

## ABSTRACT

Title of Dissertation:                   QUANTITATIVE CHALLENGES IN  
  ECOLOGY: COMPETITION, MIGRATION,  
  AND SOCIAL LEARNING

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The field of ecology has long benefitted from the application of quantitative techniques and models borrowed from other disciplines. There is a distinct need for the use of statistical and mathematical tools to address current, complex population- and species-level ecological questions. This dissertation aims to apply current mathematical and statistical approaches to answer questions regarding population dynamics, migratory behavior, and social learning. Chapter one focuses on the density-dependence of fish reproduction. I present a hierarchical model that leverages data from hundreds of populations to find statistically meaningful parameters at higher taxonomic levels. I find that reproductive density-dependence is tightly clustered within taxonomic groupings, indicating a clear evolutionary history in these population dynamics. In the second chapter, I develop a probabilistic model to look at how migratory knowledge is spread between individuals that migrate in small groups. I focus on small populations at risk of losing migratory behavior in order to ask what aspects of learning behavior, population

dynamics, and grouping structure are most important to retaining a migratory culture.

My findings highlight the importance of informed leaders, rare, large groups, and regular mixing of group composition towards the preservation of migratory behavior in small populations. In the final chapter, I use reaction-diffusion equations to look at the success of animal movement behaviors on landscapes where resources vary in space and time, and the role that memory plays in this system. I find that, while advective behaviors successfully maintain migratory movement on many landscapes, the addition of memory allows for greater populations when resources become especially scarce. This is even more effective when both behaviors are allowed to work in concert.

QUANTITATIVE CHALLENGES IN ECOLOGY:  
COMPETITION, MIGRATION, AND SOCIAL LEARNING

by

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## **Dedication**

For my mother, Linda

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## **Chapter 1:** Hierarchical analysis of taxonomic variation in intraspecific competition across fish species

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### **Abstract**

The nature and intensity of intraspecific competition can vary greatly among taxa, yet similarities in these interactions can lead to similar population dynamics among related organisms. Variation along the spectrum of intraspecific competition, with contest and scramble competition as endpoints, leads to vastly different responses to population density. Here we investigated the diversity of intraspecific competition among fish species, predicting that functional forms of density-dependent reproduction would be conserved in related taxa. Using a hierarchical model that links stock-recruitment parameters among populations, species, and orders, we found that the strength of overcompensation, and therefore the type of intraspecific competition, is tightly clustered within taxonomic groupings, as species within an order share similar degrees of compensation. Specifically, species within the orders Salmoniformes and Pleuronectiformes exhibited density-dependence indicative of scramble competition (overcompensation) while the orders Clupeiformes, Gadiformes, Perciformes, and Scorpaeniformes exhibited dynamics consistent with contest competition (compensation). Maximum potential recruitment also varied among orders, but with less clustering across species. We also tested whether stock-recruitment parameters correlated with maximum body length among species, but found no strong relationship. Our results suggest that much of the variation in the form of density-dependent reproduction among fish species

may be predicted taxonomically due to evolved life history traits and reproductive behaviors.

## **Introduction**

Intraspecific competition for resources, including food, territory, and mates, can play a large role in the survival and reproduction of individuals and thus influence population dynamics. The strength of intraspecific competition for these resources is often a limiting factor in overall population size (Pomerantz et al. 1980, Boström-Einarsson et al. 2013, Ward et al. 2013). Ecologists traditionally view intraspecific competition in terms of a dichotomy or gradient of contest versus scramble competition (Bellows 1981, Parker 2000). Just as resources are rarely split evenly among individuals (e.g., scramble competition), it is equally uncommon to observe cases where superior competitors can wholly exclude inferior individuals (e.g., contest competition; Bellows 1981). This spectrum of intraspecific competition produces a wide range of functional forms that have been used to describe density-dependent reproduction (Bellows 1981). Under contest competition, density-dependence is compensatory, such that the reproductive output of a population is greatest when the population size becomes large enough to reach the maximum number of reproductive winners that limited resources will allow. This generally occurs by reaching a maximum number of mates (Simmons and Ridsdill-Smith 2011), mating sites (Warner 1987), or territories (Marden and Waage 1990). Once the maximum number of winners is reached, additional reproductive competitors will neither increase nor decrease reproductive output, as resources are only split among the best competitors. Scramble competition, however, leads to overcompensatory density-dependence wherein production of offspring actually declines

at high densities (Zipkin et al. 2009). Limited resources are split evenly reducing the reproductive success of all individuals. This reproductive scramble competition can happen as a result of adult resource consumption, juvenile resource consumption, nest destruction, or cannibalism (Bellows 1981). Given this variety of possible outcomes, natural populations undergoing density-dependent reproduction tend to exhibit recruitment relationships somewhere along the contest – scramble gradient (which we term the “strength of overcompensation”).

Recent studies have examined the influence of evolution on aspects of population dynamics (Coulson et al. 2011, Schoener 2011, Fagan et al. 2013), suggesting that closely related species may share certain population-level dynamics due to similarities in life history traits. Such relationships are a key part of the ‘ecogenetic loop’ that links life history traits, demography, and evolution (Kokko and Lopez-Sepulcre 2007, Coulson et al. 2010). These linkages raise the question of whether the strength of overcompensation, which is rooted in life history strategy and related behaviors, may be similar across closely related species. If phenotypic variation exists in how individual reproductive output changes in response to population density, it follows that the strength of overcompensation is itself a trait under selection and suggests that there may be similarities in density-dependence among related taxa.

Body size is a key trait connecting life history characteristics to population dynamics. Research suggests that there is a link between the maximum reproductive output of a population and the maximum body size of individuals within the population for a large variety of taxa including unicellular organisms, insects, fish, and mammals (Fenchel 1974, Blueweiss et al. 1978, Honěk 1993, Savage et al. 2004). The fecundity of

an individual and population-level maximum reproductive rate have both been shown to increase with body size both within and among related species (Honěk 1993). In fisheries, maximum reproductive rate is much higher for a population when large, old females are present (Venturelli et al. 2010). Species that reach a large maximum body size are likely to be relatively more fecund and have a greater maximum reproductive rate (Goodwin et al. 2006).

Fish populations are an excellent system for studying variations in the relationship between reproductive competition and density-dependence because fish species exhibit a wide variety of dynamics and life history strategies (Rose et al. 2001). At a mechanistic level, the relationship between population density and reproductive success varies among fish species and populations because of resource limitations, habitat constraints, and potentially intrinsic, species-specific traits. For example, anadromous salmonids, which reproduce in spatially constrained rivers and creeks, are known to have poor reproductive output at high densities because spawning sites, or redds, of some individuals are destroyed by other spawners (Van Den Berghe and Gross 1989). As this behavior has the potential to reduce the fitness of all spawners roughly equally, it can be seen as a form of reproductive scramble competition. On the other end of the spectrum, older, larger females of the black rockfish, *Sebastes melanops*, lay eggs that are competitively superior to those of their younger counterparts (Berkeley et al. 2004), endowing their offspring with a survival advantage typically observed in contest competition.

Stock-recruitment relationships, or the relationships between the maximum annual number or biomass of spawners (i.e., the stock) and the annual number or biomass of offspring that reach a threshold age (i.e., recruits), vary greatly among fish species and

taxa (Myers et al. 1999). These relationships provide an ideal system to test ecological theory, as fisheries datasets are large-scale with high amounts of replication, allowing broad-scale investigations of ecosystem-level questions (Jensen et al. 2011). However, estimating the functional relationships between spawners and their recruits presents many challenges and complications. For example, decades of time series data that span a wide range of abundances are generally required to estimate individual stock-recruitment relationships accurately (Walters 1985, Myers 1997). Moreover, such time series data typically include substantial measurement error, which can lead to bias in parameter estimates (Walters and Ludwig 1981, Sethi et al. 2005, Pitchford et al. 2007). In addition, a wide variety of biotic and abiotic factors naturally leads to variation in the stock-recruit relationship. For example, changes in environmental conditions can introduce variability to the number of recruits produced from a population, with habitat changes and phenological shifts affecting recruitment success (Rijnsdorp et al. 2009).

Because of this variability in stock-recruitment data, hierarchical models (Berliner 1996, Gelman and Hill 2007) offer a valuable improvement on traditional stock-recruitment methods that estimate parameters one population at a time (Dorn 2002, Forrest et al. 2010). Hierarchical models provide a structure in which data can be grouped to observe stock-recruitment parameters at multiple levels, such as taxonomic order. Similarly, Bayesian techniques have become popular in recent decades as researchers have looked for ways to integrate data from multiple sources into one analysis (Liermann and Hilborn 1997, Stewart et al. 2013). Bayesian approaches facilitate estimation of hierarchical stock-recruitment curves by easily allowing for shared parameter estimation (Forrest et al. 2010). By integrating information from multiple

sources, hierarchical models analyzed using Bayesian methods greatly improve the accuracy of stock-recruitment models by reducing the effect of noise around the stock-recruitment relationship (Maunder and Punt 2013).

We developed a hierarchical model to investigate variation in stock-recruitment parameters, and thus types of intraspecific competition, among different taxonomic groupings of commercially harvested fish. Our multi-species model accommodates a wide range of stock-recruit functional forms in a single estimation framework using data from a large stock recruitment database (Myers et al. 1995). We used this model to examine variation in maximum recruitment per unit spawning biomass and degree of compensation at both the species and order levels. We also used maximum body length as a covariate to investigate the effect of body size on maximum recruits per spawner. We expected that the parameters governing the functional forms of stock-recruitment relationships of species would be clustered by taxonomic order, with orders that have highly spatially-constrained spawning grounds or nurseries displaying the highest levels of overcompensation. We further expected that maximum recruitment per unit spawning biomass would be greatest in highly fecund species and orders and that maximum body length would be positively correlated with the maximum recruitment per unit spawning biomass among species of the same order.

## **Methods**

### *The Dataset*

We analyzed the Myers Stock-Recruit database, which was compiled and standardized from assessments of exploited marine fisheries worldwide (Myers et al. 1995). The database includes 281 reproductively isolated subpopulations from 62 species



in 8 orders with time series ranging from 6 to 73 years (mean = 25 years) and consists primarily of marine and anadromous species with a small number of freshwater species. For each population in this database, annual stock and recruitment data were estimated using commercial catch-at-age data and/or research survey estimates. The data were standardized into spawning-stock biomass (SSB) for the stocks and thousands of metric tonnes or millions of fish for the recruits of marine fish and river-spawning salmonids, respectively (Myers et al. 1995). We then standardized the recruitment data further by dividing recruits by maximum annual spawning biomass per recruit (using values of natural mortality, maturity, and body weight at age compiled by R. A. Myers and C. Minto, pers. comm. 2015). This ensures that we regress a measure of spawning success (in units mass) against a measure of spawning potential (in units mass), such that the productivity of each population (e.g., slope at the origin) is a dimensionless quantity, comparable among stocks, that complies with the exchangeability assumption of hierarchical models (Gelman et al. 2004). A deterministic equilibrium of spawners and recruits is achieved at a ratio of 1 (i.e., the 1-1 line is replacement rate), such that the slope of the stock-recruit relationship at the origin must be greater than 1 for the population to be reproductively viable (Myers et al. 1995). All data come from assessments that used standard, species-specific procedures for aging of individuals and follow stock boundary conventions set by the Northwest Atlantic Fisheries Organization (NAFO) and the International Council for the Exploration of the Sea (Myers et al. 1995). We used this dataset instead of its successor, the RAM Legacy Stock Assessment Database (Ricard et al. 2012), because many stock and recruitment values from the latter dataset were projected from population models that assume an underlying stock-

recruitment relationships and parameters for each population, which can bias the results of meta-analysis (Ricard et al. 2012, Dickey-Collas et al. 2015). In contrast, the Myers Stock-Recruit database contains recruitment estimates from sequential population analysis methods or direct survey estimates, which do not assume any a priori stock-recruit relationship. Maximum body length values were taken for each species from the FishBase database (fishbase.org). After standardizing recruitment using natural mortality, maturity, and body size information, maximum body length values within each order were then rescaled to have a within-order mean of zero and a standard deviation of one. This rescaling was used for all subsequent analysis of the relationship between standardized maximum body length and SR parameters, and is done to ensure (1) that estimated parameters within a taxonomic order represent values given the average body length in that order, and (2) to ease mixing of Bayesian sampling.

We excluded populations with under 10 years of data because temporal autocorrelation rendered the effective sample size too small (Worm and Myers 2003, Thorson et al. 2014). We also excluded orders with fewer than five species (i.e., Lophiformes and Alopiformes). Members of the orders Osmeriformes and Esociformes (Ayu and Pike, respectively) were grouped with the Salmoniformes because those species all belong to the superorder Protacanthopterygii. These steps left us with six orders (Clupeiformes, Gadiformes, Perciformes, Pleuronectiformes, Salmoniformes, Scorpaeniformes), all of which were well-represented with 9-110 populations in 5-14 species. To avoid overparameterizing our models, we aggregated species within orders ( $n=6$ ) rather than within families ( $n=18$ ). The final 256 populations, representing 54 species in 6 orders, appear in Appendix 1.A.

### *The Stock-Recruitment Relationships*

The Beverton-Holt (1957) and Ricker (1954) stock-recruitment models are commonly used spawner-recruit models for fish populations undergoing density-dependent reproduction (Goodyear 1993, Myers 2001). The Beverton-Holt model describes a system where the number of recruits reaches a maximum at high spawner densities, beyond which additional spawners do not affect overall recruitment. This population behavior is one outcome of contest competition, where the ability to survive and reproduce varies among individuals (Brännström and Sumpter 2005). The Beverton-Holt model can also be derived from foraging arena theory and associated assumptions about risk-sensitive foraging behavior (Walters and Korman 1999). Under the Beverton-Holt model, the worst competitors decline in fitness at high densities as resources are disproportionately consumed by the best competitors. Such compensatory recruitment can be expressed as:

$$R_{t+1} = \alpha S_t / (1 + \beta S_t) \quad (1)$$

where  $S_t$  is the stock value at time  $t$  and  $R_{t+1}$  is the recruits produced at the following time step,  $t+1$ . The parameters  $\alpha$  and  $\beta$ , constrained to be non-negative, govern the shape of the stock-recruitment relationship. The parameter  $\alpha$  represents the maximum reproductive output of an individual in the absence of density-related effects, or per-capita recruitment at very low spawner abundance. Thus the slope of the stock-recruitment curve is  $\alpha$  at the origin. The parameter  $\beta$  determines the rate at which the number of recruits decreases as spawner density increases, and, in effect, determines the carrying capacity for a specified  $\alpha$ -parameter.

The Ricker (1954) model is a stock-recruitment relationship where the number of recruits reaches a maximum at an intermediate spawner density beyond which recruitment falls as spawner abundance increases. This overcompensatory behavior is generally a result of scramble competition, where reproductive success depends on competition with neighbors and access to resources is equal among individuals (Brännström and Sumpter 2005). This decline in recruits with increased spawner abundance is due to interference by neighbors, which results in lower juvenile survival at high densities. The Ricker model is written as:

$$R_{t+1} = \alpha S_t e^{-\beta S_t} \quad (2)$$

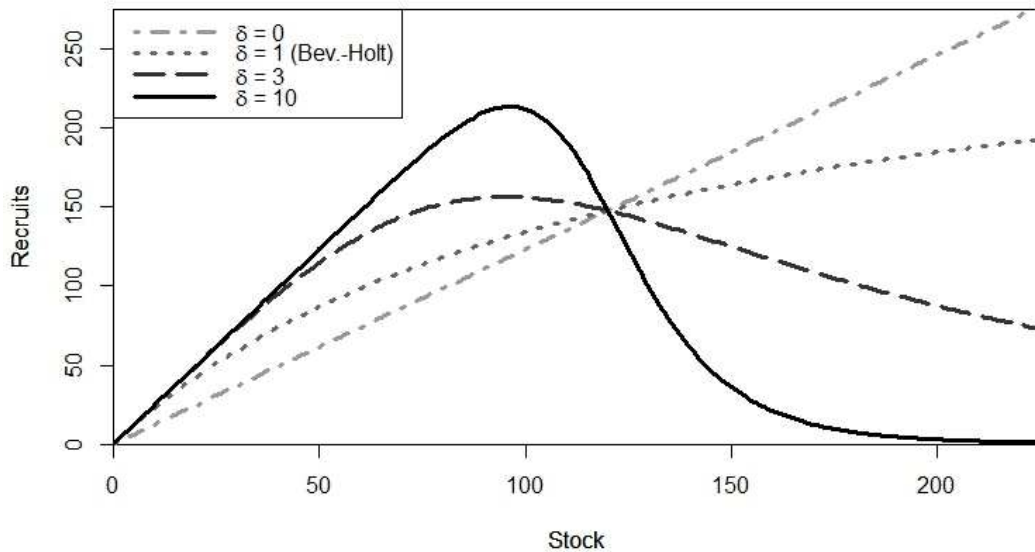
where the non-negative  $\alpha$  is directly comparable to the its estimate from the Beverton-Holt model, while  $\beta$  is not directly comparable to the Beverton-Holt model.

An alternative to the Ricker and Beverton-Holt models is the Shepherd (1982) stock-recruitment model. Through the addition of a third parameter, the Shepherd model accommodates stock-recruitment relationships that range from compensatory (as observed in the Beverton-Holt model) to overcompensatory (as observed in the Ricker model), as well as other asymptotic and non-asymptotic forms of density-dependence (Shepherd 1982). As such, the Shepherd model allows for a wide range of functional forms, spanning from contest to scramble competition, as well as density-independent dynamics (Fig. 1.1). The three parameter Shepherd model is:

$$R_{t+1} = \alpha S_t / (1 + (\beta S_t)^\delta) \quad (3)$$

where the  $\alpha$  and  $\beta$  parameters again define the maximum number of recruits per spawner and the carrying capacity, respectively. The additional non-negative parameter  $\delta$

represents the degree of compensation, or the extent to which per capita reproduction declines at high densities. When  $\delta=1$  the Shepherd model reduces to the Beverton-Holt model, and when  $\delta>1$  the model represents increased overcompensation similar to the Ricker model. When  $\delta<1$  the recruitment curve grows indefinitely at a declining rate, becoming increasingly density-independent as  $\delta$  approaches zero. At  $\delta=0$ , the relationship is exactly linear. The Shepherd model is therefore particularly useful as a general framework for analyses that span multiple taxa of fish because it does not make a priori assumptions about the structure of intraspecific competition.



**Figure 1.1** – Examples of the Shepherd model for fixed  $\alpha$  and  $\beta$  parameters ( $\alpha = 2.5$ ,  $\beta = 0.01$ ), where  $\delta$ , which regulates the degree of compensation, is varied from 0 to 10. Curve shapes range from linear ( $\delta=0$ ), to compensatory ( $0 < \delta \leq 1$ ), to overcompensatory ( $\delta > 1$ ).

### *The Hierarchical Model*

We constructed a hierarchical community model to link stock-recruitment parameters among species and compare parameter estimates across taxonomic groupings and maximum body lengths. We designed our model to test two hypotheses: 1) taxonomic orders in which fish experience substantial spatial constraints on their reproductive output, particularly the Salmoniformes and Pleuronectiformes, have higher levels of overcompensation (e.g., higher values of  $\delta$ ) compared to other orders (Clupeiformes, Gadiformes, Perciformes, and Scorpaeniformes) in the dataset; and 2) maximum recruitment per unit spawning biomass ( $\alpha$ ) correlates with the species-level maximum body length in all orders of fish. Our hierarchical model assumes that, for both  $\alpha$  and  $\delta$ , parameter estimates are related taxonomically. That is, populations of the same species should be similar dynamically, as should species belonging to the same order. We assume that there is no hierarchical relationship in the parameter  $\beta$  among populations, as carrying capacity can fluctuate greatly for a variety of abiotic reasons, and we would thus not expect  $\beta$  to be similar, either among populations within species or among species within orders (Myers et al. 2001, MacKenzie et al. 2003). At the most basic level, the Shepherd model is fit to data from each population:

$$R_{ijk,t+1} = \alpha_{ijk} S_{ijk,t} / (1 + (\beta_i S_{ijk,t})^{\delta_{ijk}}) \quad (4)$$

where  $S_{ijk,t}$  and  $R_{ijk,t+1}$  are the stock and standardized recruit values at time  $t$  and  $t + 1$ , respectively, for population  $i$  of species  $j$  within order  $k$ , and  $\alpha_{ijk}$ ,  $\beta_i$ , and  $\delta_{ijk}$  are the

Shepherd parameters for each population  $i$ .  $\beta_i$  does not have species ( $j$ ) and order level ( $k$ ) indices as it is not modeled hierarchically.

We assume that the population-level  $\delta$  and  $\alpha$  parameters each come from species-specific distributions. The logarithm of the parameter  $\delta_{ijk}$  is assumed to be drawn from a normal distribution:

$$\log(\delta_{ijk}) \sim N(\log(\mu_{\delta_{jk}}), \sigma_{\delta_j}) \quad (5)$$

where  $\log(\mu_{\delta_{jk}})$  is the log-mean value of  $\delta$  across all populations that belong to species  $j$  of order  $k$ , and  $\sigma_{\delta_j}$  is the standard deviation among populations of species  $j$ . We model  $\delta$  on the log scale so that it remains positive. The species level parameter,  $\log(\mu_{\delta_{jk}})$ , is governed by an additional, order-level parameter such that it is also a random variable that comes from a common, normal, order-level distribution:

$$\log(\mu_{\delta_{jk}}) \sim N(\log(\mu_{\delta_k}), \sigma_{\delta_k}) \quad (6)$$

where  $\log(\mu_{\delta_k})$  represents the mean of  $\log(\mu_{\delta_{jk}})$  (e.g., the mean  $\delta$  value across all species in order  $k$ ) and  $\sigma_{\delta_k}$  is the standard deviation among all species within order  $k$ .

We similarly specified  $\alpha$  at the stock level:

$$\log(\alpha_{ijk}) \sim N(\log(\mu_{\alpha_{jk}}), \sigma_{\alpha_j}) \quad (7)$$

where  $\log(\mu_{\alpha_{jk}})$  is the mean  $\alpha$  for species  $j$  in order  $k$  and  $\sigma_{\alpha_j}$  is the standard deviation of  $\alpha$  for populations in species  $j$ . At the species level, we allow maximum body length to serve as a covariate on  $\mu_{\alpha_{jk}}$  by assuming that:

$$\log(\mu_{\alpha_{jk}}) = C1_{jk} + L_{max_j} C2_{jk} \quad (8)$$

where  $L_{max_j}$  is the standardized maximum body length covariate for species  $j$  in order  $k$ , and  $C1_{jk}$  and  $C2_{jk}$  are the species-level intercept and slope terms that specify the relationship between maximum body length and  $\alpha$ . These parameters are linked at the order level as follows:

$$C1_{jk} \sim N(\log(\mu_{C1_k}), \sigma_{C1_k}) \quad (9)$$

$$C2_{jk} \sim N(\log(\mu_{C2_k}), \sigma_{C2_k}) \quad (10)$$

where  $\mu_{C1_k}$ ,  $\sigma_{C1_k}$ ,  $\mu_{C2_k}$ , and  $\sigma_{C2_k}$  are the order-level log-mean and standard deviation for the intercept and slope parameters, respectively. Recruit values were standardized using lifetime spawning biomass per recruit in the absence of fishing ( $SPR_{F=0}$ ) to ensure that  $\alpha$  was comparable among populations (Myers et al. 1999). This gives spawner and recruit values the same units such that  $\alpha$  is a dimensionless summary of the strength of lifetime compensation (i.e., maximum lifetime spawning biomass per spawning biomass) and that any differences between parameter values among taxa are meaningful.

