Demographic Stochasticity and Social Mating System in the Process of Extinction of Small Populations: The Case of Passerines Introduced to New Zealand

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ABSTRACT: Underlying the many causes of extinction of small populations is the random fate of each constituent individual or, in other words, demographic stochasticity. Demographic stochasticity is inherent to any demographic process, regardless of the environment, and its strength increases as population size gets smaller. In particular, random fluctuations in the proportion of males and females and the way they pair for reproduction (i.e., the social mating system) are usually neglected. To assess the potential importance of demographic stochasticity to the extinction process, a two-sex model with an explicit mating system was built. Extinction probabilities computed via Monte Carlo simulation were compared to real data, the case of passerines introduced to New Zealand a century ago. This minimal model of extinction allowed assessment of the importance of the mating system in the colonization process. Monogamous mating led to a higher extinction risk than did polygynous mating. Demographic uncertainty imposes high extinction probabilities on short-lived bird species as compared to long-lived bird species. Theoretical results for two-sex models are provided.

Keywords: conservation biology, demographic stochasticity, mating system, probability of extinction, two-sex models.

Demographic stochasticity results from the random fate of individuals and can never be avoided. Its effects, strictly dependent on population size, may cause extinction of small-sized populations, in addition to environmental stochasticity, natural catastrophes, inbreeding depression, and loss of genetic diversity (Lande and Barrowclough 1987; Tuljapurkar 1990; Lande 1993, 1995). Demographic sto-

chasticity could be considered as an Allee effect (Simberloff 1986; Lande 1987; Dennis 1989) and is likely to underpin the mechanism of the extinction vortex. Recent work suggests that demographic stochasticity could be a more important cause of population extinction than previously thought (Gabriel and Bürger 1992; Mode 1995; Kokko and Ebenhard 1996) because all life-cycle transitions are potentially affected by this type of variation. Consequently, modeling the main features of the life cycle of a species, such as its social system, will be crucial to population viability analysis (PVA; Soulé 1987; Boyce 1992; Burgman et al. 1993). For example, because of random fluctuations in the number of males and females, the social system will have a direct effect on the number of reproducing females. Indeed, the likelihood of finding an appropriate partner given the mating system has been seen as a potentially important Allee effect in sexual species (Saether et al. 1996), as well as one of the main costs of evolution and maintenance of sexuality (Michod and Levin 1987). It has been suspected to be the main cause driving kakapo (*Strigops habroptilus*) populations toward extinction (Trewick 1997) and to have caused the extinction of the passenger pigeon in North America (Daily and Ehrlich 1995).

In this study, we constructed a null model in the sense that demographic stochasticity, which cannot be neglected for small population sizes, was the only possible cause of extinction. Other causes, whose contribution to extinction is uncertain, were not considered. However, we incorporated all possible causes of stochastic fluctuations and examined the extent to which the mating system influenced the probability of extinction. We built a two-sex model in which pair formation was explicitly taken into account and considered several mating systems, from strict monogamy to full polygyny.

Few studies have been devoted to modeling mating systems and their influence on population dynamics (Asmussen and Hering 1983; Caswell and Weeks 1986; Mode 1995). To understand the importance of this problem in natural situations, we compared the extinction probabil-
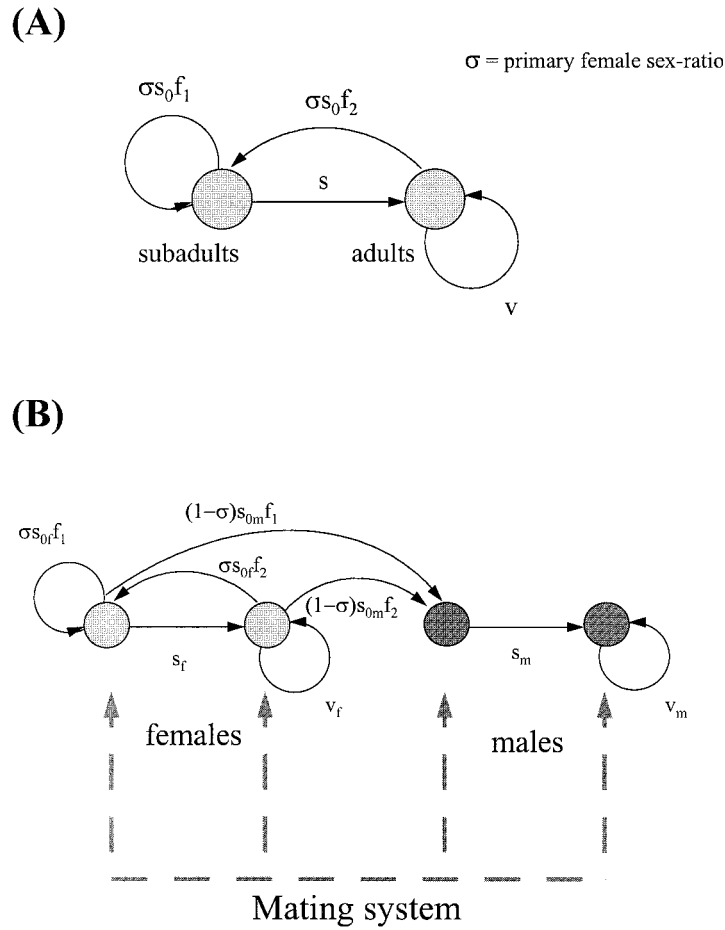
(A)

(B)

Figure 1: Two age-class life-cycle graphs for passerines. *A*, Usual one-sex model (demographic parameters as in table 1). *B*, Two-sex model with mating system.

ities predicted from a two-sex model with social monogamy to a female-based or one-sex model (Caswell 1989), using the observed extinction probability of passerine species introduced to New Zealand a century ago (Veltman et al. 1996; Duncan 1997; Green 1997). For each introduced species, the number of released individuals was obtained from the literature, and introduction success was assessed by checking whether the species was still present. This data set is particularly interesting because the number of release events is rather large and the timescale rather long, conditions that are rarely met in conservation biology (Griffith et al. 1989; Sarrazin and Barbault 1996; Wolf et al. 1996). In fact, this type of data is scarce, and the few data sets available (e.g., Moulton and Pimm 1983; Griffith et al. 1989; Berger 1990; McLain et al. 1995) lack some features needed to test stochastic population-dynamics models. We used data only on passerines (Duncan 1997) in order to avoid additional complexities of considering

species with different life-cycle characteristics. Our model was therefore built to represent an average passerine life cycle. Nevertheless, we investigated the effect of the life cycle, in particular the effect of population turnover, by examining a model with different age at maturity, fecundity, and survival.

