THE EFFECTS OF REDUCING MATING LIKELIHOOD ON POPULATION VIABILITY

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Abstract. The success a species may have invading a patch previously un-occupied is of considerable interest for pest managers and conservation ecologists. Our purpose is to examine how the presence of a reproductive Allee effect, appearing through the failure in the process of fertilization in a two-sex population, affects the survival in an invaded patch. We use a Poisson-Ricker model which includes stochastic demography and sex determination, with the females classified as successfully fertilized or not fertilized. Numerical approximations to the probabilities of extinction and the mean time to extinction are presented for fixed parameter values, from which it is possible to observe how random fluctuations in the sex ratio and mating success contribute to the risk of extinction of a species which started an invasion with small number of individuals. It can also be seen how the reproductive Allee effect changes from strong to weak as the probability of a given female to be fertilized increases.

1. **Introduction.** The role of Allee effects, sometimes called depensation, in the conservation of endangered species and the dynamics of invasions has motivated in recent years many efforts to understand the mechanisms associated with their emergence, and the development of theoretical tools which allow to broaden our understanding of the possible consequences, [3], [15]. An Allee effect is defined as the decrease of individual fitness at low conspecific densities. This decrease in fitness can be understood as a decrease in the per capita growth rate at low population densities or, equivalently, as the failure of individuals in a population to replace themselves in the following generation. In deterministic population modeling, the study of Allee effects is commonly linked to the presence of a threshold in the population density, which determines if the population survives or goes extinct. If stochasticity is introduced, the focus is instead on how the probability to extinction, the mean time to extinction or first passage probabilities are affected by the variation of parameters in the model or by the choose of initial population sizes, [3], [5].

When considering randomness in a population model, there are two types of demographic stochasticity most commonly considered by ecologists, one produced by natural, individual birth and death events within the population, and other produced by sex ratio fluctuations. Although the former reduces the time of extinction in populations of small size, it is not considered a mechanism for Allee effect, because it does not reduce the individual fitness, [3], [6]. The stochasticity

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produced by sex ratio fluctuations, however, may produce an Allee effect because variations in females' fitness will depend directly of the number of males present in the population which are able to successfully fertilize females.

In what follows, by *probability of fertilization* we mean the probability that a female finds and is fertilized successfully by at least one male during the period of reproduction. Reduced probability of fertilization at low population densities is one of the main reasons that may induce a component Allee effect, in this case called *reproductive* Allee effect, for which extensive studies have been done in recent years, see [3] and references therein. Several mechanisms may induce a reduction in the probability of fertilization, for sessile as well as mobile organisms, mainly through a decrease in fertilization efficiency, difficulties in mate finding, increased sperm limitation, decreased reproductive facilitation or sexual selection, [3]. Evidence to support the appearance of reproductive Allee effects under each of these mechanisms has been found in plant as well in animal species, [3], [6], [10], [13]. For organisms like plants or marine invertebrates which do not move during their reproductive season, or organisms that move very slowly, reproduction relies on how successful are eggs and sperm meeting in their surrounding environment, [3], thus depending on the diffusive characteristics of their medium; if organisms are quite dispersed at low densities, the diffusion of eggs or sperm may be out of range for fertilization, and therefore induce a decrease in population fitness. In contrast, mate finding is a reproductive mechanism involving encounters and direct contact between females and males. Even if individuals are able to move, reproductive Allee effects may appear if their dispersal is small, if their communities suffer of lack of aggregation or if they reproduce at irregular in time and with no synchrony, [3], [6].

Our purpose is to integrate the probability of fertilization in a probabilistic population model with non-overlapping generations, where individuals are classified as males or females, and to study the effects that changes in its value may induce on the survival of a group, assuming there is no migration. This, for instance, is subject of interest for pest managers applying control strategies on invasive species, because frequently, the target is the mating success of individuals, artificially perturbed by mating disruption, mass trapping or sterile insect release, [18], and may be the cause for a reproductive Allee effect to appear, which will naturally drive the extinction of the invader population, with no necessity of total removal of it using a eradication treatment, [12].

The probability of fertilization, which depends on the present number of males at each time, has been characterized by some reasonable properties, [1]: (1) no mating occurs in absence of individuals, (2) increases with increasing population size, and (3) for large populations where the number of males is considerably bigger than females, it is close to one. Several functions satisfying this properties have been proposed, [1], [3], for continuous and discrete time deterministic models. All those functions assume that males and females search for a couple in an environment where they are uniformly mixed.

