

The Evolution of Male-Biased Dispersal under the Joint Selective Forces of Inbreeding Load and Demographic and Environmental Stochasticity

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ABSTRACT: Sex-biased natal dispersal is widespread, and its significance remains a central question in evolutionary biology. However, theory so far fails to predict some of the most common patterns found in nature. To address this, we present novel results from an individual-based model investigating the joint roles of inbreeding load, demographic stochasticity, environmental stochasticity, and dispersal costs for the evolution of sex-biased dispersal. Most strikingly, we found that male-biased natal dispersal evolved in polygynous systems as a result of the interplay between inbreeding avoidance and stochasticity, whereas previous theory, in contrast to empirical observations, predicted male philopatry and female-biased natal dispersal under inbreeding load alone. Furthermore, the direction of the bias varied according to the nature of stochasticity. Our results therefore provide a unification of previous theory, yielding a much better qualitative match with empirical observations of male-biased dispersal in mate defense mating systems.

Keywords: sex-biased dispersal, mutation accumulation, inbreeding avoidance, mutation load.

Introduction

Life-history traits such as dispersal are shaped by evolution, and the causes and consequences of the variation in dispersal strategies observed have long been of interest. Most species exhibit some form of sex-biased dispersal, with one sex emigrating more frequently from the natal patch and/or moving a greater distance (Fontanillas et al. 2004; Douadi et al. 2007; Gauffre et al. 2009). Understanding why sex-

biased dispersal evolves is therefore a central question in evolutionary biology, yet the answer is largely unknown. Furthermore, major discrepancies exist between empirical observations and theoretical predictions.

In one of the most influential empirical reviews on sex-biased dispersal, Greenwood (1980) focused on natal dispersal and mating systems in birds and mammals and found strong and contrasting sex-biased dispersal patterns. In mammals, dispersal tends to be male biased, whereas in birds, dispersal tends to be female biased. Since Greenwood's (1980) review, a growing number of other empirical studies continue to find biases in dispersal consistent with these patterns, although there are exceptions (Clarke et al. 1997; Lawson Handley and Perrin 2007; Clutton-Brock and Lukas 2012; Mabry et al. 2013). To explain sex-biased dispersal in mammals and birds, Greenwood (1980) proposed the resource competition hypothesis. According to this hypothesis, the philopatric sex will enjoy greater benefits from familiarity with the natal area or territory—and hence from resource defense—and this will depend on the mating system. Males will be philopatric in species exhibiting resource defense strategy (males defend resources of value to females, mainly leading to social monogamy; most birds), while females will be philopatric in species exhibiting mate defense strategy (males defend access to mates and hence do not need to express site-specific dominance, mainly leading to polygyny; most mammals). The argument for philopatry in the resource competition hypothesis may be weakened, however, in species without parental care, where neither sex requires familiarity with the natal area for rearing young. This is the case, for example, for most reptiles, amphibians, fish, and insects. A number of reptile species exhibit sex-biased dispersal, and in most cases, males are more dispersive than females (Tucker et al. 1998; Rivera et al. 2006; Dubey et al. 2008; Ujvari et al.

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2008; Sheridan et al. 2010; Pernetta et al. 2011; exception: Olsson and Shine 2003). However, much less is known about dispersal in amphibians (Austin et al. 2003; Lampert et al. 2003; Palo et al. 2004; Liebgold et al. 2011), fish (Pardini et al. 2001; Hutchings and Gerber 2002; Fraser et al. 2004), and insects (Baguette et al. 1998).

Despite the many potential mechanisms proposed by empiricists, theoretical studies frequently neglect to consider the interplay of multiple pressures and instead focus on independent drivers of sex-biased dispersal. Theoreticians wishing to explore conditions favoring the evolution of sex-biased dispersal have investigated drivers such as spatiotemporal resource competition (Greenwood 1980), kin selection (Hamilton and May 1977), inbreeding avoidance (Waser et al. 1986; Perrin and Mazalov 1999; Perrin and Mazalov 2000; Lehmann and Perrin 2003), dispersal costs (Gros et al. 2008), and mating systems (Greenwood 1980; Guillaume and Perrin 2006; Guillaume and Perrin 2009). However, even with a large body of theory, the mechanisms driving the degree and direction of dispersal biases remain unclear and, in some cases, do not match empirical observations (Guillaume and Perrin 2009).

Inbreeding avoidance has been of particular interest in modeling studies because it should in principle promote the evolution of sex-biased dispersal: if siblings of only one sex disperse, the risk of mating with relatives is greatly reduced. In a promiscuous mating system, Guillaume and Perrin (2006) found that the mean dispersal of both sexes responded little and equally to low levels of inbreeding load, only increasing by one-third over expectations from models incorporating kin competition alone. However, for higher levels of inbreeding load, a bistable sex bias in dispersal emerged; that is, there was an equal probability that the dispersal bias would fall in the male or female direction. This supported previous theory where selection for inbreeding avoidance in promiscuous mating systems led to dispersal in one sex and complete philopatry in the other; however, the direction of the sex bias was random (Gandon 1999; Perrin and Mazalov 1999). A later study further explored the role of mating systems by including a polygynous mating system and found that female-biased dispersal evolved (Guillaume and Perrin 2009). However, while the results of the latter study are compelling, they are in stark contrast to empirical observations of male-biased dispersal in polygynous mating systems (Greenwood 1980; Lawson Handley and Perrin 2007).

Under the same mating systems, Gros et al. (2009) questioned whether selection for inbreeding avoidance contributes much, if at all, to the evolution of sex-biased dispersal. In polygynous mating systems, Gros et al. (2009) found that asymmetry between the sexes in between-patch variability in reproductive success, generated by demographic stochasticity, could promote slightly male-biased dispersal, even in

the absence of inbreeding load. However, biases were small for scenarios with high levels of demographic stochasticity and disappeared as soon as demographic stochasticity was reduced. Despite this, the potential roles for demographic and environmental stochasticity for sex-biased dispersal should not be overlooked. Stochasticity can greatly influence population dynamics through its effects on population densities and biotic interactions, such as local mate and resource competition (Cadet et al. 2003; Blanquart and Gandon 2011; North et al. 2011; Duputié and Massol 2013; Novak 2014). The resource competition hypothesis and some empirical studies attribute local mate competition (LMC) as the major cause for male-biased dispersal (Greenwood 1980; Lawson Handley and Perrin 2007); thus, any process potentially altering competition for mates and/or other resources could alter the evolution of sex-biased dispersal.

There is no existing work investigating both inbreeding load and demographic stochasticity as simultaneous drivers of sex-biased natal dispersal. Surprisingly, theoretical studies have focused on single mechanisms, despite empirical studies proposing multiple causes for observed patterns (Lawson Handley and Perrin 2007). Given the ecological importance of dispersal, understanding how different selective forces are likely to operate together in order to shape the evolution of sex-biased dispersal is essential. In this theoretical study, we consider the synergistic effects of inbreeding load, mating system, dispersal costs, and kin competition together with both demographic and environmental stochasticity for the evolution of sex-biased natal dispersal. By doing this, we link together previous theory and, importantly, address the gap between theoretical predictions and empirical observations (Perrin and Mazalov 2000; Gros et al. 2008, 2009; Guillaume and Perrin 2009).

