

# Kin Competition and the Evolution of Sex Differences in Development Time and Body Size

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**ABSTRACT:** One key trade-off underlying life-history evolution is the one between age and size at maturity, with earlier maturation leading to greater chances of juvenile survival at the cost of reduced fecundity as an adult. Here we model the impact of limited dispersal and kin competition on the stable resolution of this trade-off. We show that if mating is at least occasionally nonlocal, then limited dispersal favors juvenile survival over adult fecundity in females, promoting earlier female maturation at the population level; at the same time, it favors adult fecundity over juvenile survival in males, promoting later male maturation. Limited dispersal and local competition can thus drive the evolution of sexual dimorphism in the timing of maturation and consequent dimorphism in body size. At the individual level, if maturation can be flexibly adjusted in response to dispersal status, then both males and females who disperse as offspring should mature earlier than those who remain on their natal patch.

*Keywords:* kin selection, life history, age at maturity, size at maturity, trade-off.

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## Introduction

The diversity of plant and animal life histories is a consequence of inescapable trade-offs between different components of fitness (Roff 1992, 2002; Stearns 1992). One such trade-off is that between age and size at maturity: individuals that mature earlier have a greater chance of surviving to reproduce but at the same time may suffer reduced fitness as adults if they do survive, because they reach maturity at a smaller size (Roff 1984, 1992, 2000, 2002; Stearns and Koella 1986; Kozłowski and Weigert 1987; Abrams and Rowe 1996). In the most general terms, this represents one instance of the trade-off between survival as a juvenile and fitness as an adult. Similar tensions may arise in relation to the rate of

growth as well as the duration of the juvenile period, with individuals that are more active in foraging achieving greater rates of growth and thus attaining larger size at maturity but incurring greater risks of predation as a result (e.g., Arendt 1997; Biro et al. 2004; Bell et al. 2011).

Previous work on life-history evolution in structured populations has established that local competition can influence the trade-off between survival and maturation. Based on the insight that frequency-dependent selection typically leads to evolutionarily stable life-history strategies that do not maximize mean fitness (e.g., Mirmirani and Oster 1978; Abrams 1983; Day and Taylor 1996); Kawecki (1993) showed that competition among unrelated breeders in a patch favors the invasion of mutants with a slower maturation strategy than the strategy that maximizes mean fitness (see also Day and Taylor 1996). However, Day and Taylor (1997a, 2000) subsequently showed that when local competitors are related, kin selection favors earlier maturation times. The latter models, however, treat relatedness as an extrinsically specified parameter rather than an outcome of the analysis.

Here we adopt a demographically explicit approach in which local competition and local relatedness both arise from limited dispersal (e.g., Queller 1992; Taylor 1992a, 1992b; Taylor and Frank 1996; West et al. 2002; Rousset 2004; Gardner and West 2006; Lehmann et al. 2006; Lion et al. 2011), to model the impact of kin competition on age at maturity in a viscous population, assuming that the timing of maturation mediates the trade-off between juvenile survival and adult fecundity (note that the analysis is also applicable to any other trait, such as growth rate, that mediates the same trade-off). Since many studies have shown that the sexes can differ in their development times and growth rates, often leading to differences in adult size (e.g., Wiklund et al. 1991; Zonneveld 1996; Honek 1997; Blanckenhorn

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et al. 2007; Jarošik and Honek 2007; John-Alder and Cox 2007), we analyze independently the evolution of both female and male age at maturity. We also briefly consider the strategic adjustment of maturation time contingent on dispersal.

### The Model

We focus on an “infinite island,” sexually reproducing population comprising many discrete patches, each of which is occupied by  $n$  female and  $n$  male breeders (for a total of  $2n$  individuals per patch). In each, nonoverlapping generation, every female produces a large number of offspring, of which a fraction  $m$  are sired by local males, and a fraction  $(1 - m)$  by nonlocal males. The term “local” refers to individuals on the same patch and “nonlocal” to individuals on other patches; we do not explicitly model any spatial structure above the level of the patch. For simplicity, we shall suppose that the population is haploid and that gametes are produced clonally and pair to form diploid zygotes, which then undergo meiosis to form a new generation of haploid individuals.

We assume that there is a trade-off between survival as an offspring and reproductive success as an adult, mediated by age at maturity, which we denote  $\alpha_f$  for females and  $\alpha_m$  for males. This trade-off, however, takes slightly different forms for the two sexes. For adult females, age (and hence size) at maturity determines the number of offspring produced. For adult males, age (and hence size) at maturity determines the proportion of offspring sired by the focal male rather than his competitors. In other words, it is females who provide all of the investment in offspring production and care, while males simply compete for paternity of these young.