Here we extend a model that merges demographic stochasticity and stochastic sex determination presented in [14], where several mechanistic stochastic Ricker models were introduced to study the combined effects of demographic and environmental stochasticity, and demographic heterogeneity on extinction risk. We do this in the simplest model, being this extension similarly integrated to their more general models. We focus on exploring the effects that the combination of stochastic fluctuations in the sex ratio, birth and death events and the number of females

successfully fertilized in each generation may have, at low density populations, on the probabilities and mean time to extinction in an invaded patch.

2. **Model description.** The Poisson-binomial Ricker model established in [14] describes the evolution of a population with individuals of two sexes including demographic stochasticity and random sex determination. We use this model as framework to integrate the possibility of failure in the process of fertilization, which, following the same lines, can also be included in the more elaborated models presented in [14].

For convenience, let us briefly recall the first steps in the derivation of the Poisson-binomial Ricker model. Let N_t be the number of individuals at generation $t = 1, 2, ...$. Assume the number of offspring from female i in the generation t, $B_{i,t}$, is Poisson distributed with parameter β, which is the mean number of births per female, $B_{i,t} \sim Poisson(\beta)$. Then, the number of survivors from the offspring $B_{i,t}$ to the next life-cycle is $S_{i,t+1} \sim Binomial(B_{i,t}, s)$, where the parameter s is the survival probability of an individual. This parameter can be written as $s = (1 - m)e^{-\alpha N_t}$, where m is the probability of density independent mortality and α captures density dependent effects, such as cannibalistic behavior of adults on eggs (adult search rate), [14], density-dependent transmission of disease, or damage of spawning sites by other spawning adults, [7]. Then, $S_{i,t+1} \sim Poisson(\beta(1 - m)e^{-\alpha N_t})$.

Breaking down the number of individuals at generation t as

$$N_t = M_t + F_t^u + F_t^s,$$

where M_t is the number of males, F_t^s the number of females successfully fertilized and F_t^u the number of females unsuccessfully fertilized, then, the number of individuals in generation $t + 1$ is given by

$$N_{t+1} = \sum_1^{F_t^s} S_{i,t+1}.$$

The sum of random variables with Poisson distributions has also a Poisson distribution, [9], thus

$$N_{t+1} \sim Poisson\left(F_t^s \beta(1 - m)e^{-\alpha N_t}\right).$$

Let p be the probability that each male has to find and have at least one contact with a given female that leads to a successful fertilization. The value of p may depend on the individual's ability to move, their spatial distribution or the mating system, and it is the target of some control measures. For instance, the release of pheromones is a pest control strategy which affects directly the value of p, increasing the males' difficulties to locate females in space through trail confusion, [2]. For simplicity, we assume that every male has the same probability of fertilizing successfully a given female, and also that mating is promiscuous, meaning that females mate with any available males. Let $F_t = F_t^u + F_t^s$, then, the probability of fertilization, conditioned on F_t, is

$$q_t = 1 - (1 - p)^{N_t - F_t}.$$

This function clearly satisfies the three conditions for the probability of fertilization stated in the Introduction. We assume that

$$F_t \sim Binomial(N_t, z_t),$$

where z_t is the probability that an individual is born a female. For simplicity, let $z_t = z$, a constant, for all generations t. The number of mated females can be thought as distributed according to a binomial distribution,

$$F_t^s \sim Binomial(F_t, q_t).$$

Notice that if $F_t = 0$, N_t or if $N_t = 1$ then the population gets extinct in the subsequent generation. Also, if $p = 0$, no female could be fertilized and the population gets extinct. Applying the law of total probabilities, we can find the probability distribution of N_{t+1} conditioned on N_t,

$$\mathbb{P}(N_{t+1} = n|N_t) = \sum_{k=0}^{N_t} \mathbb{P}(N_{t+1} = n|N_t, F_t^s = k)\mathbb{P}(F_t^s = k|N_t)$$

$$= \sum_{k=0}^{N_t} \frac{\lambda^n e^{-\lambda}}{n!} \binom{N_t}{k} \sum_{l=k}^{N_t} \binom{N_t - k}{l - k} \left(\theta^{l-k}(1 - z)\right)^{N_t - l} \left(1 - \theta^{N_t - l}\right)^k z^l,$$

where $\lambda = k\beta(1 - m)e^{-\alpha N_t}$, and $\theta = 1 - p$, see the Appendix for derivation details. With this expression, it is straightforward to verify the conditioned expected value of N_{t+1}, given N_t, $E[N_{t+1}|N_t] = \sum_{n=0}^{\infty} n\mathbb{P}(N_{t+1} = n|N_t)$, is finite. The values of $E[N_{t+1}|N_t]$ can be estimated averaging over a large number of simulations, see Figure 1.