Methods

Life-Cycle Graph

Passerine life history was modeled by a life-cycle graph with two age classes (fig. 1*A*). The first class consisted of subadults (first-year individuals) and the second of adults (second year or older). We assumed a prebreeding census (Caswell 1989; Clobert and Lebreton 1991; McDonald and Caswell 1993). Juveniles reproduce before their first birthday, and this explains why the juvenile survival rate s_0 was

Table 1: Demographic parameters used in the models

Demographic parameters	Value	Elasticity	λ	$\overline{T}$
Passerine (two age classes):				
Juvenile survival rate (s_0)	.20	.60	1.1050	1.67
5% reduction (s_0)	.19		1.0720	...
10% reduction (s_0)	.18	...	1.0390	...
Subadult survival rate (s)	.35	.21	...	...
Adult survival rate (ν)	.50	.18	...	...
Subadult fecundity (f_1)	7.0	.38	...	...
Adult fecundity (f_2)	7.0	.22	...	...
Griffon vulture (four age classes):				
Juvenile survival rate (s_0)	.80	.10	1.0490	10.04
10% reduction (s_0)	.72	...	1.0383	...
Immature survival rates:				
s_1	.80	.10	...	...
s_2	.80	.10	...	...
s_3	.84	.10	...	...
Adult survival rate (ν)	.90	.60	...	...
Adult fecundity (f)	.80	.10	...	...

Note: λ = growth rate, $\overline{T}$ = mean generation length.

included in the transitions corresponding to reproduction. Fecundity was defined as clutch size per reproducing female (Clobert and Lebreton 1991) multiplied by the number of broods. A matrix model can be derived from the life-cycle graph, and we will call it the "linear model." The dominant eigenvalue of the matrix gives the asymptotic growth rate, λ, of the population (Caswell 1989). In the linear model, it is usually assumed that the population consists only of females, and the fecundities are multiplied by the primary female sex ratio (σ), that is, the proportion of females at birth. The growth rate $\lambda = \lambda(\sigma)$ is a continuously increasing function of σ. Because we later introduce two-sex models, the growth rate $\lambda(\sigma)$ of the linear one-sex model will be considered as the reference growth rate. Other demographic quantities, such as population structure or mean generation length, can be computed from the linear model. Average demographic parameters of passerine species have been used (table 1; see Gaillard et al. 1989; Martin and Clobert 1996). The corresponding rather favorable growth rate $\lambda = 1.1050$ is not uncommon in passerines.

Two-Sex Models with Mating System

To take both sexes into account, we built separate life-cycle graphs for males and females. These graphs were connected by arrows corresponding to reproduction, going from females to males and females, according to the primary female sex ratio σ (fig. 1*B*). We assumed a balanced sex ratio ($\sigma = 0.5$) and identical survival rates for males and females. We also modeled the way that males and females paired, that is, the social mating system. Formally, one has to consider the number of matings (A) as a deterministic or probabilistic function of the number of mature males, n_m, and the number of mature females, n_f: $A = a(n_m, n_f)$. The function (or distribution) a is assumed to have biologically realistic properties (Asmussen and Hering 1983; Caswell and Weeks 1986; Mode 1995). Alternative mating systems are displayed in figure 2. In the monogamous mating system, males and females are paired one to one, and excess males or females do not mate. The number of matings (A) is the minimum of the number of mature males and the number of mature females
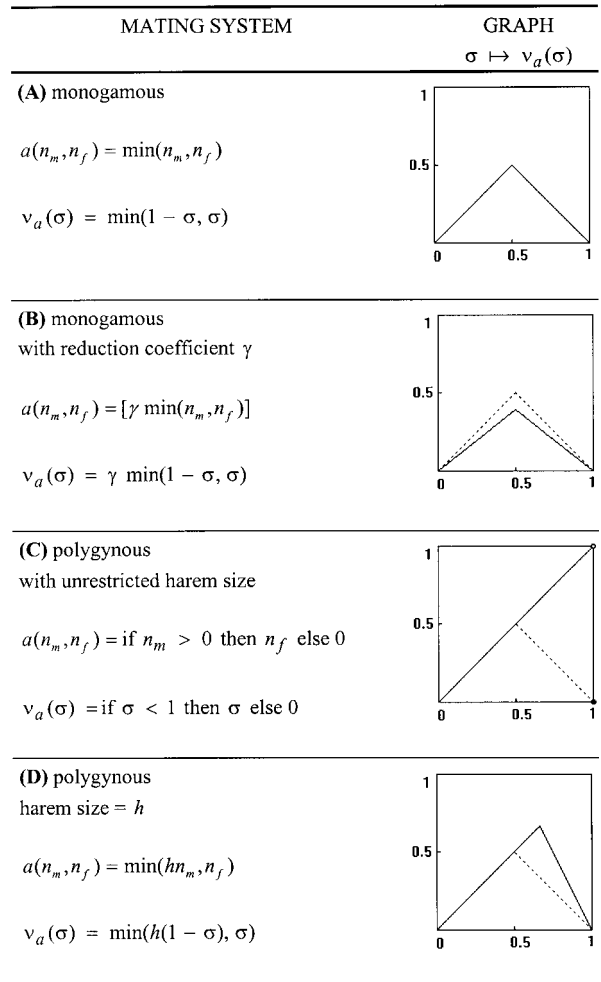

MATING SYSTEM	GRAPH $\sigma \mapsto \nu_a(\sigma)$
(A) monogamous $a(n_m, n_f) = \min(n_m, n_f)$ $\nu_a(\sigma) = \min(1-\sigma, \sigma)$	
(B) monogamous with reduction coefficient γ $a(n_m, n_f) = [\gamma \min(n_m, n_f)]$ $\nu_a(\sigma) = \gamma \min(1-\sigma, \sigma)$	
(C) polygynous with unrestricted harem size $a(n_m, n_f) = $ if $n_m > 0$ then n_f else 0 $\nu_a(\sigma) = $ if $\sigma < 1$ then σ else 0	
(D) polygynous harem size = h $a(n_m, n_f) = \min(hn_m, n_f)$ $\nu_a(\sigma) = \min(h(1-\sigma), \sigma)$	

Figure 2: Various mating systems; $n_m(n_f)$ is the number of mature males (females), σ the primary female sex ratio, $a(n_m, n_f)$ the number of matings, and $\nu_a(\sigma)$ the limit of a when the proportion of females tends toward σ. The corresponding graph $\sigma \to \nu_a(\sigma)$ is given. Dotted lines in *B–D* are given for comparison with the monogamous mating system (*A*).