We will write  $s(\alpha)$  for the probability that an individual offspring survives to maturity and  $f(\alpha)$  for fecundity (or, for a male, relative success in competition for paternity) as an adult. In our analysis, we do not specify the precise form of these functions but simply assume that  $s(\alpha)$  is strictly decreasing and  $f(\alpha)$  strictly increasing and that both functions are smooth and log concave. In the figure, however, we present results for a specific, illustrative case in which  $f(\alpha)$  takes the form of a power function (following, e.g., Roff 1984; Kozłowski and Wiegert 1987). We chose this as our illustrative case because Day and Taylor (1997*b*) have argued that models of age versus size at maturity do better to use power functions rather than conventional von Bertalanffy growth curves, although in our case a von Bertalanffy function yields very similar results to those shown. Note that we do not explicitly incorporate any fitness interaction between the timing of female and male maturation; that is, the trade-off between juvenile survival and adult fecundity for females is assumed to be inde-

pendent of male age at maturity, while the trade-off between juvenile survival and adult mating success for males is assumed to be independent of female age at maturity.

Of those offspring that survive to maturity, a fraction  $1 - d$  remain on their natal patch while a fraction  $d$  disperse to other, randomly chosen patches in the population at large. Note that we treat the rates of dispersal  $d$  and of local mating  $m$  as independent parameters, even though the two may often be correlated. After dispersal, offspring on a patch, both native and immigrant, compete for the  $n$  breeding vacancies created by the death of members of their own sex belonging to the previous, parental generation. Those offspring that fail to claim a breeding vacancy die, after which the cycle repeats.

### The Evolution of Female Age at Maturity

To model the evolution of female age at maturity in our structured population, we adopt an adaptive dynamic approach (Geritz et al. 1998; McGill and Brown 2007; Dercole and Rinaldi 2008), assuming that evolution proceeds through the successive substitution of mutations of small effect. In the appendix we derive an expression,  $w(\alpha_f + \Delta\alpha_f, \alpha_f)$  for the fitness of a mutant type that matures at age  $\alpha_f + \Delta\alpha_f$  in a population that matures at age  $\alpha_f$ . The rate and direction of evolutionary change in such a population is then proportional to the selection gradient  $\partial w(\alpha_f + \Delta\alpha_f, \alpha_f) / \partial \Delta\alpha_f$ , evaluated at  $\Delta\alpha_f = 0$ , allowing us to solve for the equilibrium female age at maturity,  $\alpha_f^*$ , at which the selection gradient is 0.

We then find that in a well-mixed population, with  $d = 1$ , the equilibrium age at maturity satisfies

$$-\frac{s'(\alpha_f^*)}{s(\alpha_f^*)} = \frac{f'(\alpha_f^*)}{f(\alpha_f^*)}, \quad (1)$$

implying that the proportional decrease in juvenile survival due to a slight increase in age at maturity (corresponding to the left-hand side of the above equation) must precisely balance the proportional increase in adult fecundity (corresponding to the right-hand side of the above equation).

More generally (allowing for  $d < 1$ ), we find that

$$-\frac{1}{2}(r_{\text{self}} - r_{\text{competing juveniles}}) \frac{s'(\alpha_f^*)}{s(\alpha_f^*)} = (r_{\text{own young}} - r_{\text{competing young}}) \frac{f'(\alpha_f^*)}{f(\alpha_f^*)}, \quad (2)$$

where  $r_{\text{self}}$  denotes the relatedness of a juvenile female to herself (i.e.,  $r_{\text{self}} = 1$ ),  $r_{\text{competing juveniles}}$  her relatedness to the other juveniles competing with her for a breeding spot,  $r_{\text{own young}}$  the mean relatedness of an adult female to her own offspring, and  $r_{\text{competing young}}$  her relatedness to the other

offspring competing with hers for a breeding spot (in the appendix, we derive formulas for these relatedness coefficients in terms of  $Q_{AA}$ , the probability of identity between copies of a gene sampled from two distinct, randomly chosen adult breeders in the same local territory, the equilibrium value of which can itself be derived from the model parameters  $d$ ,  $m$ , and  $n$ ). In a viscous population, in other words, the marginal survival cost of delaying maturity (on the left-hand side of eq. [2]) is offset by the fact that in dying, a focal juvenile female potentially clears the way for a competing juvenile to claim a breeding spot. Equally, the marginal fecundity benefit (on the right-hand side of eq. [2]) is offset by the fact that in producing offspring, a focal adult female potentially displaces competing young from a breeding spot. Note that the factor of 1/2 appears on the left-hand side of equation (2) because the survival cost of delayed female maturity applies only to females. When  $d = 1$ , in a well-mixed population, there is no inbreeding, and hence  $r_{\text{own young}} = 1/2$ , while  $r_{\text{competing juveniles}}$  and  $r_{\text{competing young}}$  are both 0, because all offspring disperse to compete with nonrelatives. Hence, under these circumstances, equation (2) reduces to equation (1).

