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# Mate choice interacts with movement limitations to influence effective dispersal

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ABSTRACT

Dispersal can augment viability of small populations, but this effect is contingent on successful post-dispersal reproduction of individuals. Nonetheless, variation in post-dispersal reproductive success is frequently ignored, such that dispersal (movement between fragments) and effective dispersal (movement followed by reproduction) are often viewed interchangeably. Mate choice by females can potentially limit or augment post-dispersal reproductive success of males and is predicted to vary with the distance dispersed. Consequently, mate choice may impact effective dispersal rates, but this issue is poorly understood. We use a multi-fragment, individual-based model to investigate if distance-mediated mate choice limits effective dispersal, in the absence of, and in combination with, distance-limited dispersal. We considered four scenarios of distance-mediated mate choice such that it was (a) spatially uniform, dispersers were (b) preferred or (c) avoided, and (d) females showed preference for dispersers that moved intermediate distances. We tested if mating system and sex-biased dispersal influence the role of mate choice on effective dispersal. We parameterized our model using previously published demographic data on the chimpanzee *Pan troglodytes*; however, we intend the model to be generalizable to many species and scenarios considered extend beyond observed chimpanzee behaviour. Mate choice induced distance-dependent patterns of effective dispersal among populations, which, under certain conditions, surpased impacts of distance-limited dispersal. When distance suppressed both dispersal and mate choice, the two additively decreased effective dispersal at large distances. When dispersers were preferred, the effects of mate choice and limited dispersal negated each other to a degree determined by the relative spatial scale of the two processes. Effects of mate choice on effective dispersal can lead to misleading conclusions on dispersal barriers when inferred through indices that reflect effective dispersal. Isolating constraints to effective dispersal can enhance our understanding of connectivity and can identify key needs for connectivity conservation.



## 1. Introduction

With widespread habitat loss, many imperilled species persist predominantly as small populations (Harcourt and Doherty, 2005). Maintenance of gene flow is an important conservation strategy for these populations to ameliorate detrimental effects of reduced genetic diversity (Keller and Waller, 2002; Doerr et al., 2011). Gene flow – defined at the scale of populations – arises from the movement of individuals between populations followed by post-dispersal reproduction (Coulon et al., 2010). In recent years, there has been an increasing interest in understanding differences in dispersal, or individual movement between two breeding populations, and effective dispersal, used here to indicate dispersal followed by subsequent non-natal successful reproduction (Greenwood and Harvey, 1982; Coulon et al., 2010). Dispersal and effective dispersal rates between populations are often implicitly assumed to serve as reliable and unbiased indices of each other, such as when inferring movement barriers from gene flow (Broquet et al., 2006; Epps et al., 2007) and the application of effective dispersal guidelines to dispersal rates (Olsson et al., 2008). Yet conditions that influence post-dispersal reproductive success can cause unexpected patterns, resulting in misleading inferences on dispersal and

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effective dispersal (e.g., de Meester et al., 2002; Riley et al., 2006; Fletcher et al., 2015). Such conditions that modify the relationship between dispersal and effective dispersal rates are highly relevant for understanding connectivity patterns across space, potential for recolonization of habitat, and for effective connectivity conservation (Riley et al., 2006; Vasudev et al., 2015).

Understanding discrepancies between dispersal and effective dispersal rates requires identifying factors that influence post-dispersal reproductive success. Multiple factors, including unfamiliarity with local surroundings, lowered fitness costs and hastened reproductive senescence (i.e., rapid ageing leading to shortened reproductive lifespan), can alter the reproductive success of dispersers (Soulsbury et al., 2008; Nevoux et al., 2013, Fletcher et al., 2015). Mate choice plays a prominent role in many of these factors (Canova and Fasola, 1994; Forero et al., 2002). The influence of mate choice can further be mediated by mating systems through limitations on reproductive success (e.g., as observed in monogamous species) and the strength of mate choice displayed by females (Clutton-Brock, 1988), in which both factors determine the variation in reproductive success across individuals. Sex-biased dispersal may accentuate, or negate, the effects of mate choice on effective dispersal (e.g., Blundell et al., 2002), depending on whether the sex that disperses is the one facing mate choice.

Dispersers can provide indirect benefits or costs as potential mates such that they can be preferred or avoided for mating. Inbreeding avoidance often leads to preferential mate selection of dispersers or unrelated individuals as compared to residents (Lehmann and Perrin, 2003). Additionally, producing heterozygous offspring may provide indirect benefits for females when these offspring show fitness advantages in terms of reproduction (Ryder et al., 2010) or survival (Landry et al., 2001). Furthermore, frequency-dependent mate choice, whereby the attractiveness of a phenotype is determined by its frequency in a population can either lead to avoidance (e.g., van Gossum et al., 2001), or preference (e.g., Kokko et al., 2007) of dispersers. Familiarity might also make more closely related individuals preferred mates (Tregenza and Wedell, 2000; de Meester et al., 2002). Furthermore, dispersers that have traversed over large distances may suffer from heightened dispersal costs (Bonte et al., 2012). Dispersal costs manifest in several ways, such as poor body condition, and may result in unrelated individuals being avoided as mates (Forero et al., 2002). Given evidence for both disperser preference and avoidance in the wild (Belichon et al., 1996; Forero et al., 2002; Griesser et al., 2008), mate choice may in reality be selective of potential mates that are of intermediate relatedness (Tregenza and Wedell, 2000). While empirical studies on post-dispersal reproductive success often dichotomize between dispersers and residents (reviewed in Belichon et al., 1996; Griesser et al., 2008), theoretical studies posit that mate choice is based, rather, on a gradient of relatedness (de Meester et al., 2002; Lehmann and Perrin, 2003). This supposition is supported by the use of self-similarity in recognizing unrelated individuals (Mateo and Johnston, 2000) and reports of post-dispersal reproductive success in natural populations varying by the distance dispersed (Forero et al., 2002; Gienapp and Merilä, 2011).