Methods

An individual-based, genetic and spatially explicit model was developed to simulate the life cycle of diploid individuals characterized by their sex and genotype. The landscape was a wrapped grid (20×20) composed of 400 discrete patches of the same carrying capacity K . A graphical depiction of the life cycle can be found in appendix A (apps. A–D available online).

Reproduction

The number of offspring a female produced was drawn from a Poisson distribution with mean λ . The mating system was either polygyny or promiscuity. Under polygyny, a single breeding male was chosen at random and fathered all offspring in a patch. Under promiscuity, every offspring produced by a female could have a different father drawn with replacement from the pool of available males within the

mother's patch. Offspring sex was assigned randomly. All adults died after reproduction, and the new population consisted of the offspring only (i.e., nonoverlapping generations).

The mutation model allowed mutation load to evolve within the population (Higgins and Lynch 2001; Guillaume and Perrin 2006, 2009). An offspring's survival w was a function of its genetic load, controlled by 1,000 unlinked diallelic diploid loci. Each offspring inherited one random allele from each of its parents. At birth, each individual had a probability U of 0.5 of a new mutation arising in its genome. Mutations were unidirectional; nondeleterious alleles were randomly drawn and became deleterious. Thus, while the genome-wide mutation rate remained constant, the gene-wise mutation rate increased as mutations accumulated. The genetic survival probability w was calculated by the multiplicative model:

$$w(i, j) = (1 - hs)^i(1 - s)^j,$$

where i is the number of heterozygote deleterious loci and j is the number of homozygote deleterious loci. Deleterious mutations had a fitness effect, $s = 0.3$, and a dominance coefficient, $h = 0.01$. Empirical data on effect sizes and dominance values for deleterious mutations are scarce; thus, mutation parameters were chosen to match with previous theoretical studies and were held constant for all simulations (Higgins and Lynch 2001; Guillaume and Perrin 2006, 2009).

Dispersal

Offspring surviving viability selection dispersed or remained philopatric according to their dispersal probability phenotype. Every individual carried two unlinked quantitative diploid loci coding for natal dispersal probability. The first locus was expressed in females, and the second locus was expressed in males. We assumed a continuum of alleles model, where allelic values ranged between 0 and 1. The natal dispersal probability of an individual was given by the mean of the two alleles at the expressed locus. We assumed global dispersal; any dispersing individual had an equal probability of reaching any other patch in the landscape and was subject to a dispersal cost ($d_c = 0.4$; Guillaume and Perrin 2006, 2009; Gros et al. 2009). Individuals inherited their dispersal genes from their parents with a probability of mutation equal to 0.001 per allele. The mutation effect size was taken from a negative exponential distribution of mean 0.2 (Guillaume and Perrin 2009). The effect was then added to or subtracted from the existing allelic value with equal probability.

Density Regulation

Ceiling density regulation was used to provide direct comparability with previous models exploring sex-biased dispersal (Guillaume and Perrin 2006, 2009). After dispersal,

in each patch the pool of male individuals was reduced to half K , and the pool of female individuals was also reduced to half K . This form of regulation assumed that competition for a limited number of breeding spots was sex specific. Ceiling regulation therefore resulted in equal sex ratios within patches and equal densities between patches when sufficient male and female offspring were present. Density regulation was random with respect to individual genotypes. In some additional simulations (app. D), we tested the effect of removing sex-specific density regulation; rather, an individual's survival was a probability determined by the density of all individuals in the patch, regardless of their sex.

Local Patch Extinction

Environmental stochasticity within simulations was introduced by including a probability of local catastrophic post-dispersal patch extinction (ε). Following an extinction event, the patch remained empty for the remainder of the generation but could be recolonized in the next generation (Poethke et al. 2003; Travis 2003).

Simulation Routine

In the first generation of all simulations, the patches were filled to carrying capacity and all individuals were initialized with a genome composed of nondeleterious alleles. An individual's dispersal alleles were drawn from a uniform distribution between 0 and 1. Using a fully factorial approach, we investigated the evolutionarily stable male (d_m) and female (d_f) dispersal probabilities evolving with inbreeding load ($U = 0.5$) for different fecundities (λ), carrying capacities (K), and local extinction probabilities (ε). Quasi-equilibrium dispersal probabilities were typically reached within 2,000 generations. Thus, all simulations ran for 4,000 generations over 30 replicates. Data and model source code underlying all results and figures are available in the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.11vb2> (Henry et al. 2016).

Results and Discussion

Our results shed new light on the discrepancy between empirical and theoretical studies of sex-biased dispersal. Indeed, our model predicted male-biased dispersal probabilities under polygyny, a result more consistent with empirical observations than previous models. For increasingly higher levels of demographic and/or environmental stochasticity (i.e., low values of K and λ and high values of ε), the dispersal bias fell toward males and, conversely, toward females with decreasing levels of stochasticity (i.e., high values of K and λ and low values of ε ; figs. 1A–1C, 2A–2C, 3). Especially strongly male-biased dispersal occurred with high dispersal costs and when