Limited dispersal and nonlocal mating can alter the equilibrium balance between survival costs and fecundity benefits and hence the equilibrium female age at maturity, because they have differing impacts on relatedness to competing juveniles and on relatedness to competing young. Assuming that mating is not strictly local (i.e.,  $m < 1$ ), then as  $d$  decreases, implying less dispersal, both  $r_{\text{competing juveniles}}$  and  $r_{\text{competing young}}$  increase. However, relatedness to competing young increases faster than does relatedness to competing juveniles, because as a juvenile, a female sired by a nonlocal male faces kin competition only with half-sibs, while by the time she becomes a breeding adult, her offspring face competition from full sibs. As a result, the fecundity benefit of delayed maturity is offset more strongly by kin competition than is the survival cost. Consequently (given our assumption that  $s$  and  $f$  are smooth and log concave), selection favors earlier female maturation.

In a similar way, assuming that there is some philopatry (i.e.,  $d < 1$ ), then as  $m$  decreases, implying less local mating, both  $r_{\text{competing juveniles}}$  and  $r_{\text{competing young}}$  decrease. However, relatedness to competing juveniles decreases faster than does relatedness to competing young, again because juveniles sired by nonlocal males escape competition with full sibs, while by the time they have become breeding adults their young may still face such competition. As a result, the survival benefit of delayed maturity is offset less strongly by kin competition than is the fecundity benefit. Once again, selection therefore favors earlier female maturation.

These effects are illustrated in figure 1, where we present results for the illustrative case in which survival to adult-

hood declines exponentially with age at maturity, while fecundity is proportional to the cube of age at maturity. To obtain these results, we derived explicit formulas for the coefficients of relatedness that appear in equations (1) and (2) in terms of the model parameters  $d$ ,  $m$ , and  $n$ , as described in the appendix, and solved the resulting equations numerically. The figure shows that there is a positive interaction between the effects of limited dispersal and of nonlocal mating but that both effects diminish as the number of breeders per patch grows.

### The Evolution of Male Age at Maturity

We can adopt a similar approach to model the evolution of male age at maturity (see appendix), which we find satisfies

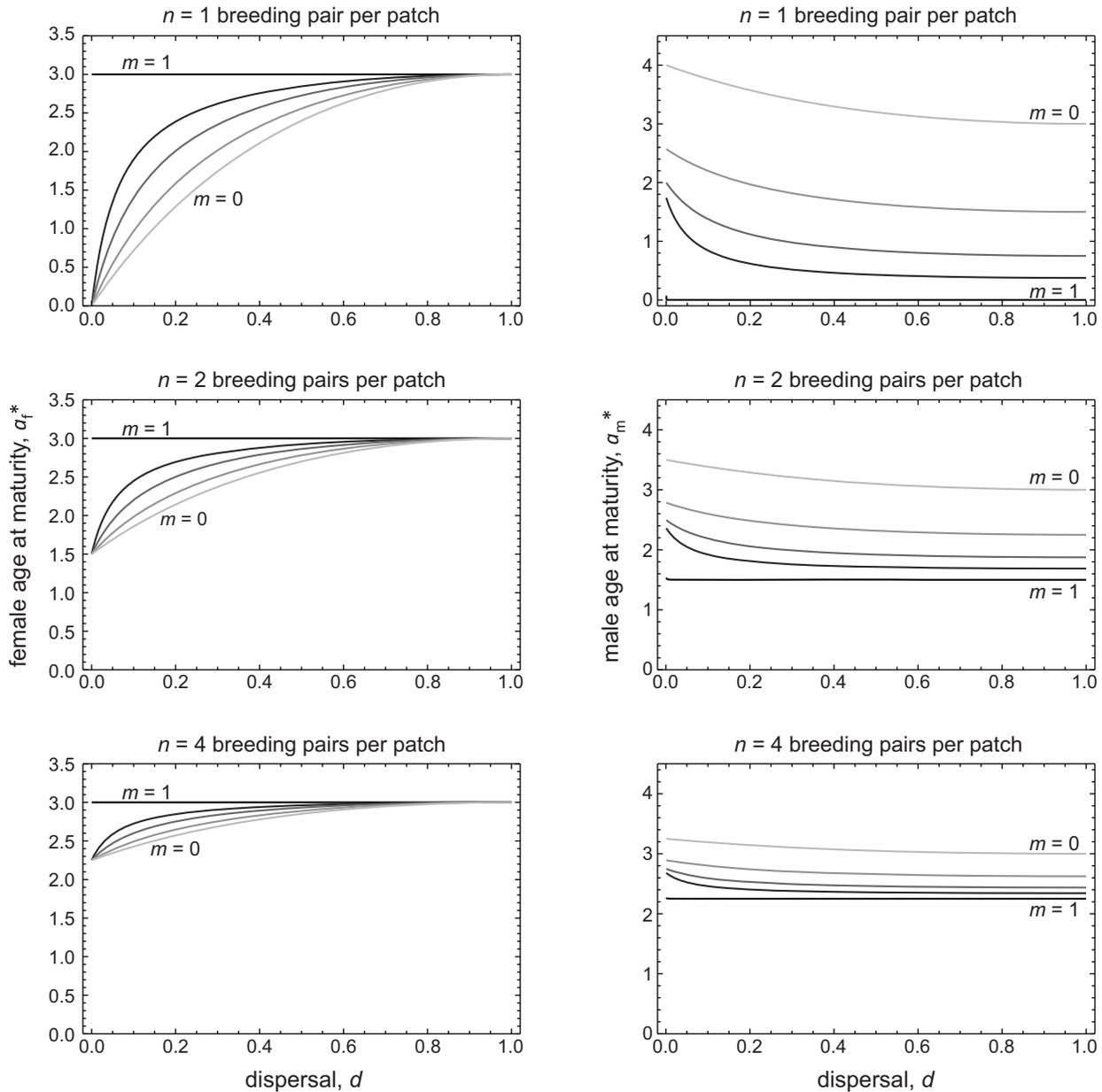
$$-\frac{1}{2}(r_{\text{self}} - r_{\text{competing juveniles}}) \frac{s'(\alpha_m^*)}{s(\alpha_m^*)} = \frac{1}{2}(r_{\text{self}} - r_{\text{competing adults}}) \frac{f'(\alpha_m^*)}{f(\alpha_m^*)}. \quad (3)$$

