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Los Angeles

Estimating the Heritability of Female Dispersal
in Yellow-bellied Marmots

A thesis submitted in partial satisfaction of the requirements
for the degree Master of Science in Biology

by

Megan Nicole Edic

2022

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ABSTRACT OF THE THESIS

Estimating the Heritability of Female Dispersal in Yellow-bellied Marmots

by

Megan Nicole Edic

Master of Science in Biology

University of California, Los Angeles, 2022

Professor Daniel T. Blumstein, Chair

Natal dispersal is the permanent movement of individuals from their natal home range to a new location for reproduction. Dispersal helps maintain genetic variation and is viewed as an adaptive behavior; however, the decision rules influencing dispersal may no longer be optimal in rapidly changing environments. Climate change creates mismatches between species' life history traits, decision rules, and the environment, and this gap may be enhanced in species whose habitats are especially sensitive to rapid change. At least two processes can permit flexible responses in a changing environment: phenotypic plasticity and/or possessing sufficient additive genetic variation to permit evolution. While numerous studies investigate species' plastic responses to altered environmental conditions, the potential to evolve when faced with long-term changes is often overlooked in ecological studies of dispersal. Here, we use the quantitative genetic mixed

model, termed the ‘animal model’, to conduct a variance decomposition of female yellow-bellied marmot (*Marmota flaviventris*) natal dispersal. We found significant heritable variation in the propensity to disperse when using a 60-year data set, but our estimate was not substantially different from zero when we used a smaller 18-year data set that permitted us to account for known environmental effects that influence dispersal. Nevertheless, these findings illustrate the importance of phenotypic plasticity in dispersal decisions in this system and, overall, suggest that should yellow-bellied marmots experience a future mismatch with their environment, they have some additive genetic variation that may allow them to evolve a new optimal response.

The thesis of Megan Nicole Edic is approved.

Kirk Edward Lohmueller

Noa Pinter-Wollman

Daniel T. Blumstein, Committee Chair

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2022

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Introduction

Natal dispersal is the permanent movement of individuals from birth sites to areas of first reproduction (Howard 1960; Greenwood 1980). Dispersal is driven by the fitness costs of remaining in local environments compared to the benefits of breeding in new locations, and the decision to disperse is likely evolved from situations where dispersal has an overall benefit (Bonte et al. 2012). Importantly, dispersal decision rules have evolved, for example, males or females predominantly disperse depending on the taxon: in mammals, males are more likely to disperse, while the opposite is true of birds (Greenwood 1980; Dobson 1982).

Dispersal decisions are also often influenced by an individual's environment. In the Anthropocene increased environmental variation is further changing the timing and utility of these cues (Parmesan and Yohe 2003). Mismatches are created when strategies evolved in response to previous environmental factors are not optimal in the current environment (Ovaskainen et al. 2013; Thackeray et al. 2016). We know that climatic conditions in both high latitude and high elevation sites are changing rapidly (Post et al. 2018), which may create mismatches that lead to suboptimal dispersal decisions (Hargreaves and Eckert 2014). Considerable research examines mismatches between changing environments and life history events in plants and their pollinators (e.g., Kudo and Ida 2013) and birds and their food sources (e.g., Both and Visser 2001).

Mammals also face considerable fitness costs from mismatches (Visser and Gienapp 2019) that may make dispersal more favorable. Mismatches increase predation risks for winter adapted mammals that are seasonally molting at different rates than snowmelt, resulting in animals that are no longer optimally camouflaged with their surroundings (Mills et al. 2013; Zimova et al. 2018). For herbivorous mammals, mismatches with timing of peak food

availability can decrease reproductive success as seen in caribou (*Rangifer tarandus*) (Post and Forchhammer 2008) and roe deer (*Capreolus capreolus*) (Plard et al. 2014). Some species of hibernating rodents are experiencing mismatches with emergence date and the timing of snowmelt. Columbian ground squirrels (*Urocitellus columbianus*) are emerging later from hibernation due to later snowmelt dates, and this is negatively impacting their fitness (Lane et al. 2012). Yellow-bellied marmots (*Marmota flaviventris*), on the other hand, are emerging earlier (Inouye et al. 2000). As mismatches become more common, a species' ability to respond and adapt to changing environments will be essential. If species are not able to respond sufficiently or rapidly enough to reduce costs of mismatches, dispersal may become more favorable.

To respond to a changing environment, organisms may have either, or both, plastic and evolved responses. Prior studies focused on the plasticity of dispersal decisions and showed that it varies based on population density (McGuire et al. 1993; Moore et al. 2006), habitat quality (Lin and Batzli 2001; Matter and Roland 2002), and competition (Dobson 1982; Waser 1985). Plasticity allows animals to adjust to changes in the environment; however, without evolutionary potential these responses cannot be passed to future generations. Evolved responses require that variation among phenotypes have a genetic basis (Lynch & Walsh, 1998). While estimating the proportion of phenotypic variation that is a function of genetic differences among individuals (i.e., heritability) is alone not sufficient for an evolved response, it permits us to assess the evolutionary potential of certain traits. However, this can be difficult to measure in wild populations, where relatedness is often not known, and individuals can be hard to follow after they disperse.

