounting
122 for year-to-year fluctuations in regional desntiy associated with for instance seed mast events
123 (Falls et al. 2007). This relative local density thus allowed us to include uncorrelated local
124 densities and regional density estimates within the same models (*sensu* van de Pol and Wright
125 2009).

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

137 *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 (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, 2) Sex Model, 3) Local Density Model, 4) Regional Density Model, 5) Raw Density Model (RWD), 6) Local and Regional Density Model, 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 model with raw local density as a fixed effect and *year* and *trapline* of initial capture as random effects on a shifting ten-year window through the time-series. This model was used because the RWD model was the simplest model with moderate support based on AIC comparisons and contained only raw local density and sex as fixed effects. 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, 4.2% (n = 142) dispersed between traplines. The proportion of the population that dispersed fluctuated between years ($\bar{x} \pm$ SE = 0.05 ± 0.008 mice dispersing in the population, n = 51 years), with no dispersal detected in

some years and a maximum of 28.6% 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 64.8% of dispersing mice being male ($X^2 = 7.7$, df = 1, $P < 0.01$). Overall, males were more likely to disperse (5.1%) than females (2.7%; Fisher Exact Test: $P = 0.006$).

Distances travelled by dispersing individuals ranged from 115m to 11.4 km ($\bar{x} \pm SE = 1.68 \pm 0.20$ km, n = 142) (Figure 2). There was no difference in dispersal distance between the sexes ($t = 0.98$, df = 92, p-value = 0.3) (Figure 2). Only 51.4% (n = 73) 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 16.9% (n = 24) 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 ($\bar{x} \pm SE = 11.15 \pm 0.81$ 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 ($\beta \pm SE = -1.035 \pm 0.15$, $Z = -6.85$, $P < 0.0001$), increased regional density ($\beta \pm SE = -0.63 \pm 0.16$, $Z = -3.9$, $P <$

0.0001), and increased local density ($\beta \pm SE = -0.091 \pm 0.026$, Z -3.52, P = 0.0004). The significant positive interaction between local and regional densities ($\beta \pm SE = 0.036 \pm 0.015$, Z = 2.44, P = 0.015) 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 fixed effect and while more males dispersed than females, the effect of sex on dispersal was not significant ($\beta \pm SE = 0.32 \pm 0.19$, Z = 1.69, P = 0.09) (Figure 3b). However, the interaction between local density and sex was in fact significant ($\beta \pm SE = 0.064 \pm 0.031$, Z = 2.1, P = 0.036), indicating 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). Initial *line of capture* was a significant random effect in this model (LRT, Deviance = 1042, X^2_1= 11.2, P = 0.0008) whereas *year* was not (LRT, Deviance = 1042, X^2_1 = 0.2, P = 0.65). Overall, the DSI model explained 11.77% of the deviance.

There was nearly strong support ($\Delta_i < 2$) for the DI model($\Delta_i = 2.2$) 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 10.05% 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 simplified model containing raw local density as a fixed effect and *year and trapline* of initial capture as random effects 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 13 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 at high densities, regardless of the scale at which density was measured. Proposed mechanisms for negative DDD include attraction to conspecifics (Danielson and Gaines 1987; Stamps 1991), range constriction in the face of high densities (Stickel 1960; Taitt 1981) and exclusionary behavior towards immigrants in periods of high density (i.e. "social fences"; Hestbeck 1982). Had trap saturation occurred in APP it could mimic a natural social fence, denying immigrants access to traps on densely populated lines and biasing our results towards the appearance of negative DDD. This seems unlikely, however, as densities on even the most highly populated traplines fell well short of saturation (i.e. average captures per 100 trap-nights across all lines throughout this study was 22.62 with SE = 0.42 and SD = 10.66; the highest capture rate on any line in any year was 73.81 captures per 100 trap-nights). Additionally, there was no obvious change in the direction of density-dependence after the traps per station were doubled in 1979.