As for females, the marginal survival cost of delaying maturity (on the left-hand side of eq. [3]) is offset by the fact that in dying, a focal juvenile male potentially clears the way for a competing juvenile to claim a breeding spot. Equally, the marginal reproductive benefit (on the right-hand side of eq. [3]) is offset by the fact that in siring offspring, a focal adult male potentially deprives competitors of paternity.

For males, as  $d$  decreases, implying less dispersal, both  $r_{\text{competing juveniles}}$  and  $r_{\text{competing adults}}$  increase. However, relatedness to competing juveniles increases faster than does relatedness to competing adults, because as an adult a male may mate nonlocally, competing with nonrelatives, even in a highly viscous population. As a result, the survival cost of delayed maturity is offset more strongly by kin competition than is the fecundity benefit, and selection thus favors later male maturation.

In a similar way, as  $m$  decreases, implying less local mating, both  $r_{\text{competing juveniles}}$  and  $r_{\text{competing adults}}$  decrease. However, relatedness to competing adults decreases faster than does relatedness to competing juveniles, again because nonlocal mating releases a male from any kin competition as an adult (while as a juvenile, even if sired by a nonlocal father, he may face competition from maternal half-sibs). As a result, the fecundity benefit of delayed maturity is offset less strongly by kin competition than is the survival cost. Once again, selection therefore favors later male maturation.

Note that  $r_{\text{competing adults}}$  is nonzero even in a well-mixed population, effectively because there is local competition among a male's own sperm. Thus, for males, even in the



**Figure 1:** Equilibrium female (left column) and male (right column) ages at maturity, as a function of the dispersal rate  $d$ , for different frequencies of local mating  $m$  when  $s(\alpha) = \exp[-\mu\alpha]$  and  $f(\alpha) = (k\alpha)^3$ . In each graph of female age at maturity, successively lower curves correspond to successively smaller values of  $m$  (1, 1/2, 1/4, 1/8, 0), while in each graph of male age at maturity, successively lower curves correspond to successively larger values of  $m$  (0, 1/8, 1/4, 1/2, 1). Different graphs show results for different values of  $n$ , the number of breeding pairs per patch. In all cases,  $\mu = 1$  and  $k = 1/3$ .

absence of limited dispersal (i.e., when  $d = 1$ ), the equilibrium balance between the marginal survival cost and fecundity benefit of later maturation depends on  $n$  and  $m$ . Nonlocal mating (i.e., smaller values of  $m$ ) and more breeders per patch (i.e., larger values of  $n$ ), tend to favor later maturation simply because they lead to stronger com-

petition for paternity, which favors greater reproductive potential (requiring a longer period of growth). In the extreme case with strictly local mating ( $m = 1$ ) and one male per patch ( $n = 1$ ), for instance, there is no value in delaying maturation at all, since a male faces no competition of any kind over mating. In this respect, selection

on males differs from that on females, because the latter benefit from greater fecundity even if they are the only breeder on their patch, due to dispersal of young.