($A = \min(n_m, n_f)$). In a polygynous mating system, a single male can mate with several females, and reproduction is optimized. If each male mates with the most females (h being harem size), the number of matings is the number of females as long as there are at least h females per male ($A = \min(hn_m, n_f)$). When the harem size is unrestricted, the number of matings is equal to the number of females, except when there are no males, in which case it is 0 ($A =$ if $n_m > 0$, then n_f, otherwise 0). To account for other factors influencing the social mating system, such as competition between eligible mates, the number of matings computed from the mating function can be further reduced by a coefficient γ ($0 < \gamma \leq 1$). For example, the number of monogamous matings can be computed as $A = [\gamma \min(n_m, n_f)]$, where the square brackets stand for the integer part. In our model, no record is kept of matings over time; that is, fidelity is not modeled.

Demographic Stochasticity and Probability of Extinction

The mathematical framework of population dynamics under demographic stochasticity is that of multitype branching processes (Harris 1963; Athreya and Ney 1972; Asmussen and Hering 1983; Gosselin and Lebreton 1999). In contrast to continuous population dynamics models, population sizes are restricted to integer values. We give here a simple description of the branching processes. Let us consider n individuals subjected to a mean survival rate s. The number of survivors, n', is computed as the sum of n Bernoulli (head and tail) trials with mean s, or, equivalently, as the realization of a binomial distribution. More generally, when n individuals go through a transition with a result of 0 with probability $1 - p$ and 1 with probability p (e.g., proportion of females, proportion of breeders), a binomial distribution binom(n, p) is used. For the fecundity transition, the number of descendants was computed as the sum of trials according to an integer-valued distribution, for example, a Poisson distribution.

When demographic stochasticity acts on the life-cycle transitions, population size over time, $n(t)$, is a stochastic process. A trajectory is a realization of the process, and the process can be identified with the set of all its possible trajectories. A trajectory is declared extinct as soon as the value 0 is reached. The (ultimate) probability of extinction p_e is the "proportion" of trajectories that go extinct among all trajectories. If a time horizon T is fixed, the probability of extinction at time T, $p_e(T)$, is the probability that a trajectory goes extinct by time $<T$. Since, at any time, all individuals in the population might leave no survivors or descendants, some trajectories necessarily go extinct and p_e is never 0. The time when extinction occurred can be associated with each extinct trajectory. This defines the extinction time of the process as a random variable t_e.

We now recall the main results for branching processes when the underlying process is linear with growth rate λ (Harris 1963; Athreya and Ney 1972). Apart from extinction, the average population mainly behaves as predicted by the underlying linear process. The growth rate of the average population is λ, and the average population structure is given by the right eigenvector with respect to λ. For $\lambda > 1$, as is assumed here, $0 < p_e < 1$ and p_e depends on initial population size and structure (for $\lambda \leq 1$, $p_e = 1$). For $\lambda \neq 1$, convergence of the process toward p_e is geometric and the mean extinction time, $E(t_e)$, is finite. To summarize, if a population with $\lambda > 1$ is not extinct at time $t \gg E(t_e)$, then it has a very high probability of escaping extinction coming from demographic stochasticity, and it will on average grow according to λ. Incorporating the mating system turns the model from a linear one to a frequency-dependent one, in the sense that the proportion of individuals in age classes affects the demographic parameters (Caswell and Weeks 1986; Chung 1994). We shall see how results obtained for linear models extend to frequency-dependent ones.

Monte Carlo Simulation

The two-sex life-cycle graph together with the mating system provide the framework for the process by which demographic stochasticity acts via binomial and Poisson distributions. Parameters subjected to demographic stochasticity were male and female survival rates, female fecundity, and primary sex ratio. More precisely, the following operations were performed at each time step: computing the number of matings according to the mating system considered, computing the number of descendants according to age-dependent fecundities, drawing the number of males and females according to the primary sex ratio, and computing the number of survivors according to age-dependent survival rates. For simplicity, we have chosen an equal number of males and females in each age class as initial population structure, close to the stable age distribution of the linear model (63% subadults and 37% adults). We have also assumed that pairings could occur with equal probability among age classes. The model was studied via Monte Carlo simulation, using the ULM (Unified Life Models) computer program (Legendre and Clobert 1995; Ferrière et al. 1996). One thousand trajectories were drawn over a 100-yr time horizon. The probability of extinction at time 100, $p_e(100)$, was close to the ultimate probability of extinction p_e. The Monte Carlo procedure was performed for a range of initial population sizes. In this way, we obtained the probability of extinction as a function of initial population size.

Passerine Species Introduced to New Zealand

The introduction of passerine species to New Zealand 100 yr ago can be seen as a natural Monte Carlo simulation. Indeed, if all introduced species are considered as several introductions of a single average passerine species, we can classify all the introduction attempts with respect to the number of released individuals, as in Green (1997) or Griffith et al. (1989). The assumption here is that each introduction is a single realization of the same stochastic process, with different initial conditions. This is obviously not completely true because the introduced passerines display some heterogeneity in their life-cycle characteristics (Sorci et al. 1998). We simply hope that this heterogeneity will be less important for the probability of extinction than the effect of demographic stochasticity on pair formation. Most species of passerines are socially monogamous, and we have used a monogamous mating system. Three polygynous species were discarded from the data set of Duncan (1997). All introduction attempts were classified into eight categories (table 2). For example, the third category of table 2 groups eight introductions with three failures and an average initial population size of 44. Those eight introductions are considered to represent eight replicates of an introduction of 44 individuals. The proportion of failures of 0.38 (3/8) can be identified with the probability of extinction of the process, with 44 individuals as initial condition. Some data show the limits of this averaging approach. *Carduelis flammea* succeeded from a single couple, while *Manorina melanocephala* never succeeded with 80, 200, and 224 individuals released. Since this last species was the only species contributing to extinction in the sixth category, this category was not used.