While the result of negative DDD runs counter to generalizations of positive DDD in mammals (Matthysen 2005), previously reported relationships between dispersal and density in *Peromyscus* spp. are inconsistent. Positive DDD has been observed in *P. maniculatus* (Fairbairn,

1978a), *P. polionotus* (Garten and Smith 1974), and genetic estimates show *P. leucopus* is more likely to disperse from high density habitat patches (Anderson and Meikle 2010). Alternatively, there is evidence of negative DDD in both *P. maniculatus* (Rehmeier et al. 2004) and *P. boylii* (Wojan et al. 2015). The spatial and temporal breadth of our study may elucidate why studies on *Peromyscus* spp., and other dispersing organisms, often yield divergent results. For while deer mice in our study consistently exhibited negative DDD, the strength with which density affected dispersal varied temporally, spatially and between sexes.

The relationship between density and dispersal varied throughout our time-series. This variation is evident when examining the time-series of regional density and movement frequency together (Figure 1a), particularly the period from 2002-2010 which visually suggests a possible positive relationship. The effect of 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 = 19) did not exhibit significant relationships between density and dispersal. Few studies investigating DDD have used 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). In an experiment using guppies (*Poecilia reticulata*), De Bona et al. (2019) recently demonstrated that over the course of a colonization event, density-dependent dispersal can change in strength and direction. Still, our findings are the first to demonstrate that the density-dispersal relationship can vary through time in an unmanipulated system and over large time-series. This highlights the value of long-term studies for drawing accurate conclusions regarding the density-dispersal relationship, as an unfortunately

281 timed relatively long-term study (i.e. 10 years) would not detect the negative effect of density on
282 dispersal that exists in this system.

283 In addition to varying temporally, the strength with which local density affected dispersal
284 was mediated by regional densities. This interaction between the regional and local density
285 effects on dispersal indicates that the negative effect of local density on dispersal is greater in
286 years of low regional density and muted in years of high regional density (Figure 3a). This
287 suggests that local density can be an important driver of dispersal, but only when examined in
288 concert with regional density, as low local densities that increase the probability of dispersal are
289 only noteworthy in years when regional densities are also low. Local and regional densities acting
290 as interacting drivers of dispersal has been observed experimentally (De Bona et al. 2019) but
291 never before in natural, unmanipulated systems. Considering local densities within the context of
292 the accompanying regional densities is important moving forward, as many studies provide only
293 densities for localized sites of emigration (Matthysen 2005), which based on our findings may
294 lead to spurious results when not considered in the context of associated regional densities. As
295 well, the few large datasets that have been used to examine DDD fail to differentiate between
296 spatial and temporal variation in densities (Matthysen, 2005; but see Pasinelli and Walters 2002;
297 Catchpole et al. 2004) despite the fact both temporal variation and interactions between densities
298 at multiple spatial scales affect dispersal.

299 Several potential mechanisms could cause this interaction between the effects of local and
300 regional densities on dispersal. Deer mice populations in APP are closely tied to maple seed
301 crops, with mouse populations peaking after seed masting (Falls et al. 2007). *Peromyscus* spp.
302 also move based on habitat quality and population density (Morris and Diffendorfer 2004). It
303 may be that individuals select habitat and disperse to high quality, maple-rich areas when
304 possible; but in years of high regional densities, local densities in high-quality habitats rise

305 enough to prevent such immigration. This process would strike a balance between traditional
306 dispersal hypotheses predicting positive DDD due to increased competition (Greenwood 1980),
307 and ideas of conspecific attraction (Stamps 1991) and habitat selection. This balance between
308 competition and facilitation amongst conspecifics has been observed previously in blue-footed
309 booby (*Sula nebouxii*), where simultaneous positive and negative DDD results from the costs of
310 competition and the advantages of increased mating choice options (Kim et al. 2009).