These effects are again illustrated in figure 1. The figure once again demonstrates that there is a positive interaction between the effects of limited dispersal and of nonlocal mating but that both effects diminish as the number of breeders per patch grows; it also highlights the contrasting impact of limited dispersal and nonlocal mating on females versus males.

### Conditional Maturation

Above we explored how the equilibrium ages at maturity for both sexes change with the population frequency of dispersal and nonlocal mating. Implicitly, our analysis was based on the assumption that the timing of maturation is under genetic control and is independent of whether an individual remains on its natal patch or disperses away. Here, however, we briefly consider how age at maturity might be expected to vary among individuals within a population, conditional on their dispersal status, if there is some flexibility in the timing of maturation. While it would also be theoretically interesting to allow for plasticity in response to paternity, that is, whether an individual was sired by a local or a nonlocal male, it seems less likely that individuals can acquire this information, so we will focus only on plastic responses to dispersal.

For an individual who disperses,  $r_{\text{competing juveniles}}$  is always equal to 0, while  $r_{\text{competing young}}$  for a female and  $r_{\text{competing adults}}$  for a male are (assuming  $d < 1$ ) positive; a female's offspring, even if she dispersed into her patch, may face competition from one another, just as a male's sperm effectively compete with one another, even if he is unrelated to any other individuals in the patch. Consequently, the fecundity benefit of delayed maturation is reduced relative to the survival cost, and selection favors earlier maturation among individuals who disperse compared to those who remain on their natal patch. This pattern holds true for both sexes. Thus, even though a higher frequency of philopatry across the population favors earlier maturation among females on average, individual philopatric females in a given population should always mature later than individual dispersing females.

### Discussion

Our analysis predicts that limited dispersal, in conjunction with nonlocal mating will indeed affect the trade-off between age and size at maturity. Most strikingly, it predicts that the effect on females will be the opposite of that on males: limited dispersal and nonlocal mating favor earlier maturation in females but later maturation in males. These

opposing effects stem from sex-differences in the intensity of kin competition across the life cycle. A female who is sired nonlocally escapes competition with full sibs as a juvenile, but by the time she has become a breeding female her offspring may face such competition. Conversely, a male who mates nonlocally escapes all kin competition as an adult, but his offspring may face competition from maternal half-sibs as juveniles. Kin competition among females is thus stronger at the adult stage, so that limited dispersal reduces the fecundity benefit of delayed maturation more than it does the survival cost, while kin competition among males is stronger at the juvenile stage, so that limited dispersal reduces the survival cost of delayed maturation more than it does the fecundity benefit. Hence, an important conclusion of this study is that local competition can drive the evolution of sexual dimorphism in the timing of maturation and consequently in body size.

To date, sex differences in development time have mainly been attributed to sex differences in the strength of sexual or fecundity selection (e.g., Wiklund and Fagerström 1977; Bulmer 1983; Iwasa et al. 1983; Wedell 1992; see Morbey and Ydenberg 2001 for a review). By contrast, limited dispersal and local competition have been largely overlooked as drivers of sexual dimorphism. Our study shows, however, that limited dispersal may well lead to accelerated female development times relative to male development times, that is, to protogyny. Although protogyny has been considered rare relative to accelerated male development (protandry; Morby and Ydenberg 2001), reevaluations of development times in insects, for example, have shown that protogyny is more common than previously thought (Honek 1997; Kranz et al. 2001; Rhainds 2010). Even in cases where other selective factors such as sexual or fecundity selection potentially favor the evolution of protandry (Bulmer 1983; Iwasa et al. 1983; Parker and Courtney 1983; Zonneveld and Metz 1991), the presence of limited dispersal could be an important weakening force, potentially contributing to the observed variation in protandry among taxa (Morbey and Ydenberg 2001; Jarošik and Honek 2007).

The patterns described above concern the relationship between dispersal, nonlocal mating, and the timing of maturation at the population level. Our model also suggests that individuals may be expected to adjust the timing of maturation according to their dispersal status. Immigrants who are unrelated to competing juveniles in the patch to which they disperse should tend to mature earlier than nondispersing individuals who remain on their natal patch. The reason is simply that immigrants experience no kin competition at the juvenile stage (while, if they attain breeding status, their own nondispersing offspring will experience competition with one another). This is similar to the selective pressure identified by El Mouden

and Gardner (2008) for harming on the part of migrants and helping on the part of natives (although they did not focus on trade-offs between different life-history stages as we do here). Such strategic adjustment of individual maturation gives rise to a superficially contradictory pattern, in which females across the population mature earlier on average as philopatry becomes more common, but philopatric individuals mature later than dispersing individuals at any given frequency of philopatry.