Results

The Importance of the Mating System with Regard to Extinction Probability

For a two-sex model with mating system, an important point is to assess the influence of the mating system on the growth rate of the population and, linked to it, on the probability of extinction. Let $\lambda_a(\sigma)$ be the growth rate of the two-sex population, with mating function a and primary female sex ratio σ. Assuming identical survival rates for males and females, we prove in the appendix that the two-sex growth rate is related to the reference growth rate $\lambda(\sigma)$ via a function $\nu_a(\sigma)$ that captures the features of the mating system:

$$\lambda_a(\sigma) = \lambda(\nu_a(\sigma)). \tag{1}$$

The function $\sigma \to \nu_a(\sigma)$ is 0 for $\sigma = 0$ or 1 and is typically convex with a single maximum at the "optimal" sex ratio

(this optimum may not be evolutionarily stable; fig. 2). Moreover, $\nu_a(\sigma) \leq \sigma$ and since $\sigma \to \lambda(\sigma)$ is a continuously strictly increasing function of σ, equation (1) shows that $\lambda_a(\sigma) \leq \lambda(\sigma)$. For example, the polygynous mating system with harem size h and mating function $a(n_m, n_f) = \min(hn_m, n_f)$ leads to $\nu(\sigma) = \min(h(1 - \sigma), \sigma)$ with a maximum at $\sigma = h/(h + 1)$ (fig. 2D). The value $h = 1$ corresponds to the monogamous mating system, and the maximum is the classical value $\sigma = 0.5$ (fig. 2A). For $\sigma \leq 0.5$, $\nu(\sigma) = \sigma$ and $\lambda_a = \lambda$, while for $\sigma > 0.5$, $\nu(\sigma) < \sigma$ and $\lambda_a < \lambda$. When the number of matings is reduced by a coefficient γ (e.g., the proportion of breeders), this has the same effect as reducing the juvenile survival rate s_0 by γ in the one-sex model, leading to a reduction in the reference growth rate λ. The expected growth rate of the two-sex model λ_a is reduced accordingly.

The case of the monotype two-sex branching process (Asmussen and Hering 1983, p. 409; their formula for the expected growth rate of the two-sex population is a special case of eq. [1]) and our simulations for multitype two-sex branching processes suggest that frequency-dependent branching processes behave roughly as linear branching processes. Indeed, after transient behavior, the realized sex ratio stabilizes, and the underlying process is close to a linear process (appendix), then general results that have been recalled for linear branching processes apply. Frequency dependence induced by the mating system mainly increases the probability of extinction and slows down convergence toward the asymptotic growth rate λ_a. For a linear model, transient oscillatory effects come from the convergence toward the stable population structure (Caswell 1989). For a two-sex frequency-dependent model, transient effects coming from the convergence toward the equilibrium sex ratio superimpose on the previous effects. Transient oscillations are more important and last longer. This explains the larger probability of extinction and the slower convergence in frequency-dependent branching processes. Since small founding populations are subject to the transient part of the dynamics, this further shows the importance of fluctuations arising from sexual behavior in colonization processes.

To assess the influence of the mating system on the demographic process, extinction probabilities were computed for the one-sex model with no mating system and for the two-sex model with various mating systems (fig. 3A). For the polygynous mating system with unrestricted harem size, extinction probabilities are close to those of the one-sex model. Probabilities of extinction of the polygynous mating system with harem size of two are similar and are not shown. Extinction probabilities of the monogamous mating system are much higher. The reason is that the extinction risk depends on the number of reproducing females: in the monogamous mating system, when

Table 2: Data for passerines introduced to New Zealand 100 yr ago

Released species	Introduction success	Release sites	Initial population size	Mean $n(0)$	p_e
Initial size, 2–9:					
Carduelis flammea	1	W	2 (1)	...	...
Carduelis spinus	0	W	2 (1)	...	...
Manorina melanophrys	0	W	2 (1)	...	...
Passer montanus	0	O	2 (1)	...	...
Piranga rubra	0	A	2 (1)	...	...
Pyrrhula pyrrhula	0	C	2 (1)	...	...
Stagonopleura bella	0	A	2 (1)	...	...
Fringilla montifringilla	0	W	3 (1)	...	...
Emberiza cirlus	1	W	4 (1)	...	...
Emberiza schoeniclus	0	O	4 (1)	...	...
Neochmia temporalis	0	O	4 (1)	5	.78
Corvus monedula	0	C	5 (1)	...	...
Sylvia atricapilla	0	A	5 (1)	...	...
Lullula arborea	0	A	5 (1)	...	...
Emberiza hortulana	0	W	6 (1)	...	...
Padda oryzivora	0	A	6 (1)	...	...
E. cirlus	1	O	7 (1)	...	...
E. schoeniclus	0	C	7 (2)	...	...
Carduelis chloris	1	O	8 (1)	...	...
Lonchura punctulata	0	A	8 (1)	...	...
S. bella	0	W	8 (1)	...	...
Turdus philomelos	1	W	8 (1)	...	...
Erithacus rubecula	0	A	9 (3)	...	...
Initial size, 10–22:					
E. rubecula	0	W	10 (1)	...	...
Gymnorhina tibicen	1	A	10 (2)	...	...
Lonchura castaneothorax	0	C	12 (1)	...	...
Malurus cyaneus	0	A	12 (1)	...	...
Poephila guttata	0	W	12 (1)	...	...
Stagonopleura guttata	0	W	12 (1)	...	...
N. temporalis	0	A	12 (2)	15	.79
P. montanus	0	A	12 (2)	...	...
Passer domesticus	1	O	14 (2)	...	...
Fringilla coelebs	1	C	16 (4)	...	...
Acridotheres tristis	0	C	18 (1)	...	...
Carduelis cannabina	0	O	20 (2)	...	...
Carduelis flavirostris	0	C	21 (1)	...	...
C. cannabina	0	W	22 (2)	...	...
Initial size, 27–46:					
L. castaneothorax	0	A	27 (2)	...	...
C. chloris	1	C	32 (2)	...	...
Corvus frugilegus	1	C	36 (4)	...	...
C. flavirostris	0	O	38 (1)	...	...
Emberiza citrinella	1	O	39 (2)	44	.38
C. cannabina	0	A	42 (4)	...	...
P. domesticus	1	C	44 (1)	...	...
Prunella modularis	1	A	46 (4)	...	...
Initial size, 49–81:					
P. domesticus	1	A	49 (2)	...	...
P. modularis	1	W	50 (3)	...	...
C. chloris	1	A	51 (3)	...	...
C. spinus	0	C	52 (2)	...	...
Carduelis carduelis	1	A	55 (2)	...	...