311 Mate availability may also influence dispersal in APP as the strength of density-
312 dependence also differed between sexes. Males dispersed more often than females, which is
313 consistent with findings of male-biased dispersal in both *Peromyscus* spp. (Fairbairn 1978a;
314 Goundie and Vessey 1986; Rehmeier et al. 2004; Mabry 2014), and other mammals (Greenwood
315 1980; Dobson 1982; Mabry et al. 2013). However, we also found evidence that dispersal in
316 females was more sensitive to changes in local density than in males, with females dispersing
317 more frequently than males when local densities were very low. Examples of sex-biased dispersal
318 switching from male-bias to female-bias within a system are rare (but see Pérez-González and
319 Carranza 2009), but have implications for understanding how mating strategies influence
320 dispersal. The predominance of male-biased dispersal in mammals (and female-bias in birds) has
321 long been attributed to mating systems, although the simplicity of this relationship has been
322 questioned (Mabry et al. 2013). If males disperse to track females and females rely on available
323 resources for reproduction (Emlen and Oring 1977), then at exceedingly low densities the lack of
324 available mates may outweigh the benefits of familiar surroundings, resulting in increased female
325 dispersal. Alternatively, if low densities indicate low food availability, this would affect female
326 dispersal to a greater extent due to their reliance on resources for reproduction (Emlen and Oring
327 1977). Differences between male and female dispersal sensitivity to local densities mean that
328 spatial variation in density could potentially affect sex ratios, in turn affecting population density.

329 As mentioned previously, our density measures did not account for variation in capture
330 probabilities. While we described the practical reasons for not being able to utilize SECR
331 methods, we recognize that this is not ideal. However, the lack of trap saturation on any of our
332 lines throughout the study, the fact that frequency of recapture of individuals within this study ($\bar{x}$
333 $\pm$ SE = 2.63 $\pm$ 0.07) did not decrease with increased regional annual densities (linear regression; β
334 $\pm$ SE = 0.012 $\pm$ 0.01, t = 1.09, P = 0.28), and the fact that the density-dispersal relationships in
335 our models were not altered by the changes in trapping methodologies that occurred throughout
336 this study all speak to the robustness of our findings.

337 *Frequency and Distance of Dispersal*

338 Generally, deer mice dispersal occurred as often as expected based on existing literature,
339 but to greater distances. Rehmeier et al. (2004) reported that over a 10-year period 4% of deer
340 mice in a tallgrass prairie undertook long-distance dispersals (LDDs, >125m); Bowman et al.
341 (2001b) similarly reported 4.2% of deer mice demonstrating LDD (>100m) in temperate forests.
342 Based on these papers, our dispersals (>115m) can be classified as LDDs and the frequency of
343 LDD by deer mice in APP (4.2%) was remarkably similar to these frequencies reported in the
344 literature. The dispersal distances in our study exceeded previous reports for *P. maniculatus*, with
345 13% (n =20) of observed dispersals exceeding the previous reported maximum long-distance
346 movement (4287 $\pm$ 10m, in Wood and McKinney 2015). Our observed maximum dispersal
347 distance of 11.3km represents a 164% increase on that previous maximum. As well, we detected
348 more frequent movements of great distances than previous studies, with 3.1% of mice dispersing
349 over 200m compared to 1% of mice dispersing beyond 200m in previous studies (Brant 1962;
350 Groves and Keller 1986). We also observed 2.7% and 2.1% of mice dispersing beyond 300m and
351 500m respectively, while roughly 1% of populations travelled those distances in previous studies