Parent-offspring regressions were used in a few cases to estimate the heritability of dispersal in wild populations of great reed warblers (*Acrocephalus arundinaceus*) (Hansson et al.

2003) and collared flycatchers (*Ficedula albicollis*) (Doligez et al. 2009), and were used to study the heritability of dispersal distance in great tits (*Parus major*) (Greenwood et al. 1979). Parent-offspring regressions often do not account for confounding effects such as shared environmental conditions which may bias heritability estimates (Kruuk and Hadfield 2007). Unbiased estimates of heritability, such as those potentially estimated using a mixed model termed the ‘animal model’ (Kruuk 2004), separate genetic and environmental influences and are needed to accurately determine the evolutionary potential of dispersal decisions.

We studied the heritability of the propensity to disperse in female yellow-bellied marmots by decomposing the variance in dispersal into its genetic and environmental components, using an animal model. The animal model is a mixed model that uses both fixed and random effects and integrates the fact that individuals are genetically related using a pedigree (Kruuk 2004). The model corrects for fixed effects that explain variation in a given trait and partitions the phenotypic variance among the random effects, including additive genetic and residual variance. By using a pedigree, we can estimate the expected genetic relatedness matrix, which includes the relatedness of all pairwise combinations of individuals in a population, not just parent-offspring and sibling-sibling pairs (Kruuk 2004). Because individuals in the population share genes and are not independent, individual identity associated with a pedigree is given as a random effect. The additive genetic variation, or the variation in the genetic effect of the phenotype for each individual relative to the mean phenotype, can then be estimated (Wilson et al. 2010). The animal model can explore complex relationships in wild populations and estimate the relative effect size of many variables that influence phenotypes while also accounting for common environment. Thus, variance decomposition analyses using the animal model are ideal to identify and separate factors that influence dispersal and to estimate any additive genetic variation.

Yellow-bellied marmots are an ideal species to decompose variance components of dispersal because approximately half of females disperse (Armitage and Downhower 1974) creating a substantial amount of variation to investigate. Additionally, since 1962, yellow-bellied marmots located in the Upper East River Valley, near Gothic, Colorado, USA have been under intensive study. Summer survival and dispersal can be estimated and since 2003, we have collected detailed environmental and social variables that have been known to influence dispersal decisions (Brody and Armitage 1985; Blumstein et al. 2009; Armitage et al. 2011). This analysis differs from these previous studies of dispersal because we not only investigated known social, environmental, and body condition factors that may explain dispersal, but we also estimated the heritability of dispersal and studied maternal and paternal presence effects. In addition, we have a comprehensive molecular genealogy that dates back to 2001 and was used to identify genetic variation in the propensity to be bullied (Lea et al. 2010), allocate time to antipredator vigilance (Blumstein et al. 2010), explain variation in alarm call structure (Blumstein et al. 2013) and, finally, to explain variation in the emergence date from hibernation (Edic et al. 2020).

We fitted three animal models to estimate the heritability in dispersal and environmental influences of dispersal. Based on previous results, showing that individuals interacting more had a lower probability of dispersing (Blumstein et al., 2009; Armitage, 2012; Armitage et al., 2011), we expected to find that sociality, and specifically, a female's social embeddedness – the degree to which an individual is integrated in their group (Moody and White 2003) – would explain a significant amount of variation in the propensity to disperse as a yearling. While there is a cost of inbreeding (Olson et al. 2012), we did not expect paternal presence to influence dispersal decisions, because mother-daughter relationships have a greater impact on who is

recruited into a matriline (Armitage 2014). Additionally, body condition may influence both the benefits and costs of dispersal and therefore could influence dispersal decisions.

Materials and Methods

Study Species and Site

Data were collected on a population of yellow-bellied marmots in and around the Rocky Mountain Biological Laboratory (RMBL) located in Gothic, Colorado. We studied marmots living in colonies distributed along a 5 km latitudinal gradient between 2700 and 3100 m.a.s.l. that divides the population into two valley positions, up valley and down valley. Marmots were regularly trapped by placing Tomahawk-live traps near known burrow entrances, and upon capture, transferred to cloth handling bags to be sexed, weighed, and checked for reproductive status. We collected hair samples for genetic assignment of maternity and paternity (Blumstein et al. 2010). Each marmot was assigned a unique ear tag number for both ears and a unique dorsal pelage marking using Nyanzol fur dye that permitted identification from afar, which we used to determine residency and to observe social interactions (described below). Since 2003, most marmot colonies were observed most of the days of the week, and we used a combination of observations and trapping to follow marmots through their summer active season. Virtually all individuals were trapped for the first time as pups or yearlings and therefore most individual's ages were known precisely. For individuals with unknown birth years, body mass was used to assign individuals to an age class (Ozgul et al. 2010).