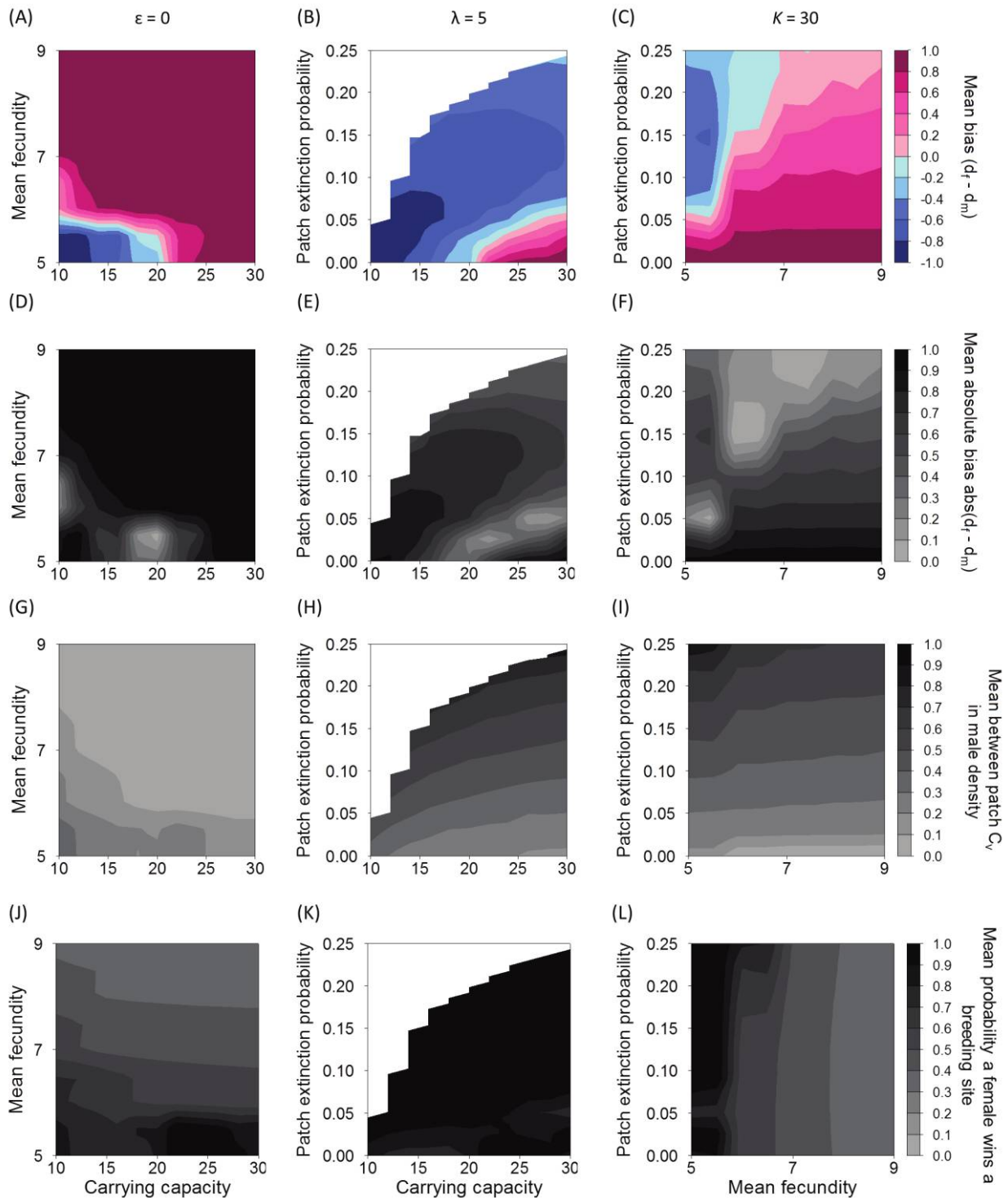


Figure 1: Effects of demographic and environmental stochasticity under conditions of polygyny with inbreeding load ($U = 0.5$). A–C, Mean dispersal bias (calculated as $d_f - d_m$). Increasing blue tones represent male bias, and increasing pink tones represent female bias. D–F, Mean absolute dispersal bias (calculated as the absolute value of $d_f - d_m$). G–I, Mean between-patch coefficient of variation in male density after density regulation and before reproduction. J–L, Mean probability a female juvenile wins a breeding site in her natal patch (calculated as $K/\text{number of females}$). Contours are interpolated over the mean of the last 100 generations of 30 replicates. White regions are areas of parameter space where populations did not persist. Parameters held constant are $d_c = 0.4$ (all cases), $\varepsilon = 0$ (A, D, G, J), $\lambda = 5$ (B, E, H, K), $K = 30$ (C, F, I, L).

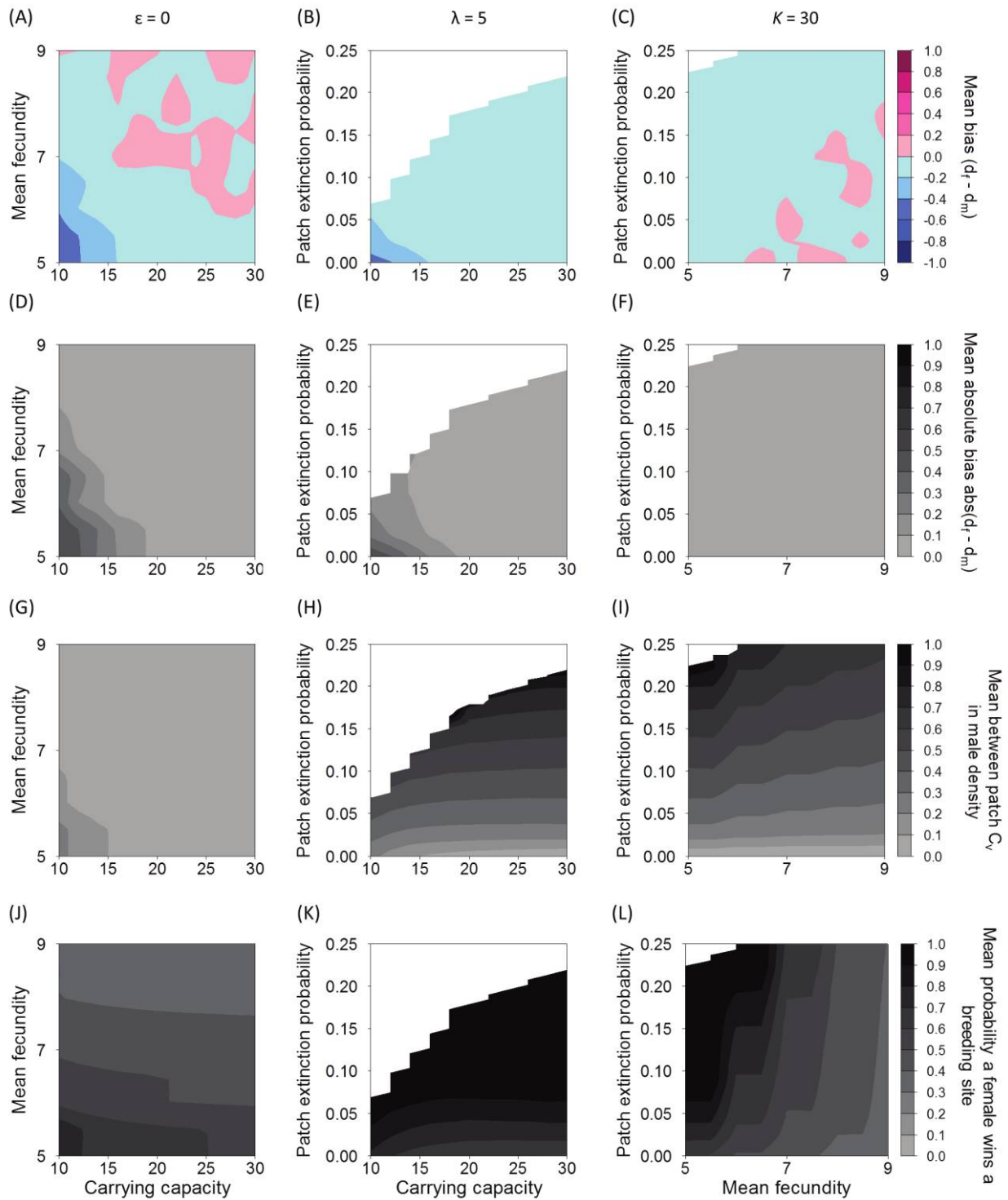


Figure 2: Effects of demographic and environmental stochasticity under conditions of promiscuity with inbreeding load ($U = 0.5$). A–C, Mean dispersal bias (calculated as female dispersal probability – male dispersal probability). Increasing blue tones represent male bias, and increasing pink tones represent female bias. D–F, Absolute dispersal bias (calculated as the absolute value of female dispersal probability – male dispersal probability). G–I, Mean between-patch coefficient of variation in male density after density regulation and before reproduction. J–L, Mean probability a female juvenile wins a breeding site in her natal patch (calculated as $K/\text{number of females}$). Contours are interpolated over the last 100 generations of 30 replicates. White regions are areas of parameter space where populations did not persist. Parameters held constant are $d_c = 0.4$ (all cases), $\varepsilon = 0$ (A, D, G, J), $\lambda = 5$ (B, E, H, K), $K = 30$ (C, F, I, L).