Remark 1. The value of p can be thought, more accurately, as a variable depending on the density of males and on females' ability to find males in a given area. In [4], a dependence relation between the probability of successful fertilization, the area searched by a male and the number of individuals in a patch is established. The description of this dependence may also include other situations than only the searched area, such as pheromone diffusion for static females, for instance. Following [4], where the number of mating encounters that a female has in an effective area searched a during breeding time, $X(a)$, is modeled as an homogeneous birth process, we assume the probability that a female finds a male after searching a small area Δa is proportional to the number of males, i.e. $\mathbb{P}(X(a + \Delta a) = x + 1|X(a) = x) = B(N_t - F_t)\Delta a$. Then, the probability of having no contact leading to fertilization can be written as $e^{-aB(N_t - F_t)}$. Therefore, the probability of fertilization of a female at generation t is

$$q_t = 1 - e^{-aB(N_t - F_t)}$$

and the expression for $\mathbb{P}(N_{t+1} = n|N_t)$ is the same as before, but with $\theta = e^{-aB}$.

Remark 2. If we let $p = 1$, i.e. every male in the population has at least one contact with a female which leads to a successful fertilization, then $q_t \equiv 1$ and all the females are successfully fertilized, $F_t^s = F_t$, thus

$$\mathbb{P}(N_{t+1} = n|N_t) = \sum_{k=0}^{N_t} \mathbb{P}(N_{t+1} = n|N_t, F_t = k)\mathbb{P}(F_t = k|N_t)$$

$$= \sum_{k=0}^{N_t} \frac{\lambda^n e^{-\lambda}}{n!} \binom{N_t}{k} z^k (1 - z)^{N_t - k},$$

which is the Poisson-binomial Ricker model proposed in [14].
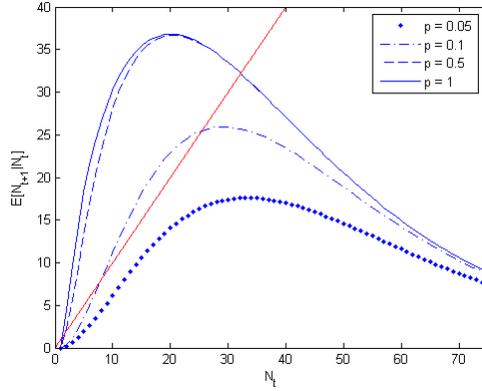
FIGURE 1. The graph of $E[N_{t+1}|N_t]$ presents a sigmoidal shape at low values of p. As the value of p increases, the curves rapidly approach the limit curve with $p = 1$, crossing in their way the straight line with slope one, and creating two equilibrium points for the conditioned expected value, which is typical in deterministic models including some type of Allee effect. At $p = 1$, when all females are successfully fertilized, the sigmoidal shape is lost, and the curve is described by the Ricker model $N_{t+1} = N_t R e^{-\alpha N_t}$, where R is the density-independent mean per capita growth rate. The values of the parameters used are $z = 0.5, \beta(1-m) = 10, \alpha = 0.05$, [14].

3. **Population viability analysis.** The likelihood of extinction of a population is an object of fundamental importance for conservation and pest management. Here we use the model just described in the last section to analyze the population viability of an invading species, applying the widely available elementary theory of finite Markov chains, which allows to compute numerically extinction probabilities and, because we are considering populations with no migration, the mean time to extinction.

The population dynamics is described by an absorbing Markov chain, where the states of the process consist of the number of individuals in the population at each generation, with only one absorbing state, 0. In the model, there is no bound for the number of possible states. However, it is possible to obtain useful information assuming the number of states finite, but large enough. This assumption is physically reasonable: starting with small a population, a large population may be achieved in the next generation with a very low probability, and if that event ever happens, the population suffers in the subsequent generation a considerable reduction, due to density dependent mortality.