We modeled each population by additionally assuming that the recruit data could contain process and/or sampling error that is not adequately captured with the recruitment function (Myers 2001). To account for this potential error, we assumed that each of the recruit data points is drawn from a normal distribution centered on the “true” recruitment value:

$$\tilde{R}_{i,t+1} \sim N(R_{i,t+1}, R_{i,t+1} \sigma_{R_i})$$



Here,  $\tilde{R}_{i,t+1}$  is the recruit data point for year  $t + 1$  for population  $i$ ,  $R_{i,t+1}$  is the expected recruitment value for population  $i$ , and  $\sigma_{R_i}$  is the population-specific standard deviation around the mean recruitment value.

We analyzed our model with a Bayesian approach using Markov chain Monte Carlo (MCMC) to obtain samples from the posterior distributions of all model parameters. MCMC allows us to easily estimate model parameters and directly present the probability that a parameter has a certain value. We specified vague prior probabilities for all parameters in our model to represent a lack of knowledge on the order-level means, the variations among stocks, species and orders, and the carrying capacity within stocks:

$$\mu_{\delta_k} \sim N(3,10) \quad \mu_{\delta_k} \geq 0$$

$$\beta_i \sim N(0.01,0.1) \quad \beta_i \geq 0$$

$$\mu_{C1_k} \sim N(3,10) \quad \mu_{C1_k} \geq 0$$

$$\mu_{C2_k} \sim N(0,10)$$

$$\sigma_{\delta_j}, \sigma_{\delta_k}, \sigma_{\alpha_j}, \sigma_{C1_k}, \sigma_{C2_k} \sim U(0,100).$$

The first parameter in each normal distribution is the mean and the second is the standard deviation. The first and second parameters in the uniform distribution represent the limits of that distribution. These prior distributions cover a range much larger than the expected possible parameter values, such that each prior is relatively flat over the expected parameter ranges. Normal distributions were chosen over uniform distributions for mean parameter values because of improved model convergence. We analyzed our model

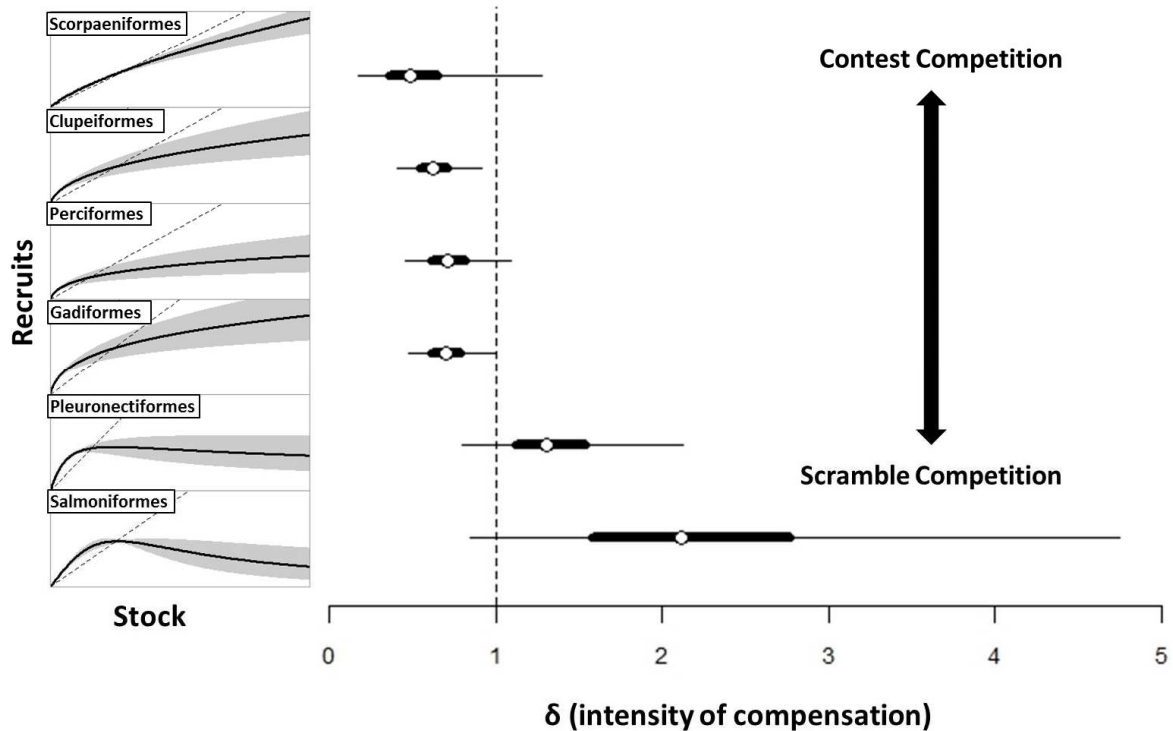
using the programs R and JAGS (Plummer 2003) to estimate posterior parameter distributions. We ran 100,000 MCMC iterations and thinned the chains by keeping only every 20<sup>th</sup> iteration after a burn-in of 40,000. We analyzed model convergence using the Gelman-Rubin statistic  $\hat{R}$  (Appendix 1.B). Further tests of fit and validation of our model are found in Appendix 1.C, and figures showing posteriors produced without fitted data are found in Appendix 1.D for comparison. We tested hypothesized differences in stock-recruitment behavior among orders by comparing posterior distributions of parameters among species and order groups.

## **Results**

### Order-level Results

Parameter estimates from order-level stock-recruitment curves suggest a wide range of dynamics across orders ranging from scramble competition to varying degrees of contest competition (Fig. 1.2). Posterior distributions of  $\delta$  for Clupeiformes, Gadiformes, Perciformes, and Scorpaeniformes exhibited low degrees of density-dependence, as credible intervals (CIs) ranged primarily between  $\delta = 0$  (density-independent) and  $\delta = 1$  (Beverton-Holt-form compensation) (Fig. 1.2). Curves with these values of  $\delta$  have a declining slope, but never fully reach a saturated recruitment value (although an equilibrium population size still exists at the intersection of the recruitment curve and the 1-1 replacement line). The orders Pleuronectiformes and Salmoniformes, however, had 50% credible intervals completely above the  $\delta = 1$  line. These results correspond to an overcompensatory stock-recruitment relationship (similar to the Ricker model), suggesting that populations within these two orders generally display overcompensation.

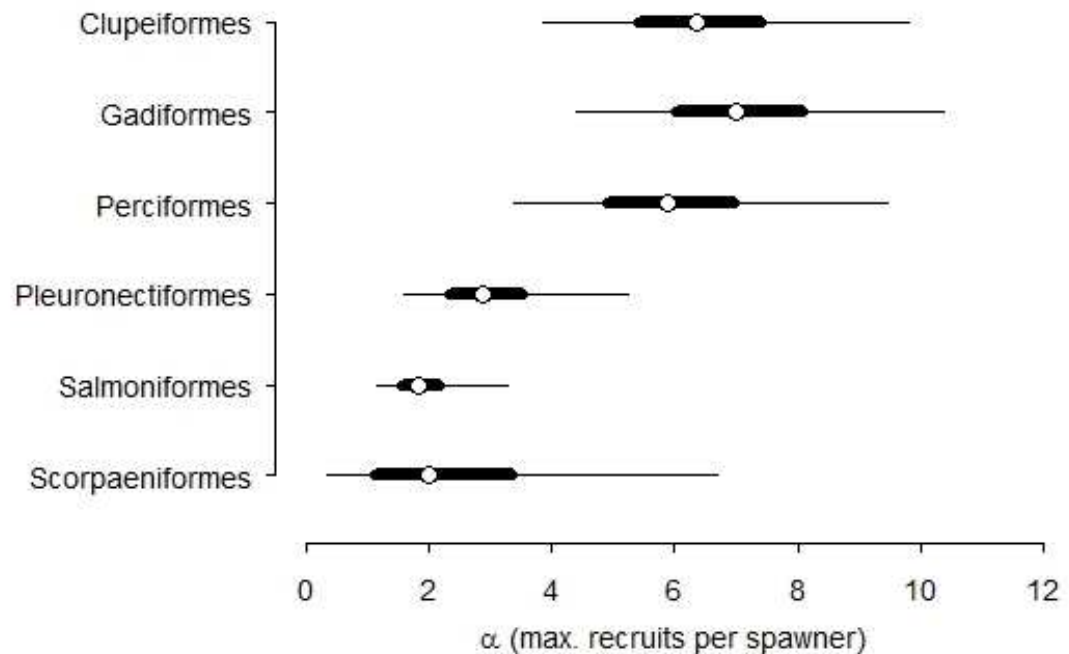
These two orders reach maximum total recruitment at stock values that vary by species and then show a decline in recruitment at populations beyond this size.



**Figure 1.2**– Order-level stock recruitment curves showing intraspecific competition ranging from contest/compensatory competition (top panels) to scramble/overcompensatory competition (bottom panels). On the left, median order-level stock-recruitment relationships (black lines) are shown with 50% credible intervals (grey shading), as estimated using the Shepherd model. Dotted lines indicate the 1:1 line of stock and recruits. Axes vary in size between orders to facilitate comparisons among functional forms rather than carrying capacity. Values of  $\beta$  for each were determined by averaging median  $\beta$  values across all populations of a species and all species of an order. Stock and Recruit units are not given, as population sizes vary greatly within orders. On the right, the 95% (thin lines) and 50% (thick lines) credible intervals for order level  $\delta$

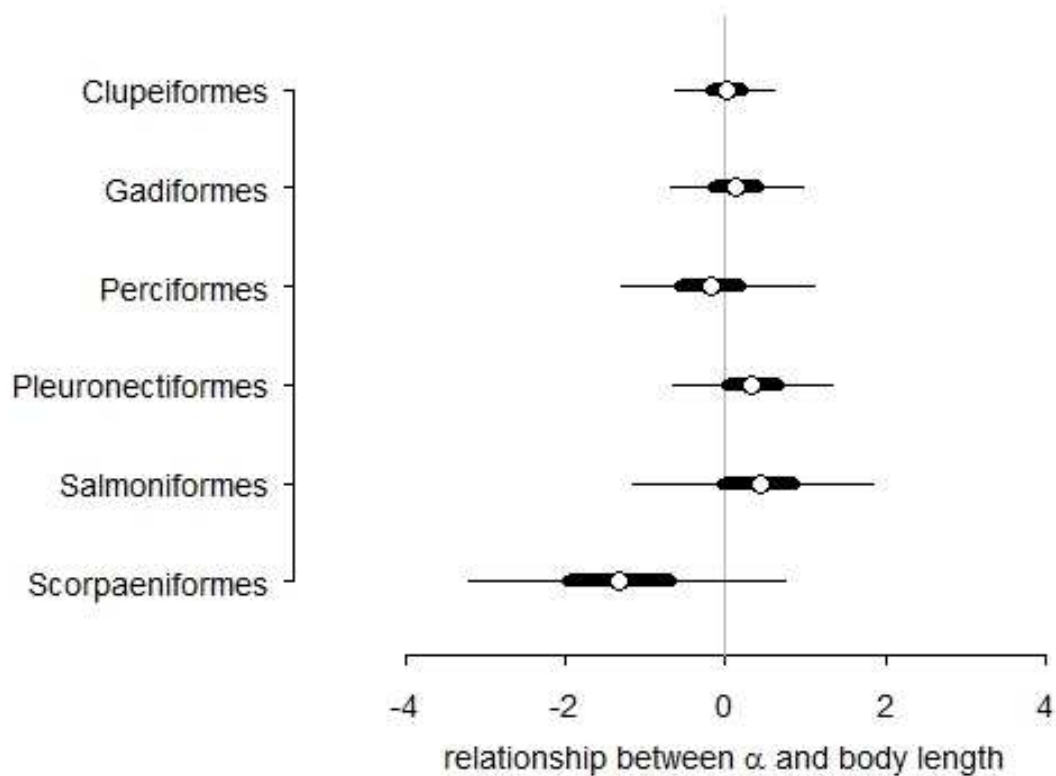
(intensity of compensation) values. Median values are represented by open circles. The dashed line at  $\delta = 1$  indicates where the Shepherd model is equivalent to the Beverton-Holt Model.

The parameter  $\alpha$  was highest in the Clupeiformes, Gadiformes, and Perciformes, all with median parameter values of  $\alpha > 4$  (Fig. 1.3), suggesting high maximum lifetime spawners per spawner for species in these orders. The orders Pleuronectiformes, Salmoniformes, and Scorpaeniformes had comparatively lower median  $\alpha$  parameter values (median  $\alpha < 3$  for all orders).



**Figure 1.3** – The 95% (thin lines) and 50% (thick lines) credible intervals for order-level  $\alpha$  (per capita recruitment at low densities) values. Median values are represented by open circles.

There was no strong relationship between  $\alpha$  and maximum body length (mean order-level covariate,  $\mu_{C2_k}$ ) for any of the orders (Fig. 1.4). The 50% credible interval for Gadiformes and Pleuronectiformes both overlap zero, suggesting no relationship between  $\alpha$  and  $L_{max}$  whereas Perciformes and Scorpaeniformes have positive order-level slopes and the Clupeiformes and Salmoniformes have negative order-level slopes. When the order-level structure was removed from our model (e.g., all species were grouped together), no relationship was found between  $\alpha$  and maximum body length. When similarly tested,  $\delta$  also showed no relationship with maximum body length (Appendix 2.E).

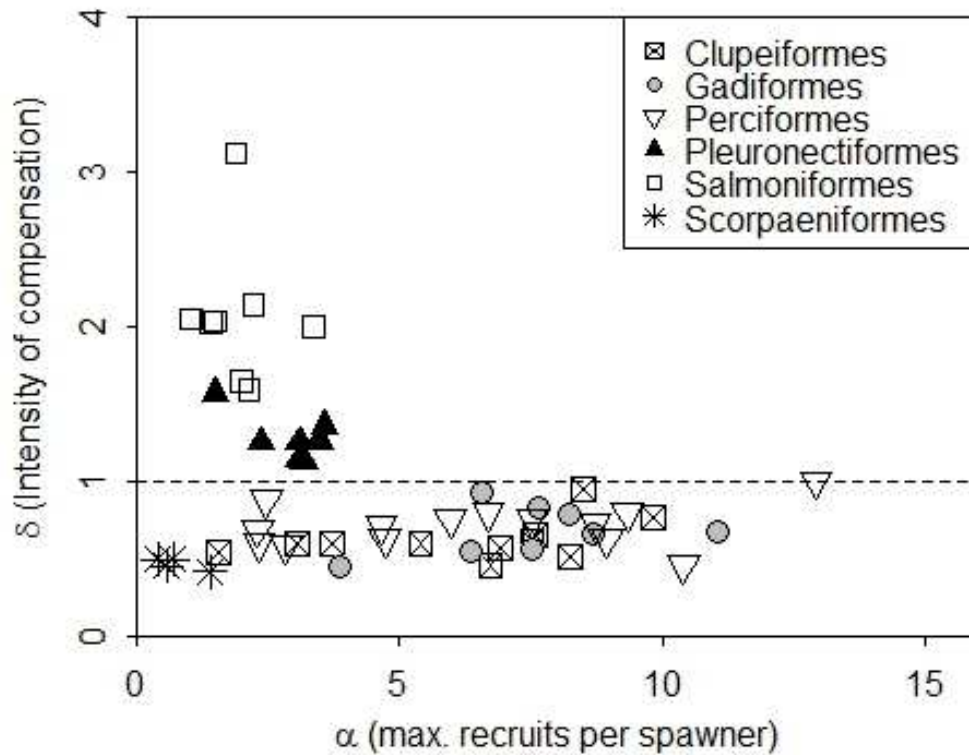


**Figure 1.4** – Order level effects of maximum body length on the parameter  $\alpha$ . A value of 0 indicates no relationship while a positive (negative) value indicates a positive (negative) relationship between maximum body length and maximum per-capita recruitment. Open circles represent median values and the lines indicate the 50% (thick lines) and 95% (thin lines) credible intervals.

### Species-level Results

We found that, within a given order, species generally exhibit clustered values of  $\delta$  and more variation in  $\alpha$ . All species within the orders Pleuronectiformes and Salmoniformes had median  $\delta$  values in the range of overcompensation ( $\delta > 1$ ). Species of all other orders lie within the range between a linear and a compensatory stock-

recruitment relationship ( $0 < \delta < 1$ ). The  $\alpha$  parameter has a much greater amount of variation among species, especially within the Clupeiformes, Gadiformes, and Perciformes orders (Fig. 1.5). Exploratory analysis showed that the sample mean of delta among species was similar in a model lacking grouping by order with some shrinkage of the variance (results not shown).



**Figure 1.5** – Median  $\alpha$  plotted against median  $\delta$  for all 54 fish species included in our model. Species are grouped into symbols based on taxonomic order. The dashed line at  $\delta = 1$  indicates pure contest competition. Values above the line indicate scramble competition. Values below the line indicate weak intraspecific competition.

## Discussion

Our analyses document striking divergence in the strength of overcompensation and intraspecific competition among orders and species. We found that the degree of intraspecific competition ( $\delta$  parameter) for the Salmoniformes (here defined as salmonids and relatives, including other members of the superorder Protacanthopterygii) and Pleuronectiformes (flatfishes) lies primarily in the overcompensatory range (Fig. 1.2), suggesting that for these taxa, high stock levels can depress recruitment. This result agrees with the common use of the Ricker model and observations of overcompensation in salmonids (Walters 1975, Krkošek et al. 2008), and with observed spawner-recruit relationships found in some studies of flatfish (Iles 1994, Rijnsdorp and Van Leeuwen 1996, Van Der Veer et al. 2000, Wilderbuer et al. 2002, Wilderbuer et al. 2013, Archambault et al. 2014).

The results for both of these orders accord with our prediction that fish with spatially constrained reproduction are severely suppressed by intraspecific competition at high abundances. For stream-dwelling salmonids, such scramble competition may come about via several mechanisms. One example involves limitation on suitable spawning habitat (Armstrong et al. 2003) and redd superimposition (destruction of existing nests by subsequent spawners), which can cause strong overcompensation through the loss of a large percentage of eggs laid (Van den Berghe and Gross 1989, Fukushima et al. 1998). Moreover, immediately following emergence, juvenile salmonids at high densities also experience high mortality as severe competition and less efficient foraging behavior lead to greater mortality through starvation than when fry densities are low (Nislow et al. 2011). Flatfish similarly experience density-dependence due to spatially constrained nursery habitats. Eggs and larvae for many flatfishes drift in a pelagic phase before



becoming demersal juveniles and concentrating in nurseries (Rijnsdorp et al. 1995). Density-dependent processes come into effect and the concentration of individuals relative to nursery carrying capacities may limit successful recruitment (Beverton 1995, Rijnsdorp et al. 1995). The spatial constraint of nurseries with limited seabed habitat promotes competition, and strong density-dependence is observed in populations with high juvenile concentrations in these habitats (Archambault et al. 2014).

The four other orders included in our model (Clupeiformes, Gadiformes, Perciformes, and Scorpaeniformes) exhibit competition between density-independent ( $\delta=0$ ) and compensatory ( $\delta=1$ ) dynamics (Fig. 1.2). For density-dependence in the range  $0 < \delta < 1$ , recruitment can increase indefinitely with increasing spawning output. We note that this does not suggest an indefinitely growing population, as there is an equilibrium abundance (e.g., carry capacity) whenever  $\delta>0$ , which is identified as the point where the stock-recruit curve crosses the 1-1 replacement line. Beyond this point, increasing spawner abundance will continue to increase recruitment, but at a net loss. The functional form of these orders differ from those found in studies that investigate stock-recruitment dynamics across taxa, such as in Scorpaeniformes (Dorn 2002, Forrest et al. 2010), as few studies have used models that allow for variation in the degree of compensation. It is clear from their low values of  $\delta$  that these orders have similar forms of intraspecific competition that are distinctly on the contest side of the contest-scramble gradient. Overall, our  $\delta$  parameter results suggest that even though the degree of compensation varies widely across taxa, much of that variation among fish species may be predicted taxonomically as a function of evolved life history traits and reproductive behaviors.

Our results demonstrated that the  $\alpha$  parameter of the Shepherd model differs greatly among fish orders (Fig. 1.3). Because  $\alpha$  is a standardized reproductive output of individuals at low population levels without density-dependent effects (i.e., maximum lifetime spawners per spawner), we expected that orders with greater fecundity and higher per-capita spawning biomass would have greater  $\alpha$  values (Andersen et al. 2008). Many of the species of the orders Clupeiformes, Gadiformes, and Perciformes do indeed have high fecundity, while the Salmoniformes are generally much less fecund (Mertz and Myers 1996). The fecundity values for the orders Pleuronectiformes and Scorpaeniformes are much less consistent, but fish belonging to those orders do generally have higher fecundities than members of the Salmoniformes. As fecundity is only one part of the recruitment process, other factors that affect survival of juveniles, such as predation or habitat quality, could greatly affect reproductive output at low densities (Karatayev et al. 2015). Large, late-maturing fish have been associated with relatively higher fecundities, small eggs, and few reproductive bouts per season (Winemiller and Rose 1992). Specifically, Scorpaeniformes tend to have small eggs and low maximum replacement rates (Winemiller and Rose 1992, Myers et al. 1999), which would indicate a low  $\alpha$  parameter value. Our results suggest that there are distinct differences in  $\alpha$ , among fish orders, which appear to follow similar differences in fecundity and life history.

Contrary to expectation, we did not find a consistent effect of maximum body length on the maximum lifetime replacement rate ( $\alpha$  parameter) (Fig. 1.4). The allometric dependence varied from positive to negative by order, but no strong pattern emerged. When we analyzed all taxa together, we found no effect of maximum body length on  $\alpha$ . This appears to indicate that, at these broad levels, body size does not show

a strong effect on maximum lifetime compensation, contrary to previous hypotheses (Andersen et al. 2008).

We found strong clustering by order when looking at the species-level  $\alpha$  and  $\delta$  Shepherd model parameters (Fig. 1.5). This is especially true for the  $\delta$  parameter. Median parameter estimates suggest that all species of the Pleuronectiformes and Salmoniformes orders exhibit overcompensatory dynamics, whereas none of the species of any of the four other taxonomic orders show a similar response. This implies that the type and degree of intraspecific competition is maintained through taxonomic groupings, mediated perhaps through similarities in life history and behavior. The lack of similar clustering in the  $\alpha$  parameter within taxonomic orders indicates a much higher variation in maximum recruitment per unit spawning biomass between taxa, as the orders Clupeiformes, Gadiformes, and Perciformes have especially high variation in  $\alpha$  among species.