Table 2 (*Continued*)

Released species	Introduction success	Release sites	Initial population size	Mean $n(0)$	p_e
Alauda arvensis	1	A	62 (2)	…	…
E. rubecula	0	O	62 (3)	63	.42
C. frugilegus	0	A	66 (2)	…	…
A. tristis	0	W	70 (2)	…	…
Manorina melanocephala	0	O	80 (1)	…	…
C. flammea	1	O	81 (2)	…	…
G. tibicen	1	O	81 (5)	…	…
Initial size, 98–126:					
P. modularis	1	O	98 (2)	…	…
F. coelebs	1	O	99 (3)	…	…
A. arvensis	1	O	100 (3)	…	…
A. arvensis	1	W	108 (2)	…	…
Sturnus vulgaris	1	A	109 (3)	…	…
F. coelebs	1	A	113 (4)	113	.17
F. montifringilla	0	C	117 (4)	…	…
C. carduelis	1	O	118 (4)	…	…
C. cannabina	0	C	119 (4)	…	…
T. philomelos	1	A	125 (2)	…	…
S. vulgaris	1	C	125 (4)	…	…
F. coelebs	1	W	126 (4)	…	…
Initial size, 138–236:					
Turdus merula	1	O	138 (5)	…	…
T. philomelos	1	O	145 (5)	…	…
S. vulgaris	1	O	169 (3)	…	…
T. merula	1	A	170 (4)	…	…
C. carduelis	1	W	177 (3)	…	…
M. melanocephala	0	C	200 (1)	189	.18
P. domesticus	1	W	200 (1)	…	…
C. flammea	1	A	209 (1)	…	…
P. modularis	1	C	210 (6)	…	…
M. melanocephala	0	W	224 (4)	…	…
E. citrinella	1	C	236 (3)	…	…
Initial size, 260–345:					
G. tibicen	1	W	260 (1)	…	…
C. carduelis	1	C	265 (4)	…	…
S. vulgaris	1	W	298 (5)	…	…
T. philomelos	1	C	299 (7)	301	.0
G. tibicen	1	C	313 (9)	…	…
C. flammea	1	C	326 (5)	…	…
E. citrinella	1	A	345 (6)	…	…
Initial size, 434–477:					
A. arvensis	1	C	434 (5)	…	…
T. merula	1	C	477 (7)	455	.0

Source: Duncan 1997.

Note: Introduction events have been classified according to similar initial population sizes. Release sites: A = Auckland; C = Canterbury; O = Otago; W = Wellington. Numbers in parentheses are the number of release events. Mean $n(0)$ = average initial population size for each class; p_e = proportion of failures for each class.
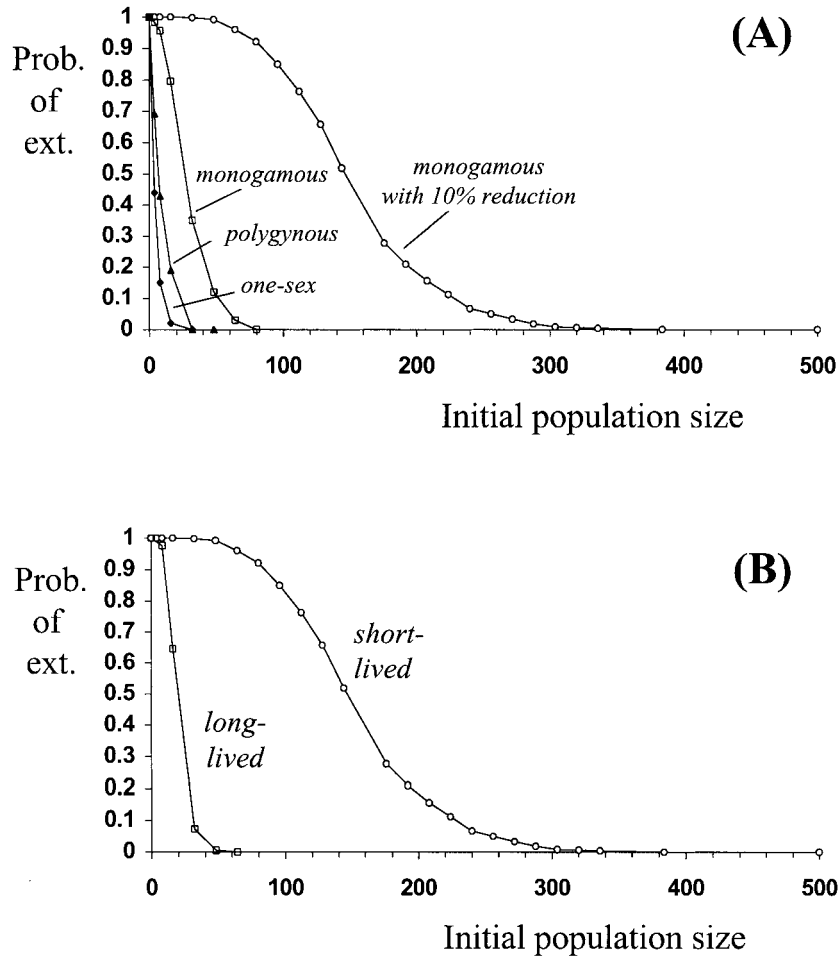
Figure 3: Probability of extinction at time 100, $p_e(100)$, as a function of initial population size, $n(0)$. *A*, Passerine model, various mating systems (cf. fig. 2; growth rate $\lambda = 1.1050$ in all cases): one-sex model, no mating system (*solid diamonds*); polygynous mating system with unrestricted harem size (*solid triangles*); monogamous mating system (*open squares*); competitive monogamous mating system with 10% reduction in the number of matings (*open circles*; number of matings $A = [0.9 \min(n_m, n_f)]$). *B*, Short-lived (passerine, growth rate $\lambda = 1.1050$) versus long-lived (griffon vulture, growth rate $\lambda = 1.0490$). In both cases, the number of monogamous matings is reduced by 10%.

random fluctuations lead to fewer males than females, unpaired females do not reproduce, while in the polygynous mating system, all females reproduce. Incorporating a cost of polygyny, such as reduced paternal care, could change this result. When a realistic coefficient γ affecting the number of monogamous matings is introduced (the number of matings is reduced by 10%), extinction probabilities increase dramatically (fig. 3*A*). Thus, a slight variation in the number of breeders has a considerable impact on population viability.