The spatial configuration of populations plays an important role in determining patterns of dispersal in landscapes (MacArthur and Wilson, 1967), such as increasing distance between populations leading to a decline in dispersal rates ('distance-limited dispersal' hereafter, Koenig et al., 1996). In addition, distance between population-pairs can act as a proxy for relatedness through genetic isolation (Wright, 1943) and local adaptation to increasingly divergent environments (de Meester et al., 2002). Such a distance-dependant gradient of relatedness, by leading resident females to choose (or avoid) unrelated dispersers as mates, could lead to augmentation (or suppression) of reproductive success of long-distance dispersers and ultimately lead to spatial patterns of effective dispersal imposed through distance-dependant mate choice (Fig. 1).

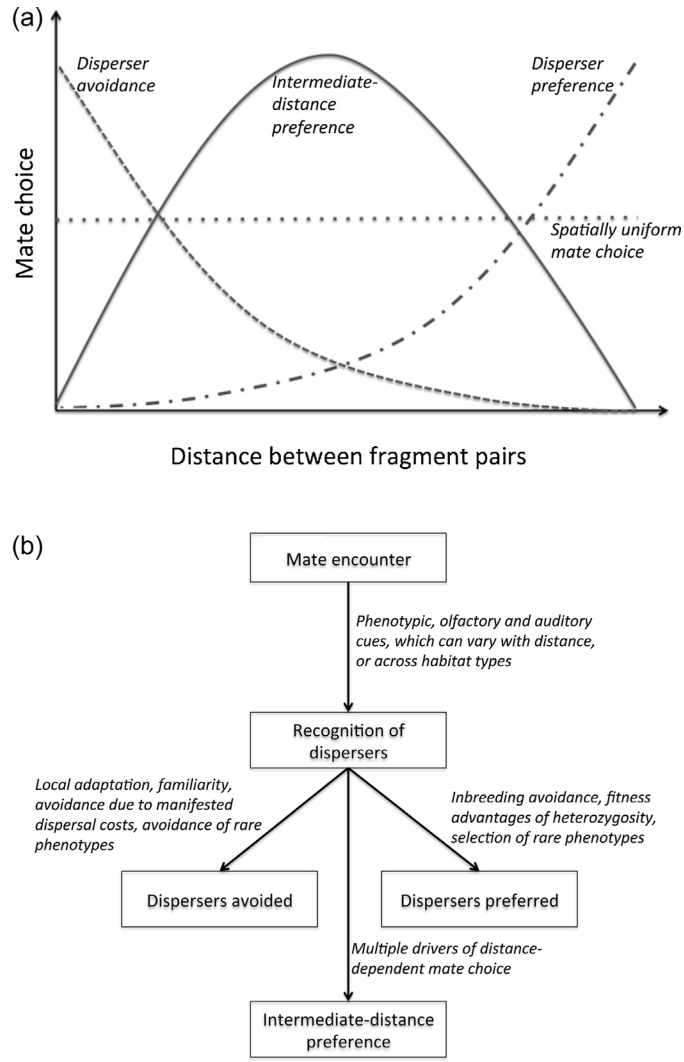


**Fig. 1.** (a) Scenarios of distance-mediated mate choice considered in this study. We consider spatially uniform mate choice (dotted line), mate choice decreasing with distance, or disperser avoidance (dashed line) and mate choice increasing with distance, or disperser preference (dotted and dashed line). The last scenario includes an initial increase of mate preference with distance, a peak in mate preference at intermediate distances and subsequent suppression of mate choice (intermediate-distance preference; solid line). (b) A framework for distance-dependent mate choice, showing potential drivers of disperser avoidance, disperser preference, or selection for dispersers of intermediate distance.

While theory suggests that mate choice may vary with dispersal distance (or relatedness, de Meester et al., 2002; Lehmann and Perrin, 2003) and empirical evidence suggest that dispersers and residents often differ in their reproductive success (Belichon et al., 1996), it is unclear if, and the extent to which, such effects influence population connectivity (Kool et al., 2013). Connectivity, or functional linkages between populations (or habitats), forged by effective dispersal can influence population dynamics and viability through a variety of mechanisms, including demographic rescue, inbreeding avoidance and colonization of unoccupied habitat (Keller and Waller, 2002; Doerr et al., 2011). Unfortunately, empirical evidence of post-dispersal reproductive success from natural populations is rarely of sufficient scale to detect distance-dependent patterns of mate choice and relate them to connectivity (Belichon et al., 1996; but see Riley et al., 2006, Fletcher et al., 2015). Simulation models form an ideal alternative method to provide a