Let $p_{ij} = \mathbb{P}(N_{t+1} = j | N_t = i)$ be the transition probabilities between states and notice that this probabilities are time independent,

$$\mathbb{P}(N_{t+1} = j | N_t = i) = \mathbb{P}(N_{r+t+1} = j | N_{r+t} = i),$$

for all $r = 1, 2, ...$. Thus, we express the transition matrix for any generation t as

$$\mathbf{P} = \begin{pmatrix} 1 & 0 & 0 & 0 & \cdots \\ 1 & 0 & 0 & 0 & \cdots \\ p_{20} & p_{21} & p_{22} & p_{23} & \cdots \\ p_{30} & p_{31} & p_{32} & p_{33} & \cdots \\ \vdots & \vdots & \vdots & \vdots & \ddots \end{pmatrix} = \begin{pmatrix} 1 & \mathbf{0} \\ \mathbf{R} & \mathbf{T} \end{pmatrix}.$$

We remark, for later use, that each state i, $i \geq 2$, is transient. This means that if we start with a population of i individuals, the probability of reaching the state i again, at a different time, is strictly less than one. We justify the former claim as follows. First, notice that $p_{ij} > 0$ for all $i \geq 2$ and $j = 0, 1, 2, ...$, and the probability of reaching the absorbing state 0, starting at $i \geq 2$, is p_{i0}. Then, the probability of not returning to i, at any time, is greater than p_{i0}. Therefore, the probability of returning to the state i is less than $1 - p_{i0} < 1$.

3.1. **Probability of extinction.** If a species invades an unoccupied patch, our interest is the likelihood that the invader survives after invasion starts. If the invasion begins with a small number of individuals it would be prone to a reproductive Allee effect. Below, we compute approximations to the extinction probabilities for the first generations of invaders.

Let $\mathbb{P}_{ext}(t, N_1)$ be the probability of extinction at generation t starting with a population N_1, (here thought as the first generation). Defining $p_k = \mathbb{P}(N_2 = k | N_1)$, $k = 1, 2, ...$, we can write

$$
\begin{aligned}
\mathbb{P}_{ext}(t, N_1) &= \sum_{k_{t-2} \geq 1} \sum_{k_{t-3} \geq 1} \cdots \sum_{k_1 \geq 1} p_{k_1} p_{k_1, k_2} \cdots p_{k_{t-3}, k_{t-2}} p_{k_{t-2}, 0} \\
&= \begin{cases} \mathbf{a} \left(\mathbf{T}'\right)^{t-3} \mathbf{R} & \text{if } t \geq 3, \\ \mathbb{P}(N_2 = 0 | N_1) & \text{if } t = 2, \end{cases}
\end{aligned}
$$

where $\mathbf{T}'$ is the transpose of $\mathbf{T}$, and $\mathbf{a}$ is the row vector with the k-th entry equal to p_k. Figure 2 shows a sequence of snapshots of the evolution in time of the probability of extinction al low population densities during the first generations.

The fundamental matrix of the Markov chain, defined as $\mathbf{N} = (\mathbf{I} - \mathbf{T})^{-1}$ is of use for computing the overall extinction probabilities for an invader population, which can be obtained through the product $\mathbf{NR}$, where the component $(\mathbf{NR})_i$ is the probability that the absorbent state 0 is reached given that the Markov chain starts at the transient state i. In Figure 3 we observe how the reproductive Allee effect shapes the probability of extinction at low initial population values. We recall that it is not possible to remain forever jumping among transient states, and that absorption occurs with probability one, [8].