In an earlier model, Pen (2000) showed that population viscosity favors greater reproductive effort, leading to higher fecundity. This may appear to contrast with our prediction that, in females, viscosity favors earlier maturation (at the population level), leading to lower fecundity (see also Day and Taylor 2000). The contrasting predictions arise because Pen (2000) considers the trade-off between fecundity and adult survival, while we consider the trade-off between fecundity and juvenile survival. In reality, both trade-offs ideally should be addressed simultaneously, allowing for coevolution of age/size at maturity and reproductive effort as an adult; the net impact of viscosity on adult fecundity would then depend on the relative sensitivity of juvenile and adult survival to increased investment in reproduction. It is worth pointing out, however, that whether one focuses on timing of maturation or on reproductive investment as an adult, viscosity tends to favor a more “accelerated” life history, with females maturing earlier and dying sooner (as a result of greater reproductive effort). Faster life histories are favored because they ameliorate kin competition, with early death clearing the way for replacement by relatives (Ronce and Promislow 2010).

Our results on the evolution of female age at maturity resemble those of some previous analyses but arise for rather different reasons. In the analysis of Day and Taylor (2000), relatedness among individuals on a patch favored earlier maturation times because of their assumption that prematuration growth of a focal individual slows growth of others in the same patch, while postmaturation reproduction has no such negative impact on the fitness of local competitors. By contrast, in our analysis, early maturation affects both pre- and postmaturation competition, with the result that it is only when mating occurs nonlocally and the intensity of kin competition therefore changes

across the life cycle that limited dispersal influences the timing of maturation. De Jong et al. (2000) explicitly modeled the evolution of maturation time in a metapopulation of monocarpic perennial plants and found that due to the possibility of local extinctions, limited dispersal favors shorter generation times. By contrast, we have assumed a constant patch size with no local extinctions, so that the opportunity does not arise in our model (as in theirs) for early maturing types to take advantage of reduced juvenile competition in young populations following extinction.

In addition to fixed patch sizes, there are many other assumptions in our model that could be relaxed or modified in future work. For instance, we have assumed that dispersal rates are fixed, rather than free to coevolve with age and size at maturity, and that they are the same for both sexes. Sex differences in dispersal can favor helping in the more philopatric sex and harming in the less philopatric sex and in populations with overlapping generations can give rise to sex-specific changes in relatedness with age (Johnstone and Cant 2008, 2010; Gardner 2010). Such changes will influence the trade-off between juvenile survival and adult fecundity and thus affect the evolution of age at maturity. We have also assumed that all individuals of a given generation reproduce alongside one another—delayed maturation decreases the chance of an individual surviving to reproduce as an adult, though yielding a benefit in terms of adult fecundity, but since generations do not overlap, the delay is never so great that the focal individual “misses” a breeding season, nor can it end up breeding alongside the offspring of a contemporary. A more general model would allow for overlapping generations (following Taylor and Irwin 2000; Irwin and Taylor 2001), but this would entail a great increase in complexity, as it would be necessary to track relatedness and reproductive value of individuals of multiple age classes in patches of all possible age compositions.

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## APPENDIX

### Kin Competition and the Evolution of Sex Differences in Development Time and Body Size

#### *Fitness Expressions*

*Female Age at Maturity.* Assuming weak selection, the fitness of a focal allele  $\alpha_f^i$  that influences female age at maturity can be approximated as

$$\begin{aligned}
& w(\alpha_f^i, \alpha_f^{ff}, \alpha_f^{fm}, \alpha_f^{jf}, \alpha_f^{jm}, \alpha_f^{pop}) = \\
& \frac{1}{4} \left\{ f(\alpha_f^i) \left[ \frac{(1-d)s(\alpha_f^i)}{(1-d)f(\alpha_f^{ff})s(\alpha_f^{jf}) + df(\alpha_f^{pop})s(\alpha_f^{pop})} + \frac{ds(\alpha_f^i)}{f(\alpha_f^{pop})s(\alpha_f^{pop})} \right] \right. \\
& + f(\alpha_f^i) \left[ \frac{(1-d)}{(1-d)f(\alpha_f^{ff}) + df(\alpha_f^{pop})} + \frac{d}{f(\alpha_f^{pop})} \right] \\
& + mf(\alpha_f^{fm}) \left[ \frac{(1-d)s(\alpha_f^i)}{(1-d)f(\alpha_f^{fm})s(\alpha_f^{jm}) + df(\alpha_f^{pop})s(\alpha_f^{pop})} + \frac{ds(\alpha_f^i)}{f(\alpha_f^{pop})s(\alpha_f^{pop})} \right] + (1-m) \frac{s(\alpha_f^i)}{s(\alpha_f^{pop})} \\
& \left. + mf(\alpha_f^{fm}) \left[ \frac{(1-d)}{(1-d)f(\alpha_f^{fm}) + df(\alpha_f^{pop})} + \frac{d}{f(\alpha_f^{pop})} \right] + 1 - m \right\}, \tag{A1}
\end{aligned}$$

where  $\alpha_f^i$  denotes the age at maturity of a female bearing the focal gene copy;  $\alpha_f^{ff}$  (or  $\alpha_f^{fm}$ ) the average age at maturity of local females, when the focal gene copy is borne by a female (or male);  $\alpha_f^{jf}$  (or  $\alpha_f^{jm}$ ) the average age at maturity of a locally produced juvenile female when the focal gene copy is borne by a female (or male); and  $\alpha_f^{pop}$  the population average female age at maturity.