Fitting the Model with the Data

The probabilities of extinction computed from the average passerine model were plotted against the observed prob-

abilities of extinction as a function of initial population size (fig. 4). We used the reference growth rate $\lambda = 1.1050$, and the number of monogamous matings was reduced by 5% ($A = [0.95 \min(n_m, n_f)]$). To estimate the goodness of fit, we regressed the observed probabilities against those predicted by the model. The predicted values explained 90% of the variance in the observed values ($P = .001$; $R^2 = 0.90$; SAS Institute 1992). Considering approximately the same set of species, Green (1997) used three ranges of initial population sizes—$2 \leq n(0) \leq 10$, $10 < n(0) \leq 100$, and $n(0) > 100$—and computed the corresponding probabilities of extinction, 0.85, 0.75, and 0.08, respectively. His results, which are consistent with those of Griffith et al. (1989), agree with those of our model. So far, for each introduced species, we have considered
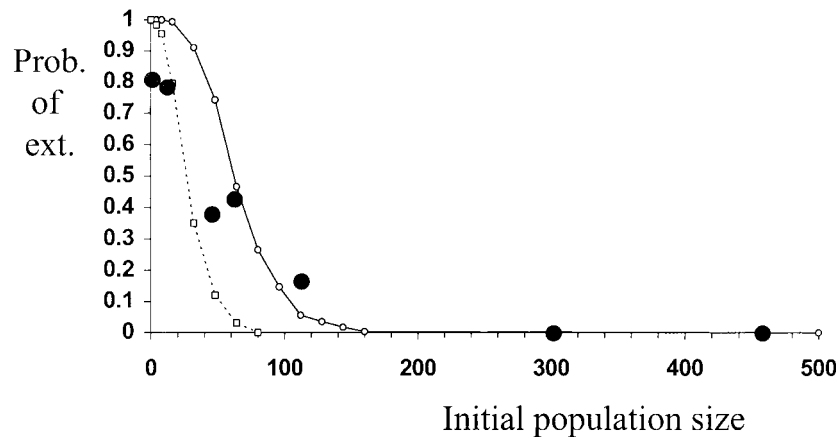
Figure 4: Results of the model against observed extinction in the case of passerines introduced to New Zealand (from Duncan 1997): probability of extinction at time 100 as a function of initial population size; observed probabilities of extinction, as given in table 2 (*solid circles*), and computed probabilities of extinctions, as given by the model (growth rate $\lambda = 1.1050$), monogamous (*open squares*), and monogamous with 5% reduction in the number of matings (*open circles*).

that all release events took place simultaneously, as if only one release event had occurred (e.g., four releases of 20 individuals every 4 yr is considered as a single release of 80 individuals). As a check, we simulated the introduction of the same number of individuals either in a single release event or in several release events with various time lags between events (some cases are reported in fig. 5). It appeared that, when demographic stochasticity was the sole factor of uncertainty, the probability of extinction depended mainly on the number of released individuals (it increased with the number of release events and with the time lag between events). This result also held for the long-lived species considered below. However, taking environmental stochasticity into account would modify this conclusion (Haccou and Iwasa 1996).

Short Lived versus Long Lived

To compare the introduction success of short-lived and long-lived birds, the corresponding two-sex model with monogamous mating system was built for a long-lived bird species (griffon vulture *Gyps fulvus*). Demographic parameters given in Ferrière et al. (1996) have been altered in order to obtain a lower reference growth rate (table 1; $\lambda = 1.0490$ against $\lambda = 1.1050$ for passerine). For our passerine model, mean generation length is 1.7 yr, while it is 10.0 yr for the griffon vulture. In both cases, the number of monogamous matings was reduced by 10%. The coefficient $\gamma = 0.9$ affecting the number of possible matings is the proportion of breeders that has been observed for the griffon vulture (F. Sarrazin, personal communication). It appears that extinction probabilities are much higher

for the short-lived species (fig. 3B). For short-lived and long-lived life cycles, the demographic parameters with fluctuations that have the strongest impact on the growth rate are not the same, and this can be measured by sensitivity analysis (Caswell 1989; see also Fox 1993). For the short-lived species, the most sensitive parameter is juvenile survival rate while for the long-lived species, it is adult survival rate (table 1). A reduction in the number of breeders has the same effect as a reduction in juvenile survival rate (s_j) in the underlying linear model, and it reduces the growth rate (λ), which in turn increases the probability of extinction. This reduction in growth rate is more important for short-lived than for long-lived species. This explains why the mating system has the strongest impact on the probability of extinction in the former species due to stochastic fluctuations in the number of matings. If the reference growth rates are corrected to take into account the reduction in the number of matings, we obtain $\lambda = 1.0390$ for the short-lived and $\lambda = 1.0383$ for the long-lived species (table 1). Thus, identical growth rates lead to very different probabilities of extinction for species with different generation time. Short-lived bird species have a rapid turnover, which amplifies the stochastic fluctuations in the number of descendants because of the combined chance realizations of the number of matings, the number of fledglings, and the primary sex ratio. For the long-lived species, these fluctuations are buffered by the pool of individuals that remain from one year to the next.

Discussion

We developed a two-sex model by duplicating a female-based model and adding a mating function. The growth
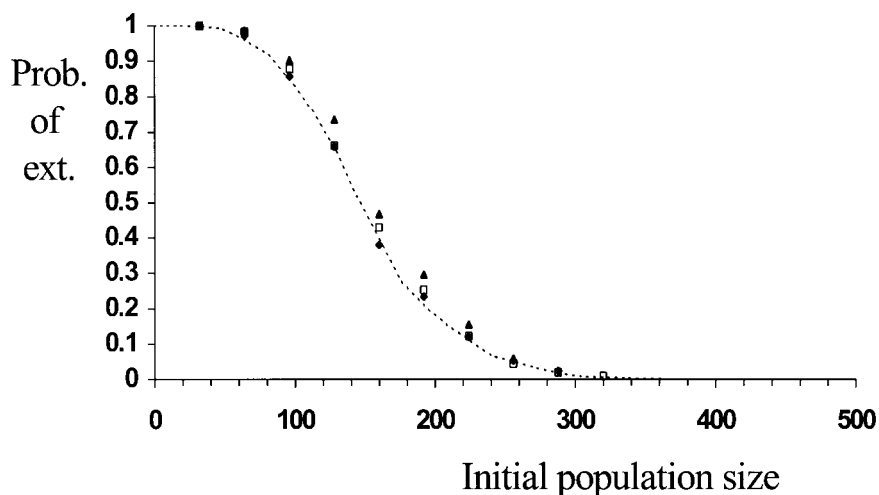
Figure 5: Probability of extinction at time 100 as a function of initial population size for various release scenarios (passerine, $\lambda = 1.1050$, number of matings $A = [0.9 \min (n_m, n_f)]$): one release event, all individuals released simultaneously (*dotted line*); four release events with 1 yr between events (*solid diamonds*); four release events with 4 yr between events (*solid triangles*); two release events with 4 yr between events (*open squares*).