A key strength of the hierarchical modeling approach is that it can leverage population-level variation in reproductive rate and the strength of compensation (whether that variation manifests from reaction norms or from genotypic variation) to yield species-level and order-level insights relevant for management. Often, recruitment models are selected based on convention, model selection techniques, or by prior usage in related species. These decisions are based on biological considerations at some level, but in cases where data are poor or limited, it can be difficult to determine which model is most appropriate for a particular species. There is no standard approach for choosing a stock-recruitment model for a particular fish species, whether large amounts of data exist

or not. Our modeling approach provides insight into the most appropriate density dependent models for a number of species.

We found that the type and degree of intra-specific competition are tightly clustered within orders indicating strong similarities in the form of intra-specific competition among related species. In contrast, maximum lifetime replacement rate shows a greater spread across species. Overall, these results indicate that evolutionary history leaves a clear signal in the population dynamics of fish through tight, within-taxa clustering of reproductive density-dependence, likely mediated by taxonomic similarities in life history and behavior. Ultimately these findings may provide a pathway for leveraging information across species to further explore the ecology, evolutionary trajectories, and management of fish species.

## **Chapter 2:** Social transmission of migratory knowledge: quantifying the risk of losing migratory behavior

In press in *Theoretical Ecology*

### **Abstract**

When migration is a learned behavior, small populations have a significant problem of maintaining migratory knowledge across generations. These populations risk losing migratory behavior entirely, which may exacerbate existing stressors on population size. Here we investigated the success of various behavioral, demographic, and social factors towards maintaining migration within small populations. Using a discrete-time probabilistic model to simulate repeated migrations, we found that migratory group size plays an important role in maintaining migratory knowledge within the population. Rare, large groups allow for migratory knowledge to be spread to many individuals at once. When a population learns migration information incrementally, the presence of individuals that can learn quickly, therefore transitioning rapidly into leaders, has a profound impact on migrational persistence. Furthermore, small populations are better able to maintain migratory behavior when groups rely on informed leaders as compared to using collective group knowledge, even when that collective knowledge is heavily weighted towards knowledgeable individuals. Finally, we found that both species with short lifespans and species that migrate with fixed group compositions are at especially high risk of losing their migration behavior at small population sizes.

## Introduction

Group migration occurs when individuals that share breeding (or non-breeding) habitats organize into smaller, sub-population level groups to complete their migratory journey. This form of collective behavior presents a unique challenge for persistence when the migratory behavior is partially or completely learned from other individuals (Fagan et al. 2012). In particular, successful navigation by a small migratory group hinges upon each group having at least one experienced individual that is capable of navigating the migratory pathway. Such individual-level differences in navigation ability can be achieved either through differences in innate sensing and navigation of the environment (Pratt 1954, Wiltschko & Wiltschko 2003) or differences in learned migratory routes (Dodson 1988, Alerstam et al. 2003, Couzin et al. 2005).

If individuals are innately programmed and can use environmental cues for migration without the need for learning, migratory behavior may persist independent of population size. However, small migratory populations may face strong Allee effects (Berdahl et al. 2016) and risk losing migratory behavior (Fagan et al. 2012). If migratory behavior has a learned component, the persistence of migratory culture within a population may depend on demography, the social interactions of individuals, and the mechanisms for learning migratory pathways (Alerstam et al. 2003, Wilcove & Wikelski 2008, Fagan et al. 2012). The impact of demography and the learning process is highlighted in the case of species for which individual migrational ability improves with repeated migrations (Mueller et al. 2013). If migratory knowledge can be acquired as a benefit of successful small group migrations, then the spread of migratory information within a population will vary greatly. The rate of learning will also depend on grouping

dynamics and the nature of decision-making within a group. In the context of collective behavior, different modes of group decision-making include leader-following, quorum sensing, and environmental modification (Couzin 2009). Of particular interest is how these different kinds of decision-making behaviors may interact with processes of group formation, dissolution, and reassembly (Conradt & Roper 2003) to impact migratory outcomes.

All populations face challenges when their numbers are declining. With migratory species that rely on learning, such declines can be especially problematic because there is the added risk of losing migratory culture. At the same time, population declines can themselves result from loss of migratory behavior (Bolger et al. 2008, Newmark 2008), setting up a devastating feedback cycle that exacerbates population losses. Thus, there are special challenges involved in maintaining a migratory culture that is either partially or completely learned. Nelson (1998) has explored this issue for white-tailed deer (*Odocoileus virginianus*), demonstrating that migratory knowledge is not under rigid genetic control. Similarly, taking an experimental approach, Chernetsov et al. (2004) has used white storks (*Ciconia ciconia*) to demonstrate that juveniles isolated from adult migrants initiate their migrations in erratic directions and suffer high levels of mortality en route.

The repeated successful transmission of knowledge required for learned migration is highlighted by the “adopted-migrant hypothesis” (McQuinn 1997), which is used in fisheries to explain the transmission of breeding ground knowledge between generations for Atlantic herring (*Clupea harengus*) and other fish species. According to this hypothesis, migration can be a fragile behavior to maintain because information about

specific migratory locations is directly passed from older generations to first-time migrants. For this reason, much uncertainty exists regarding the stability of migratory behavior within small populations of endangered species that rely on learned migratory routes, for example the whooping crane (*Grus americana*) or the southern right whale (*Eubalaena australis*) (Urbanek et al. 2010, Valenzuela et al. 2009). From these perspectives, understanding what behavioral and demographic conditions are favorable to the persistence of migratory behavior can help to inform management decisions and better identify the biological scenarios under which partially or fully learned migratory behavior should be expected.

Small group migration with a learned component can be found across a wide range of life histories. This includes short lived species that migrate in large groups, such as Atlantic herring (*Clupea harengus*) (Huse et al. 2010) or greater white-fronted geese (*Anser albifrons*) (Hayakawa & Furuhashi 2012), long-lived species that migrate in large groups, like the Mexican free-tailed bat (*Tadarida brasiliensis*) (Williams et al. 1973, McCracken & Gustin 1991), and long-lived species that migrate in small groups, such as whooping cranes (*Grus americana*) (Mueller et al. 2013), goitered gazelle (*Gazella subgutturosa*) (Blank et al. 2012) and orcas (*Orcinus orca*) (Higdon et al. 2011). In contrast, there is little evidence of short-lived species maintaining learned, small-group migrations, but it is unclear if this is due to biological limitations or biases in species studied.

Here we present a probabilistic model of small group migration with which we explore how changes to grouping dynamics, learning behavior, and population structure affect the persistence of migratory cultural knowledge. We use this model to investigate



which of these population characteristics and grouping conditions alter the likelihood of persistence versus loss of migratory culture. To better understand the mechanisms behind these outcomes, we explore different scenarios for transmission of migratory information within populations and identify the factors that most contribute to the persistence of migratory knowledge. From heuristic arguments, we can formulate several hypotheses. First, learned migratory knowledge will be less likely to persist in short-lived species and those species prone to migrate in the smallest groups. Second, migration in small groups cannot persist without decision-making that defers towards informed leaders. Third and last, species with partial learning states will maintain migratory knowledge longer than species experiencing all-or-nothing learning due to the increased proportion of individuals with some capacity to successfully lead migrations.

## **Methods**

### *Model Description*

Here we present a discrete-time probabilistic model describing learned migration in a population that migrates in small groups. In this model we make the reasonable assumption that migratory information (e.g., migratory routes, stopover sites) is learned during migration. In this context, individuals only have the chance to learn from other, already knowledgeable individuals in their migratory group, and migratory information is equally available to all individuals in the group.

In our base model, at any time  $T$ , a population of  $N$  individuals comprises  $L_T$  individuals that have migratory knowledge (which we term learned individuals), and  $N -$

$L_T$  individuals that are naive. Each migratory time-step of the model (one round-trip migration) contains four Stages (Fig. 2.1). These are: Stage 1) formation of migratory groups, Stage 2) determination of migratory success or failure, Stage 3) updating of learning status of surviving individuals, and Stage 4) occurrence of births and non-migratory deaths.

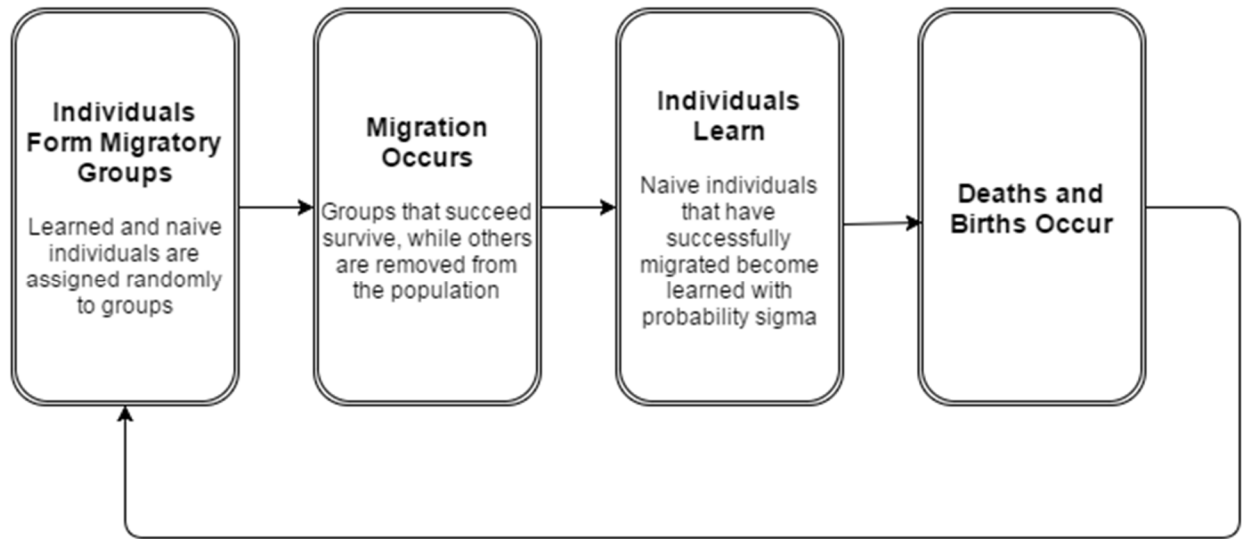


Fig. 2.1 – Figure describing model, showing steps of migratory process

We first consider two strategies for group formation (Stage 1). In Strategy 1, the Probabilistic Strategy, individuals are randomly assigned to equal-sized groups, which can differ among migrations. This random reassignment between migrations allows for horizontal transmission of migratory knowledge from learned individuals to naïve ones. In Strategy 2, the Fixed-Association Strategy, individuals are assigned to equal-sized groups, and group membership remains constant for life. This permanent assignment represents vertical transmission, where individuals learn from parents and relatives, as contrasted with the horizontal transmission found in the Probabilistic Strategy. Later, we

consider non-equal group sizes by allowing for group sizes drawn from a probability distribution (See *Grouping Dynamics*).

Migratory success (Stage 2) is determined on a group-by-group basis and depends on the presence of a learned individual. This migration is assumed as one round trip to and then from non-breeding grounds for simplicity. In the base model, any group with at least one learned individual is deemed to have migrated successfully, whereas a group without a learned individual is deemed unsuccessful, resulting in the death of all group members. Initially, we do not consider any incremental benefit from having more than one learned individual. Later, however, we consider both age-structured populations, where individuals have increasing abilities to successfully lead a migratory group as they become more experienced (See *Age Structure and Incremental Learning*) and group decision-making, where the composition of the entire group is important to migratory success (See *Spontaneous Learning and Leadership*).

Naive individuals that complete the migration by migrating in the company of learned individuals may then transition to learned status (Stage 3) with a probability,  $\sigma$ . We calculate this transition on an individual basis, where a successful migration may result in none, some, or all of the naive individuals in the group progressing to learned status. In the age-structured model this learning probability is replaced by a set of transition matrices that span the range of possible learning types (See *Spontaneous Learning and Leadership*).

Finally, our base model allows for the death of successful migrants (Stage 4), where learned and naive individuals die at a rate  $\delta$ , followed by a birth process, where any dead individuals are replaced by newborn, naive individuals. In our first model

formulations, this step, which acts outside of the migrational process, represents a precise balance between birth and death, and ensures a constant, inter-seasonal group size. In the Fixed Association strategy, we do not model a mechanism for the creation of new groups. However, we do subsequently explore the effects of variable birth processes where we allow population size to increase or decrease through a separate birth step (See *Variable Birth Processes*).

Considering the requirements of successful migration, learning, and survival, the probability of an unlearned individual becoming learned and surviving in our base model is:

$$\sigma(1 - \delta) \left( 1 - \frac{(N - L_T - 1)! (N - G)!}{(N - L_T - G)! (N - 1)!} \right)$$

where  $\sigma$  is the probability of learning the migration,  $(1 - \delta)$  is the survival rate, and the final term represents the odds of an unlearned individual being in a group with a learned individual, and therefore migrating successfully. Here,  $G$  is group size.

### *Grouping Dynamics*

To consider variable group size, we also explore scenarios in which grouping can occur based on group size distributions. For each migration, group sizes are drawn from a beta distribution,  $\beta(a, b)$  with shape parameter  $a$  and scale parameter  $b$ , spanning the proportion of the population from 0 to 1. Samples of random group size are drawn from the distribution until the cumulative number of individuals equals the migrating population. If a group is drawn whose size exceeds that of the total remaining population, the distribution is resampled for the entire population. This is done instead of

resampling only for the final group in order to greatly reduce skew towards small group sizes compared to other methods. Individuals are then randomly assigned as in our Probabilistic Strategy in the base model. We initially set  $a=2$  and  $b=20$ .

Using this group size distribution, we explore migratory success as functions of mean group size and expected lifespan. We vary the mean group size in Stage 1 by adjusting  $b$  such that  $\mu = \frac{1}{1+\frac{b}{a}}$  where  $\mu$  is our distribution mean. We vary the death probability,  $\delta$  (Stage 4) to vary our expected lifespan. We measure the probability of maintaining migratory knowledge over 200 migrations while varying our expected lifespan, measured in number of migrations, from 1 (death after one migration) to 10, and varying mean group size from 1 to 10.

To determine the effect of rare, large groups, we use our base model with fixed group sizes. We maintain group sizes of 4 individuals for all groups except one, which varies from 4 to 40 individuals. In three separate simulations, we look at this large group occurring every one, two, or five migrations. We simulate this system across a variety of expected lifespans (by varying the death probability,  $\delta$ ), ranging from 2 to 5 migrations. We then calculate the probability of migration loss, or the proportion of simulations that had lost migratory knowledge within 200 migrations.

### *Variable Birth Processes*

To test how the persistence of migratory behavior scales from a stable population to a growing population, we additionally explore the case where the birth and death terms are not equal, allowing for variation in population size. In this model, we introduce a separate birth process before deaths, where  $\gamma$  represents the birth rate per individual. We

explore the range from  $0.95\delta \leq \gamma \leq 1.05\delta$  to determine migration persistence as population dynamics vary from moderate population decline to stability to population growth. In these scenarios, we use our variable group size process to form migratory groups, as changing population size raises the possibility of different group sizes for each migration.

### *Age Structure and Incremental Learning*

To test our hypotheses regarding the success of incremental learning, we create a model that allows for individuals to learn migratory information in increasing experience levels over repeated migrations.

We consider an age-structured model with  $n$  experience levels of migratory knowledge. Within this model, we consider multiple cases for gaining knowledge. First we consider 1-step learning, where in any given migration individuals may only progress to the next level. In this case, the probability of learning,  $\sigma$ , is fixed at one, and an individual's extent of migratory knowledge corresponds to its age. Alternatively, we consider 1-step stochastic learning ( $\sigma < 1$ ). This represents delayed learning, where individuals can successfully migrate and age but not increase in their migratory knowledge. We examine both of these cases for models with both 2 and 5 experience levels.

For this age-structured model, each level of experience,  $i$ , has a learnedness values of  $l = \frac{i-1}{n-1}$  where the first experience level corresponds to  $l = 0$ , or the complete inability to lead a successful migration, and the final level corresponds to  $l = 1$ , a guaranteed ability to successfully lead a migration. Learnedness levels are thus equally

spaced within the range (0,1). Given this multi-level model, the probability of a naive individual successfully migrating, learning, and surviving becomes

$$\sigma(1 - \delta)(l_{leader})$$

where  $l_{leader}$  represents the probability of successful migration, giving the experience level of the ‘leader’ of the migratory group (which we define as the individual with the highest learnedness level).

To provide a legitimate comparison between the 2- and 5-level models, we maintain the same expected lifespan and time until full learning. This means that, in the 2-level model, an individual must successfully migrate four times before moving to the 2<sup>nd</sup> learned level. This corresponds to a 5-level model where  $l = 0$  for the first 4 experience levels and  $l = 1$  for level 5. Alternatively, we also consider the 2-level case of “fast learners,” where the expected time until learning remains 4 migrations, but is modeled stochastically. Here, we allow the learning probability to maintain the same expected time to full learning as in our 5-level model by setting  $\sigma = 0.25$ . This introduces variability in the learning ability of individuals into the model.

We further explore our multi-level model through comparison of different learning capabilities. Specifically, using transition matrices, we look at five types of learning. These are a) 1-step learning, b) 1-step stochastic learning, c) stochastic multi-step learning, d) jump-to-leader, and e) jump-to-leader stochastic learning. 1-step learning, as described above, models individuals progressing exactly one level when they successfully migrate in the same group as a more learned individual. In 1-step stochastic learning, these same individuals fail to progress to the next level with some probability,

which we set here as 0.5. Stochastic multi-step learning indicates that an individual will have an equal probability of staying in their level,  $i$ , moving to the leader's level,  $j$ , or moving to any level in-between with probability equal to  $\frac{1}{1+j-i}$ . Jump-to-leader and jump-to-leader stochastic learning model scenarios where successfully migrating individuals have the potential to increase their learnedness to exactly the level of the leader of their group (respectively without or with some probability of staying in their current state). These matrices are shown and described in detail in appendix 2.A.

### *Spontaneous Learning and Leadership in Age-structured Populations*

To explore the effects of learning in the absence of more knowledgeable individuals, we introduce a parameter,  $\omega$ , which controls the degree of spontaneous learning. When  $\omega = 0$ , individuals that are the most knowledgeable migrants in their groups, or 'leaders', are unable to progress to the next experience level even after a successful migration (because no individuals in their groups are more knowledgeable than they are). In contrast, when  $\omega = 1$ , surviving 'leaders' can learn spontaneously, progressing to the next experience level independent of the presence of a more knowledgeable individual. We explore how spontaneous learning affects the retention of migratory knowledge in our 5-level model by allowing the individuals with the highest experience levels to move up a level at a probability of  $\omega = 0.5$ . This means that, if they are not already in the highest experience level, half of the group 'leaders' will on average to progress to the next level.

As a final complexity, we investigate the importance of leaders, comparing leader-based migration (where the survival of a group depends only on its most-knowledgeable



individual), with aggregate-decision migration (where each individual contributes to the group's ability to migrate successfully). For aggregate-decision migration, we calculate  $l$ , the probability of successful migration, in three ways: 1) the mean  $l$  of all individuals in the group, 2) a weighted  $l$ , where individual contributions scale arithmetically with experience level (1, 2, 3... $n$ ) and 3) a weighted  $l$ , where individual contributions scale quadratically with experience level (1, 4, 9... $n^2$ ).

#### *Parameter Summary and Comparison against Analytical Solutions*

All simulations were run using R programming language. Table 2.1 presents a summary of all parameters appearing in the base model and scenarios, along with a description of their purpose. Results for the scenarios outlined above are, for the most part, determined through numerical simulations. Table 2.2 gives the parameter values for each simulation. However, under the assumption of fixed population and fixed group sizes, we can obtain explicit mathematical formulae for the probabilities of migratory culture loss using combinatoric approaches. These comparisons against analytical solutions appear in appendix 2.B.

Symbol	Name	Description
$N$	Population size	Number of individuals in the population
$L_T$	Learned individuals	Number of individuals knowledgeable of migration route at time T
$\sigma$	Learning probability	Probability a naive individual will become learned after a successful migration
$\delta$	Death probability	Probability of death for an individual that has successfully migrated
$G$	Group size	Size of migratory groups when constant through the population
$\beta(a,b)$	Beta distribution	Beta distribution with shape parameter $a$ and scale parameter $b$
$\mu$	Mean group size	Mean size of migratory groups when variable though the population
$\gamma$	Birth rate	Birth rate per individual
$\lambda$	Finite rate of increase	Average per-capita change in population over one time step
$i$	Level of experience	The experience level of an individual in our multi-level learning model
$l$	Learnedness value	The probability, tied to experience level, that an individual can successfully lead migratory group
$l_{leader}$	Leader learnedness	The highest experience level of an individual in a given group
$\omega$	Spontaneous learning	The probability of a group leader progressing to the next level of experience, given that the leader is not at the highest experience level

**Table 2.1** – List of variables included in our model

Simulation	Description	N	$L_0$	$\sigma$	$\delta$	$G$	$\gamma$	Experience Levels	$I$	$\omega$
Fig. 2.2	Group size vs. expected lifespan	200	100	0.2	0.1-1	beta(2,var.)	1-10	2	1	0
Fig. 2.3	Fixed vs. random group association	12	4	0.2	0.1	4	---	2	1	0
Fig. 2.4	Effect of rare, large groups	200	100	0.1	0.2-0.5	4+	---	2	1	0
Fig. 2.5	Effect of the finite rate of increase	200	100	0.1	0.5	beta(2,20)	0.95-1.05	2	1	0
Fig. 2.6	Age structure & spontaneous learning	200	N/A	Var.	Var.	beta(2,50)	1	2-5	0-1	0 - 0.5
Fig. 2.7	Comparison of learning mechanisms	100	N/A	0.5	Var.	beta(2,80)	1	5	0-1	0
Fig. 2.8	Leadership and decision-making	250	N/A	1	0.1-0.9	beta(2,20)	1	5	Var.	0

0 **Table 2.2** – List of simulation parameter values

## Results

In the base model with variable group sizes, long-lived populations that aggregate in large groups best maintained migratory knowledge within small populations over many generations (Fig. 2.2). For lifespans exceeding 4 years and group sizes exceeding 3 individuals, migratory culture consistently persisted over the simulation period of 200 migrations. Through our analyses we will consider persistence for 200 migrations as successfully maintaining migratory knowledge. In contrast, populations in which individuals were shorter-lived or in which migration occurred in smaller groups consistently lost migratory behavior within this same time period.