The lower four rows in formula (A1) correspond, respectively, to the expected number of surviving daughters produced when the focal gene copy is borne by a female, the expected number of surviving sons produced when the focal gene copy is borne by a female, the expected number of surviving daughters produced when the focal gene copy is borne by a male, and the expected number of surviving sons produced when the focal gene copy is borne by a male. In each case, we consider both surviving offspring that remain on their natal patch and those that disperse (and when the focal gene copy is borne by a local male, both offspring sired locally and those sired nonlocally). The sum of these four rows is multiplied by 1/4 to give overall fitness because there is a probability of 1/2 that the focal gene copy will be found in a breeder of specified sex and a probability of 1/2 that any given offspring of that breeder will inherit its gene copy from the parent in question. Note that since we are concerned here with a gene that influences only female age at maturity, the survival of sons is independent of whether or not they inherit the focal gene copy.

The derivation of these expressions in each row is straightforward: to illustrate, in the first row, the fecundity of a female carrying the focal gene copy is given by  $f(\alpha_f^i)$ , and any daughters she produces either remain in the local patch, with probability  $1-d$ , or disperse to a remote patch, with probability  $d$ . In both cases, the survival probability of a daughter carrying the focal allele is given by  $s(\alpha_f^i)$ . Successful establishment as an adult breeder in the local patch is determined by the total number of locally competing female juveniles in the denominator: the average fecundity of local adult females (including the focal adult female) is given by  $f(\alpha_f^{ff})$ , of whose female offspring a fraction  $1-d$  stay in the local site, where they survive with a probability of  $s(\alpha_f^{jf})$ . In addition, juvenile females migrate into the patch with probability  $d$ , and the number of immigrants depend on the population average female age at maturity  $f(\alpha_f^{pop})$ . Each immigrant female juvenile subsequently survives with probability  $s(\alpha_f^{pop})$ . Similarly, daughters of the focal female that disperse to a remote site compete with a total of  $f(\alpha_f^{pop})s(\alpha_f^{pop})$  juvenile females.

#### Male Age at Maturity.

$$\begin{aligned}
& w(\alpha_m^i, \alpha_m^{mm}, \alpha_m^{jm}, \alpha_m^{jf}, \alpha_m^{pop}) = \\
& \frac{1}{4} \left\{ \frac{(1-d)s(\alpha_m^i)}{(1-d)s(\alpha_m^{jf}) + ds(\alpha_m^{pop})} + \frac{ds(\alpha_m^i)}{s(\alpha_m^{pop})} \right. \\
& + 1 \\
& + m \frac{f(\alpha_m^i)}{f(\alpha_m^{mm})} \left[ \frac{(1-d)s(\alpha_m^i)}{(1-d)s(\alpha_m^{jm}) + ds(\alpha_m^{pop})} + \frac{ds(\alpha_m^i)}{s(\alpha_m^{pop})} \right] + (1-m) \frac{f(\alpha_m^i)}{f(\alpha_m^{pop})} \frac{s(\alpha_m^i)}{s(\alpha_m^{pop})} \\
& \left. + m \frac{f(\alpha_m^i)}{f(\alpha_m^{mm})} + (1-m) \frac{f(\alpha_m^i)}{f(\alpha_m^{pop})} \right\}. \tag{A2}
\end{aligned}$$

Again, the lower four rows in the formula given in equation (A2) correspond, respectively, to the expected number of surviving daughters produced when the focal gene copy is borne by a female, the expected number of surviving sons produced when the focal gene copy is borne by a female, the expected number of surviving daughters produced when the focal gene copy is borne by a male, and the expected number of surviving sons produced when the focal gene copy is borne by a male.

