The Annals of Applied Probability
1993, Vol. 3, No. 1, 198–211

ON THE GALTON–WATSON PREDATOR–PREY PROCESS

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We consider a probabilistic, discrete-time predator–prey model of the following kind: There is a population of predators and a second one of prey. The predator population evolves according to an ordinary supercritical Galton–Watson process. Each prey is either killed by a predator in which case it cannot reproduce, or it survives and reproduces independently of all other population members and according to the same offspring distribution with mean greater than 1. The resulting process $(X_n, Y_n)_{n \ge 0}$, where X_n and Y_n, respectively, denote the number of predators and prey of the nth generation, is called a Galton–Watson predator–prey process. The two questions of almost certain extinction of the prey process $(Y_n)_{n \ge 0}$ given $X_n \to \infty$, and of the right normalizing constants d_n, $n \ge 1$ such that Y_n/d_n has a positive limit on the set of nonextinction, are completely answered. Proofs are based on a reformulation of the model as a certain two-district migration model.

1. Introduction and main results. Let $(\Omega, \mathscr{A}, (P_{x,y})_{x,y \in \mathbb{N}_0}, (X_n, Y_n)_{n \ge 0}, (\xi_{i,j})_{i,j \ge 1}, (\eta_{i,j})_{i,j \ge 1}, (\nu_{i,j})_{i,j \ge 1})$ be a stochastic model which satisfies the following assumptions:

(a) For all x, y, $P_{x,y}$ is a probability measure on $(\Omega, \mathscr{A})$ such that $P_{x,y}(X_0 = x, Y_0 = y) = 1$.

(b) Under each $P_{x,y}$, $(\xi_{i,j})_{i,j \ge 1}$, $(\eta_{i,j})_{i,j \ge 1}$ and $(\nu_{i,j})_{i,j \ge 1}$ are mutually independent sequences of i.i.d. $\mathbb{N}_0$-valued random variables whose joint distributions do not depend on x, y and have finite means $\mu = E\xi_{1,1}$, $m = E\eta_{1,1}$ and $\alpha = E\nu_{1,1}$. [Here and in the following we write $P[E]$, $P_{x,\cdot}[E_{x,\cdot}]$ and $P_{\cdot,y}[E_{\cdot,y}]$ for probabilities (expectations) w.r.t. $P_{x,y}$ which do not depend on, resp., (x,y), y and x.]

(c) For each $n \ge 1$,

$$(1.1) \qquad X_n = \sum_{j=1}^{X_{n-1}} \xi_{n,j} \quad \text{and} \quad Y_n = \left(\sum_{j=1}^{Y_{n-1}} \eta_{n,j} - \sum_{j=1}^{X_n} \nu_{n,j} \right)^+ .$$

This model has recently been introduced by Coffey and Bühler (1991) in order to describe the evolution of a predator–prey population with X_n the number of predators in the nth generation and Y_n the associated number of prey not eaten by these predators before having produced offspring. $\xi_{n,j}$ clearly represents the number of offspring of the jth predator in the nth generation, $\nu_{n,j}$

Received September 1991; revised March 1992.
AMS 1991 *subject classifications*. Primary 60J80; secondary 60G42, 60F99.
Key words and phrases. Galton–Watson predator–prey process, extinction probability, normalizing constants, martingales, two-district migration model.

the number of prey eaten by him and $\eta_{n,j}$ the number of offspring of the jth surviving prey in that generation. According to the assumptions, $(X_n)_{n \geq 0}$ forms an ordinary Galton–Watson process whereas $(Y_n)_{n \geq 0}$, though based on the same principle of independent reproduction, is additionally subject to shrinkage due to the predators. More precisely, each prey produces offspring only if it survives its full potential life length of one time unit without being killed by a predator. We call $(X_n, Y_n)_{n \geq 0}$ a Galton–Watson predator–prey process (GWPPP). The analysis of predator–prey models dates back to Lotka (1925) and Volterra (1926) who studied deterministic versions. Hitchcock (1986) and Ridler-Rowe (1988) are recent references for probabilistic variants which, however, are very different from the one given above. We also mention these works for further literature cited therein.