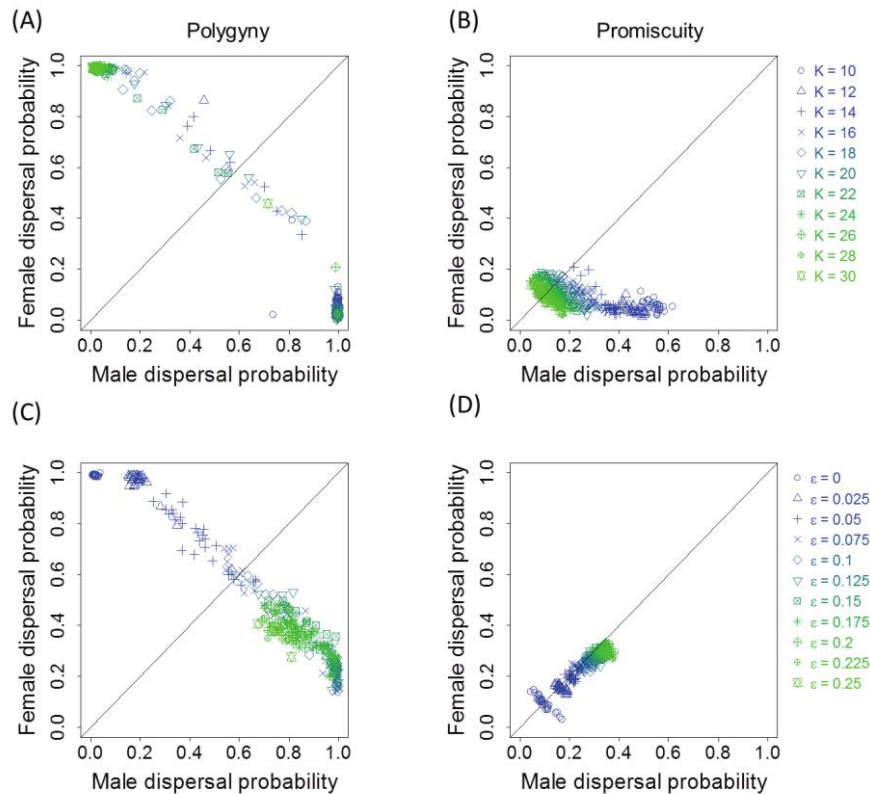


Figure 3: Evolved dispersal probability under polygyny (A, C) and promiscuity (B, D) with inbreeding load ($U = 0.5$) across a range of carrying capacities (K ; A, B) and local patch extinction probabilities (ϵ ; C, D). Each point represents the mean dispersal probability over the last 100 generations in one of 30 independent replicates. When held constant, parameter values are $\lambda = 5$, $\epsilon = 0$, $K = 30$, $d_c = 0.4$.

local populations experienced high demographic and/or environmental stochasticity (fig. 1A–1C). Strong stochasticity led to a high risk of local extinction. Thus, the result of strong male-biased dispersal is largely applicable to empirical examples of male-biased dispersal in populations experiencing high levels of disturbance, for example, small or fragmented populations (Stow et al. 2001; Stow and Sunnucks 2004; Gauffre et al. 2009; Oklander et al. 2010). The incorporation of stochasticity outweighed the effects of inbreeding load in the polygynous scenarios and converted a female-biased dispersal strategy (as previously found in Guillaume and Perrin 2009) into a male-biased strategy. This result also highlights the potential for changes in dispersal if increasing habitat destruction or climate change increases local extinction risk or dispersal costs. For example, in the Cunningham's skink (*Egernia cunninghami*), habitat fragmentation inhibited female dispersal more than male dispersal, leading to male-biased dispersal in fragmented sites (Stow et al. 2001). While strong female- or male-biased dispersal evolved under polygyny, for equivalent parameter values, the absolute bias was much reduced under promiscuity (cf. fig. 1 with fig. 2D–2F). The

wide range of evolutionary outcomes predicted by our model can be explained by the mating system and the degree of demographic and environmental stochasticity, modifying the relative strengths of resource competition, kin competition, and inbreeding avoidance.

Effect of Demographic and Environmental Stochasticity

In both mating systems, females were competing for space resources (LRC) while males were competing for mates (LMC). Stochasticity increased spatiotemporal heterogeneity in population size, and dispersing individuals could therefore realize fitness benefits associated with lower competition in less-crowded patches (McPeck and Holt 1992). In figures 1A–1C and 2A–2C, the blue regions correspond to higher between-patch variation in male density, shown in figures 1G–1I and 2G–2I. Male-biased dispersal therefore emerged when high levels of stochasticity increased the between-patch variation in male density. If male density varied between patches, then the intensity of male-male competition varied between patches. Thus, by dispersing, a male increased his chance of breeding

in a patch with fewer competing males and more female mates. Of course, the opposite was also true; a male could disperse to a patch with more males and fewer females. However, particularly under polygyny when LMC was high, the benefit outweighed the risk; all males in a patch were competing to be the sole mating male, and a successful immigrant male's fitness greatly increased by dominating all mating opportunities within a patch (Gros et al. 2009). Patches were filled with fewer juveniles after reproduction when stochasticity was high. Thus, selection for female dispersal also declined as LRC for breeding territories between females reduced. In figures 1J–1L and 2J–2L the probability of a female juvenile surviving density regulation and hence winning a breeding territory in her natal patch was higher when stochasticity was higher. Furthermore, while males were always competing for mates, as long as there was at least one male present, females were guaranteed a mate. Male-biased dispersal under high stochasticity therefore emerged as a consequence of increased male dispersal due to bet-hedging to reduce LMC and also increased female philopatry as LRC reduced. Furthermore, stronger male-biased dispersal emerged under polygyny than under promiscuity because LMC for males was higher. Indeed, in a similar study, Gros et al. (2009) found that the strength of male-male competition within patches was much higher under polygyny than under promiscuity, the strength of competition for relevant resources was higher for males than females under polygyny, and the strength of competition for relevant resources was similar between the sexes under promiscuity.