rate of the two-sex model was lower than or equal to the growth rate of the one-sex model. Including demographic stochasticity extended the time at which the population was at risk (transient phase). Although the model was based on several assumptions (similar life cycles for males and females, mating function irrespective of age or density, absence of individual heterogeneity), it produced a close fit to extinction probabilities observed for passerine species introduced to New Zealand a century ago. The effect of demographic stochasticity on pair bond formation depended on generation time; the extinction probability of long-lived species was not very sensitive to this parameter.

Two-Sex Model and Demographic Stochasticity

Finding a mate has long been thought to be a potentially important cost associated with the evolution of sexuality (Michod and Levin 1987). Sexuality appears to increase the probability of extinction (Lynch et al. 1993, 1995*a*, 1995*b*), and at least in some species, parthenogenesis may have evolved secondarily because of high probability of extinction linked to the maintenance of sexuality when populations are small and isolated (Gerritsen 1980; Bernstein et al. 1985). Maintaining sexuality in small-sized populations appears to be costly. We showed that the number of individuals required to achieve a given probability of extinction increased by a factor of two or even 10, when going from the one-sex model to the two-sex model (see fig. 3*A*). This largely exceeds the effect of inbreeding or mutation accumulation (Lynch et al. 1995*a*), at least for short-term persistence. Polygynous mating systems are less

sensitive to demographic stochasticity than monogamy, and it may be predicted that a polygynous mating system should be selected for in small-sized populations for reasons other than simple competition for suitable breeding territories or mates (Orians 1969; Davies 1992). We assumed that the life cycle was identical for males and females, which may not be the case. The difference between male and female life cycle may reveal further complexities in the role of sex in small-sized populations (McLain et al. 1995; Sorci et al. 1998). For example, modeling the competition for mates in two-sex models has revealed the possibility of quasi-periodic or even chaotic dynamics because of the frequency-dependent nature of these models (Caswell and Weeks 1986; Chung 1994).

The difficulty of finding a mate has often been proposed as an Allee effect (Andrewartha and Birch 1954; Dennis 1989; Sutherland 1996). However, few if any documented cases of a decrease in demographic parameters when density decreases have been reported for vertebrates (Fowler and Baker 1991; Myer et al. 1995; Saether et al. 1996). Beside the fact that estimating demographic parameters in small-sized populations is a difficult task and may preclude the detection of any Allee effect (Saether et al. 1996), adding demographic stochasticity to the probability of finding a mate has the effect of reducing the average reproductive success. The first consequence of taking into account the mating system is that the proportion of individuals that will participate in reproduction will be lowered with respect to a one-sex model. This was formally demonstrated by deriving an analytical expression (eq. [1]; appendix) that links the growth rate of a two-sex model to the growth

rate of the corresponding one-sex model by the introduction of the mating function. The magnitude of the decrease will also depend on population size because of demographic stochasticity. Given that the proportion of reproducing females in a given stage or age is particularly difficult to estimate, especially for birds (Clobert 1995), it is not surprising that few cases have been reported. Nonetheless, demographic stochasticity acting on the probability of finding a mate induces an increase in extinction probability, as shown by the comparison with the introduction success of passerines in New Zealand.

Extinction Probabilities of Passerines Introduced to New Zealand

Approximately 137 species of exotic birds have been introduced by humans to New Zealand before 1907 and 20% are still present (Veltman et al. 1996). We selected passerines (Duncan 1997) because, as a group, they have similar life cycles. For each introduced species, two key variables are available: the number of released individuals and the number of release events. We therefore decided to use this data set (table 2) to check whether our null model, based solely on demographic stochasticity, could satisfactorily predict the fate of these introductions in New Zealand. We calculated extinction probabilities by assuming that each species introduction attempt was a trial of a single process where only propagule sizes differed. Comparison with the simulated probabilities of extinction derived from a two-sex passerine life cycle with average demographic parameters was satisfactory. However, for small propagule sizes, a higher extinction risk was predicted by our model. In the data set of Duncan (1997), introduction success of a species on a site is assessed by its actual presence, which might bias the true extinction frequency. Indeed, the presence of a bird species in a site could come from later immigration from another site where it succeeded. This is the case for *Gymnorhina tibicen*, whose introduction at Otago (81 individuals) is reported as a success, while Long (1981) states that it went extinct by the late 1920s but later appeared again because of natural immigration from Canterbury (313 individuals introduced). Also, unreported introductions that succeeded could conceal the failure of introductions reported as successful and raise initial population sizes. Nevertheless, the match of the model against the data for passerines suggests that the probability of finding a mate is an important factor for the persistence of these species. We found that, for a given number of introduced individuals, the type of mating system strongly influences the probability of extinction. Our result highlights the need to study the mating systems in conservation biology, at least for short-lived species (Berger 1996; Höglund 1996; Saether et al. 1996). There are other causes of introduction failure, such as the suitability of the area of introduction (Griffith et al. 1989), competition between introduced species (Moulton and Pimm 1983; Duncan 1997), temporal variability (Griffith et al. 1989), or transplantation cost (Massot et al. 1994; Sarrazin et al. 1994; Wolf et al. 1996). In this study, we do not exclude these causes as possible explanations for the observed extinctions. They would reduce the demographic parameters, merely amplifying the sampling effect of demographic stochasticity. We suggest that, for short-lived bird species, the main contribution to extinction could come from demographic stochasticity, implying that initial population size is a strong predictor of colonization success. We assumed that all individuals of a species were released on one single occasion instead of several. Simulations showed (fig. 5) that, within realistic bounds, the number of release events for a single species had little influence on the probability of extinction as long as temporal variations in the environment were low compared to the effect of demographic stochasticity. In other words, sustained introduction of species for which demographic stochasticity is the main contributor to extinction would not improve introduction success. Our results are therefore in accord with Griffith et al. (1989) and Wolf et al. (1996), who found that the number of released individuals correlated strongly with translocation success but did not find a consistent relationship between translocation success and the number of release events.