352 (Diffendorfer et al. 1999; Rehmeier et al. 2004). This indicates that the tail of the dispersal
353 distance distribution of this species has previously been underestimated.
354 Dispersal distances tend to follow leptokurtic distributions; many individuals disperse
355 short distances with few LDDs. Understanding the rate and extent of LDDs, represented by the
356 tail of the distribution of dispersal distances, is important as they determine the spread of a
357 species in a landscape (Kot et al. 1996; Levin et al. 2003; Green and Figuerola 2005). Species
358 with "fat-tailed" dispersal distributions exhibit more rapid spread throughout landscapes (Kot et
359 al. 1996). This can influence persistence in the face of climate change (Schloss et al. 2012),
360 which small mammals in this region are already responding to (Myers et al. 2009), and the spread
361 of zoonotic diseases (Mundt et al. 2009), of which *Peromyscus* spp. are vectors (Meerburg et al.
362 2009; Gaitan and Millien 2016). These distribution tails are notoriously difficult to quantify
363 (Koenig et al. 1996), and LDD in deer mice is generally reported anecdotally or with little detail
364 (Jung et al. 2005; Wood and McKinney 2015). Our absolute frequencies of dispersal should be
365 interpreted cautiously as mark-recapture studies have limited ability to detect dispersal. The
366 majority of small mammal studies utilize trapping grids too small to detect LDDs (< 2ha, from
367 Bowman et al. 2001a), and comparisons with radio-tracking and genetic dispersal estimates show
368 that mark-recapture methods underestimate dispersal distances (Koenig et al. 1996).
369 Unfortunately, expanding trapping grids is often impractical, as increasing the maximum distance
370 across a grid exponentially increases area and monitoring effort. Our study takes an alternate
371 approach by instead using many smaller transects, reducing our ability to detect individual
372 dispersal events, but overcoming this via extensive temporal replication. Our results suggest that
373 deer mice LDDs are more common than the literature suggests, reinforcing claims that relatively
374 small-scale mark-recapture monitoring techniques fail to accurately capture LDD (Koenig et al.
375 1996).

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, by demonstrating that LDD by deer mice is not uncommon. This reinforces that dispersal distributions estimated from short-term mark recapture studies may be underestimated, which is potentially important for future conservation.

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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	1059.8	0	-520.8	0.686	1
Density interaction model (DI): ~ Local Density + Regional Density + Sex + Closest Distance + Local Density:Regional Density	8	1062.0	2.2	-523.0	0.228	2
Local and regional density model : ~ Local Density + Regional Density + Sex + Closest Distance	7	1065.3	5.5	-525.7	0.044	4
Raw density model (RWD): ~ Raw Density + Sex + Closest Distance	6	1065.6	5.7	-526.8	0.040	3
Regional density model: ~ Regional Density + Sex + Closest Distance	6	1071.4	11.6	-529.7	0.002	5
Local density model: ~ Local Density + Sex + Closest Distance	6	1074.7	14.9	-531.4	<0.001	6
Sex model: ~ Sex + Closest Distance	5	1081.0	21.2	-535.5	<0.001	7
Biological null model: ~ Closest Distance	4	1085.4	25.6	-538.7	<0.001	8

Note: 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

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

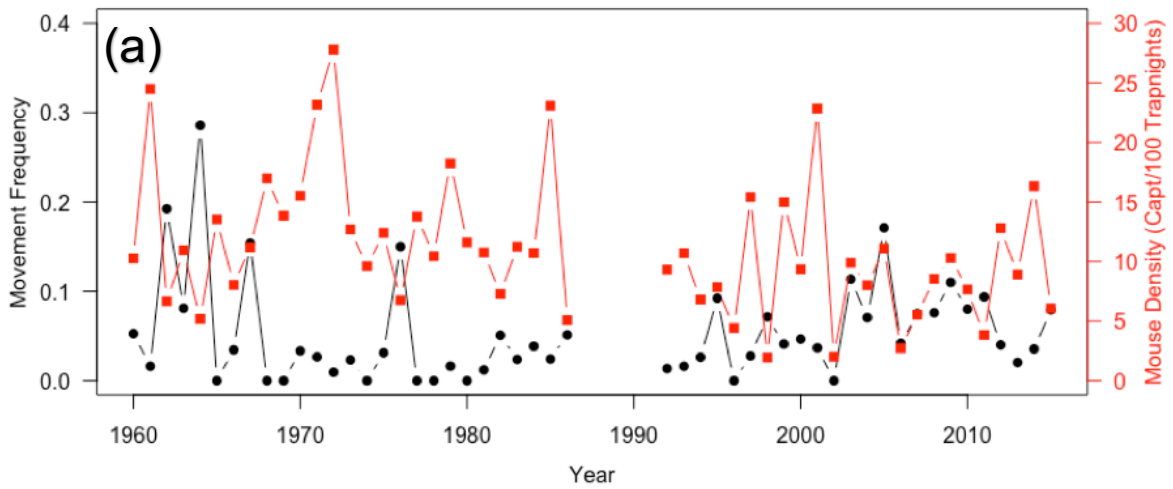
Variable – Variable Type	β ± SE	Z	∂^2	X^2	P
Closest Distance - Fixed	-1.035 ± 0.15	-6.85	-	-	<0.0001
Sex (Male) - Fixed	0.32 ± 0.19	1.69	-	-	0.09
Local Density - Fixed	-0.091 ± 0.026	-3.52	-	-	0.0004
Regional Density - Fixed	-0.63 ± 0.16	-3.98	-	-	<0.0001
Local Density : Reg. Density - Fixed	0.036 ± 0.015	2.44	-	-	0.01
Local Density : Sex (male) - Fixed	0.064 ± 0.031	2.10	-	-	0.04
Year - Random	-	-	1042	0.2	0.65
Initial Trapline – Random	-	-	1042	11.2	0.0008