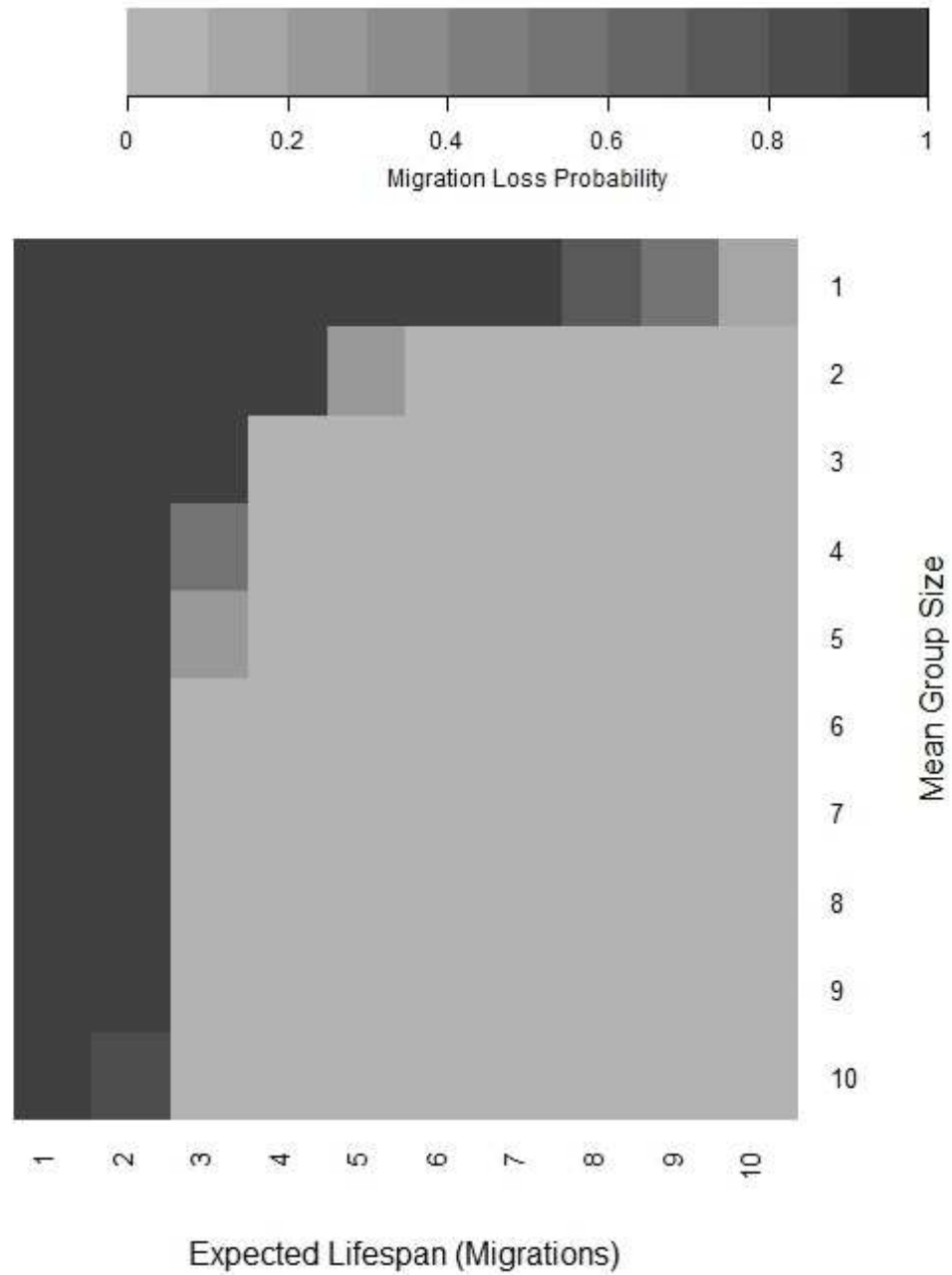


Fig. 2.2 – The probability of migratory culture loss depends on an interaction between mean group size and expected lifespan. Populations with either small group sizes or short-lived individuals are most at risk. Parameters for this simulation were  $N = 200$ ;  $L_0 = 100$ ;  $\sigma = 0.2$ ;  $l = 1$ ;  $\omega = 0$  while  $\delta$  and  $\gamma$  varying along our axes.

The Fixed Association strategy, where individuals remain in the same migratory group for life, caused migratory persistence to decline rapidly compared with the Probabilistic Strategy, where groups re-formed after each migration (Fig. 2.3). We view these two strategies as bounds on what could be expected in real populations, and assume that most real species are likely to have a group association that falls between these two extremes. Rare, large groups increased the probability of migratory persistence, even if they only occur every five migrations (Fig. 2.4). The size of the rare, large groups required to maintain migratory behavior becomes greater as its occurrence becomes more infrequent (Fig. 2.4).

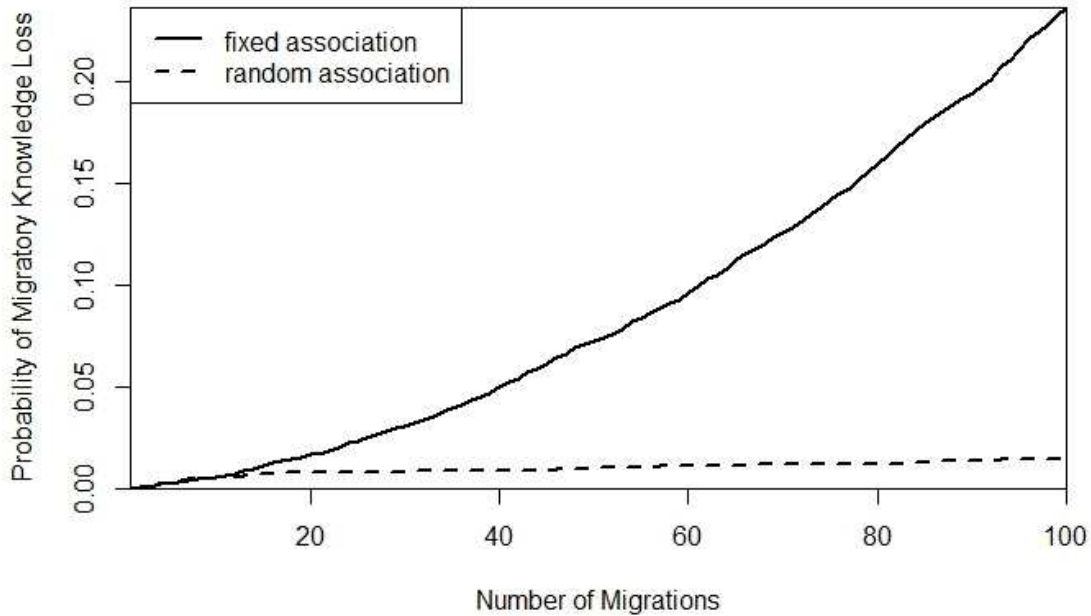
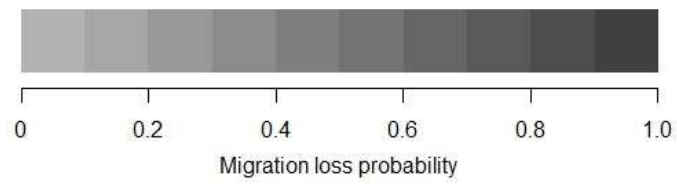
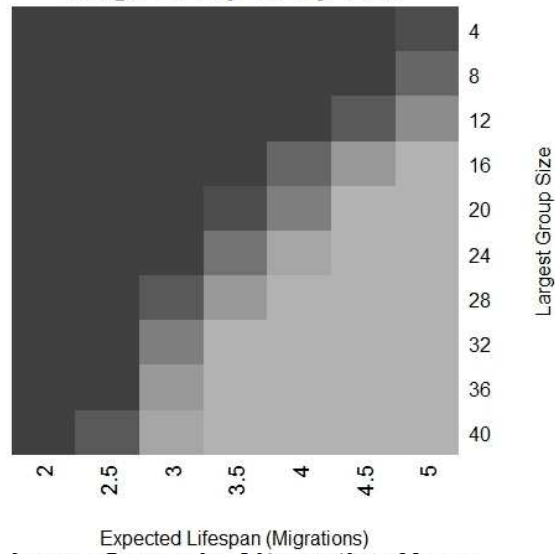


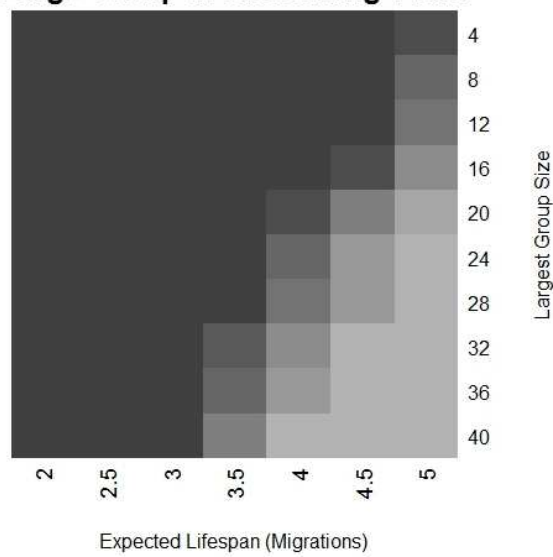
Fig. 2.3 – Strategies for group formation (fixed association versus random association) differ greatly in their predicted influences on the probability of culture loss across successive migrations. Plotted are results for  $\sigma = 0.2$ ,  $\delta = 0.1$ , with  $N = 12$  individuals in 3 groups of four individuals. Initially, there were three learned individuals ( $L_0 = 3$ ) with one learned individual in each group. Other parameters used in this simulation are  $l = 1$ ;  $\omega = 0$ .



**Large Group Every Year**



**Large Group in Alternating Years**



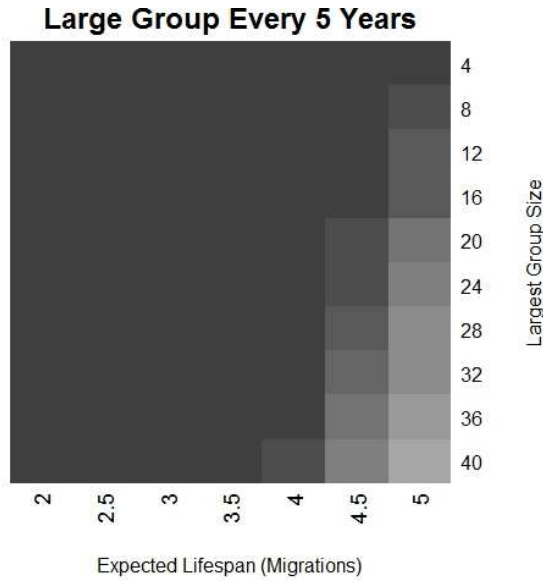


Fig. 2.4 –Migratory persistence as a function of variation in lifespan (x-axes) and the largest group in the population (y-axes). One group in each population is fixed at this largest size, and all other groups are of size 4. These largest groups occur every year (Panel 1), every other year (Panel 2), and every five years (Panel 3). Parameters for this simulation were  $N = 200$ ;  $L_0 = 100$ ;  $\sigma = 0.1$ ;  $l = 1$ ;  $\omega = 0$  while  $\delta$  varies along the x axis.

The finite rate of increase for the population did not greatly affect the probability of migration loss at small perturbations from steady state ( $\lambda = 0.99, 1.01$ ) (Fig. 2.5). With rapid population growth ( $\lambda = 1.05$ ), the migratory behavior was stable over 100 years. However, with rapid population decline ( $\lambda = 0.95$ ), the probability of retaining migratory behavior steadily declined over time. This loss of migratory behavior in the  $\lambda = 0.95$  model is in the same timeframe as we would expect the population to become lost through decline: a population with  $\lambda = 0.95$  is expected to be under 1% of its original size after 100 time steps.



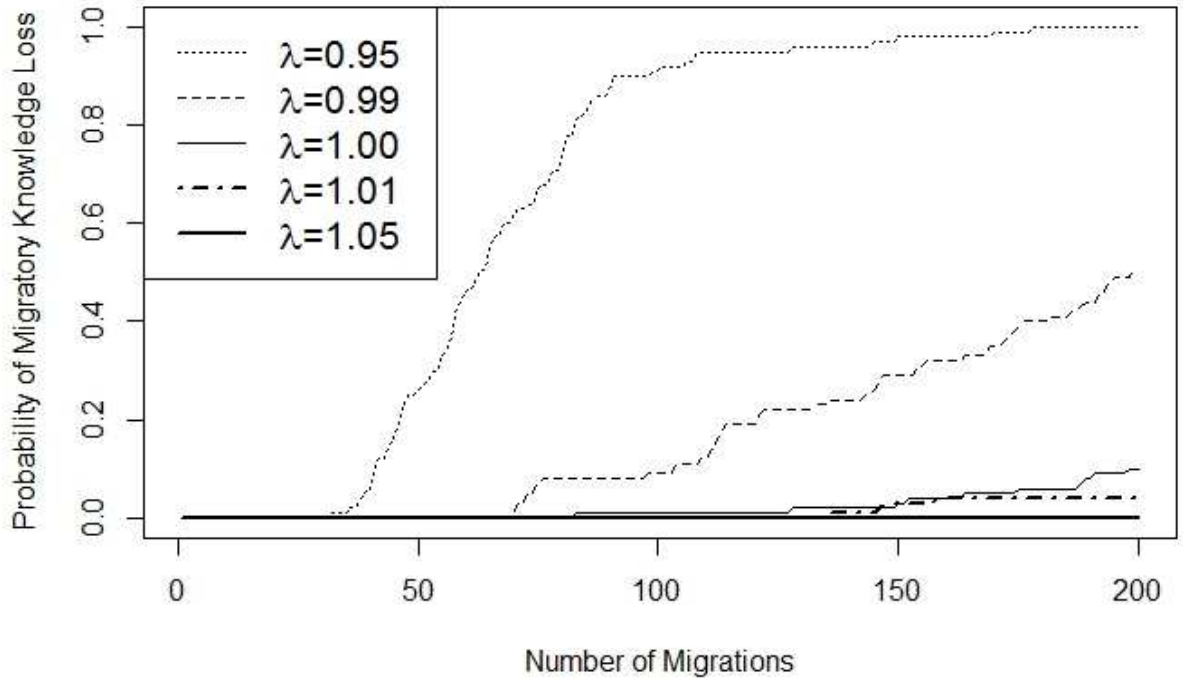


Fig. 2.5 – How the finite rate of increase ( $\lambda$ ) influences the loss of migratory culture when migration occurs in groups. This figure presents results from a 2-level learning model where a naive individual can progress to the learned state with probability  $\sigma=0.1$  after successfully completing a migration. Individuals die with  $\delta = 0.5$ , and initial populations consist of  $N_0 = 200$  with  $L_0 = 100$ . Further parameters for this simulation were  $l = 1$ ;  $\omega = 0$ .

Of our multi-level models, our 2-level model with “fast learners” showed the best retention of migratory culture, with no migratory loss over 200 migrations (Fig. 2.6). Of the populations undergoing 5-level gradual learning, those with Spontaneous Learning (i.e., individuals could progress to the next experience level after a successful migration without the presence of a more learned individual) were the most successful at maintaining migratory culture, but less so than the 2-level model with “fast learners.” Furthermore, we found that those learning processes that allowed for non-zero

probabilities of skipping experience levels (i.e., the stochastic multi-step, jump-to-leader stochastic learning, and jump-to-leader models of learning) all maintained migratory culture more successfully than those that only allowed incremental progression (Fig. 2.7).

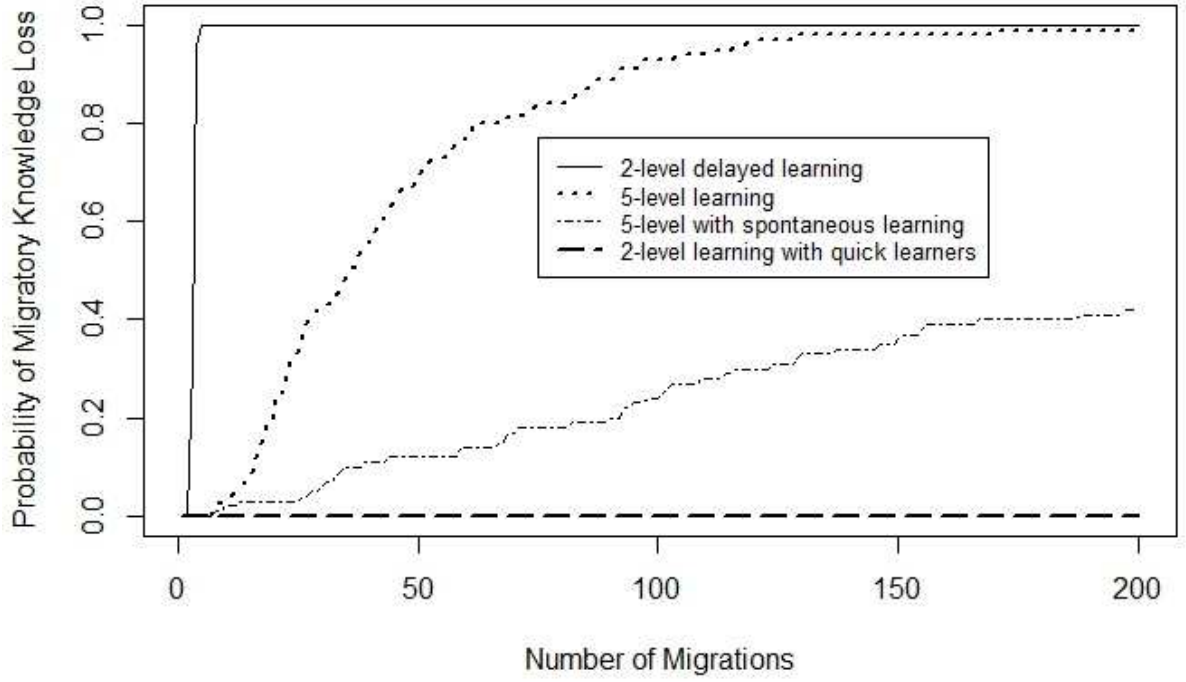


Fig. 2.6 – The loss of migratory culture as a function of age-structured learning. Learning models are defined in the Methods subsection *Age Structure and Incremental Learning*. Here,  $N = 200$  with equal numbers of individuals initially in each experience level.  $\delta \in \{0.1, 0.3, 0.5, 0.7, 0.9\}$  for sequential experience levels in all cases except for 2-level learning with quick learners, where  $\delta \in \{0.1, 0.9\}$ .  $\sigma = 1$  for all learning models except for 2-level learning with quick learners, where  $\sigma = 0.25$ , meaning that all models have an expected time until complete knowledge of 4 migrations. Ability to successfully a migratory group ranged from complete ( $l = 1$ ) at the highest experience level to absent ( $l = 0$ ) at the lowest experience level, with intermediate levels being distributed evenly in that range.  $\omega = 0.5$  for the 5-level with spontaneous learning simulation, while  $\omega = 0$

for all others.  $\gamma = 1$  for all simulations.

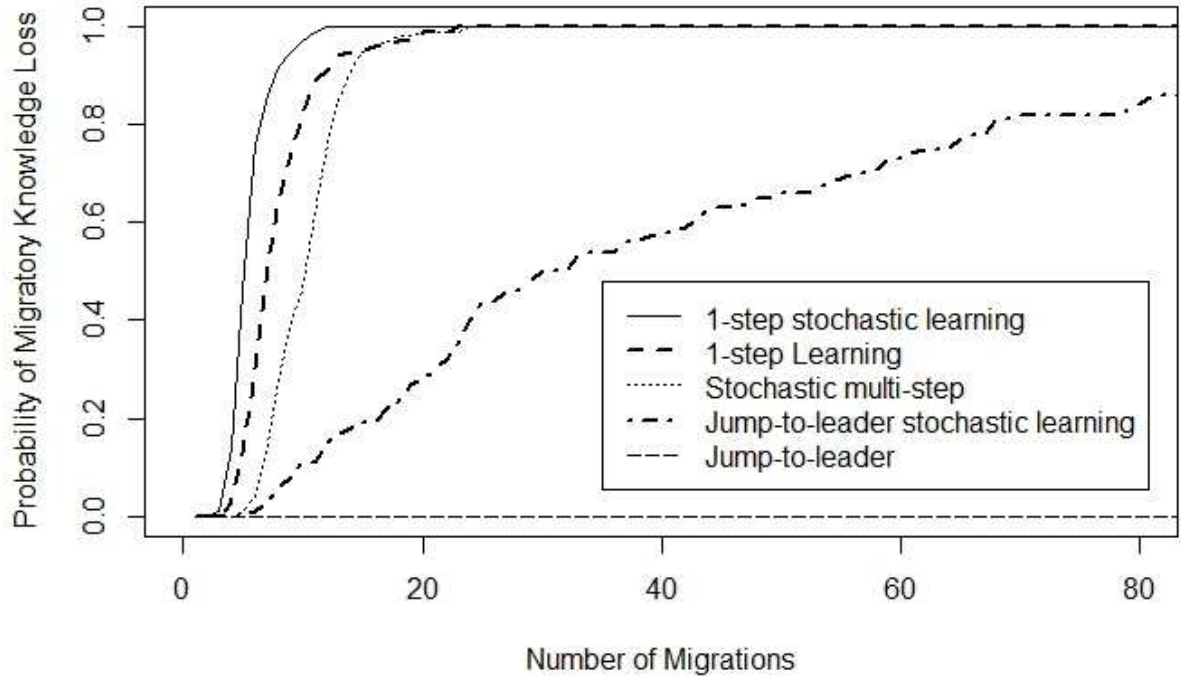


Fig. 2.7 – How different Learning Mechanisms affect the loss of migratory culture. All results are for a population size of  $N = 100$  individuals and a learning model with 5 experience levels each initially containing 20 individuals. Learning probabilities are described in *Age Structure and Incremental Learning* and Appendix 2.A.  $\delta \in \{0.1, 0.3, 0.5, 0.7, 0.9\}$  and  $\gamma = 1$ .

Leader-based migration, where migratory success was determined by the knowledge status of the most experienced individual in a migratory group, greatly outperformed the other decision-making mechanisms (i.e., averaged decision-making, arithmetic weights and quadratic weights; Fig. 2.8). Arithmetic and quadratic weights offered only modest improvements in the persistence of migration compared to averaged decision-making.

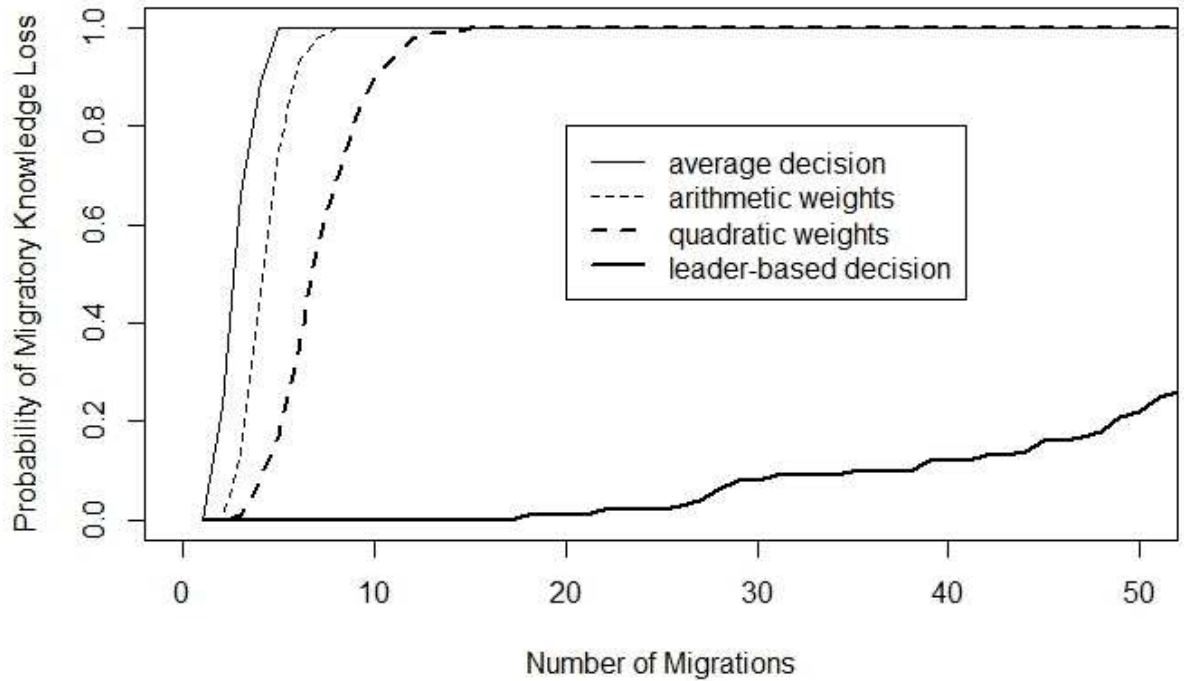


Fig. 2.8 – Effects of different kinds of decision-making on the loss of migratory knowledge. Leader-based decision-making holds a clear advantage against other kinds of group decision-making, where all individuals in the migratory group contribute regardless of their experience levels. This comparison uses the 5-level model. Here,  $N = 250$  with equal numbers of individuals initially in each experience level.  $\delta \in \{0.1, 0.3, 0.5, 0.7, 0.9\}$ ,  $\sigma = 1$ , and  $\gamma = 1$ .