Natal Dispersal

We defined natal dispersal as those yearlings who were last observed or trapped within our study site before 1 August (day of year = 213) and not seen the following spring. Most yearlings disappear within 10 days of the colony's first pup emergence date (Armitage 1991) however, this

date can vary by colony location and year, and we used 1 August as the cutoff because pups at all colony locations would have emerged by this time. While most dispersal resulted in individuals leaving our study sites, some dispersal occurred between colonies, and we added animals that were observed or trapped when they were two years old in a colony location other than their birth colony. We excluded individuals from our analysis that had observed deaths or were seen after a prolonged absence because we could not be certain if absences were a dispersal event or not. Thus, we inferred dispersal when marmots were not seen in late summer and there was no evidence of death. Dispersing female yearlings have relatively high annual survival rates (0.73) compared to resident female yearlings (0.87) (van Vuren and Armitage 1994). However, we recognize that some individuals might have died undetected.

Some individuals were born outside our study site, had unknown parents, and appeared at a known colony location as adults (≥ 2 years old). We classified these immigrants as dispersers and their inclusion expanded the number of dispersers for quantifying heritability and permitted us to track their descendants' dispersal decisions.

Our data spanned six decades and some of this time interval did not have consistent observational data, so we limited dispersal events to seven colony locations that were consistently observed. These colonies included five down valley sites: Avalanche, Bench, Gothic townsite, Horse Mound, River, and two up valley sites: Marmot Meadow and Picnic. Avalanche and Horse Mound were intermittently occupied; the rest of the sites were continuously occupied since the study began.

DNA Extraction and Parentage Assignment

We created a pedigree of all individuals in our data set and their parents to calculate the additive genetic variance. Constructing the pedigree for our study began by determining parents of each

individual using DNA samples collected from 2001 to 2020. DNA was extracted from hair samples and known microsatellite sequences were amplified by PCR using a QIAamp Mini Kit (Qiagen Inc., Valence, CA, USA). Microsatellite sequences were genotyped and used to match parent and offspring at 12 loci. Following Blumstein et al. (2010), we used GENEMAPPER software to determine allele frequencies for each individual and assigned parentage using CERVUS 3.0 (Kalinowski et al. 2007) to calculate the likelihood of each mother and father to a given offspring. CERVUS conducts a parentage simulation and compares critical values to likelihood scores while considering sampling proportion of parents, loci mistyped, and relatedness values (Olson et al. 2012). Parents were determined for an offspring simultaneously at a 95% confidence level for the trio. Since females form matriline and typically remain in birth colonies, candidate mothers were all adult females for a given colony who showed signs of pregnancy. Candidate fathers were determined more broadly because males may breed in nearby colonies. Males were grouped by valley position and matched with offspring based on colony location. We assumed a sampling proportion of 99% for mothers and 96% for fathers in CERVUS, as most females are trapped and known in each colony and males move between areas. Females are typically highly related, so for each year we estimated the average relatedness among females in the population and provided it as an extra parameter in CERVUS. In addition to identifying parents, the entire pedigree was used in subsequent analyses.

Social Embeddedness

The degree to which a female yearling is socially connected to her groupmates explains significant variation in her propensity to disperse (Armitage et al., 2011; Blumstein et al., 2009). Female yearlings who are more interactive and socially embedded within their colonies are less likely to disperse (Blumstein et al. 2009). Conversely, almost all yearling males disperse after

their first winter, due to agonistic interactions with adult males (Armitage and Downhower 1974). To account for the proportion of phenotypic variation that contributed to an individual's connectedness, we calculated social embeddedness – a social network measure that quantifies how connected to the group an individual is and is based on the number of independent links to others in the group (Moody and White 2003) – for each yearling based on social networks built from detailed social observations.

At each colony location, marmots shared burrows and space with a subset of all possible individuals at that colony. Therefore, we defined social groups based on space-use overlap (two individuals seen or trapped at the same location and time, or observed using the same burrow, within a one-day interval). To do so, we determined simple-ratio pairwise association indices (Cairns and Schwager 1987) using SOCPROG (Whitehead 2009) for yearlings and adults annually. Association indices were based on the space-use overlap and the proportion of time a pair of individuals were seen together. From these indices, we used the random walk algorithm Map Equation (Csardi and Nepusz 2006; Rosvall and Bergstrom 2008; Rosvall et al. 2009) to identify social group membership. This algorithm assigns each individual to only one social group. However, as social interactions with adult males may play a large role in how embedded an individual is in their group and because adult males often mate with females from multiple matriline, we added adult males to each group for which they had at least one social interaction with a member of that group. This addition enabled more accurate embeddedness measures for potential dispersing individuals to be calculated as we maintained all dispersing individual's social ties with adult males.