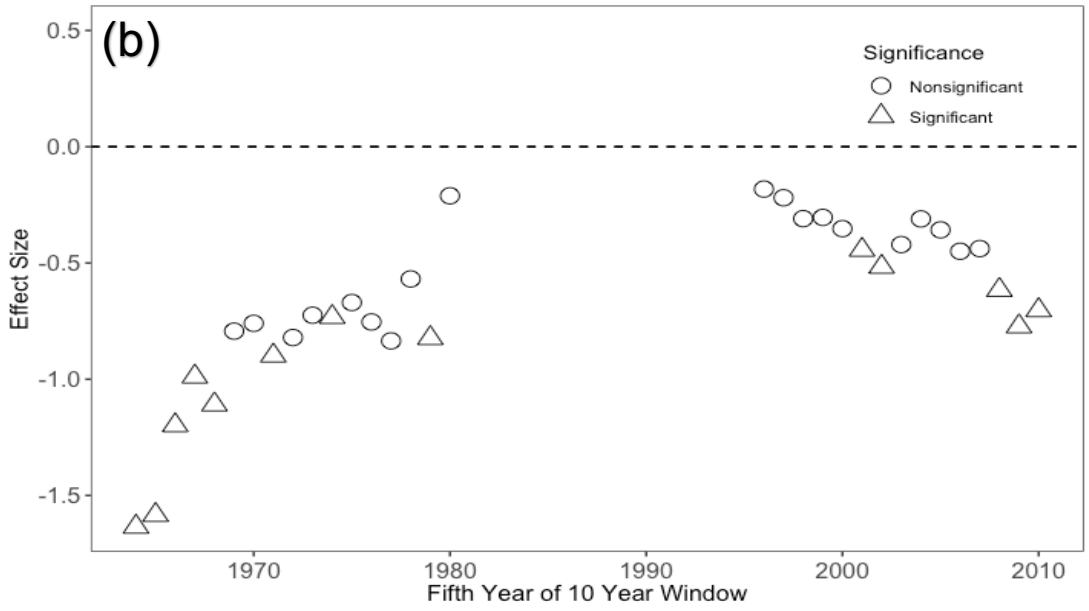
583 Note: This model best fitted the observed dispersal data and had strong support based on model comparisons using AIC.
584 Likelihood ratio tests were used to assess the significance of each random effect.