## Discussion

The persistence or loss of migratory behavior in species with group migration and social learning is not solely determined by population-specific factors, grouping dynamics, or learning processes. Rather, the summation of all three of these factors can contribute to migratory loss. We will address each of these causes in turn to better understand their importance in maintaining migration in small populations.

The size of migratory groups affects how well information can be spread within a population. Similarly, average lifespan determines the number of migrations an individual will perform. Consequently, both group size and species lifespan are key variables determining how well a small population will maintain migratory behavior. We found that populations with the most persistent migratory behavior were those with long lifespans and relatively large group sizes (Fig. 2.2). In populations with a longer average lifespan, the average learned individual is able to share knowledge with naive individuals over repeated migrations. Likewise, in populations with larger migratory groups, a single learned individual can, on average, spread migratory knowledge to more individuals per migration. Conversely, our model predicts low migratory success for populations in which individuals are short-lived and migrate in small groups. We believe this corresponds with the dearth of examples of animals that fall into this category, as short-lived species would likely require very large population sizes to maintain learned migration due to low individual transmission rates. This fits with the expectation that species with a socially learned migratory behavior are likely to be long-lived with highly social behavior (Bauer et al. 2011). Species exhibiting partially or completely learned migration tend to be long-lived (Higdon et al. 2011, Blank et al. 2012), have large group sizes (Huse et al. 2010, Hayakawa & Furuhashi 2012), or both (Nelson 1998, Chernetsov et al. 2004).

Migratory success also varies based on the importance of leaders and the role of knowledgeable individuals during the migratory process. As expected, we found leader-based migratory behavior to produce the highest persistence of migratory knowledge (Fig. 2.7), as this behavior relies on the best information present in each migratory group.

Interestingly, not only did average decision-making perform poorly, but weighted decision making also produced rapid decline of migratory culture, even when quadratically weighted, which made more experienced individuals disproportionately important. In some species, for example whooping cranes (Mueller et al. 2013), migratory efficiency is closely linked to the presence of older, more experienced individuals and is relatively insensitive to the composition of the rest of the group, including variation in group size. In some fish, the level of experience in an environment, independent of age, determines individuals to be followed (Reebs 2000). However, quorum sensing, or collective behavior that follows the preference of the majority, suggests an alternative to leader-based movement that can improve movement accuracy (Ward et al. 2008). As quorum sensing necessitates large group sizes for accurate consensus-making, smaller groups would therefore be unusually reliant on leader-based decision-making in comparison. Indeed, with even a moderately higher cost for leading than following, models have suggested that small groups will rely on few individuals to lead, a proportion that decreases with group size (Guttal & Couzin 2011). Conversely, the notion that larger groups necessitate a higher number of individuals capable of leading would make a single-leader strategy less viable at large group sizes.

The manner in which migratory groups are formed in a small population can greatly restrict or permit the transfer of migratory information within the population. We found that fixed group association, similar to vertical transmission of knowledge, severely underperformed random association in terms of migratory persistence (Fig. 2.3). This is not surprising, because deterministic group associations can be thought of as a metapopulation model with no connectivity. That is, once a migratory group loses its last

learned individual, the group is unable to be rescued by any other group. By contrast, random association provides mixing similar to increased connectivity in metapopulations. Although true group formation is likely to lie somewhere between fixed group associations and fully random associations, these two scenarios set limiting bounds on the rate of migratory culture loss. Social aggregations can be determined by relatedness for some species (Richard et al. 1996), whereas others form independently of kinship (Mueller et al. 2013). In bottlenose dolphins, these strategies are both present, causing some social groupings to be fixed and others more liable to change (Krützen et al. 2003). Furthermore, fixed group associations may only exist in one life stage, such as mother humpback whales migrating with their calves, where further migratory groups are unrelated (Valsecchi 2002). Despite the lower performance of fixed group strategies at low population levels (Fig. 2.3), these strategies can be found in real species with larger populations, where other benefits, such as kin altruism, may make the strategy favorable.

Furthermore, we found that the relative sizes of the migratory groups within a population greatly influenced whether that population remained migratory (Fig. 2.4). Given constant population size, persistence of migratory behavior increases as the largest group size increases. From a learning perspective, mass migration, or having the entire population migrate in one group, would permit the greatest spread of information, as one individual could teach the entire population under our assumed dynamics. Indeed, we can see the importance of rare, large groups in Fig. 2.4, as few simulations of groups of four individuals maintained migratory behavior over 200 migrations. In contrast, having a slightly larger group every migration or a rare, large group increased the probability of migratory persistence for many lifespans. This might be of particular importance in

species such as herring, where individuals exhibit partially-learned migration in large groups varying from hundreds to millions of individuals (Misund 1993, Huse et al. 2010). As it is theorized that these herring require a certain percentage of learned individuals to successfully target their destination (Huse et al. 2002), smaller groups sizes might be prohibited by a low ability to learn or other factors (such as information exchange) that would slow the spread of migratory knowledge.

The mechanisms by which individuals learn are empirically harder to measure than group size or longevity, but such mechanisms nevertheless greatly influence the persistence of migratory culture. Some species, including some fish (Kieffer and Colgan 1992) and whooping cranes (Mueller et al. 2013), have incremental learning whereas others, such as golden shiners (Reebs 2000), ravens (Foley et al. 2008), and elephants (Wright et al. 2003) have defined “leaders” and “followers” (King & Cowlshaw 2009). We found that a population with 5 levels in which learning occurred incrementally was able to maintain its migratory culture far longer than a population with leaders that learn all at once (stepwise) after 4 migrations (2-level delayed learning) (Fig. 2.6). In contrast, when we leveled the playing field so that groups had equal expected times until complete learning, a “leaders” and “followers” behavior with variation in how quickly individuals learn (2-level learning with quick learners) more successfully maintained migration in a small population as compared to incremental learning. To expand on this, even though a population with 2-level learning may have more completely naive individuals than a population of equivalent size in which learning occurs gradually over 5 experience levels, the possibility that a small number of individuals can become completely informed after the first or second migration can prevent the loss of migratory culture. In contrast,



populations experiencing 2-level delayed learning have neither a buffer of partially learned individuals nor quick learners, making this strategy much less successful.

Spontaneous learning was another learning behavior that provided a mechanism for the persistence of migratory behavior. In our 5-level model of incremental learners, allowing for spontaneous learning (where successfully migrating individuals could progress to the next experience level without having joined a group with a more knowledgeable individual) provided a substantial buffer against the loss of migratory culture (Fig. 2.6). To conceptualize spontaneous learning, we can think of a populations where groups are migrating with some element of randomness. Of those moving randomly, individuals in groups that succeed retain the ability to complete this journey in future migrations, in effect causing them to learn without being taught by other individuals in the group. In our model, adding spontaneous learning allowed a parameterization that had previously seen complete loss of migratory behavior within 100 migrations to improve to roughly a 50% chance of persisting through 200 migrations (Fig. 2.6). In a migrating population, this would represent the difference between less-informed migratory groups failing to become better leaders and the more successful strategy of these groups learning by trail-and-error.

In general, the ability to skip experience levels (whether by the stochastic multi-step mechanism or the jump-to-leader mechanism) proved far more successful than incremental learning as a means of maintaining migratory behavior. Indeed, allowing individuals to skip experience levels had a far greater effect than removing the possibility of not learning (Fig. 2.7). Again, this implies that quick learners provide great benefit in small migratory populations. This is contrary to the observed concept of reinforcement

learning, where satisfactory outcomes reinforce behaviors over time (Sutton et al. 1992). However, reinforcement learning is computationally simple (Sutton et al 1992), and slower learning may provide a mechanism to deal with variable quality of migratory knowledge. Given limited capacity for memory, the ability to reinforce and maintain the most current information allows individuals to update route information as environmental conditions change (Fagan et al. 2013). It is worth noting that, given time and stability, a population undergoing the “jump-to-leader” behavior will eventually lose intermediate experience levels and become a 2-level structured population, independent of the probability of jumping. Therefore, this population would seem to only persist with a multiple-level learning behavior in changing environmental conditions, where the information being passed among individuals has some varied utility, such as changing migratory routes.

## **Conclusions**

Our results highlight the importance of experienced individuals to migration persistence. In some cases experience will vary directly with age, whereas in other cases experience derives from particularly fortuitous social interactions. In either case, these models emphasize that a small number of individuals with particular trait values (here, experience level) can have outsized conservation relevance. These results are intriguing because they parallel findings from other systems of conservation interest. For example, a few robust, mature males may contribute differentially to the reproductive health of wildlife populations, but these same males are desired as hunting trophies (Coltman et al. 2003). Likewise, in marine fisheries, a few females of extraordinary size may have

massively disproportional impacts on recruitment rates on when reproductive potential scales nonlinearly with size (Trippell 1995, Baskett et al. 2005).

One limitation of our model is that we generally assume that uninformed migrants die because they fail to migrate successfully to the correct destination. While migratory pathways for obligate species may remain consistent over long periods of time, straying (i.e, deviating from an established migratory route) is certainly not an exclusively fatal behavior. Indeed, within the framework of the “adopted-migrant hypothesis” (McQuinn 1997), novel breeding grounds may arise in years of high reproductive output where many naive individuals migrate without learned individuals but nonetheless arrive in suitable habitats (Huse et al. 2002, Huse et al. 2010). However, in the context of our model, reducing the penalties for uninformed movement should not qualitatively alter our conclusions. Overall, our findings suggest that rare, large migratory groups and regular mixing between groups are key to the persistence of learned migratory behavior in small populations. The opportunity for “quick learners,” even if rare, can provide a vital mechanism for sustaining migratory behavior in small populations. Species with short lifespans appear to be at particular risk of migratory loss when faced with declining numbers.

## **Chapter 3: The rescue of animal migration using memory-based movement on sparse resource landscapes**

### **Abstract**

Animal migration is an important mechanism in maintaining population integrity, yet is a globally at-risk behavior. Partial differential equations provide a good system for modelling this movement and the resource landscape that it is driven by. We use a system of reaction-diffusion equations to investigate the interplay between behavior types and ability to follow resources that are increasingly sparse in space and time. We look at parameterizations where populations exhibiting advection, or the following of a resource gradient, and diffusion are unable to persist, and investigate the effect that memory has on their survival. We model memory as a form of advection responding to the resource landscape at a previous point in time. We also investigate a combined approach, including advection on local and previous time scales. We find that when resources become scarce, resource-following becomes increasingly important for the survival of populations. However, in resource scenarios where advection fails to maintain migration, and therefore sufficient population size, we find that memory will, in certain scenarios, provide a rescuing effect. Furthermore, allowing a population to react to the resource landscape based on memory and local observation produced the largest final populations, as information leading towards a resource was available for the longest period of time in this scenario.

### **Introduction**

The migration of animals over long distances is a globally threatened phenomenon (Wilcove and Wikelski 2008), and the loss of migratory behavior often

results in the drastic reduction of the population size (Bolger et al. 2008). Even when the cause of the cessation of migration is removed, such as the removal of fencing for overland migration, migratory behavior does not always resume (Boone and Hobbs 2004). Yet, our understanding of the behavioral mechanisms leading to the development of migration is still incomplete. Depending on the information present, animals may be able to sense environmental clues and adjust migratory behavior in-transit, or they may be forced to rely on individual memory or ancestral knowledge (Winkler et al. 2014). The migratory behavior of species relying on memory may be especially threatened with a rapidly changing environment. An understanding of how migration develops in response to an information-poor environment is therefore important for the conservation of species whose migration has come under threat. Specifically, determining the interplay between behavior types and resource distributions is vital to understanding what features are important towards maintaining the migratory phenomenon when resource-tracking alone is not enough to explain migratory formation.

From a modeling standpoint, partial differential equation (PDE) systems allow for a useful amount of variation in both the distribution of resources and the type of animal behaviors modeled. Due to this versatility, PDE frameworks have been used to model ecological processes that include dispersal and invasion, the spread of disease, critical patch size, and species coexistence (Holmes et al. 1994, Garlick et al. 2011). By allowing a continuously changing resource landscape, PDEs provide an ideal modeling framework for studying drivers of migration. Through the application of reaction-diffusion equations, a specific form of PDE, to animal movement (Skellam 1951), we also allow movement behavior to be broken down into two components: diffusion and

advection. Diffusion is a random, Brownian motion that ecologically represents random searching or dispersal. Advection, however, represents a directed movement along a gradient, representing the perception and processing of environmental data by the individual followed by reactive movement.

However, variations in model formulation expand these reaction-diffusion models away from their limitation that individuals respond only to information that is local in space and time. In one deviation, studies have used non-local information to model perceptual ranges of animals, where dispersal is determined by a range of surrounding information (Pe'er & Kramer-Schadt 2008, Fagan et al. 2017). Also useful, and key to this study, is the addition of memory to animal movement models. Agent-based models have been a popular choice for modeling spatial memory (Börger et al. 2008, Fagan et al. 2013), as including memory can help individuals avoid areas they have previously visited (Fronhofer et al. 2013, Schlägel & Lewis 2014) or seek out high-quality patches as return points (Van Moorter et al. 2009, Boyer & Walsh 2010, Berger-Tal & Avgar 2012, Riotte-Lambert et al. 2015). However, only a few ecological studies (e.g. Potts et al. 2014, Potts and Lewis 2016) have looked at memory in an Eulerian system, such as a reaction-diffusion formulation. We propose here a method to allow populations to also react to resource and population distributions at a previous time step. This will allow for populations to follow gradients of resources from their collective memory, potentially providing useful movement cues when information about the resource is scarce.

Here we investigate how memory interacts with advective movement and the role that memory plays in low-information resource environments. We first look at competing populations exhibiting advective-diffusive movement without memory to see

how the competitive outcomes and stable population sizes change across parameter space. We then, using parameterizations where advection fails, investigate the effects of memory as a potential rescue mechanism. We hypothesize that populations using both advection and diffusion will, on all resource landscapes, outcompete populations using just diffusion and that, in cases where advection and diffusion alone cannot maintain a migratory population, memory will serve as a successful behavior to increase equilibrium population size.

## Methods

### *Reaction-diffusion equations*

To do so, we will look at two competing populations using the following set of reaction-diffusion equations:

$$(1) \quad d_u \partial_{xx} u - a_u \partial_x u \partial_x r(x, t - \delta_u) + (r(x, t) - u - v)u = \partial_t u$$

$$d_v \partial_{xx} v - a_v \partial_x v \partial_x r(x, t - \delta_v) + (r(x, t) - v - u)v = \partial_t v$$

on  $\Omega = (-15, 15)$

$$d_u \partial_x u - a_u u \partial_x r(x, t - \delta_u) = 0$$

$$d_v \partial_x v - a_v v \partial_x r(x, t - \delta_v) = 0$$

on  $\partial\Omega$

Here, the first terms, of the form  $d_i \partial_{xx} i$ , represent the diffusive process in the equation.

The value of  $d_i$  for each population  $u$  and  $v$  determines the strength of the diffusion for

that population. The term  $a_i \partial_x i \partial_x r(x, t - \delta_i)$  gives both our advection and memory components, where the parameter  $a_i$  determines the strength of advection. The parameter  $\delta_i$  determines the time scale at which the memory component of advection acts. The resource,  $r(x, t)$ , is given as a function of both position on our axis and time. The term  $(r(x, t) - v - u)i$  describes the response of the population to the resource level as well as the population levels of both the  $u$  and  $v$  populations

When  $a_i = 0$  and  $d_i$  is nonzero, these equations give the behavior class of pure diffusion. When both  $d_i$  and  $a_i$  are nonzero and  $\delta_i = 0$  the population exhibits the behavior of diffusion with advection. Finally, when  $\delta_i \neq 0$ , a memory component is added to advective behavior, where the population responds to the location of a resource  $\delta_i$  amount of time in the past.

### *Resource landscapes*

We consider three dynamic, one-dimensional resource landscapes. These time-varying functions are a Gaussian distribution that translates between two endpoints, a Gaussian distribution that pulses between two poles, and an approximately uniform distribution that pulses between two poles.

The translating Gaussian distribution can be written as

$$(2) \quad r(x, t) = \frac{1}{\sqrt{2\pi}\sigma_x} e^{-(x-x_0(1+\xi_x \cos(\pi \frac{2t}{T})))^2 / (2\sigma_x^2)}$$

where  $\sigma_x$  is the standard deviation of the Gaussian resource distribution,  $x_0$  is the mean position of the resource distribution,  $x_0 \xi_x$  is the maximum deviation of the distribution



away from the mean position, and  $T$  is the length of each oscillatory period. For our analyses  $\sigma_x = 1$ ;  $x_0 = 15$ ;  $\xi_x = 5$  and  $T$  is variable.

Similarly, we write the pulsing Gaussian distribution as

$$(3) \quad r(x, t) = \frac{1}{\sqrt{2\pi\sigma_x}} e^{-(x-x_0)^2/(2\sigma_x^2)} \sum_{i=0}^{n_T} e^{-(t-iT)^2/(2\sigma_t^2)} +$$

$$\frac{1}{\sqrt{2\pi\sigma_x}} e^{-(x+x_0)^2/(2\sigma_x^2)} \sum_{i=0}^{n_T} e^{-(t-(i+\frac{1}{2})T)^2/(2\sigma_t^2)}$$

where  $n_T$  is the number of oscillatory periods in the length of our model,  $T$  is the length of each oscillatory period, and  $\sigma_t$  is the standard deviation of the normal distribution describing the pulse. These values vary by analysis.  $\sigma_x$  remains the standard deviation of the Gaussian resource distribution while  $x_0$  now represents the mean position of each resource pulse, located symmetrically around  $x = 0$ .

Finally, we approximate the uniform distribution using the Fourier series of a rectangular pulse wave

$$(4) \quad h_{x_0}(x) = \frac{\tau}{P} + \sum_{n=1}^M \frac{2}{n\pi} \sin\left(\frac{\pi n \tau}{P}\right) \cos\left(\frac{2\pi n}{P}(x \pm x_0)\right) \left(1 - \left(\frac{n}{M}\right)^2\right)$$

where  $\tau$  represents the width of the pulse,  $P$  is the spatial period between pulses,  $M$  is the number of series coefficients used, and  $x_0$  represents the locations, positive and negative, or our two pulses. Here,  $\tau = 2$ ,  $P = 30$ , the length of our simulated space,  $M = 100$ , and  $x_0 = 5$ . Adding in our time variation, we get the formulation of our resource function

$$(5) \quad r(x, t) = h_5(x) \sum_{i=0}^{n_T} e^{-(t-iT)^2/(2\sigma_t^2)} +$$

$$h_{-5}(x) \sum_{i=0}^{n_T} e^{-(t-(i+\frac{1}{2})T)^2/(2\sigma_t^2)}$$

where  $n_T$ ,  $T$ , and  $\sigma_t$  are the same as in the pulsing Gaussian distribution. These values vary by analysis.

Symbol	Name	Description
u, v	Populations	The two competing populations in our model
$d_i$	Diffusion Rate	The rate of random movement for population $i$
$a_i$	Advection Rate	The rate that a population $i$ moves up a resource gradient
$\delta_i$	Memory Time Scale	The time before present at which population $i$ senses the landscape
$r(x, t)$	Resource Landscape	Resources changing both in space and time
$\sigma_x$	Std. Dev. - Space	Standard deviation of the resource along x
$x_0$	Mean position	Mean position of translating Gaussian resource function
$x_0\xi_x$	Max. Deviation	Maximum deviation away from $x_0$ for translating Gaussian resource function
$T$	Oscillatory Period	The length of time required for one full resource cycle
$n_T$	Total No. of	The number of periods in our modelled length of

	Periods	time
$\sigma_t$	Std. Dev. - Time	The standard deviation describing the normal distribution of our two pulsing resource functions
$\tau$	Width of Pulse	The width of the non-zero part of our uniform resource function
$P$	Spatial Period between Pulses	The space between pulses in a pulse wave Fourier transform, trivial in this case, as each end of the function has only one pulse
$M$	Series coefficients	The number of series coefficients used for our Fourier approximation

**Table 3.1.** Names and descriptions of symbols used in this study.

### *Solutions*

We solve the reaction diffusion equations numerically for each scenario using Mathematica's built in NDSolve function. We find numeric solutions modeling both one diffusion-only population and one diffusion and advection population. We run this formulation for each resource function at three different period lengths ( $T \in \{20,40,60\}$ ), for three diffusion parameterizations ( $d \in \{0.2,0.5,1.0\}$ ), and across ratios of advection to diffusion ( $a/d$ ) ranging from 0 (no advection) to 25 (heavy advective movement).