From these group assignments we constructed undirected and unweighted social networks based on affiliative interactions (e.g., greeting, allogrooming, play) using the R

package, version 4.1.2, “igraph”, version 1.2.11 (Csardi and Nepusz 2006; R Development Core Team 2021). Social interactions were recorded during hours of peak activity over the entire active season from distances that limited the observer effect and then classified using a detailed ethogram described in Blumstein et al. (2009). We focused on affiliative interactions because they relate to marmot dispersal (Blumstein et al. 2009) and because they comprised 88% of social interactions. Networks consisted of yearling and adult females and males. Pups were not included in the social networks as approximately half of them die their first winter (Armitage and Downhower 1974), they emerge mid-season, and primarily only interact with each other and their mother. Social networks were constructed from 34,189 social interactions between 678 unique individuals. This produced 209 social groups from 2003-2020, when social networks were constructed.

From these social networks, we calculated embeddedness following Blumstein et al. (2009), which used the calculations developed by Moody and White (2003). Briefly, an individual’s social embeddedness is the largest k-component to which it belongs. A k-component is a maximal subset of individuals (nodes) in which all social connections (paths) are mutually reachable by at least k node-independent paths using only nodes in the subset. Paths are node-independent if the paths share no nodes. Maximal means that no other node can be added to the set while ensuring that all members still be k connected. Thus, the larger the embeddedness value, the more integrated into the group the individual is. Embeddedness values are an integer ≥ 1 . However, some marmots do not have an embeddedness value as they are not a member of a social group yet, and thus should not be excluded from our dispersal analysis since less embedded marmots are more likely to disperse (Blumstein et al. 2009). Therefore, these individuals were assigned an embeddedness value of zero to represent their lack of group

membership, as an individual who is a member of a social group cannot have an embeddedness value of zero. This allows for these isolated and potentially more likely to disperse individuals to still be included in our analysis.

Statistical Analysis

To extend our data set and accurately estimate heritability of dispersal, we fitted three different animal models. First, to maximize the model's full potential to estimate additive genetic variation we fitted a model of all available data on dispersal including yearlings from 2001-2020 and data on immigration for adult females. We did not include all adult females pre-2001, but only the ones that were ancestors to yearlings observed between 2001-2020 to maximize pedigree information. We did not include fixed effects or common environmental effects in this model because many of the individuals from before 2001 did not have good observational data. Additionally, we wanted to include as many immigrants as possible to expand the model's power to estimate genetic variation despite not having data on immigrants as yearlings. We included colony as a random effect to account for micro-environmental effects affecting dispersal decisions. With the exception of one detailed multi-year study (van Vuren and Armitage 1994), we have not followed yearlings who leave our study site, and thus only know the colony yearlings dispersed from but not the colony where they settled in, apart from the few that dispersed within our population (<10%). Immigrants, on the other hand, dispersed from outside our study area, so we do not have information on where they dispersed from and only observed where they settled. We therefore used the colony location immigrants settled in and used the colony individuals dispersed from for all yearlings as the colony effect. This was to not overestimate the amount of variation in dispersal contributing to colony effect by grouping immigrants together in their own colony. In other words, we did not distinguish between

dispersers and immigrants in the model and therefore assume that the effect of colony location is similar between dispersal and immigration. We included additive genetic (individual identity linked to the pedigree) and year of dispersal as additional random effects in the model. Year of dispersal was estimated for each immigrant as the year an individual was a yearling and quantified as the year before they arrived in one of our colony locations, since all immigrants are first seen as adults and estimated to be 2 years old. This data set consisted of 388 females with a dispersal rate of approximately 41% including yearlings and adult dispersers (138 dispersed as yearlings and 22 immigrated as adults).

Second, to eliminate any potential biases of not knowing the colony immigrants dispersed from or yearlings dispersed to and to fully estimate any potential genetic variation in dispersal, we fitted a similar model but without the colony effect. However, we acknowledge that additive genetic estimates without controlling for confounding environmental effects could be overestimated.