Generation Time and Extinction Probability

The number of individuals to be released in order to maximize the chances of successful establishment decreased with species generation time. We compared two life cycles, one that may represent a passerine life cycle and one that may represent a large scavenger or marine bird. For example, to obtain a 90% probability of persistence 100 yr after an introduction, more than 200 individuals are needed for short-lived species while only 30 are needed for long-lived ones (fig. 3*B*). As long as body size is a good indicator of species generation time (Gaillard et al. 1989), our results are consistent with the observation that large-bodied animals seem to be better colonizers than small-bodied ones (Pimm et al. 1988) or to have a better translocation success (Griffith et al. 1989). Demographic stochasticity turns out to have a greater impact on short-lived species than on long-lived ones, especially at introduction. Similarly, the probability of finding a mate has much less effect as generation time increases. Indeed, demographic stochasticity on mate acquisition mainly affects recruitment parameters whose fluctuations have less impact on the population growth rate as generation time increases (Lebreton and Clobert 1991). In such cases, other sources

of extinction such as natural catastrophes or temporal variations in the environment may predominate (Ewens et al. 1987; Goodman 1987; Shaffer 1987; Lande 1993). These sources of extinction are no longer related to population size above some threshold value. Indeed, the probability of extinction is an exponentially decreasing function of initial population size (depending on the mating system and generation time) for demographic stochasticity, while it is, in the long run, independent of initial population size for environmental stochasticity (Tuljapurkar 1990). Taking density dependence into account would complicate this scheme (Lande 1993). However, the data set of Griffith et al. (1989) shows that, above some propagule size, the probability of extinction is nearly constant.

Conclusion

Demographic stochasticity could be one of the most important sources of extinction for small-sized populations of short-lived bird species. For these species, taking into account the mating system is of prime importance to predict accurately the probability of extinction. The simultaneous effect of the mating system and demographic stochasticity principally affects the proportion of breeding females, which has a high impact on the population growth rate. Long-lived species are less sensitive to both factors. Future studies need to incorporate more details on the mating system and, in particular, its modification with population density. Then it will be possible, for populations kept in small numbers for a long period of time, to study the interplay between the evolution of the mating system, the probability of extinction and the colonization ability.

Acknowledgments

APPENDIX

Two-Sex Matrix Model with Mating System

We start from a usual age-structured model with age classes (k) and matrix

$$\mathbf{X}(\vec{\alpha}) = \begin{pmatrix} \alpha_1 f_1 & \cdots & \alpha_{k-1} f_{k-1} & \alpha_k f_k \\ s_1 & \cdots & 0 & 0 \\ \vdots & \ddots & \vdots & \vdots \\ 0 & \cdots & s_{k-1} & v \end{pmatrix},$$

where $f_1, ..., f_k$ are female fertilities; $s_1, ..., s_{k-1}$ are subadult survival rates; v is adult survival rate ($v = 0$ gives the Leslie matrix); and $\vec{\alpha} = (\alpha_1, ..., \alpha_k)$ is a set of parameters. The one-sex model has matrix $\mathbf{X}(\vec{\sigma})$ with $\vec{\sigma} = (\sigma, ..., \sigma)$, where σ is the primary female sex ratio (proportion of females at birth), and we denote by $\lambda(\sigma)$ the corresponding dominant eigenvalue (the matrix is primitive for $v \neq 0$, and we assume primitivity when $v = 0$).

For the two-sex model, our first assumption is that males and females have identical life cycles (in particular, identical survival rates). The two-sex matrix with mating system is built from the duplicated life-cycle graph (fig. 1A shows the case of two age classes) and is a block matrix

$$\begin{pmatrix} \mathbf{X}(\vec{0}) & \mathbf{Y}((1-\sigma)\vec{\beta}) \\ O & \mathbf{X}(\sigma\vec{\beta}) \end{pmatrix}.$$

Matrix $\mathbf{X}(\vec{0})$ corresponds to the male life cycle and has null entries in the first row. Matrix $\mathbf{X}(\sigma\vec{\beta})$ corresponds to the female life cycle, with the first row accounting for female offspring. Matrix $\mathbf{Y}((1-\sigma)\vec{\beta})$ corresponds to male offspring and has null entries except in the first row. The population vector is $(n_{m1}, ..., n_{mk}, n_{f1}, ..., n_{fk})'$, with $n_{mi}(n_{fi})$ as the number of males (females) in the ith age class. Our second assumption describes how the mating system is modeled, $n_m(n_f)$ being the number of reproducing males (females) and a the mating function.

Second, at each time step, the total number of matings, $A = a(n_m, n_f)$, is computed, and the matings are dispatched equitably among reproductive age classes. The third series of assumptions concerns the mating function, supposed to have biologically realistic properties (Asmussen and Hering 1983; Caswell and Weeks 1986), and the existence of a limit function capturing its main features.

In the third assumption, the mating function a has a limit when the proportion of females tends toward the primary female sex ratio:

$$\nu_a(\sigma) = \lim_{(n_f/n)\to\sigma} \frac{a(n_m, n_f)}{n}, \tag{A1}$$

with $n = n_m + n_f$.

Examples of limit functions ν_a are given in figure 2. In the two-sex block matrix, $\vec{\beta} = (\beta_1, ..., \beta_k)$ accounts for the matings with

$$\beta_i = \frac{(n_{fi}/n_f)A}{n_{fi}} = A/n_f.$$

By the third assumption, $\beta_i \to \nu_a(\sigma)/\sigma$ and the block matrix converges toward

$$\mathbf{X}_a(\vec{\nu}) = \begin{pmatrix} \mathbf{X}(\vec{0}) & \mathbf{Y}\left(\dfrac{1-\sigma}{\sigma}\vec{\nu}\right) \\ O & \mathbf{X}(\vec{\nu}) \end{pmatrix},$$

with $\vec{\nu} = (\nu_a(\sigma), ..., \nu_a(\sigma))$. The dominant eigenvalue $\lambda_a(\sigma)$ of the block matrix $\mathbf{X}_a$ is that of its block $\mathbf{X}(\vec{\nu})$, and we obtain

$$\lambda_a(\sigma) = \lambda(\nu_a(\sigma)). \tag{A2}$$

In fact, what precedes proves that, under our assumptions, the realized sex ratio converges toward the primary sex ratio.

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