### *Memory*

After identifying a resource parameterization where advection and diffusion fail to maintain a strong population, we also find numeric solutions for populations that use

memory-based advection. Initially, we look at our original formulation for memory (1). As a final complexity, we also include a population that advects to both the current resource landscape and the resource landscape at a previous time. This modifies (1) to now read

$$(6) \quad d_u \partial_{xx} u - a_u \partial_x u \partial_x r(x, t) - a_u \partial_x u \partial_x r(x, t - \delta_u) + (r(x, t) - u - v)u = \partial_t u$$

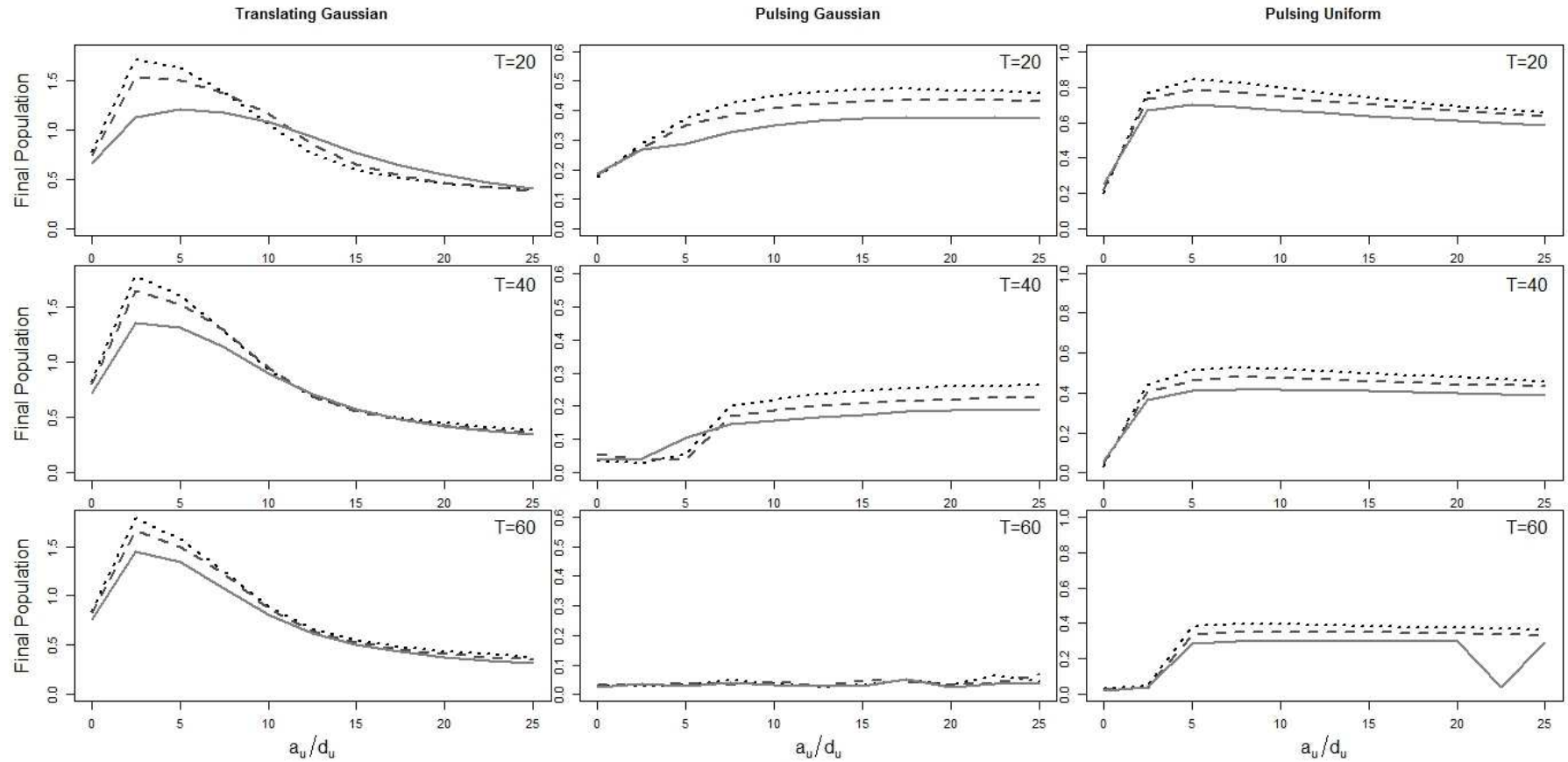
we vary the time scale upon which memory is acting from  $\delta_i = 0$  to  $\delta_i = T$ .

## Results

### *Translating Gaussian Resource Function*

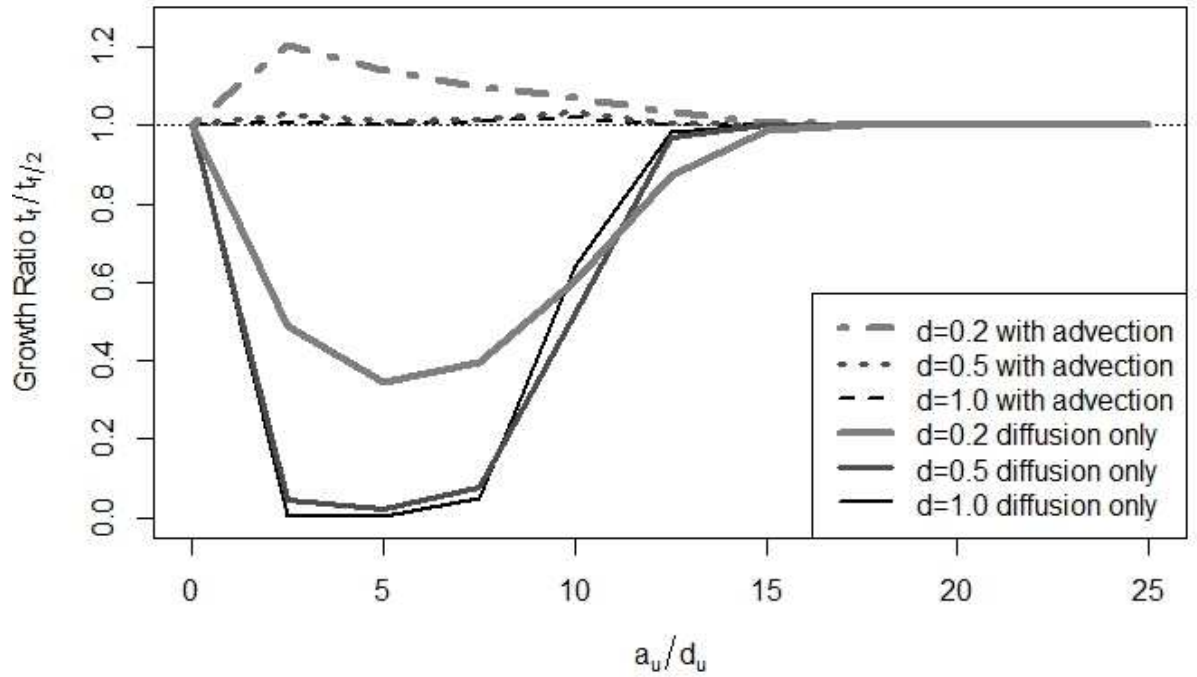
On the translating Gaussian resource landscape we found that as we increased the ratio of advection to diffusion we crossed a threshold from the advective population having an extremely high population level at the end of our time period ( $>1.7$  at  $a/d = 2.5$ ) to the final population crashing ( $< 0.4$  at  $a/d = 25$ ) (Fig. 3.1). This trend was consistent between all resource translation speeds ( $T \in \{20, 40, 60\}$ ) and all diffusion parameterizations ( $d \in \{0.2, 0.5, 1.0\}$ ). Consistently, advective populations with higher diffusion rates, and therefore higher advection rates, had higher ending populations than populations with the same  $a/d$  ratio (Fig. 3.1). The transition to declining ending populations in our model corresponded with a transition between the advective population excluding the purely diffusive population and coexistence between the two (Fig. 3.2). Results were similar for all other resource translation speeds (not shown).





**Figure 3.1.** An advective-diffusive population competing against a purely diffusive population. Y-axis values give the final total population of the advective-diffusive population after 600 time steps. Y-axis ranges are preserved within, but not between columns. Each column represents one of the three resource landscapes used in this study. The x-axis represents the

ratio between the advective and diffusive parameter values, with increasing value of  $a/d$  representing increasing advective behavior. Each plot contains three lines, representing different values of diffusive parameters,  $d = 0.2$  (solid grey line),  $d = 0.5$  (dashed line), and  $d = 1.0$  (black, dotted line).



**Figure 3.2.** The ratio of the population at the numerically solved period's end to the population at the halfway point ( $t_f/t_{f/2}$ ) shown for parameterizations between a population undergoing diffusion with advection (dashed lines) and a population undergoing pure diffusion (solid lines) at different diffusion strengths. A growth ratio of 1.0 indicates a stable population size while anything less indicates a population being outcompeted and anything greater represents a growing population. Analyses were run for 600 time steps, or 30 migration cycles with a resource translation period of 20 time steps.

### *Ecological Interpretation*

In an environment where resources are consistently available and individuals can move freely, low levels of resource-tracking (advection), in concert with random searching (diffusion), greatly outcompetes exclusive random searching. This is



independent of the rate that the location of the resource changes (Fig. 3.1). However, populations with higher affinity for resource-tracking, while still successful, fail to exclude species dependent on random searching (Fig. 3.2). Instead, we see coexistence which is possibly explained as resource partitioning. This would occur if the two species end up differentially occupying the resource space, with the resource-tracking population occupying the highest-quality habitat while the random searching population has higher abundances in lower quality habitat.

#### *Pulsing Gaussian Resource Function*

When the Gaussian resource function pulsed between two poles instead of translating, we found that our final population levels were much smaller (all less than 0.5) (Fig. 3.1). For both our  $T = 20$  and  $T = 40$  scenarios, as we increased the ratio of advection to diffusion, our advective population consistently performed better, leveling off at a maximum final population. The increase in final population size for the  $T = 40$  scenario corresponded with the exclusion of the diffusive-only population (not shown). However, for the panel where the period between resource pulses was 60 time steps, all parameterizations failed to maintain populations (Fig. 3.1).

#### *Ecological Interpretation*

When resources are found seasonally only at two poles, populations must be able to span the low-resource gap between them to survive. Here, the drive to move along even faint resource gradients has an important advantage over populations employing only random searching. As the tendency to follow resource gradients increases, the final population size of our resource-tracking population increases to a plateau where added

gradient-following does not increase the population size. However, once the gap between resource availability becomes too great ( $T = 60$ ), all behavior types are unable to persist (Fig. 3.1).

### *Pulsing Uniform resource function*

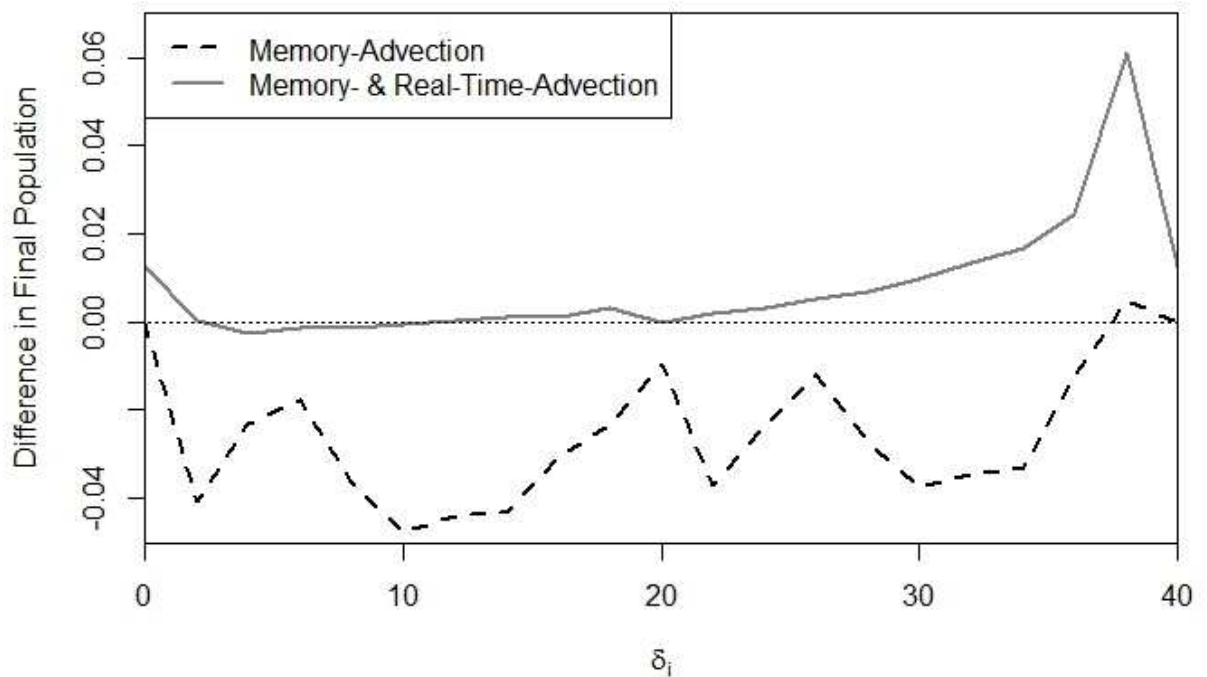
In a resource environment with a relatively flat resource landscape that pulses in and out with time between poles, the success of advective behavior is similar to that in a pulsing Gaussian function. Again, upon reaching a certain threshold of  $a/d$ , final population sizes increased to a stable plateau. However, population sizes in general were much larger than those found in our Gaussian resource function (Fig. 3.1). Advective populations were also able to become stable at all three values of  $T$ . The primary difference in this resource function is the uniformity of resource quality, making it unlikely that this habitat would be susceptible to spatial resource partitioning.

### *Addition of Memory*

We found a parameterization from Figure 3.1 where advective behavior failed to maintain a substantial population size on one of our resource functions. The parameterization  $T = 40$ ,  $d = 0.5$ ,  $a/d = 2.5$  was selected for its proximity to a more successful advective population ( $a/d = 5$ ), indicating a possibility of rescue through the addition of memory. We found that substituting memory-based advection for advection increased the total population size, but only at values of  $\delta$  close to one full resource period (Fig. 3.3). In a completely periodic resource landscape, these values of  $\delta$  equate to advection along what the resource gradient will be in the coming time steps. At all

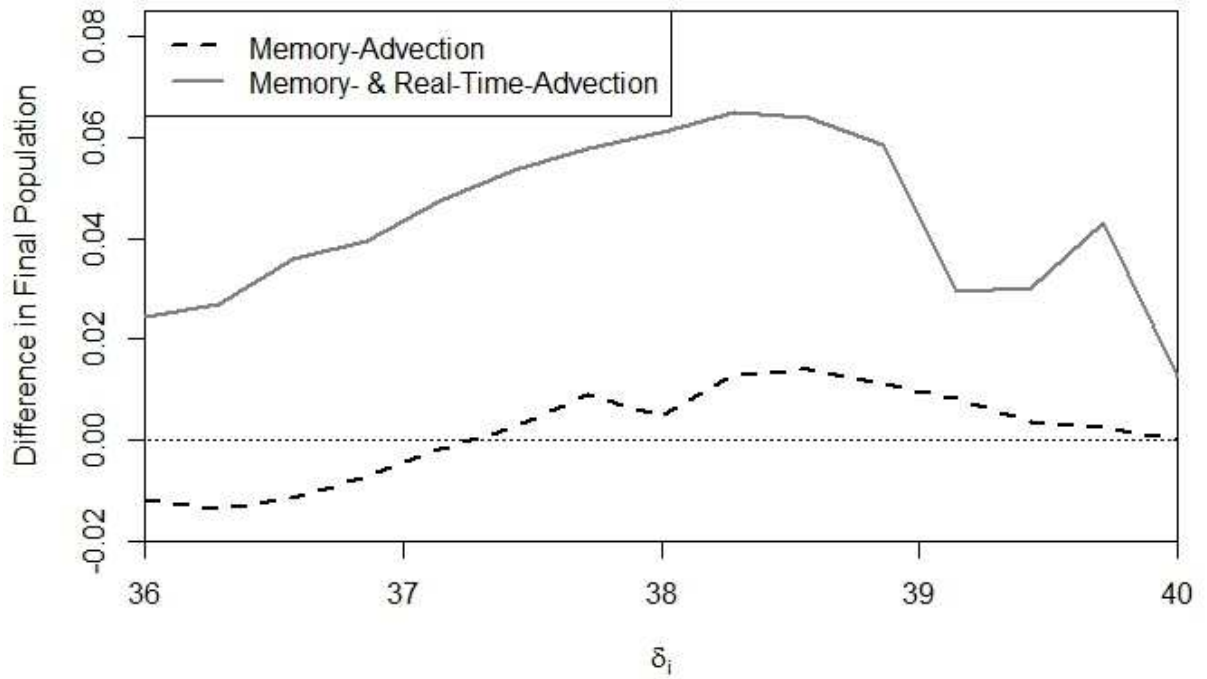
other values of  $\delta$ , population performance decreased, as unsynchronized memory-based advection led individuals in directions where resources would not soon appear.

However, when a population was allowed to balance both memory-based advection and real-time advection, final population size increased at a wider range of memory time scales (Fig. 3.3). This combination of two time scales allows for an individual to weigh both memory and local perception of the landscape when making movement decisions. By having this increased deductive power, there is likely to be a greater proportion of each period where the individual has a strong gradient, either in real-time or using memory, off which to advect.



**Figure 3.3a.** The effect of memory-based advection (dashed, black line) and both memory-based and real-time advection (solid, grey line) on final population sizes when

compared to an advective population without memory. Values above the  $y=0$  line indicate increased population sizes as a result of memory, whereas values below the line indicate decreased population sizes.  $T = 40$ ,  $d = 0.5$ , and  $a/d = 2.5$



**Figure 3.3b.** A higher-resolution version of Figure 3.3a from  $t_{offset} = 36$  to  $t_{offset} = 40$

## Discussion

When we analyze the success of advective behavior across our three resource landscapes we find, when resources are continually abundant, like in our translating Gaussian resource distribution, that advective behavior beyond a small  $a/d$  ratio reduces the size of the population (Fig. 3.1). We find that this reduction in population size

corresponds with a transition in our competitive outcome, as at low values of  $a/d$ , the advective population outcompetes the diffusive population, causing its exclusion. However, at  $a/d \approx 12.5$ , these two species begin to coexist, both maintaining stable populations (Fig. 3.2). We see evidence of resource partitioning in this scenario, as there is a higher advective population at the highest quality parts of the resource patch, and a greater diffusive population at many of the lower quality resources. A similar result was found in Fagan et al. (2017), where, as advection strength increases, diffusion switches from inhibiting foraging success to enhancing it. In an ecological framework, it behooves an individual to make use of available lower value habitat when competition for resources is high. In this case, movement strategies that allow for both directed movement and searching give rise to higher populations. We see the benefit of combining directed movement with random searching occur in populations as diverse as marine predators (Humphries et al. 2010), birds (Roshier et al. 2008), and insects (Reynolds and Frye 2007), indicating that this sort of combined movement approach is successful in a wide range of systems.

In contrast, as resource gradients become scarcer, populations become more reliant on advective behavior to find these resources. In Figure 3.1, we see that when the resource landscape changes from being a translating Gaussian distribution to a Gaussian distribution pulsing between two poles, strong advection goes from being a hindrance towards maintaining large population sizes to being a requirement. Furthermore, in this second resource distribution (pulsing Gaussian), when advection levels are high enough to provide sufficient tracking of the resource, increasing the diffusion coefficient while maintaining the ratio of  $a/d$  further increases maximum population size. It seems likely

that this outcome is due to the increased strength of diffusion and advection promoting a faster acquisition of resources as they appear.

Both advective and diffusive behaviors become insufficient to maintain a population when the distance between resources in space and time becomes too large. When our Gaussian pulse resource distribution reached  $T = 60$ , no populations were able to sustain any notable population after 600 time steps (Fig. 3.1). In purely diffusive systems, when boundaries between patches are inhospitable, the size of the patch required to maintain a stable population increases in comparison to when those conditions are relaxed (Ludwig et al. 1979). In our case, resource patches have boundaries in both space and time, implying that as barriers to movement between patches are increased diffusion, and eventually advection, will fail to maintain a viable population. However, this is also a scenario when memory could serve a role to strengthen migratory behavior between resource patches. We found that, in a parameterization where advective-diffusive behavior failed, advecting behavior acting at a time scale of almost one resource pulse prior ( $\delta \rightarrow T$ ) caused an increase in final population size (Fig. 3.3). This should be expected, as, when resources are predictable, acting on environmental cues prior to their arrival through the usage of memory should increase a population's ability to find resources. This usage of memory is consistent with the concept of return points, where individuals might seek out a location where they have prior knowledge of favorable resources (Fagan et al. 2013). Depending on scale, this concept can be used as a way of building a home range, efficiently searching a landscape, or developing a migratory pattern. But, this form of memory benefitted the population only up to a point. Memory time scales between 0-37 time steps (out of the 40 time steps in a period) decreased

population size compared to advection alone (Fig. 3.3). This is far from surprising, as acting on memory time scales near half of the resource's period will lead to a population being completely out of synch with the resource, consistently following cues towards locations where resources will not remerge for some time. This is related to phenological mismatches, where changes in environmental cues cause errors in timing of important events. Whether describing emergence (Kudo & Ida 2013), development timing (Miller-Rushing et al. 2010), or migration (Visser et al. 2012), errors in timing can have disastrous effects. This suggests that timing-based memory, while beneficial in a stable environment, might also carry risks in a changing environment.

With the addition of our final complexity, we found that populations exhibiting all of diffusion, real-time advection, and memory-based advection maintained the largest population sizes, independent of memory time scales (Fig. 3.3). As this behavior was not as reliant on exact timing of memory, it would carry fewer risks related to environmental change. However, the greatest improvement in performance still occurred in a similar range to only memory-based advection ( $\delta \rightarrow T$ ). This memory strategy ends up providing the benefits of both pure advection and memory-based advective movement. A population displaying this behavior can move towards remembered high-quality patches, but will not be as likely to leave abundant resources early.

We conclude that, while the ability to detect and move along a resource gradient is often more successful of a movement strategy than random searching, diffusion can become beneficial in concert with advection. Furthermore, in scenarios where gradients are too faint or distant to be followed, reliance on memory can help develop and maintain migratory behavior. We also presented a new parameterization of advective memory,

where individuals balance abilities to navigate both by memory of previous resource gradients as well as along a current gradient. This strategy, while complex, eventually provides the individuals with better information with which to guide their movement.