Third, to account for environmental effects that influence dispersal, we fitted a model of only yearlings after 2003, since this is when detailed social and environmental observations at our study location began, and included fixed effects known to influence dispersal. We used June mass as a condition of individual fitness and local conditions (Maldonado-Chaparro et al. 2015), which could be a proximate correlate of dispersal (Bonte and de La Peña 2009). June 1st mass for each individual was estimated as a BLUP using a linear mixed effect model with a restricted maximum likelihood method (see Maldonado-Chaparro et al. 2015 for more details). Social embeddedness (described above) was used to account for social variation that may drive dispersal. Parents' presences were quantified based on if the mother or father was seen or trapped that summer and was used to control for maternal and paternal effect. Mother's reproductive

status was quantified as weaned or did not wean a litter that summer. Fixed effects included 1 June mass, social embeddedness, dam presence, sire presence, dam's reproductive status, and valley position. We fitted additive genetic, year of dispersal, colony individual dispersed from, and litter effect as random effects in our model. Litter effect, which we coded as year and mother's ID, was used to control for common environmental effect. Colony was defined as the location where dispersers left, or where philopatric individuals were as yearlings. This data set consisted of 265 yearling females with a dispersal rate of approximately 30% (80 dispersers).

Models were fitted using R version 4.1.2 (R Development Core Team 2021) and the package MCMCglmm (Hadfield 2010). Given that dispersal is a binary trait of dispersed (1) or did not disperse (0), we fitted an animal model with a binomial distribution. Following de Villemereuil (2021) we used expanded priors with a chi-square distribution for random effects. These priors are better suited for estimates of heritability in binary traits because they allow for a more equal spread between 0 and 1 for the prior distribution of the heritability. We used the suggested priors ($V = 1$, $\nu = 1000$, $\alpha \cdot \mu = 0$, $\alpha \cdot V = 1$) for all random effects. Because the residual variance can't be accurately measured with a binary trait, we fixed it at 1 (de Villemereuil 2021). Models ran for 510,000 iterations with a 10,000 burn-in period, thinning interval of 500, and sample size of 1000 so that the autocorrelation for each parameter was below 0.05. We performed a Heidelberg stationary test to check for convergence (Heidelberger and Welch 1981) that passed all random effects and had p-values > 0.05 , supporting our model had converged. Effects were considered significant when their highest posterior density intervals (HDPI) did not include zero and the variation was substantially different from zero. We reported outputs as a posterior mode with the lower and upper 95% HDPI. Our models were fitted with a threshold family that put the liability and latent scale at the same level and allowed us to

calculate heritability on the liability scale as the proportion of the phenotypic variation (V_p) due to additive genetic variation (V_a), or V_a/V_p .

Results

The first model that included yearlings and immigrants, revealed substantial additive genetic variation ($V_a = 0.754$, 95% HDPI 0.000 – 3.763) and non-zero heritability ($h^2 = 0.421$ 95% HDPI 0.038 – 0.784, Fig. 1) in dispersal (Table 1). Neither colony nor year explained variation in dispersal.

The second model without a colony effect resulted in a higher heritability estimate with a smaller interval ($h^2 = 0.636$ 95% HDPI 0.362 – 0.887, Table 1). However, because we did not control for any confounding effects in this model, the heritability was potentially overestimated.

Our third model showed that social embeddedness was a significant predictor of dispersal (Table 1), with less embedded individuals more likely to disperse (Fig. 2), as supported by previous studies (Blumstein et al., 2009). The other fixed effects, 1 June mass, dam presence, sire presence, valley position, and dam reproductive status were all nonsignificant and did not affect dispersal likelihood. We found that litter effect explained 29% of the variation in dispersal ($litter^2 = 0.294$ 95% HDPI 0.000 – 0.519, Table 1) but year and colony had no significant influence. We found low levels of additive genetic variance in dispersal in this smaller analysis ($V_a = 0.059$, HDPI 0.000 – 9.370 Table 1). However, the posterior mode density plot for the heritability estimate showed a bimodal peak (Fig. 1) suggesting that the data does reflect genetic variation in dispersal but with little power. The first and smaller peak represents a combination of small effect, and priors with a higher weight close to zero, whereas the second peak is only driven by the data.

Discussion

By decomposing the variation in natal dispersal of yellow-bellied marmots, we were able to estimate non-zero heritability and determine drivers of dispersal. This finding suggests that offspring of dispersers are more likely to leave their birth areas than offspring born to philopatric females, but that female yearlings also respond to environmental cues that may influence the costs and benefits of remaining in natal areas. However, we also found that to calculate the heritability of dispersal in free-living yellow-bellied marmots and to account for environmental effects, a large data set is required.

Our 60-year data set had several limitations that prevented us from including potentially important fixed effects to accurately account for all environmental variation. Additionally, because we did not follow dispersers once they left our study site, and because 90% of yearling females who disperse leave our study site, we were limited in the power we had to estimate genetic variation. Our novel solution to this problem was to include the dispersal status of ancestors by saying that immigrants were also dispersers. This approach increased our model's power to estimate genetic variation but created two new problems. First, we were not certain of the location from which immigrants dispersed from which prevented us from comprehensively estimating the colony effect. Second, parents of immigrants were unknown and thus, for these individuals, we could not account for maternal and paternal effect.