3.2. **Time to extinction.** The computation of the mean time to extinction can be done using the formula $\mathbf{m} = \mathbf{Ne}$, where $\mathbf{e}$ is the column vector with all the entries equal to one, [8], and the i-th component is the mean time to extinction given i initial individuals. The numerical results using the parameters $z = 0.5, \beta(1 - m) = 5, \alpha = 0.05$ are displayed in Figure 4. We observe that for small values of p the value of the mean time of extinction has a sigmoidal increasing shape as the number of initial individuals in the population increases. This indicates the presence of a strong Allee effect. If the values of p increase, the sigmoidal shape is lost and is transformed in a hyperbolic type shape, indicating the Allee effect is now weak.
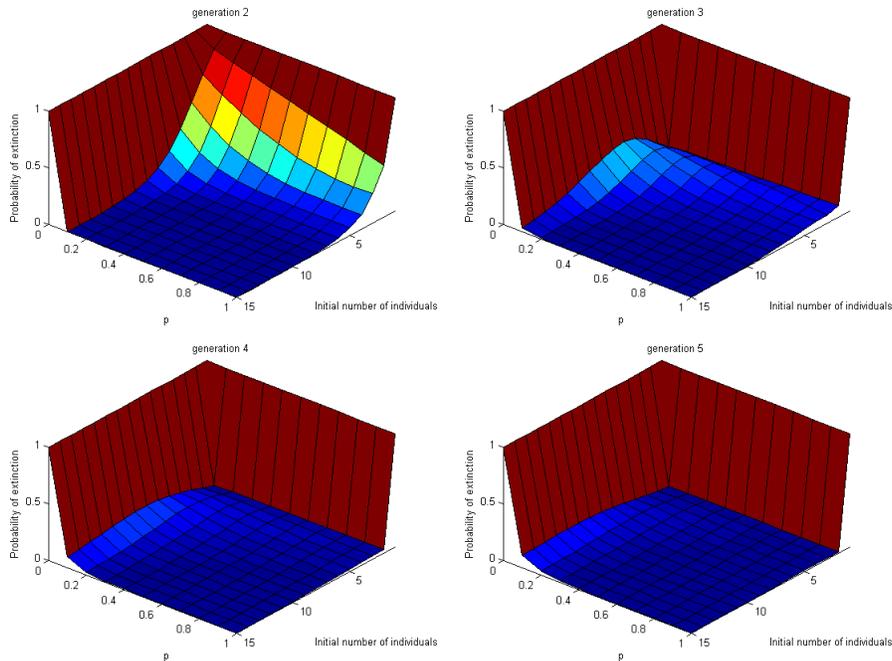
FIGURE 2. This sequence of snapshots shows the evolution of the probability of extinction during the first generations (here, the first generation is the initial population). The probability of extinction is relatively high at the generation subsequent to the invasion if the value of p is small and the number of individuals introduced are small. The parameters used are the same as in Figure 1.

4. **Discussion.** Sex ratio fluctuations, which arise from random sex determination in the offspring and from demographic stochasticity in male/female deaths, in combination with low population densities, can be very effective in reducing individual fitness through mate-finding mechanisms. As mentioned before, reproductive Allee effects have been successfully observed, for instance, in Glanville fritillary, the gypsy moth, smooth cordgrass, and many other species of animals and plants, [16], [6]. In contrast, if the population grows, the sex ratio is approximately 1:1, and most likely every individual would find a mate, causing therefore the disappearance of reproductive Allee effects. Thus, in an attempt to understand and quantify the conditions under which Allee effects may take place, and their potential consequences in the survival of a species, many mathematical models have being introduced and studied. But, as more details are added into the models from the biological context, such as two sex population or variations in the sex ratio, the complexity and difficulty to analyze them increases, [17].

Because Allee effects are phenomena occurring at low population densities, and being deterministic models suitable for describing the mean behavior at large populations, it seems reasonable to think that information obtained from stochastic models would be more helpful, especially in the evaluation of extinction risk for invasion and conservation management. But we remark that, the need for theoretical understanding of reproductive Allee effects does not come only from conservation
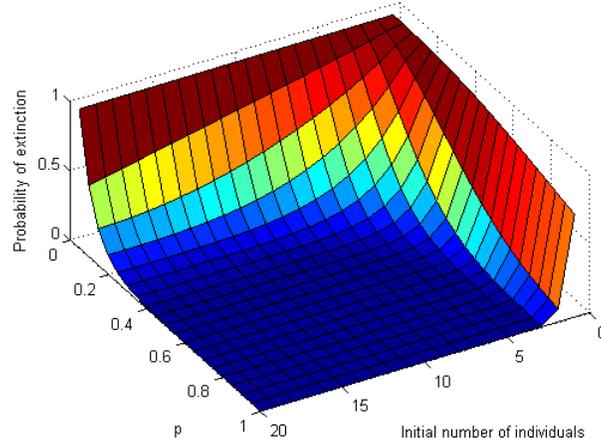
FIGURE 3. As the values of p decrease, the probability of extinction increases. In this example, for a reproductive Allee effect to appear as a result of control measures, it is necessary to reduce considerably the value of p, otherwise the it will be difficult to eradicate the invader.
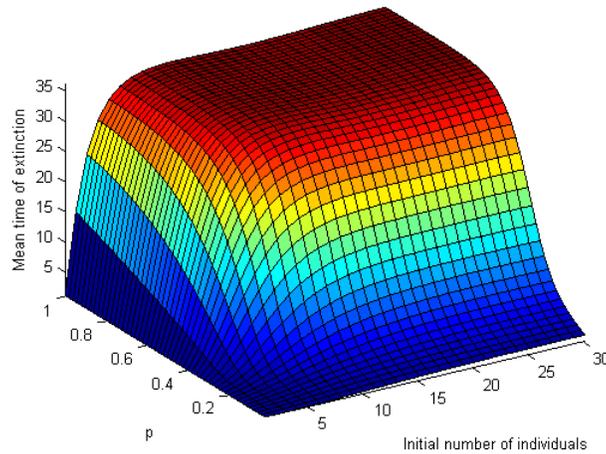