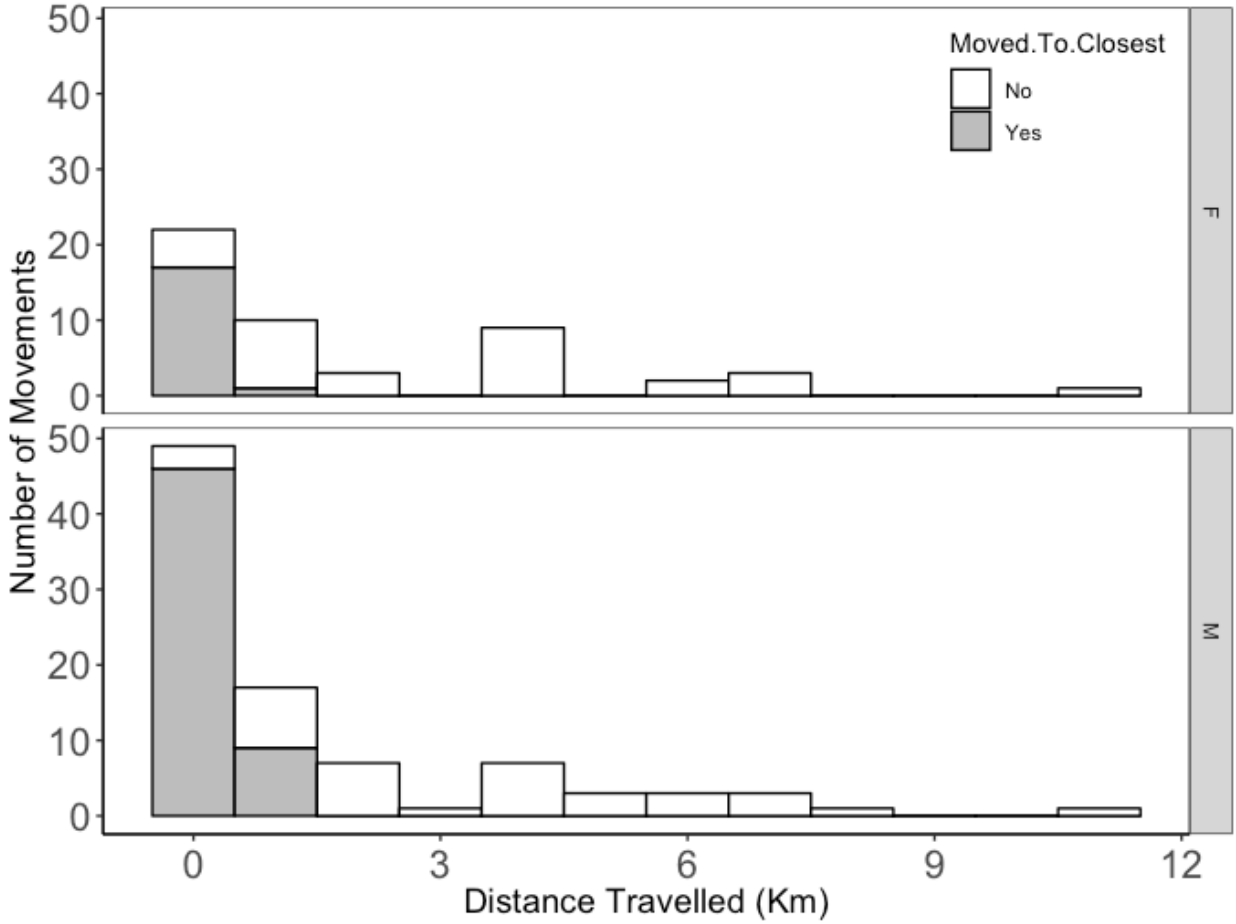
Fig 1: a) Proportion of possible dispersers that dispersed each year plotted alongside the density of the deer mouse (*Peromyscus maniculatus*) population in APP between 1960-2015. b) the effect size and significance of the relationship between raw density and dispersal probability as analyzed in 32 ten-year shifting windows using a model with raw local density as a fixed effect and *year* and *trapline* of initial capture as random effects. 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. Windows where the relationship is significant are represented with triangles and lack of significance is represented with squares. Significance determined at $\alpha = 0.05$.

Fig 2: Distances travelled by dispersing deer mice (N = 142). (F) is for females while (M) represents 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 ($t = 0.98$, $df = 92$, p-value = 0.3)