Nonetheless, and despite these potential shortcomings, we found that there was non-zero genetic variation in dispersal when using the large data sets that included yearling ancestors. As we restricted this data set and controlled for maternal, paternal, and common environment effects, the heritability estimate decreased. Yet, there was an unresolvable issue with this analysis; the posterior mode density plot for heritability had a bimodal peak with a large portion

of the posteriors sampling around 0.4 (Fig. 1). The second peak with an estimate of 0.4 was similar to heritability estimates in our other models. We believe this reflects lack of power for the model with the restricted data set and fixed effects. The priors we used for the heritability estimate allowed for a more even spread between 0 and 1 in the heritability estimate but still with a higher probability close to zero. In absence of genetic variation, we would expect to obtain a highly skewed posterior distribution with only one peak at zero. The second peak was thus driven by the data, but without a signal strong enough to avoid small effects and prior influence. As expected, we found that social embeddedness was an important driver of dispersal (Fig. 2) and that there is phenotypic plasticity in the decision to disperse. Female yearlings that were more socially connected with marmots they shared space with, were less likely to leave. This supports previous findings (Blumstein et al. 2009) and shows that social interactions greatly influence which female yearlings are recruited into the matriline and which ultimately leave.

Other studies show that maternal effect greatly influences dispersal decisions (Armitage et al. 2011), where mother's presence and the greater number of interactions with the mother make individuals less likely to disperse. However, our results showed that mother's presence and mother's reproductive status had no significant effect on dispersal. This could be explained because the last analysis on dispersal in yellow-bellied marmots was conducted over a decade ago when the population was much larger. Our data set incorporated this timeframe but also included data much more recent, including a time when the population was reduced by half and mother's influence may not be as prevalent as it once was or at decreased population densities. Paternal presence and body mass did not have a significant affect on female yearling dispersal, consistent with past studies (Armitage et al. 2011), suggesting that inbreeding avoidance is not a

driver of dispersal and that larger individuals do not necessarily fare better in unknown environments.

For female yearlings, the cost of dispersal versus the cost of remaining in natal matriline, may be similar. Females that disperse do not join existing matrilines and must establish new ones, a potentially costly process, and face predation while in transit and unknown conditions. However, females that are recruited to matrilines and remain in our study site are often reproductively suppressed (Armitage 1991), may experience similar levels of predation to that outside of our study site (van Vuren and Armitage 1994), and are facing earlier snowmelt each spring (Inouye et al. 2000). Yellow-bellied marmots at Gothic, Colorado are already responding to changing conditions by emerging from hibernation earlier than they did in the 1980's (Inouye et al. 2000), and these changes have increased summer survival yet decreased winter survival (Cordes et al. 2020). With winter survival on the decline due to dryer and longer summers, dispersal to more favorable environments could become a key component of this population's survival.

Dispersal is an important mechanism that maintains a population's genetic diversity and influences the ability to adapt to changing conditions and the rate of this adaption (Bohonak 1999). Understanding the drivers of dispersal is critical in predicting how species will respond to and persist in the face of climate change (Cote et al. 2010). Together our results show that marmot dispersal is, like many traits, explained by some degree of plasticity as well as some degree of heritability. Thus, marmots at our site seem to have the ability to respond to environmental changes if needed and adapt to climate change if mismatches arise and/or fitness costs increase.

Figures & Tables

	Model 1			Model 2			Model 3		
	95% HDP intervals			95% HDP intervals			95% HDP intervals		
	Estimate	Lower	Upper	Estimate	Lower	Upper	Estimate	Lower	Upper
Fixed effects									
Intercept	0.014	-0.416	0.568	0.590	0.022	1.401	0.250	-2.579	3.648
1 June mass							0.000	-0.001	0.002
Dam presence							-0.745	-3.197	0.071
Sire presence							-0.262	-1.810	0.596
Social embeddedness							-0.242	-0.554	-0.051
Valley [up]							0.190	-1.361	3.024
Dam reproductive status [wean]							0.765	-0.399	1.977
Variance components									
V_a	0.754	0.000	3.763	1.326	0.240	6.733	0.059	0.000	9.370
V_{colony}	0.001	0.000	0.316				0.012	0.000	1.101
V_{year}	0.003	0.000	0.243	0.004	0.000	0.422	0.009	0.000	2.012
V_{litter}							0.690	0.000	4.776
V_R	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
V_P	1.472	1.017	5.076	2.378	1.246	7.911	3.481	1.471	15.564
Conditioned variance ratio									
h^2	0.421	0.038	0.784	0.636	0.362	0.887	0.002	0.000	0.702
$colony^2$	0.000	0.000	0.122				0.001	0.000	0.158
$year^2$	0.001	0.000	0.093	0.001	0.000	0.103	0.002	0.000	0.223
$litter^2$							0.294	0.000	0.519