FIGURE 4. Low values of p produce a sigmoidal shape in the mean time to extinction, indicating the presence of a strong Allee effect. This shape changes to a hyperbolic shape as the value of p increases, indicating the presence of a weak Allee effect.

and invasion issues. Interestingly, it also comes from the suggestion that they may have been driving evolutionary changes in mating systems, leading species to adapt mechanisms in order to avoid low densities, or mechanisms allowing mate-finding at low densities, [6].

The novelty presented here is the inclusion of the probability of fertilization in a stochastic Poisson-Ricker model, which already integrates random sex determination, and show how numerical computations, through the use of elementary Markov chains theory, can be done to obtain the extinction probabilities and the mean time to extinction. As a result, it is possible to determine the presence of weak or strong reproductive Allee effects and its capacity to drive a low density population to extinction.

For the specific computations made, the presence of a strong Allee effect in the region of low values of p is clearly observed in the mean time to extinction, through the presence of a sigmoidal shape. As the values of p increase, the sigmoid changes into a hyperbolic curve, meaning that the strong Allee effect turns into a weak Allee effect. Also, in Figure 3, we observe how the Allee effect makes the probability of extinction increasing as the value of p decrease. The computation of the probabilities of extinction for the first generations allows to observe how the mass of the distribution is radically reduced in time. This may suggest that pest control strategies, such as the mass release of phermones, would better applied when an invasion, with small number of individuals, has just started, that is, when the probability of extinction is high due to the reproductive Allee effect.

Any strategy for conservation or eradication on species that require sexual recombination for reproduction should consider the extent to reproductive Allee effects may impact the population viability. The analysis made here represents a basic approach with further extensions in different directions. Of particular interest would be the inclusion of accurate descriptions of spatial relations, given that they are directly related with the appearance of reproductive Allee effects.

5. **Appendix.** Here we deduce the formula for $\mathbb{P}(N_{t+1} = n | N_t)$ presented in Section 2. First, notice that

$$
\begin{aligned}
\mathbb{P}(F_t^s = k | N_t) &= \sum_{l=k}^{N_t} \mathbb{P}(F_t^s = k | F_t = l) \mathbb{P}(F_t = l) \\
&= \sum_{l=k}^{N_t} \binom{l}{k} q_t^k (1 - q_t)^{l-k} \binom{N_t}{l} z^l (1-z)^{N_t - l}, \\
&= \sum_{l=k}^{N_t} \binom{N_t}{k} \binom{N_t - k}{l - k} q_t^k (1 - q_t)^{l-k} z^l (1-z)^{N_t - l},
\end{aligned}
$$

the second equality coming from the fact that $F_t^s \sim Binomial(F_t, q_t)$ and $F_t \sim Binomial(N_t, z)$. Replacing this expression in

$$
\mathbb{P}(N_{t+1} = n | N_t) = \sum_{k=0}^{N_t} \mathbb{P}(N_{t+1} = n | N_t, F_t^s = k) \mathbb{P}(F_t^s = k | N_t),
$$

with $\theta = 1 - p$, and recalling that $N_{t+1} \sim Poisson\left(F_t^s \beta (1-m) e^{-\alpha N_t}\right)$, gives de desired equality.

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