The form of stochasticity mattered for the evolution of male-biased dispersal because environmental stochasticity increased only the degree of male-biased dispersal when it exaggerated population fluctuations already caused by demographic stochasticity; otherwise, it could reduce the bias. The absolute bias decreased as patch extinction rates increased when K and λ parameters were held constant (fig. 1E, 1F). When demographic stochasticity was low (e.g., high mean fecundities and high carrying capacities), same-sex competition was high because occupied patches were full. Thus, individuals of both sexes could still benefit from dispersal into a patch made empty by a local extinction event. For females, local extinction increased dispersal when occupied patches were saturated. However, when local extinction exaggerated population fluctuations, creating patches below saturation, dispersal decreased (Ronce et al. 2000). We therefore found that increasing local extinction could decrease the degree of male-biased dispersal because female dispersal simultaneously increased or remained high. For example, under promiscuity, male-biased dispersal did not emerge because female dispersal simultaneously increased (fig. 3D), and under polygyny for high extinction values ($\varepsilon = 0.25$), female dispersal remained at around 0.4 (fig. 3C). Complete philopatry in one sex is rarely observed (Richard et al. 1993; Kerth et al.

2002; Lawson Handley and Perrin 2007), and slightly more balanced dispersal is potentially a more realistic theoretical result than complete philopatry in one sex.

Sex-specific ceiling regulation assumes that competition for breeding sites differs between the sexes. Indeed, in some species, density-dependent survival appears to be more strongly influenced by the density of the same sex than the density of the opposite sex (Clutton-Brock et al. 1985, 1987; Wauters et al. 2004; Bonenfant et al. 2009; Michler et al. 2011). Ceiling regulation resulted in equal sex ratios within patches and no variation in density between patches (if there were sufficient males and females before regulation). However, for some species, density-dependent survival may not be sex specific (Bonenfant et al. 2009; Bassar et al. 2013; Cubaynes et al. 2014). Because of the importance of demographic stochasticity for between-patch variance in LMC, relaxing the assumption of sex-specific ceiling regulation had important implications for the evolution of male-biased dispersal (app. D). Using stochastic sex-independent density regulation resulted in uneven sex ratios within patches and differing densities between patches, even when sufficient male and female offspring were present. This consequently increased demographic stochasticity and between-patch variability in LMC. Increased between-patch variance in LMC resulted in strong male-biased dispersal for all values of K , even in the absence of inbreeding load (fig. D1C; figs. A1, B1, C1, D1 available online). The incorporation of inbreeding load then further increased the strength of male-biased dispersal (fig. D1D). Now that we have a better understanding of the different and synergistic mechanisms at play across previous studies (Guillaume and Perrin 2006; Gros et al. 2009), an important avenue for future work would be to investigate the roles of density dependence for driving sex-biased dispersal.

Effect of Kin Competition

Kin competition selects for higher natal dispersal probabilities, because individuals increase their inclusive fitness by competing with unrelated individuals in foreign patches rather than competing with kin in the natal patch (Hamilton and May 1977). Selection for dispersal to avoid kin competition was weaker under promiscuity than polygyny because under promiscuity competitors were less likely to be related, while under polygyny competitors were always half- or full siblings. Without mutation load, we found that dispersal rates were indeed higher under polygyny than promiscuity for the equivalent parameter values (app. B). Kin competition was therefore a cause for the overall higher dispersal rates and higher absolute bias under polygyny than promiscuity (cf. fig. 1C, 1D with fig. 2C, 2D). Under promiscuity but not under polygyny, however, stochasticity could alter kin structure and, in turn, alter the influence of kin competition on dispersal. Under promiscuity, we expect kin com-

petition to increase as stochasticity increases because competitors are more likely to be related when patch densities decreased (Poethke and Hovestadt 2002; Poethke et al. 2007; app. B). Thus, increasing male-biased dispersal under promiscuity with increasing demographic stochasticity can be interpreted as a response to between-patch variation in LMC and increasing kin competition between males. Under complete polygyny, increased stochasticity is not expected to change the kin structure and degree of kin competition because offspring in a patch share the same father, regardless of patch density (Gros et al. 2009). Thus, although dispersal probabilities are overall higher under polygyny, the increasing strength of male-biased dispersal under polygyny with increasing stochasticity arose through increasing between-patch variance in LMC but not increasing kin competition.

Effect of Inbreeding Load

Similar to kin competition, the response to inbreeding load was much stronger under polygyny than under promiscuity. Inbreeding load had two effects. First, it exaggerated population fluctuations because it reduced the number of offspring surviving at birth. For example, a female's realized fecundity was reduced by up to one-third on average (app. C). Unless λ was sufficiently high and such losses removed only the doomed surplus (Errington 1934; Kokko and Lindström 1998), inbreeding load further exaggerated demographic stochasticity. Second, inbreeding load generates heterosis, resulting in selection for increased dispersal probabilities as an inbreeding avoidance strategy, especially when relatedness is high under polygyny (Guillaume and Perrin 2006, 2009). Selection to avoid inbreeding was highest for females under polygyny, because female fecundity was determined by one event with one—potentially related—male. For a polygynous breeding male, however, the much greater overall fecundity could buffer offspring losses due to inbreeding load. Consequently, selection for females to avoid inbreeding remained strong, and female-biased dispersal probabilities evolved when selection pressures from local competition and kin competition were similar between the sexes (low stochasticity), as previously found by Guillaume and Perrin (2009). In figure 1A–1C, the pink regions (female bias) correspond to large values of absolute bias in figure 1D–1F; thus, there was a strong bias in the female direction. Under promiscuity, the effective population size in a patch is expected to be larger; females could therefore spread the risk of inbreeding by mating with multiple males rather than by dispersing. Thus, under promiscuity, female-biased dispersal emerged, but the magnitude of the bias was smaller than under polygyny. In figure 2A–2C, the pink regions (female bias) correspond to only small values of absolute bias in figure 2D–2F.

Inbreeding avoidance selects for dispersal in at least one of the sexes; however, we expect female-biased dispersal

when LRC is high for females (especially if it is between kin) and male-biased dispersal when LMC varies between patches. Thus, our results support Greenwood's (1980) hypothesis and the mechanism proposed by Gros et al. (2009) and, more recently, Hovestadt et al. (2014); sex-biased dispersal emerges owing to asymmetric spatiotemporal variability in competition between the sexes. Nonetheless, the relative push and pull of all the selective forces, kin competition, inbreeding avoidance, and local competition determined the degree of the bias. As such, when the accumulative strength of selection pressures for dispersal became similar between the sexes, the dispersal bias became less certain. In the majority of simulations, the bias tended toward the sex with the stronger incentives to disperse, but given the stochastic nature of the simulations, the outcome was never certain. On occasion, we found more symmetrical dispersal rates or variability in the direction of the bias. For example, under polygyny with high values of K , usually females dispersed and males were philopatric; however, in some replicates, the opposite occurred (fig. 3A). Under promiscuity, the evolutionarily stable dispersal rates found between replicates were much less scattered (fig. 3B). Furthermore, dispersal probabilities tended to settle rapidly, because if one sex dispersed, the pressure to disperse to avoid inbreeding was immediately reduced in the other sex, particularly when dispersal incurred a cost.