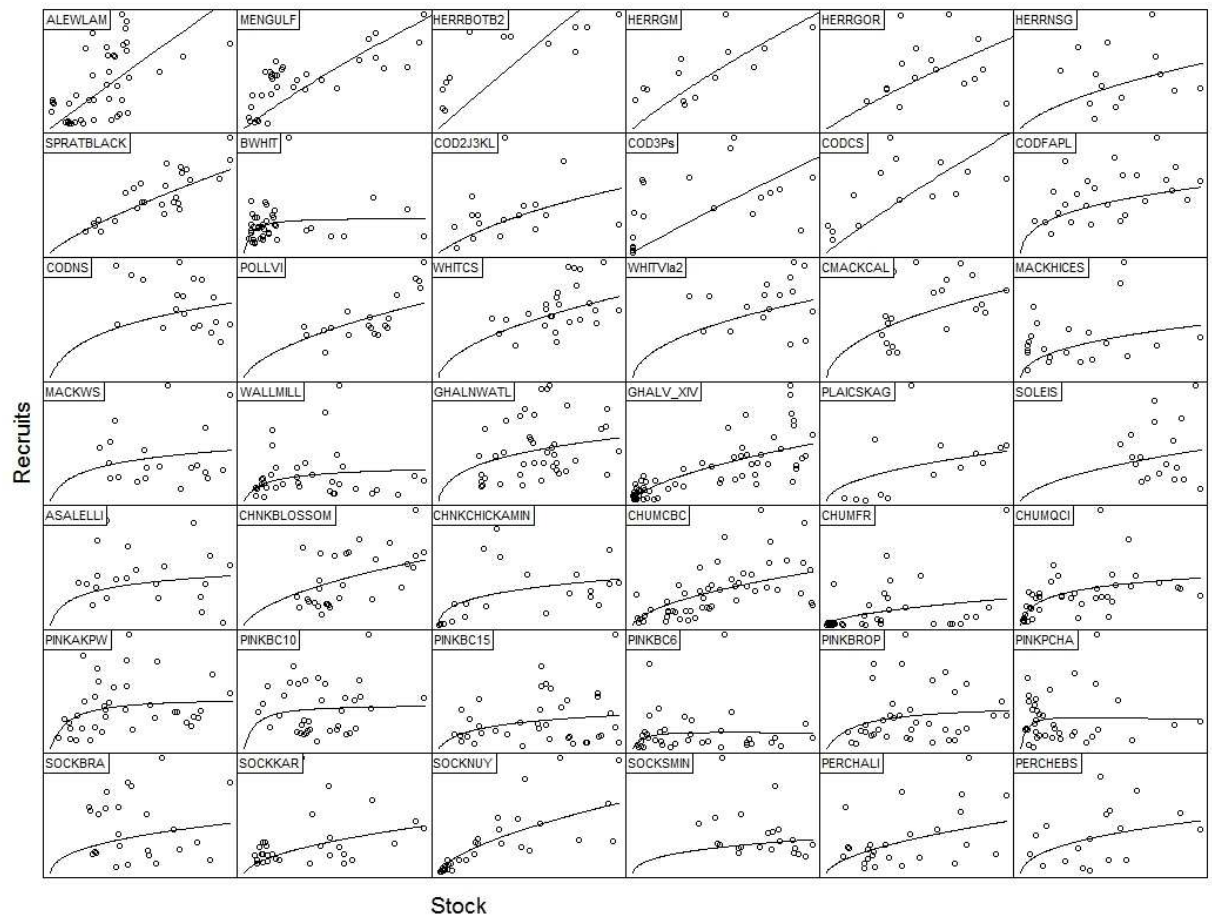
## Appendices

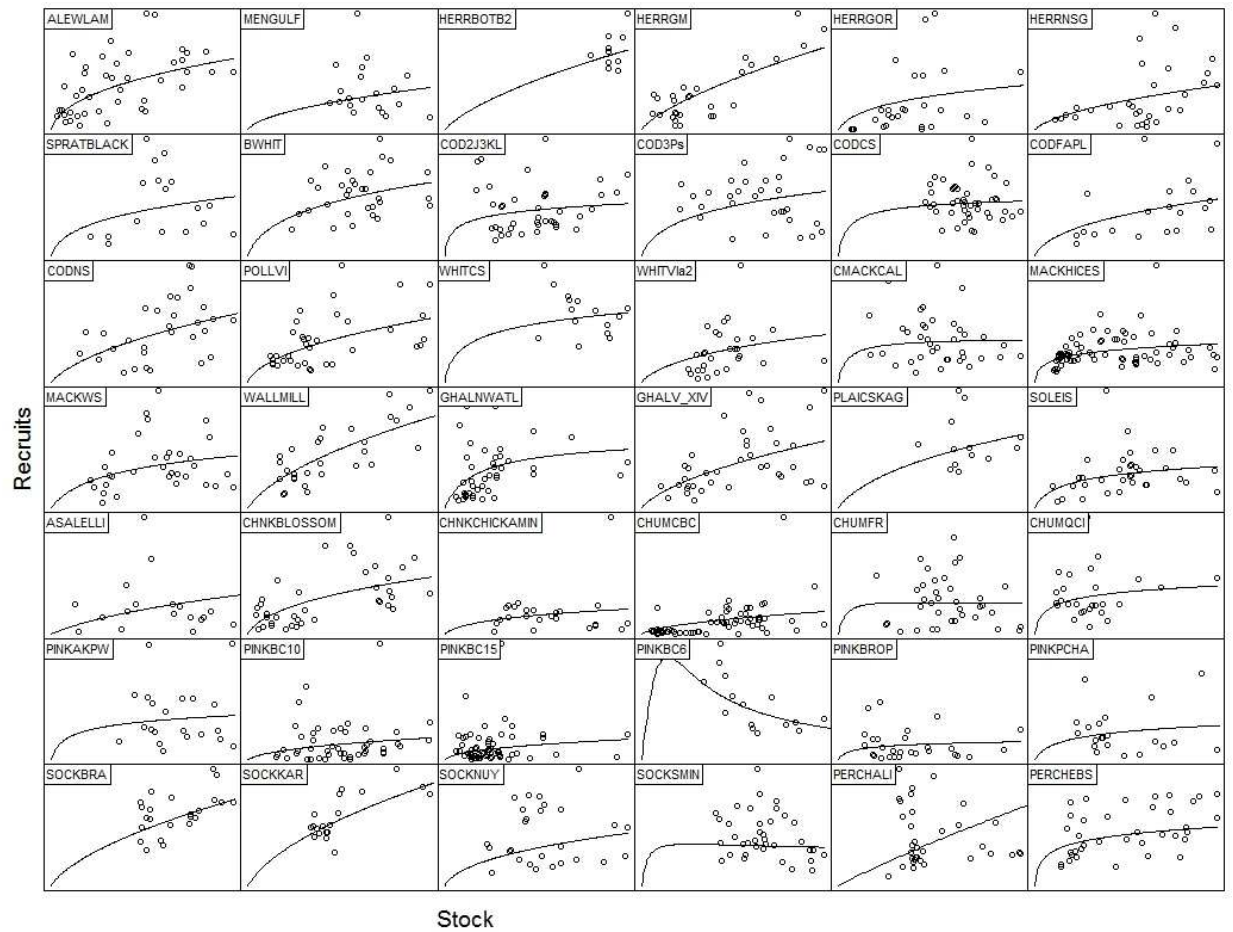
**Appendices 1.A-1.B** are considered too large for this document and are available online in the Ecological Archives associated with the publication of the first chapter at <http://onlinelibrary.wiley.com/doi/10.1890/15-0733.1/full>

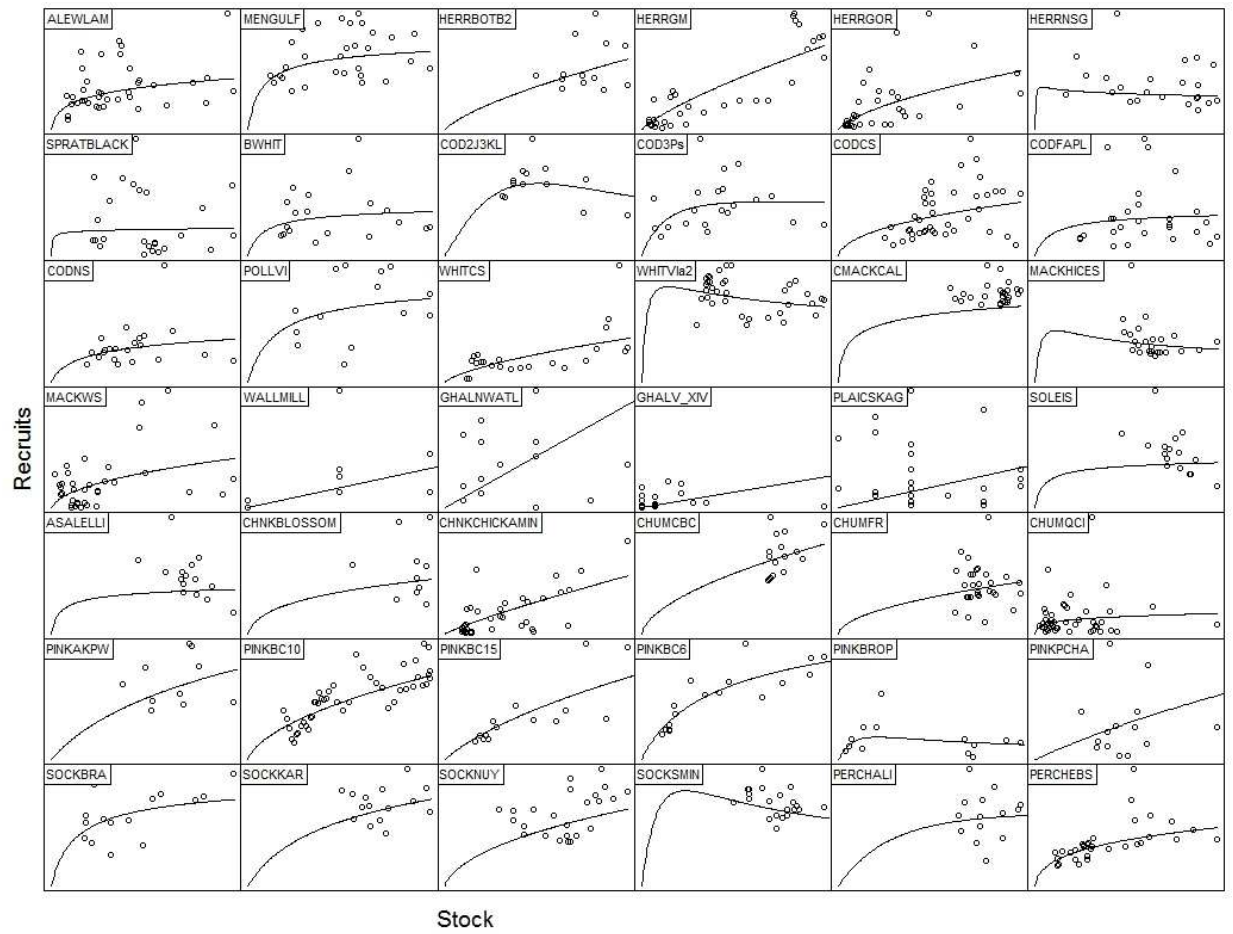
### Appendix 1.C

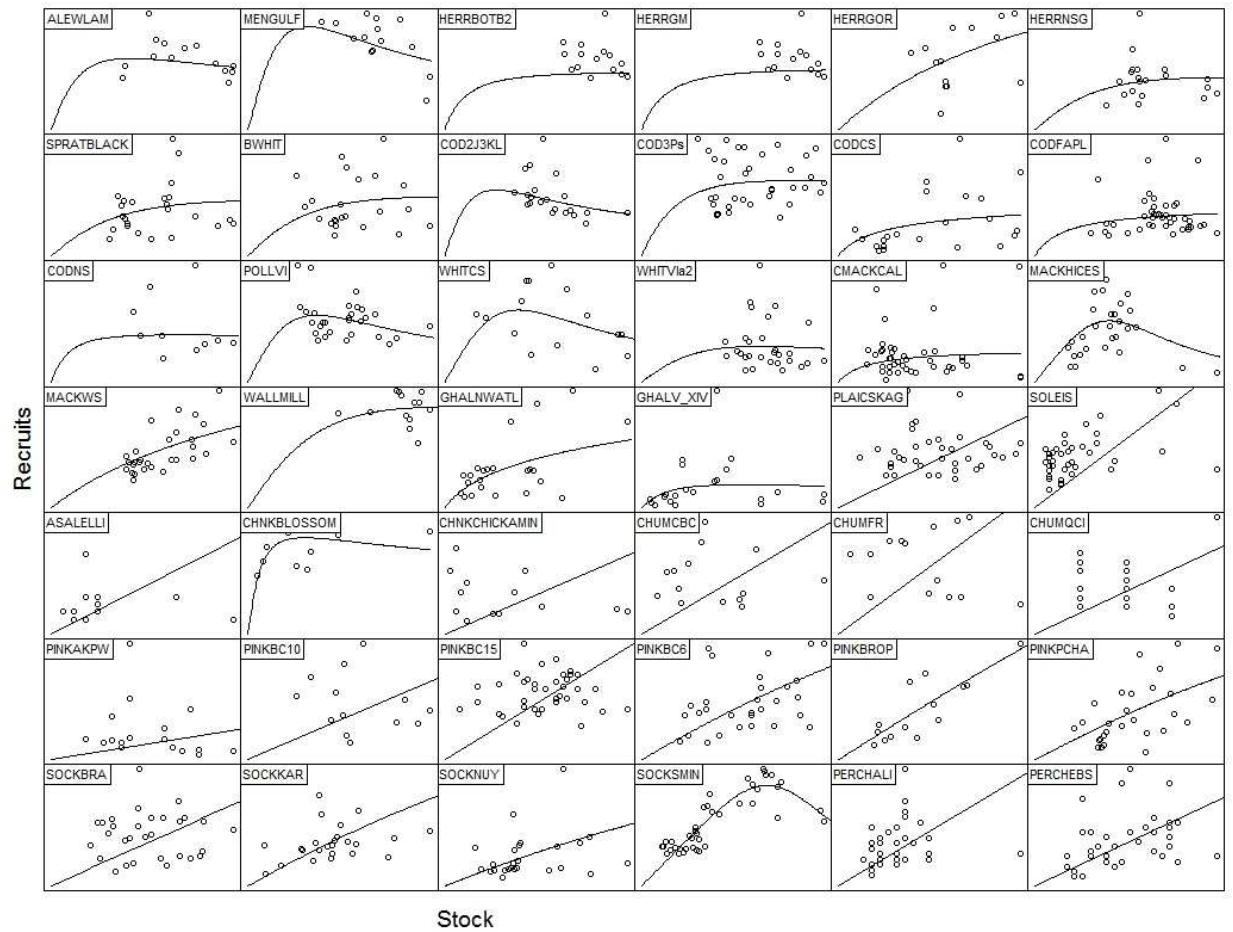
The following plots are included as indicators of fit, variability, and contrast in our data and results.

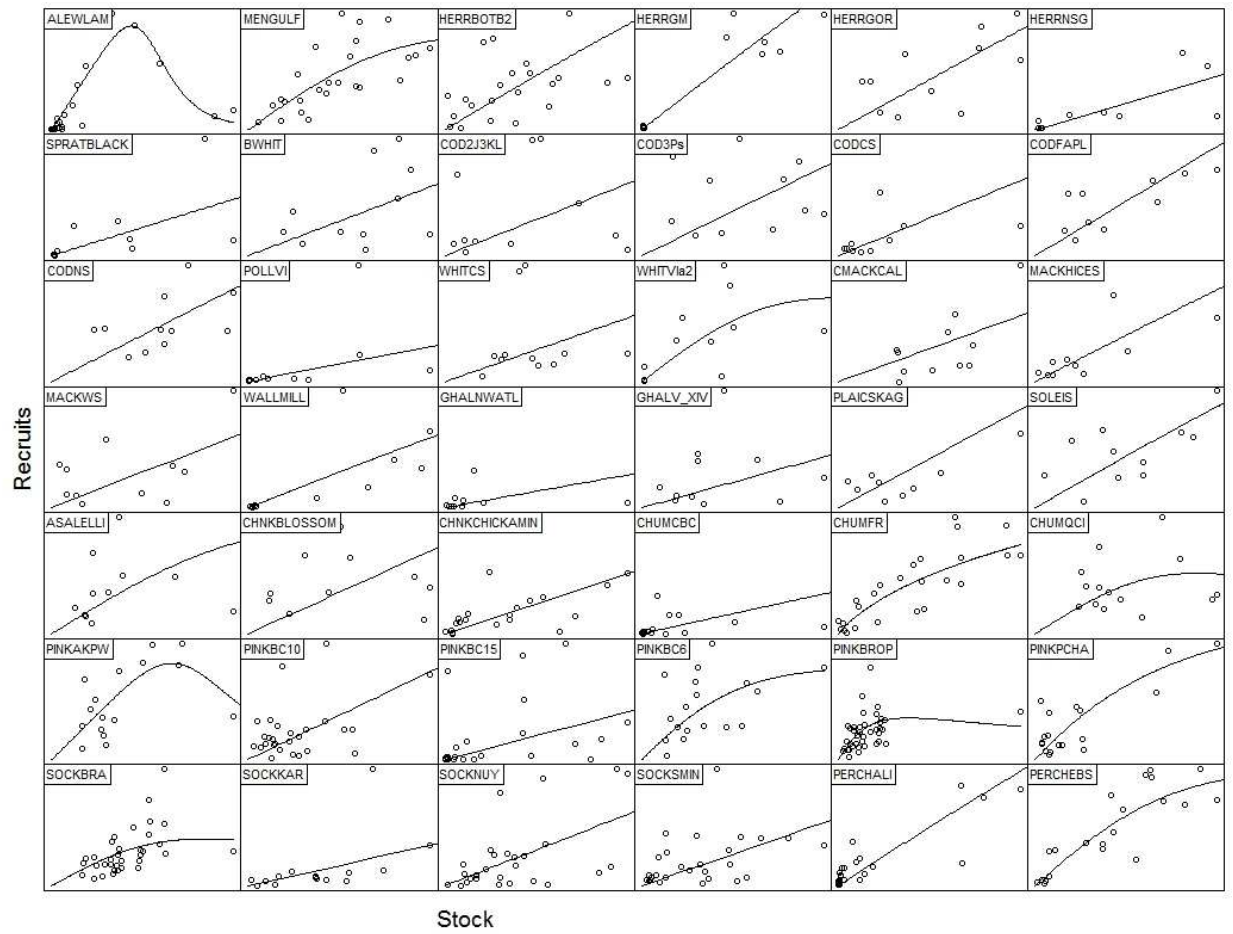
**Figure 1.C1.** Plots of the data for all 254 populations and the Shepherd model fit for those data using the median values for alpha, beta, and delta from the posterior distributions. This figure gives a visual for the fit of our model posterior parameters to the stock-recruitment data.

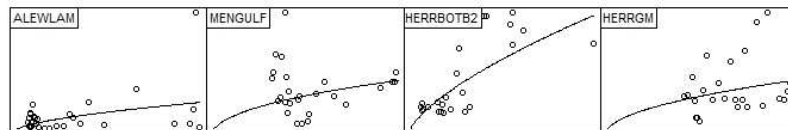
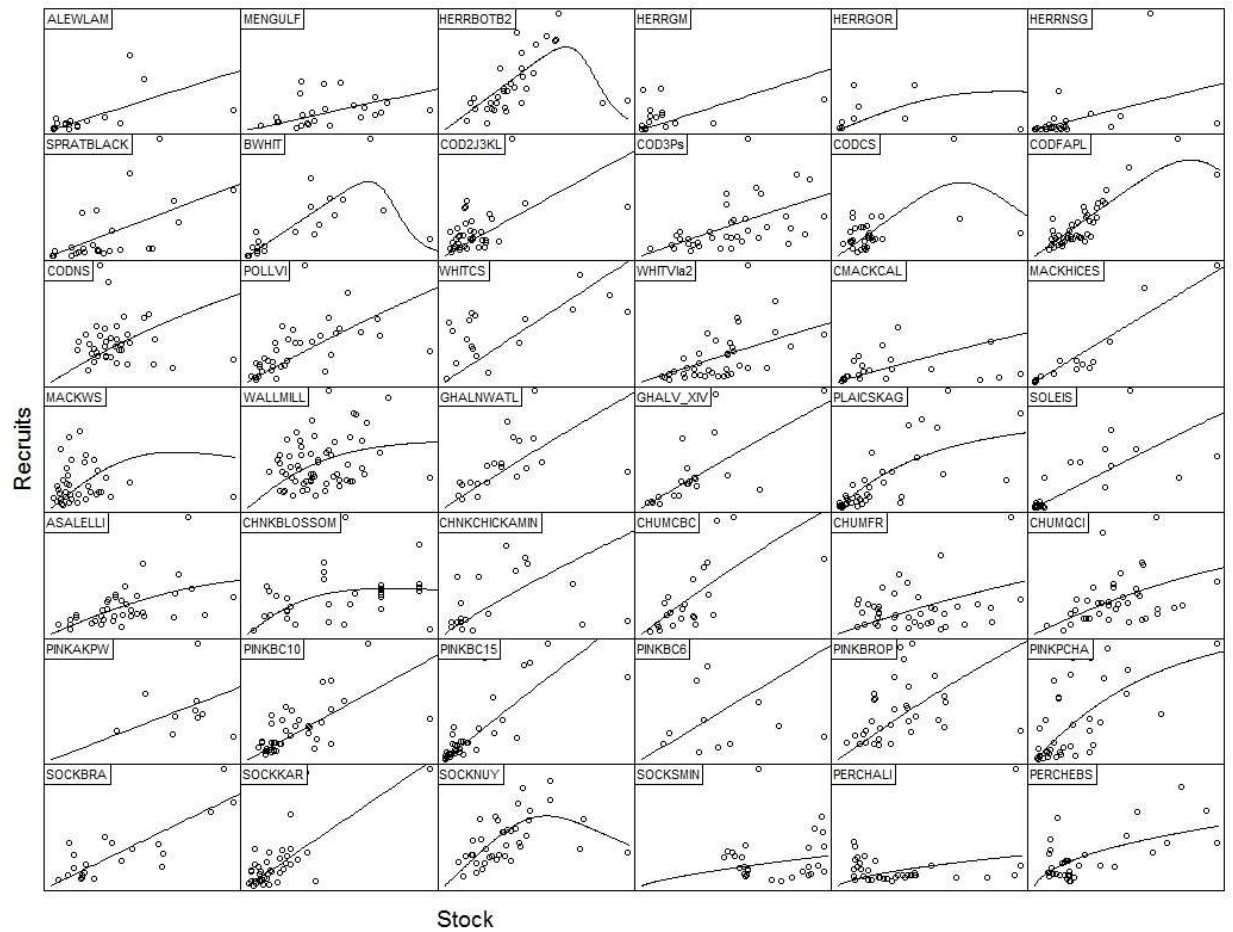