### Selection Gradients

We derive selection differentials that determine the rate of evolutionary change in  $\alpha_f$  and  $\alpha_m$  using a direct fitness approach (Hamilton 1964; Taylor and Frank 1996; Taylor et al. 2007):

$$\frac{dw}{d\alpha_f} = \left( \frac{\partial w}{\partial \alpha_f^i} + r_{jf} \frac{\partial w}{\partial \alpha_f^{jf}} + r_{jm} \frac{\partial w}{\partial \alpha_f^{jm}} + r_{ff} \frac{\partial w}{\partial \alpha_f^{ff}} + r_{fm} \frac{\partial w}{\partial \alpha_f^{fm}} \right) \Bigg|_{\alpha_f^i = \alpha_f^{ff} = \alpha_f^{fm} = \alpha_f^{jf} = \alpha_f^{jm} = \alpha_f^{pop} = \alpha_f}, \quad (A3)$$

$$\frac{dw}{d\alpha_m} = \left( \frac{\partial w}{\partial \alpha_m^i} + r_{jm} \frac{\partial w}{\partial \alpha_m^{jm}} + r_{jf} \frac{\partial w}{\partial \alpha_m^{jf}} + r_{mm} \frac{\partial w}{\partial \alpha_m^{mm}} \right) \Bigg|_{\alpha_m^i = \alpha_m^{mm} = \alpha_m^{jf} = \alpha_m^{jm} = \alpha_m^{pop} = \alpha_m}.$$

where  $r_{ff}$  denotes the relatedness between two adult females sampled randomly with replacement from the same patch,  $r_{fm}$  the relatedness between a female and a male from the same patch,  $r_{jf}$  the relatedness between a juvenile and a female from the same patch, and so on.

Solving for  $dw/d\alpha_f = 0$ , we obtain

$$-\frac{1}{2} \left[ 1 - \frac{1}{2} h(r_{jf} + mr_{jm}) \right] \frac{s'(\alpha_f)}{s(\alpha_f)} = \left[ \frac{1}{2} (1 + mr_{fm}) - \frac{1}{2} h(r_{ff} + mr_{fm}) \right] \frac{f'(\alpha_f)}{f(\alpha_f)}, \quad (A4)$$

where, for notational convenience, we have introduced the term  $h \equiv (1 - d)^2$ . Equation (5) from the main text can then be derived from the above, noting that  $r_{self} = 1$ ,  $r_{competing\ juveniles} = (1/2)h(r_{jf} + mr_{jm})$ ,  $r_{own\ young} = (1/2)(1 + mr_{fm})$ , and  $r_{competing\ young} = (1/2)h(r_{ff} + mr_{fm})$ .

Solving for  $dw/d\alpha_m = 0$ , we obtain

$$-\frac{1}{2} \left[ 1 - \frac{1}{2} h(r_{jf} + mr_{jm}) \right] \frac{s'(\alpha_m)}{s(\alpha_m)} = \frac{1}{2} (1 - mr_{mm}) \frac{f'(\alpha_m)}{f(\alpha_m)}, \quad (A5)$$

which yields equation (3) from the main text, noting that  $r_{competing\ adults} = mr_{mm}$ .

### Relatedness Coefficients

We now derive expressions for the aforementioned relatedness coefficients. Writing  $Q_{AA}$  for the probability of identity between copies of an age at maturity gene sampled from two distinct, randomly chosen adult breeders in the same local territory (i.e., sampling without replacement), we obtain the following recursion:

$$Q_{AA,t+1} = \frac{1}{4} h \left( \frac{1}{n} + \frac{n-1}{n} Q_{AA,t} \right) + \frac{1}{2} hm Q_{AA,t} + \frac{1}{4} hm^2 \left( \frac{1}{n} + \frac{n-1}{n} Q_{AA,t} \right), \quad (A6)$$

where the first part on the right-hand side reflects the probability that alleles are sampled from two females (probability 1/4) that are both locally born (probability  $h = [1 - d]^2$ ). With probability 1/n, both females descend from the same parent, whereas with probability  $(n - 1)/n$ , the females descend from different parents, which share alleles with probability  $Q_{AA,t}$ . The second part on the right-hand side reflects the probability that two alleles are sampled from a locally breeding male and a female. Note that a male breeds locally with probability  $m$ . The last part reflects the probability that two alleles are sampled from locally breeding males, where the probability that both males are local is  $h$  and also breed locally is  $m^2$ . We can solve equation (A6) to obtain an equilibrium value  $Q_{AA}$ , which is not particularly informative, so we do not show it here.

We can then express the relatedness coefficients that appear in equation (A3) in terms of  $Q_{AA}$ :

$$r_{ff} = \frac{1}{2} \left( \frac{1}{n} + \frac{n-1}{n} Q_{AA} \right) + \frac{1}{2} m Q_{AA},$$

$$r_{jm} = \frac{1}{2} Q_{AA} + \frac{1}{2} m \left( \frac{1}{n} + \frac{n-1}{n} Q_{AA} \right),$$

$$r_{ff} = r_{mm} = \frac{1}{n} + \frac{n-1}{n} Q_{AA},$$

$$r_{fm} = Q_{AA}.$$

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