Male-Biased Dispersal: A Result of Multiple Selective Pressures

The evolution male-biased dispersal due to the combined effects of inbreeding avoidance, dispersal costs, and stochasticity is similar to hypotheses proposed in some empirical studies. For example, in American black bears (*Ursus americanus*), male-biased dispersal and female philopatry resulted in low levels of inbreeding. This suggests that male-biased dispersal is effective as an inbreeding avoidance strategy (Costello et al. 2008). However, male dispersal rates were also higher in areas with high male bear density compared with areas of low male bear density, and the likelihood of young males breeding successfully was lower in high-density areas. This indicates that male-biased dispersal rates could also be modified by LMC between males (Costello et al. 2008). Similarly, for brook trout (*Salvelinus fontinalis*), Hutchings and Gerber (2002) suggested that male-biased dispersal was a consequence of inbreeding avoidance and LMC. Males were recaptured at greater distances from tagging locations during spawning than during nonspawning, thus suggesting that male dispersal was associated with mating and competition for mates (Hutchings and Gerber 2002). In our model, females choose mates at random, but Lehmann and Perrin (2003) also found that female mate choice to avoid kin could drive up male dispersal. Alternatively, inbreeding load could

also lead to variation in male quality, with females choosing higher-quality males with less load (Kempnaers 2007; Fromhage et al. 2009). This could potentially act as a form of purging through higher reproductive success of individuals carrying less mutational load (Mitton et al. 1993) and reduce selection for higher dispersal probabilities to alleviate mutation load. Evolution of female choice for male quality related to mutational load is thus another avenue for future research into male-biased dispersal.

Our multifaceted theoretical approach relates well to empirical patterns of sex-biased dispersal, in particular providing an improved match to empirical observations of male-biased dispersal in mate defense systems. In our study, the result of strong male-biased dispersal under sex-specific ceiling density regulation is largely applicable to empirical examples of male-biased dispersal in populations experiencing high levels of disturbance, such as small or fragmented populations (Stow et al. 2001; Stow and Sunnucks 2004; Gauffre et al. 2009; Oklander et al. 2010). Thus, an important further step would be to reduce dispersal costs and local extinction pressure within the model to investigate the evolution of male-biased dispersal for species existing in apparently more stable environments (Packer and Pusey 1987; Clutton-Brock et al. 1997; Keogh et al. 2007). An outstanding major challenge for models of dispersal evolution is to add sufficient realism so quantitative predictions can be made for the eco-evolutionary dynamics of particular species. Existing studies explicitly linking models and empirical data on sex-biased dispersal and its evolution are rare. However, Blyton et al. (2015) recently used simulation and empirical data to investigate the effectiveness of sex-biased dispersal as an inbreeding avoidance strategy in the mountain brushtail possum (*Trichosurus cunninghami*). Simulation results and empirical results were congruent; moreover, the study is a vital demonstration of the utility of validating simulation results against empirical data. To achieve greater realism, future theoretical work will have to consider more carefully the form of density dependence incorporated, since this can alter the intensity of competition experienced by individuals, as well as model more explicitly the genetic architecture underlying dispersive traits. With such a modeling framework, we can begin to address, in greater detail, the gap between empirical patterns and theoretical results to further our understanding of sex-biased dispersal.

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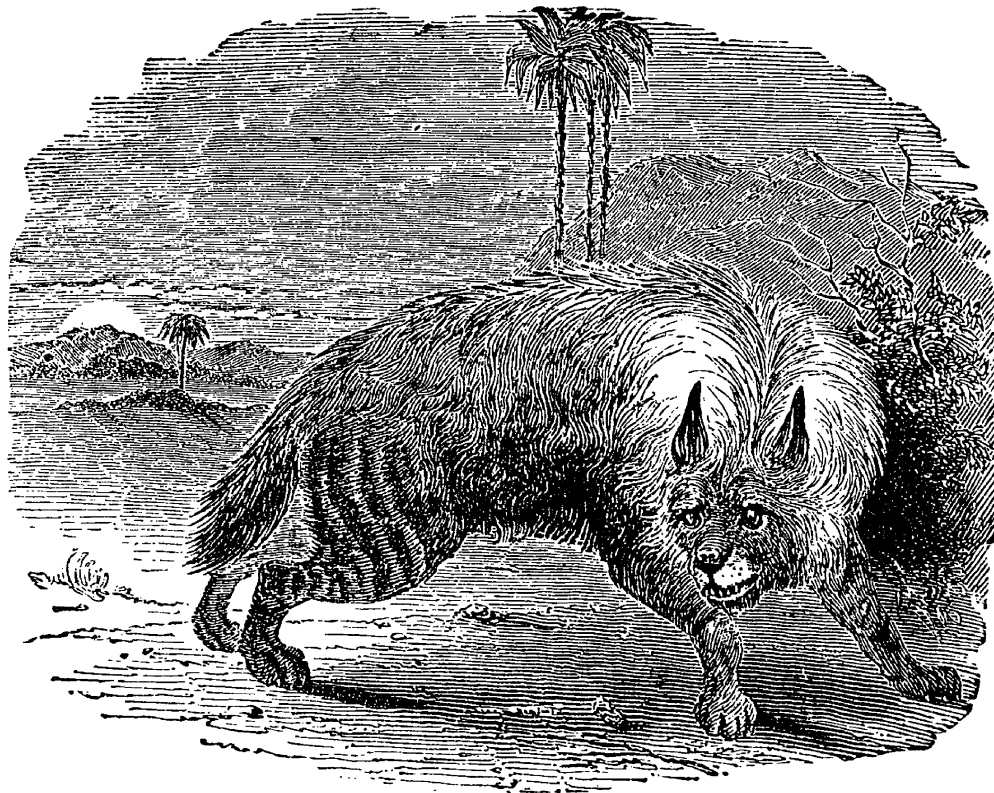
Literature Cited