Table 1. Variance estimates using three fitted animal models for yellow-bellied marmot dispersal. Model 1 and Model 2 included female yearlings from 2001-2020, their female ancestors pre-2001 and several random effects. Model 3 included only female yearlings from 2003-2020 and all fixed and random effects. V_a , V_{colony} , V_{year} and V_{litter} are the additive genetic, colony yearlings dispersed from (and immigrants dispersed to if applicable), year of dispersal, and litter variance respectively. V_R is the residual variance fixed at 1 for a binary trait. V_P is the total phenotypic variance in the model. h^2 is the heritability, estimated as V_a/V_P . Results that substantially differ from zero or do not include zero in the 95% highest posterior density intervals (HDPI) are in bold.

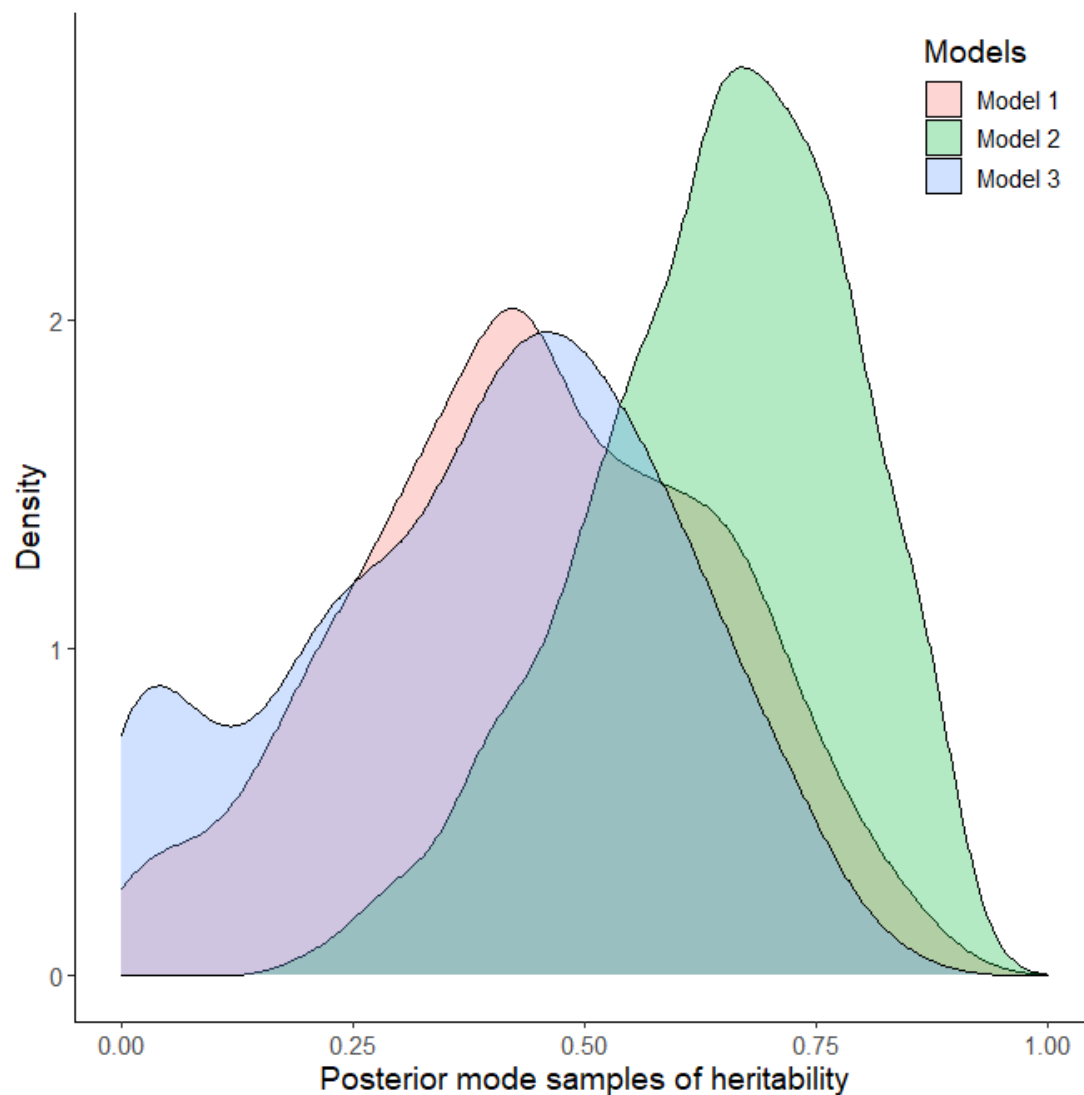


Figure 1. Posterior mode density plot of the heritability estimates for three fitted animal models. Model 1 included female yearlings from 2001-2020 and their female ancestors when colony was a combined effect, and no fixed effects were included. Model 2 included the same data but without colony effect. Model 3 included only yearlings from 2003-2020 and all fixed and random effects. Each model had a sample size of 1000.