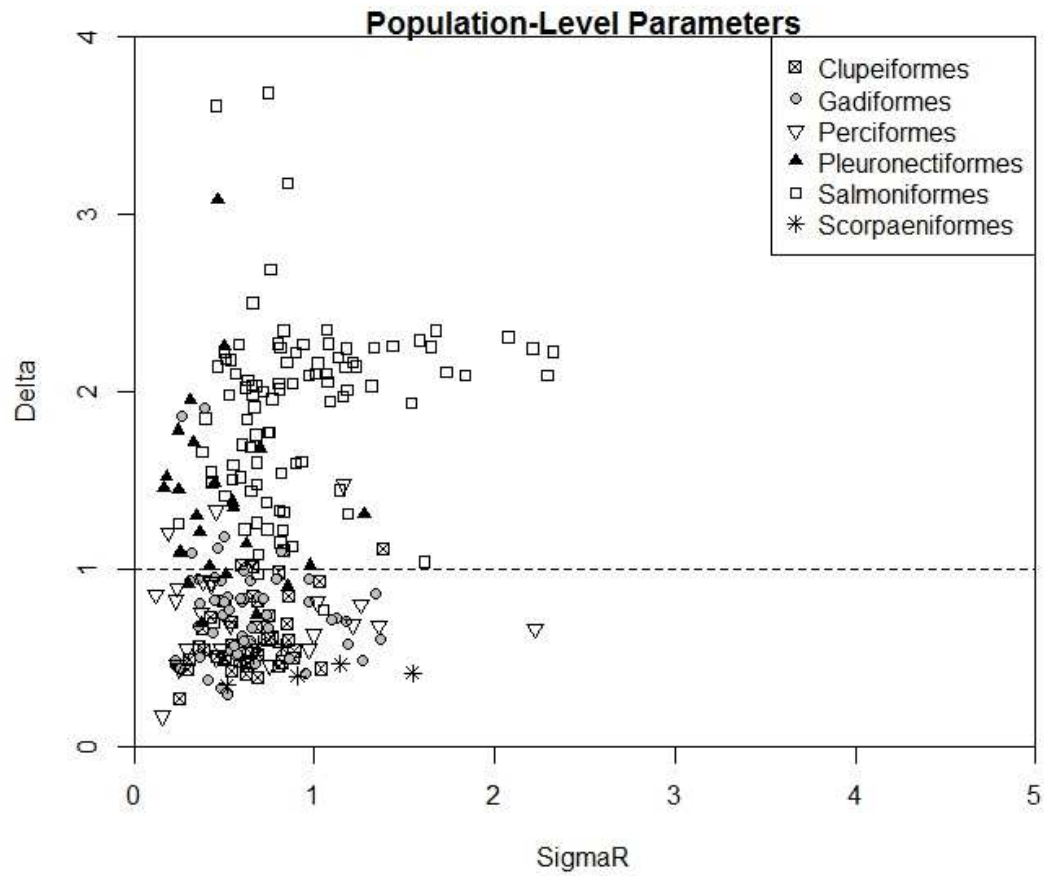






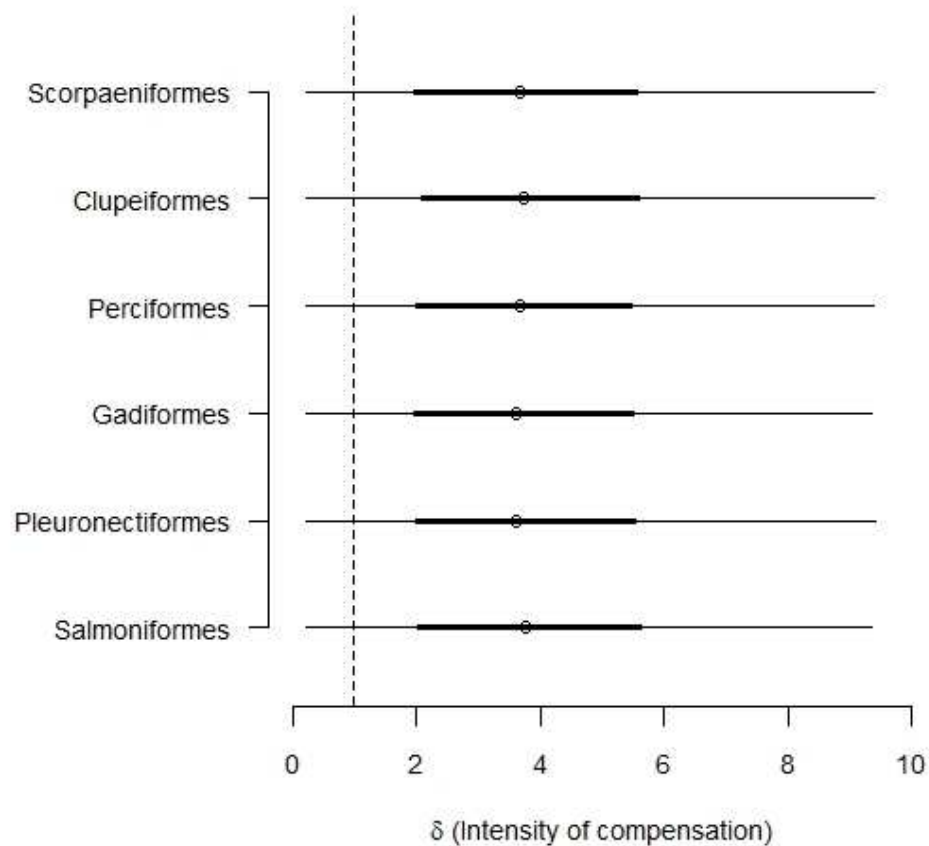


**Figure 1.C2.** Population-specific standard deviation around the mean recruitment value,  $\sigma_{R_i}$ , compared to median posterior delta values for each population. Symbols represent the taxonomic order for each population.

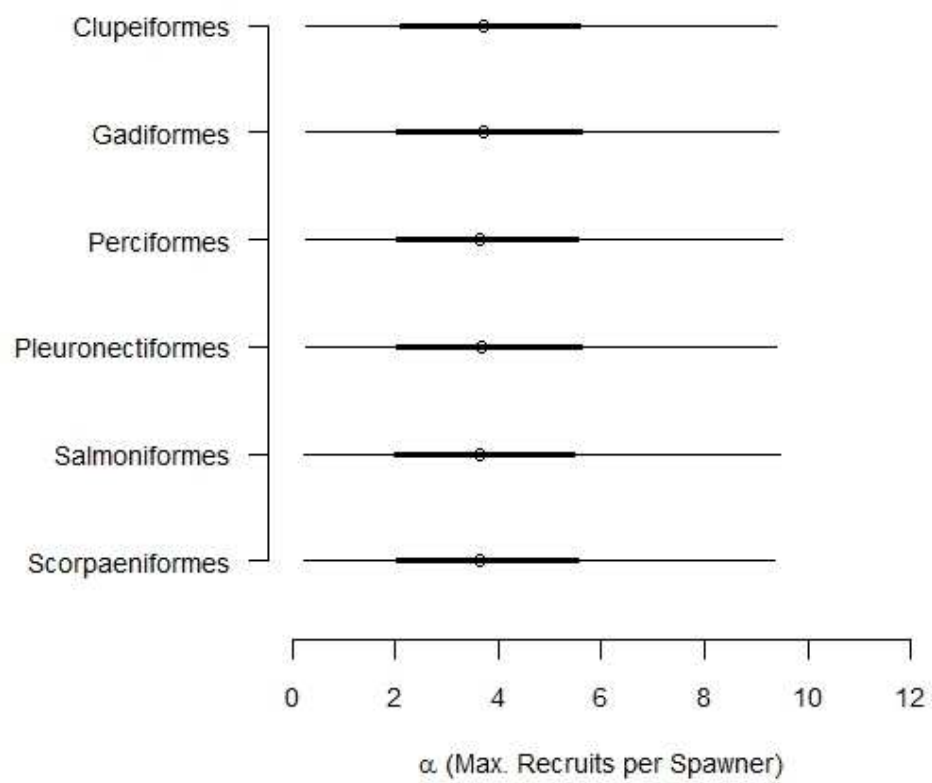


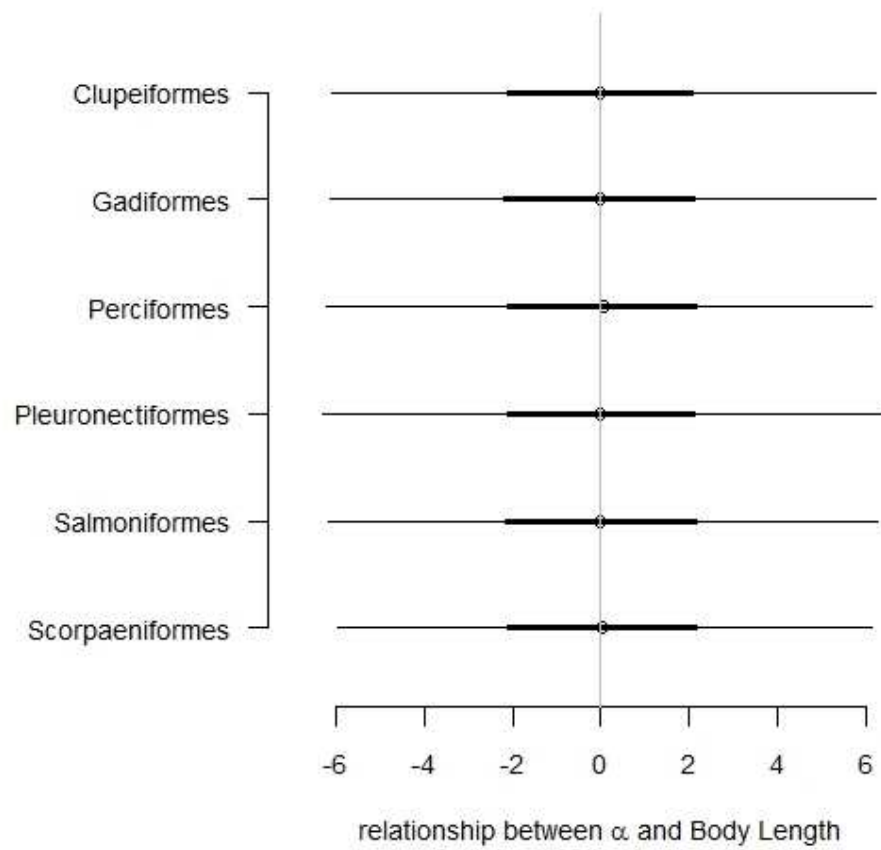
## Appendix 1.D

Figures showing the prior distributions for  $\delta$ ,  $\alpha$ , and the relationship between  $\alpha$  and maximum body length for each order. Priors are estimated by running the model with no data and then plotting the resulting (uninformed) posterior distributions for each parameter. Open circles represent median values and the lines indicate the 50% (thick lines) and 95% (thin lines) credible intervals.



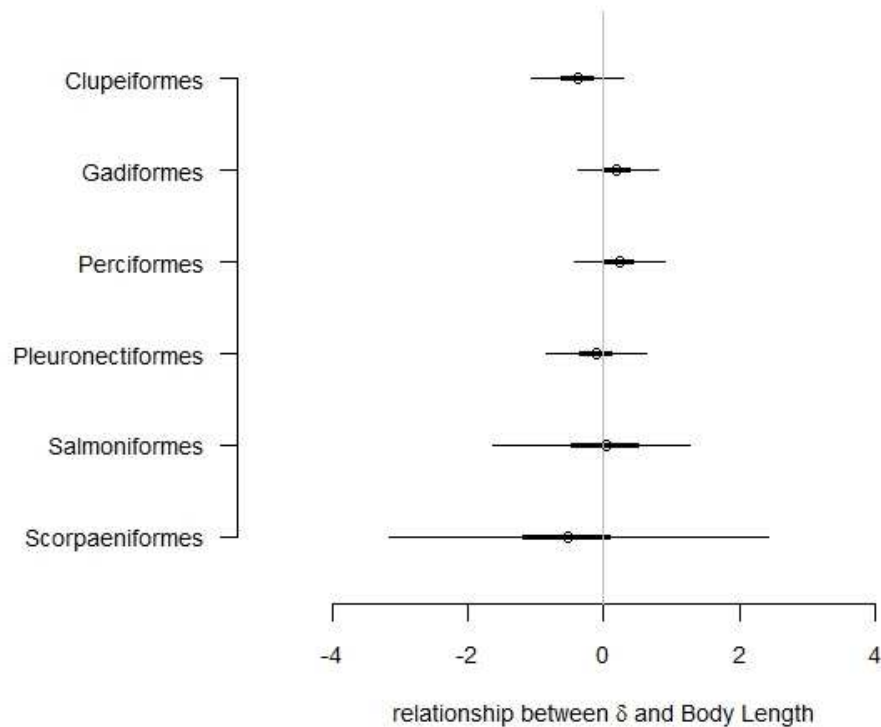






## Appendix 1.E

Figure showing covariate estimates for the relationship between  $\delta$  and maximum body length for each order. These results were obtained from a separate model in which we estimated the effect of maximum body length on  $\delta$  (rather than on  $\alpha$ , as is presented in the main text). A value of 0 indicates no relationship while positive and negative values indicate positive and negative correlations, respectively. Open circles represent median values and the lines indicate the 50% (thick lines) and 95% (thin lines) credible intervals.



## Appendix 2.A – Derivation of Transition Matrices For Different Learning Mechanisms

Below are the transition matrices that describe the different Learning Mechanisms described in our multi-level model. These examples use a four-level model, but can be generalized for any number of levels. Rows represent the current and potential experience levels of the individual, columns represent the levels of the leader within the group, and the values represent the probabilities of those transitions.

a) 1-step learning

$$\begin{array}{c}
 \begin{array}{cccc}
 & 1 & 2 & 3 & 4 \\
 \begin{array}{l}
 1 \rightarrow 1 \\
 1 \rightarrow 2 \\
 1 \rightarrow 3 \\
 1 \rightarrow 4 \\
 2 \rightarrow 2 \\
 2 \rightarrow 3 \\
 2 \rightarrow 4 \\
 3 \rightarrow 3 \\
 3 \rightarrow 4 \\
 4 \rightarrow 4
 \end{array}
 & \begin{pmatrix}
 1 & 0 & 0 & 0 \\
 0 & 1 & 1 & 1 \\
 0 & 0 & 0 & 0 \\
 0 & 0 & 0 & 0 \\
 0 & 1 & 0 & 0 \\
 0 & 0 & 1 & 1 \\
 0 & 0 & 0 & 0 \\
 0 & 0 & 1 & 0 \\
 0 & 0 & 0 & 1 \\
 0 & 0 & 0 & 1
 \end{pmatrix}
 \end{array}
 \end{array}$$

b) 1-step stochastic learning

$$\begin{array}{c}
 \begin{array}{cccc}
 & 1 & 2 & 3 & 4 \\
 \begin{array}{l}
 1 \rightarrow 1 \\
 1 \rightarrow 2 \\
 1 \rightarrow 3 \\
 1 \rightarrow 4 \\
 2 \rightarrow 2 \\
 2 \rightarrow 3 \\
 2 \rightarrow 4 \\
 3 \rightarrow 3 \\
 3 \rightarrow 4 \\
 4 \rightarrow 4
 \end{array}
 & \begin{pmatrix}
 1 & 0.5 & 0.5 & 0.5 \\
 0 & 0.5 & 0.5 & 0.5 \\
 0 & 0 & 0 & 0 \\
 0 & 0 & 0 & 0 \\
 0 & 1 & 0.5 & 0.5 \\
 0 & 0 & 0.5 & 0.5 \\
 0 & 0 & 0 & 0 \\
 0 & 0 & 1 & 0.5 \\
 0 & 0 & 0 & 0.5 \\
 0 & 0 & 0 & 1
 \end{pmatrix}
 \end{array}
 \end{array}$$

c) stochastic multi-step learning

$$\begin{array}{c}
1 \rightarrow 1 \\
1 \rightarrow 2 \\
1 \rightarrow 3 \\
1 \rightarrow 4 \\
2 \rightarrow 2 \\
2 \rightarrow 3 \\
2 \rightarrow 4 \\
3 \rightarrow 3 \\
3 \rightarrow 4 \\
4 \rightarrow 4
\end{array}
\begin{pmatrix}
1 & 0.5 & 0.\bar{3} & 0.25 \\
0 & 0.5 & 0.\bar{3} & 0.25 \\
0 & 0 & 0.\bar{3} & 0.25 \\
0 & 0 & 0 & 0.25 \\
0 & 1 & 0.5 & 0.\bar{3} \\
0 & 0 & 0.5 & 0.\bar{3} \\
0 & 0 & 0 & 0.\bar{3} \\
0 & 0 & 1 & 0.5 \\
0 & 0 & 0 & 0.5 \\
0 & 0 & 0 & 1
\end{pmatrix}$$

d) jump-to-leader

$$\begin{array}{l} 1 \rightarrow 1 \\ 1 \rightarrow 2 \\ 1 \rightarrow 3 \\ 1 \rightarrow 4 \\ 2 \rightarrow 2 \\ 2 \rightarrow 3 \\ 2 \rightarrow 4 \\ 3 \rightarrow 3 \\ 3 \rightarrow 4 \\ 4 \rightarrow 4 \end{array} \begin{pmatrix} 1 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 \\ 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 1 \\ 0 & 1 & 0 & 0 \\ 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 1 \\ 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 1 \\ 0 & 0 & 0 & 1 \end{pmatrix}$$

e) jump-to-leader stochastic learning

$$\begin{array}{l} 1 \rightarrow 1 \\ 1 \rightarrow 2 \\ 1 \rightarrow 3 \\ 1 \rightarrow 4 \\ 2 \rightarrow 2 \\ 2 \rightarrow 3 \\ 2 \rightarrow 4 \\ 3 \rightarrow 3 \\ 3 \rightarrow 4 \\ 4 \rightarrow 4 \end{array} \begin{pmatrix} 1 & 0.5 & 0.5 & 0.5 \\ 0 & 0.5 & 0 & 0 \\ 0 & 0 & 0.5 & 0 \\ 0 & 0 & 0 & 0.5 \\ 0 & 1 & 0.5 & 0.5 \\ 0 & 0 & 0.5 & 0 \\ 0 & 0 & 0 & 0.5 \\ 0 & 0 & 1 & 0.5 \\ 0 & 0 & 0 & 0.5 \\ 0 & 0 & 0 & 1 \end{pmatrix}$$

## Appendix 2.B – Validation of simulations

Suppose that there are  $N$  individuals in the population and that they form groups of size  $G$  to migrate. If, prior to migration, there are  $L_T$  learned individuals, then we define the following probability

$$\rho_{u_i/L_t} = \frac{\alpha_i \binom{N/G}{u_i}}{\binom{N}{N-L_T}} \quad (1.a)$$

where  $u_i = \text{floor}\left(\frac{N-L_t}{G}\right) - i$  is the number of groups without a learned individual and

$$\alpha_i = \binom{N - G u_i}{N - L_T - G u_i} - \sum_{k=0}^{i-1} \alpha_k \binom{\frac{N}{G} - u_i}{i - k} \quad (1.b)$$

In (1),  $\rho_{u_i/L_t}$  is the probability that there will be  $u_i$  groups without a learned individual, given that there were a total of  $L_t$  learned individuals in the population. If there are  $u_i$  groups without a learned individual, then  $U_i = G u_i$  individuals did not have an opportunity to learn and

$$S_i = N - U_i - L_t = N - G \left( \text{floor}\left(\frac{N-L_T}{G}\right) - i \right) - L_T \quad (2)$$

individuals were newly exposed to the route. Consequently,  $\rho_{u_i/L_t} = \Omega_{S_i/L_t}$  where  $\Omega_{S_i/L_t}$  is the probability of having  $S_i$  newly exposed individuals, given that there were  $L_t$  learned individuals prior to migration. However, not all exposed individuals will learn the route. If the probability of learning is  $\sigma$ , then we define the following probability

$$p_{A/S_i} = \binom{S_i}{A} \sigma^A (1 - \sigma)^{S_i - A} \quad (3)$$

where  $p_{A/S_i}$  is the probability of having  $A$  newly learned individuals given that  $S_i$  individuals were exposed. From (1-3) we define the probability of having  $L_{t+1}$  learned individuals after migration, given that there were  $L_t$  learned individuals before migration as

$$P_{L_{T+1}/L_T} = \sum_{i=0}^{\text{floor}\left(\frac{N-L_T}{G}\right)} p_{L_{T+1}-L_T/S_i} \Omega_{S_i/L_T} \quad (4)$$

$$P_{L_{T+1}/L_T} = \sum_{i=0}^{\text{floor}\left(\frac{N-L_T}{G}\right)} \left( N - G \left( \text{floor}\left(\frac{N-L_T}{G}\right) - i \right) - L_t \right) \sigma^{L_{T+1}-L_T} (1 - \sigma)^{N-G\left(\text{floor}\left(\frac{N-L_T}{G}\right)-i\right)-L_{T+1}} \frac{\alpha_i \binom{N/G}{\text{floor}\left(\frac{N-L_T}{G}\right)-i}}{\binom{N}{N-L_T}} \quad (5)$$

This defines the transition matrix for the migration step.

Suppose that death happens after migration. If the probability of dying after migration is  $\delta$  and keeping the total population fixed, the probability that there are  $L_{t+2}$  learned individuals after death given that there were  $L_{t+1}$  learned individuals prior to death is

$$d_{L_{T+2}/L_{T+1}} = \binom{L_{T+1}}{L_{T+1} - L_{T+2}} \delta^{L_{T+1} - L_{T+2}} (1 - \delta)^{L_{T+2}} \quad (6)$$

This defines the transition matrix for the death step.

The probability of having a specific number of learned individuals after  $T$  time-steps is then given by

$$\mathbf{C}_T = (\mathbf{dP})^T \mathbf{C}_0 \quad (7)$$

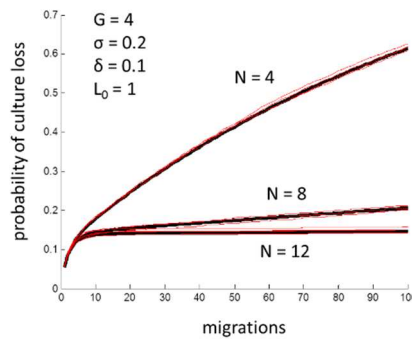
where  $\mathbf{C}_0$  is a vector defining the probability of having a certain number of learned individuals at the initial time and  $\mathbf{C}_T$  is a vector defining the probability of having a certain number of learned individuals at time  $t = T$ .

The previous derivation assumed that groups formed completely at random. At the other extreme, there may be perfect affinity to a single group (i.e., individuals are born into a group and remain with the group until death). To model this scenario, we can use the previous derivation, modified slightly. For  $N$  individuals that form groups of size  $G$ , we can calculate the probability of having a certain number of learned individuals, assuming perfect affinity to a group, as

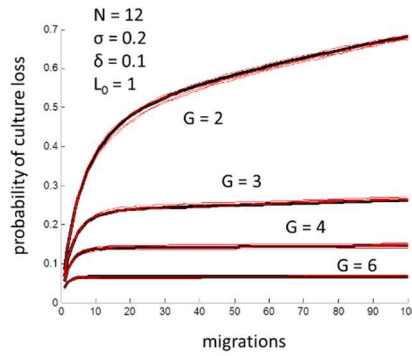
$$\mathbf{C}_T = (\mathbf{C}_{T,N/G})^{N/G} \quad (7)$$

where  $\mathbf{C}_{T,N/G}$  is  $\mathbf{C}_T$  calculated for a population of size  $N/G$  assuming evenly distributed learned individuals, i.e.  $L_0/G$  learned individuals per group.

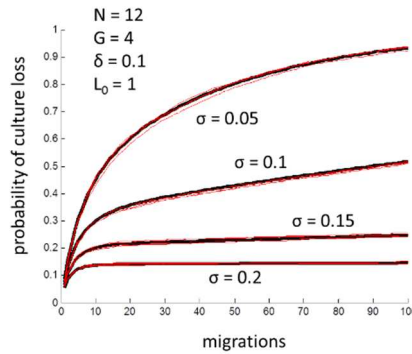
Below we present results:



**Fig. 2.B1** Probability of culture loss for three different population sizes and assuming random grouping. Red lines are simulations (average of 5000 trials), black lines are exact results.

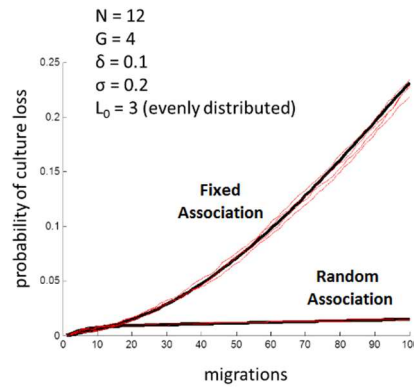


**Fig. 2.B2** Probability of culture loss for four different group sizes and assuming random grouping. Red lines are simulations (average of 5000 trials), black lines are exact results.



**Fig. 2.B3** Probability of culture loss for four different learning probabilities and assuming random groupings. Red lines are simulations (average of 5000 trials), black lines are exact results.





**Fig. 2.B4** Probability of culture loss for random vs. fixed-association groupings. Red lines are simulations (average of 5000 trials), black lines are exact results. One would expect that associations between fully random and fully fixed would lie between these two curves.

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