- Austin, J. D., J. A. Dávila, S. C. Lougheed, and P. T. Boag. 2003. Genetic evidence for female-biased dispersal in the bullfrog, *Rana catesbeiana* (Ranidae). *Molecular Ecology* 12:3165–3172.
- Baguette, M., C. Vansteenwegen, I. Convi, and G. Nève. 1998. Sex-biased density-dependent migration in a metapopulation of the butterfly *Proclissiana eunomia*. *Acta Oecologica* 19:17–24.
- Bassar, R. D., A. Lopez-Sepulcre, D. N. Reznick, J. Travis, A. E. E. D. Brodie, and E. M. A. McPeck. 2013. Experimental evidence for density-dependent regulation and selection on Trinidadian guppy life histories. *American Naturalist* 181:25–38.
- Blanquart, F., and S. Gandon. 2011. Evolution of migration in a periodically changing environment. *American Naturalist* 177:188–201.
- Blyton, M. D. J., S. C. Banks, and R. Peakall. 2015. The effect of sex-biased dispersal on opposite-sexed spatial genetic structure and inbreeding risk. *Molecular Ecology* 24:1681–1695.
- Bonenfant, C., J. Gaillard, T. Coulson, M. Festa-Bianchet, A. Loison, M. Garel, L. E. Loe, et al. 2009. Empirical evidence of density-dependence in populations of large herbivores. *Advances in Ecological Research* 41:313–357.
- Cadet, C., R. Ferrière, J. A. J. Metz, and M. van Baalen. 2003. The evolution of dispersal under demographic stochasticity. *American Naturalist* 162:427–441.
- Clarke, A., S. Bernt-Erik, and E. Roskaft. 1997. Sex biases in avian dispersal: a reappraisal. *Oikos* 79:429–438.
- Clutton-Brock, T. H., and D. Lukas. 2012. The evolution of social philopatry and dispersal in female mammals. *Molecular Ecology* 21:472–492.
- Clutton-Brock, T. H., M. Major, S. D. Albon, and F. E. Guinness. 1987. Early development and population dynamics in red deer. I. Density-dependent effects on juvenile survival. *Journal of Animal Ecology* 56:53–67.
- Clutton-Brock, T. H., M. Major, and F. E. Guinness. 1985. Population regulation in male and female red deer. *Journal of Animal Ecology* 54:831–846.
- Clutton-Brock, T. H., K. E. Rose, and F. E. Guinness. 1997. Density-related changes in sexual selection in red deer. *Proceedings of the Royal Society B: Biological Sciences* 264:1509–1516.
- Costello, C. M., S. R. Creel, S. T. Kalinowski, N. V. Vu, and H. B. Quigley. 2008. Sex-biased natal dispersal and inbreeding avoidance in American black bears as revealed by spatial genetic analyses. *Molecular Ecology* 17:4713–4723.
- Cubaynes, S., D. R. MacNulty, D. R. Stahler, K. A. Quimby, D. W. Smith, and T. Coulson. 2014. Density-dependent intraspecific aggression regulates survival in northern Yellowstone wolves (*Canis lupus*). *Journal of Animal Ecology* 83:1344–1356.
- Douadi, M. I., S. Gatti, F. Levrero, G. Duhamel, M. Bermejo, D. Vallet, N. Menard, et al. 2007. Sex-biased dispersal in western lowland gorillas (*Gorilla gorilla*). *Molecular Ecology* 16:2247–2259.
- Dubey, S., G. P. Brown, T. Madsen, and R. Shine. 2008. Male-biased dispersal in a tropical Australian snake (*Stegonotus cucullatus*, Colubridae). *Molecular Ecology* 17:3506–3514.
- Duputié, A., and F. Massol. 2013. An empiricist's guide to theoretical predictions on the evolution of dispersal. *Interface Focus* 3:20130028.
- Errington, P. L. 1934. Vulnerability of bobwhite populations to predation. *Ecology* 15:110–127.
- Fontanillas, P., E. Petit, and N. Perrin. 2004. Estimating sex-specific dispersal rates with autosomal markers in hierarchically structured populations. *Evolution* 58:886–894.