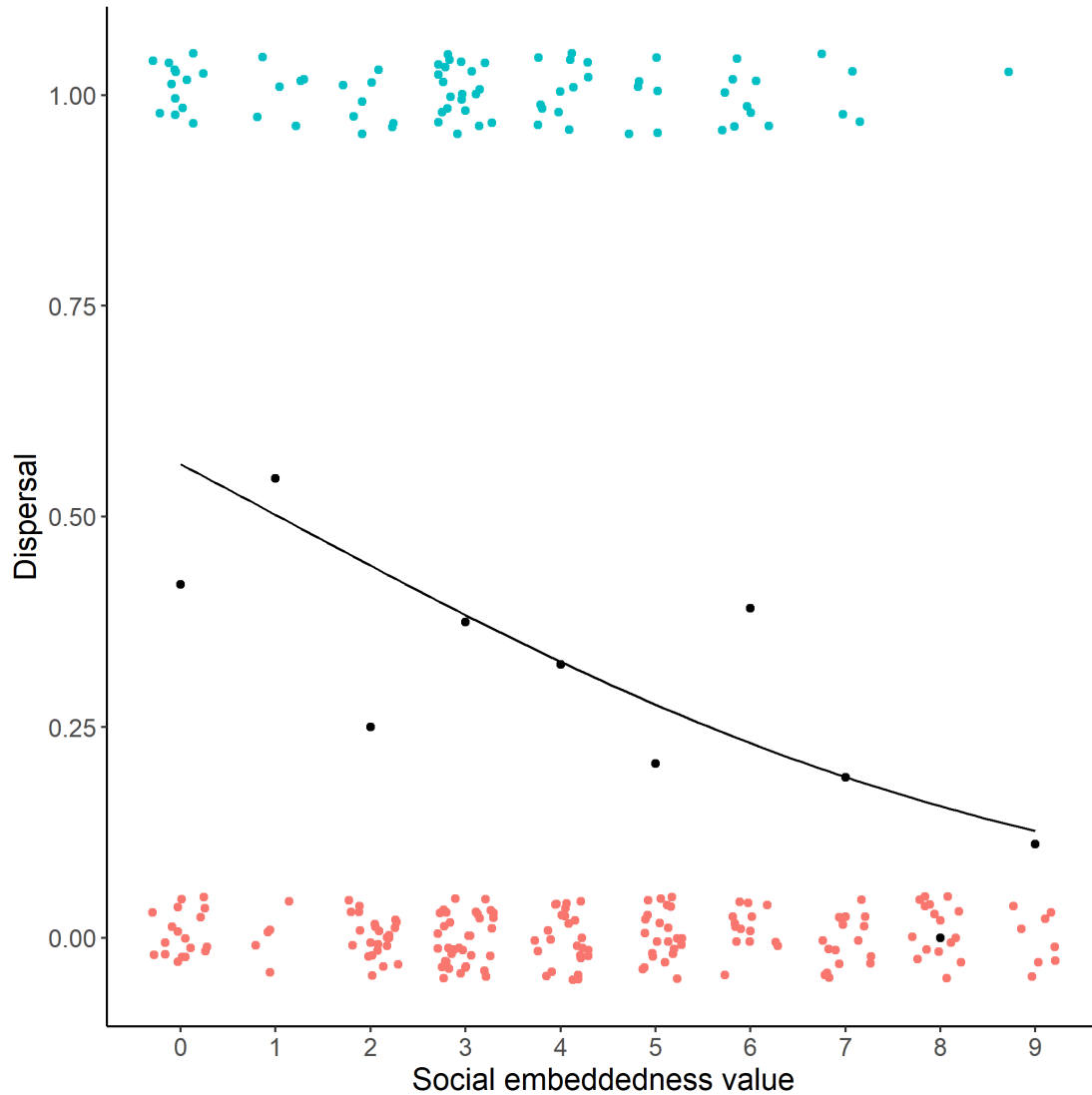


Figure 2. Relationship between dispersal and social embeddedness for female yearlings from 2003-2020. Colored datapoints represent number of dispersing (blue) and non-dispersing (red) individuals for each social embeddedness value. Higher social embeddedness values indicate an individual is more embedded in their social group. A social embeddedness value of 0 was assigned to individuals who did not have a social group. Black datapoints show the ratios of dispersed individuals versus all individuals for each social embeddedness value and the black line indicates the relationship predicted by the model.

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