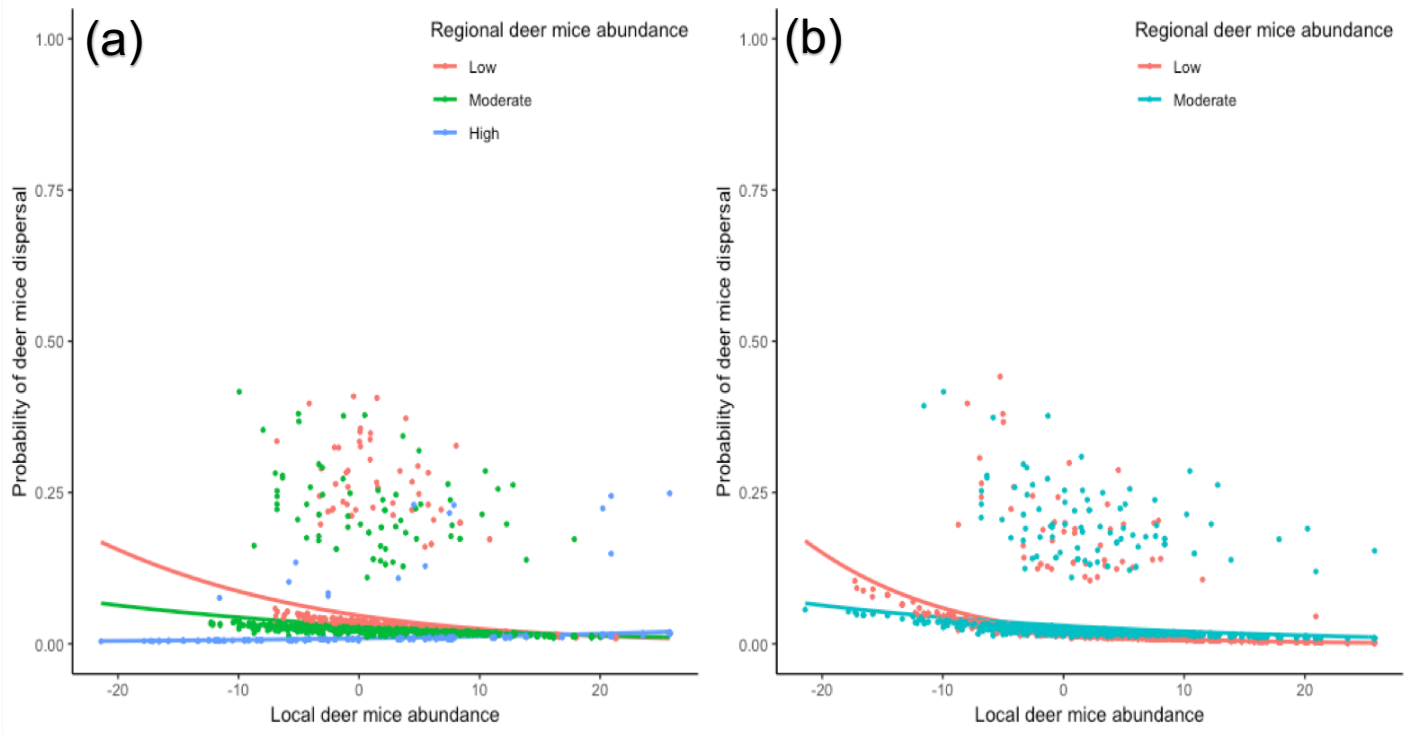
Fig 3: a) Partial plot of the interaction between Regional Density and Local Density from the DSI model ($\beta \pm SE = 0.036 \pm 0.015$, $Z = 2.44$, $P = 0.015$). Regional Density is grouped by tertile. The positive interaction can be seen to make the negative density-dependent dispersal in response 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. b) Partial plot of the interaction between Local Density and Sex (F=Female, M = Male) from the DSI model ($\beta \pm SE = 0.064 \pm 0.031$, $Z = 2.10$, $P = 0.036$). 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.


(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


Moved.To.Closest
No
Yes
F
M
Number of Movements
Distance Travelled (Km)
0
10
20
30
40
50
0
3
6
9
12

2


(a)
Regional deer mice abundance
Low
Moderate
High
Probability of deer mice dispersal
1.00
0.75
0.50
0.25
0.00
-20
-10
0
10
20
Local deer mice abundance
(b)
Regional deer mice abundance
Low
Moderate
Probability of deer mice dispersal
1.00
0.75
0.50
0.25
0.00
-20
-10
0
10
20
Local deer mice abundance

3