- Fraser, D. J., C. Lippé, and L. Bernatchez. 2004. Consequences of unequal population size, asymmetric gene flow and sex-biased dispersal on population structure in brook charr (*Salvelinus fontinalis*). *Molecular Ecology* 13:67–80.
- Fromhage, L., H. Kokko, and J. M. Reid. 2009. Evolution of mate choice for genome-wide heterozygosity. *Evolution* 63:684–694.
- Gandon, S. 1999. Kin competition, the cost of inbreeding and the evolution of dispersal. *Journal of Theoretical Biology* 200:345–364.
- Gauffre, B., E. Petit, S. Brodier, V. Bretagnolle, and J. F. Cosson. 2009. Sex-biased dispersal patterns depend on the spatial scale in a social rodent. *Proceedings of the Royal Society B: Biological Sciences* 276:3487–3494.
- Greenwood, P. J. 1980. Mating systems, philopatry and dispersal in birds and mammals. *Animal Behaviour* 28:1140–1162.
- Gros, A., T. Hovestadt, and H. J. Poethke. 2008. Evolution of sex-biased dispersal: the role of sex-specific dispersal costs, demographic stochasticity, and inbreeding. *Ecological Modelling* 219:226–233.
- Gros, A., H. J. Poethke, and T. Hovestadt. 2009. Sex-specific spatio-temporal variability in reproductive success promotes the evolution of sex-biased dispersal. *Theoretical Population Biology* 76:13–8.
- Guillaume, F., and N. Perrin. 2006. Joint evolution of dispersal and inbreeding load. *Genetics* 173:497–509.
- . 2009. Inbreeding load, bet hedging, and the evolution of sex-biased dispersal. *American Naturalist* 173:536–541.
- Hamilton, W. D., and R. M. May. 1977. Dispersal in stable habitats. *Nature* 269:578–581.
- Henry, R. C., A. Coulon, and J. M. J. Travis. 2016. Data from: The evolution of male-biased dispersal under the joint selective forces of inbreeding load and demographic and environmental stochasticity. *American Naturalist*, Dryad Digital Repository, <http://dx.doi.org/10.5061/dryad.11vb2>.
- Higgins, K., and M. Lynch. 2001. Metapopulation extinction caused by mutation accumulation. *Proceedings of the National Academy of Sciences of the USA* 98:2928–2933.
- Hovestadt, T., O. Mitesser, and H.-J. Poethke. 2014. Gender-specific emigration decisions sensitive to local male and female density. *American Naturalist* 184:38–51.
- Hutchings, J., and L. Gerber. 2002. Sex-biased dispersal in a salmonid fish. *Proceedings of the Royal Society B: Biological Sciences* 269:2487–2493.
- Kempnaers, B. 2007. Mate choice and genetic quality: a review of the heterozygosity theory. *Advances in the Study of Behavior* 37:189–278.
- Keogh, J. S., J. K. Webb, and R. Shine. 2007. Spatial genetic analysis and long-term mark-recapture data demonstrate male-biased dispersal in a snake. *Biology Letters* 3:33–35.
- Kerth, G., F. Mayer, and E. Petit. 2002. Extreme sex-biased dispersal in the communally breeding, nonmigratory Bechstein's bat (*Myotis bechsteinii*). *Molecular Ecology* 11:1491–1498.
- Kokko, H., and J. Lindström. 1998. Seasonal density dependence, timing of mortality, and sustainable harvesting. *Ecological Modelling* 110:293–304.
- Lampert, K. P., S. Rand, U. G. Mueller, and M. J. Ryan. 2003. Fine-scale genetic pattern and evidence for sex-biased dispersal in the tungara frog, *Physalaemus pustulosus*. *Molecular Ecology* 12:3325–3334.
- Lawson Handley, L. J., and N. Perrin. 2007. Advances in our understanding of mammalian sex-biased dispersal. *Molecular Ecology* 16:1559–1578.
- Lehmann, L., and N. Perrin. 2003. Inbreeding avoidance through kin recognition: choosy females boost male dispersal. *American Naturalist* 162:638–652.
- Liebigold, E. B., E. D. Brodie III, and P. R. Cabe. 2011. Female philopatry and male-biased dispersal in a direct-developing salamander, *Plethodon cinereus*. *Molecular Ecology* 20:249–257.
- Mabry, K. E., E. L. Shelley, K. E. Davis, D. T. Blumstein, and D. H. Van Vuren. 2013. Social mating system and sex-biased dispersal in mammals and birds: a phylogenetic analysis. *PLoS ONE* 8: e57980.
- McPeck, M. A., and R. D. Holt. 1992. The evolution of dispersal in spatially and temporally varying environments. *American Naturalist* 140:1010–1027.
- Michler, S. P. M., M. Nicolaus, R. Ubels, M. van der Velde, C. Both, J. M. Tinbergen, and J. Komdeur. 2011. Do sex-specific densities affect local survival of free-ranging great tits? *Behavioral Ecology* 65:1975–1986.
- Mitton, J. B., W. S. F. Schuster, E. G. Cothran, and J. C. de Fries. 1993. Correlation between the individual heterozygosity of parents and their offspring. *Heredity* 71:59–63.
- North, A., S. Cornell, and O. Ovaskainen. 2011. Evolutionary responses of dispersal distance to landscape structure and habitat loss. *Evolution* 65:1739–1751.
- Novak, S. 2014. Habitat heterogeneities versus spatial type frequency variances as driving forces of dispersal evolution. *Ecology and Evolution* 4:4589–4597.
- Oklander, L. I., M. M. Kowalewski, and D. Corach. 2010. Genetic consequences of habitat fragmentation in black-and-gold howler (*Alouatta caraya*) populations from northern Argentina. *International Journal of Primatology* 31:813–832.
- Olsson, M., and R. Shine. 2003. Female-biased natal and breeding dispersal in an alpine lizard, *Niveoscincus microlepidotus*. *Biological Journal of the Linnean Society* 79:277–283.
- Packer, C., and A. E. Pusey. 1987. Intrasexual cooperation and the sex ratio in African lions. *American Naturalist* 130:636–642.
- Palo, J. U., D. Lesbarrères, D. S. Schmeller, C. R. Primmer, and J. Merilä. 2004. Microsatellite marker data suggest sex-biased dispersal in the common frog *Rana temporaria*. *Molecular Ecology* 13:2865–2869.
- Pardini, A. T., C. S. Jones, L. R. Noble, B. Kreiser, H. Malcolm, B. D. Bruce, J. D. Stevens, et al. 2001. Sex-biased dispersal of great white sharks. *Nature* 412:139–140.
- Pernetta, A. P., J. A. Allen, T. J. C. Beebee, and C. J. Reading. 2011. Fine-scale population genetic structure and sex-biased dispersal in the smooth snake (*Coronella austriaca*) in southern England. *Heredity* 107:231–238.
- Perrin, N., and V. Mazalov. 1999. Dispersal and inbreeding avoidance. *American Naturalist* 154:282–292.
- . 2000. Local competition, inbreeding, and the evolution of sex-biased dispersal. *American Naturalist* 155:116–127.
- Poethke, H. J., and T. Hovestadt. 2002. Evolution of density- and patch-size-dependant dispersal rates. *Proceedings of the Royal Society B: Biological Sciences* 269:637–645.
- Poethke, H. J., T. Hovestadt, and O. Mitesser. 2003. Local extinction and the evolution of dispersal rates: causes and correlations. *American Naturalist* 161:631–640.
- Poethke, H. J., B. Pfenning, and T. Hovestadt. 2007. The relative contribution of individual and kin selection to the evolution of density-dependent dispersal rates. *Evolutionary Ecology Research* 9:41–50.
- Richard, A. F., P. Rakotomanga, and M. Schwartz. 1993. Dispersal by *Propithecus verreauxi* at Beza-Mahafaly, Madagascar: 1984–1991. *American Journal of Primatology* 30:1–20.

- Rivera, P. C., C. N. Gardenal, and M. Chiaraviglio. 2006. Sex-biased dispersal and high levels of gene flow among local populations in the Argentine boa constrictor, *Boa constrictor occidentalis*. *Austral Ecology* 31:948–955.
- Ronce, O., F. Perret, and I. Olivieri. 2000. Evolutionarily stable dispersal rates do not always increase with local extinction rates. *American Naturalist* 155:485–496.
- Sheridan, C. M., J. R. Spotila, W. F. Bien, and H. W. Avery. 2010. Sex-biased dispersal and natal philopatry in the diamondback terrapin, *Malaclemys terrapin*. *Molecular Ecology* 19:5497–5510.
- Stow, A. J., and P. Sunnucks. 2004. High mate and site fidelity in Cunningham's skinks (*Egernia cunninghami*) in natural and fragmented habitat. *Molecular Ecology* 13:419–430.
- Stow, A. J., P. Sunnucks, D. A. Briscoe, and M. G. Gardner. 2001. The impact of habitat fragmentation on dispersal of Cunningham's skink (*Egernia cunninghami*): evidence from allelic and genotypic analyses of microsatellites. *Molecular Ecology* 10:867–878.
- Travis, J. M. J. 2003. Climate change and habitat destruction: a deadly anthropogenic cocktail. *Proceedings of the Royal Society B: Biological Sciences* 270:467–473.
- Tucker, A. D., H. I. Mccallum, and K. R. McDonald. 1998. Sex-biased dispersal in a long-lived polygynous reptile (*Crocodylus johnstoni*). *Behavioural Ecology and Sociobiology* 44:85–90.
- Ujvari, B., M. Dowton, and T. Madsen. 2008. Population genetic structure, gene flow and sex-biased dispersal in frillneck lizards (*Chlamydosaurus kingii*). *Molecular Ecology* 17:3557–3564.
- Waser, P. M., N. Austad, and B. Keane. 1986. When should animals tolerate inbreeding. *American Naturalist* 128:529–537.
- Wauters, L. A., E. Matthysen, F. Adriaensen, and G. Tosi. 2004. Within-sex density dependence and population dynamics of red squirrels *Sciurus vulgaris*. *Journal of Animal Ecology* 73:11–25.

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“Prominent among the mammalian scavengers are the hyenas [illustrated], the ugliest in their general appearance of all the flesh eaters. These well-known animals are at present confined to the warm regions of Africa and Asia, where they feed upon animals which they find dead, and such parts of animals as have been left from the feasts of the lion, tiger, and others of the nobler kinds of the typical carnivora.” From “A Few Words About Scavengers” by Sanborn Tenney (*The American Naturalist* 1877, 11:129–135).