Two theorems will be proved in this paper. The first one is concerned with the extinction probability function

$$q(x, y) = P_{x,y}(Y_n \to 0 | X_n \not\to 0), \qquad x, y \in \mathbb{N}$$

under the assumption that $\mu > 1$, $m > 1$ and $\alpha > 0$. It extends Coffey and Bühler's main result and completely answers the question when $q(x, y) < 1$ holds true. The second theorem provides the right normalizing constants d_n such that Y_n / d_n tends to a positive limit on the event $\{Y_n \not\to 0\}$ of nonextinction. It is the counterpart of the Heyde–Seneta theorem for ordinary Galton–Watson processes.

The statement of the results requires for some further notation. Put $\xi = \xi_{1,1}$, $\eta = \eta_{1,1}$, $\nu = \nu_{1,1}$, define

$$\begin{aligned} p_n(\xi) &= P(\xi = n), \\ \xi_* &= \inf\{n \geq 1; p_n(\xi) > 0\}, \\ \xi^* &= \sup\{n \geq 1; p_n(\xi) > 0\}, \\ f^{(\xi)}(s) &= \sum_{n \geq 0} p_n(\xi) s^n = E_{1,\cdot}(s^{X_1}) \quad \text{for } |s| \leq 1, \\ f_n^{(\xi)} &= f^{(\xi)} \circ \cdots \circ f^{(\xi)} \qquad (n \text{ times}) \end{aligned}$$

and similarly $p_n(\eta), p_n(\nu), \eta_*, \eta^*, \nu_*, \nu^*, f^{(\eta)}, f_n^{(\eta)}, f^{(\nu)}, f_n^{(\nu)}$. Let $q_{(\eta)}$ be the minimal root of $f^{(\eta)}(s) = s$ which is less than 1 because $m > 1$. Thus $f^{(\eta)}$ has an inverse $g^{(\eta)}$ on $[q_{(\eta)}, 1]$ with its n-fold iteration $g_n^{(\eta)}$ being the inverse of $f_n^{(\eta)}$.

Define next $Z_0 = Y_0$ and

$$Z_n = \sum_{j=1}^{Z_{n-1}} \eta_{n,j} \quad \text{for } n \geq 1. \tag{1.2}$$

$(Z_n)_{n \geq 1}$ is nothing but the ordinary GWP originating from Y_0 ancestors if no predators interfere. By the Heyde–Seneta theorem [see Jagers (1975), Theorem (2.7.1)], there are constants d_n, for example, $d_n = -1/\log g_n^{(\eta)}(s)$ for some $s \in (q_{(\eta)}, 1)$,

$$\lim_{n\to\infty} \frac{d_n}{a^n} = \begin{cases} \infty, & \text{if } a < m, \\ 0, & \text{if } a > m, \end{cases} \quad \text{and} \quad \lim_{n\to\infty} \frac{d_{n+1}}{d_n} = m, \tag{1.3}$$

such that for all $y \in \mathbb{N}$,

$$\frac{Z_n}{d_n} \to Z \qquad P_{\cdot,y}\text{-a.s.}, \tag{1.4}$$

for some finite random variable Z which satisfies $P_{\cdot,y}(Z > 0) = P_{\cdot,y}(Z_n \to \infty)$. Note that (1.3) implies $Z_{n+1}/Z_n \to m$ $P_{\cdot,y}$-a.s. on $\{Z_n \to \infty\}$. If $E\eta \log(1 + \eta) < \infty$, one can choose $d_n = m^n$ and $E_{\cdot,y}Z = y$ holds; otherwise $d_n/m^n \to 0$, as $n \to \infty$, and $E_{\cdot,y}Z = \infty$. By the same theorem there are constants c_n satisfying (1.3) with m replaced by μ such that

$$\frac{X_n}{c_n} \to X \qquad P_{x,\cdot}\text{-a.s.}, \tag{1.5}$$

for all $x \in \mathbb{N}$ and some finite random variable X which satisfies $P_{x,\cdot}(X > 0) = P_{x,\cdot}(X_n \to \infty)$. Moreover $X_{n+1}/X_n \to \mu$ $P_{x,\cdot}$-a.s. on $\{X_n \to \infty\}$.

Theorem 1 shows that the question whether the prey population has a positive chance of survival essentially depends on the growth of Z_n relative to that of X_n. However, rather than simply comparing the reproduction means m and μ the formal condition reads $\sum_{n\geq 1} c_n/d_n < \infty$ or $= \infty$. Note that the latter sum is finite if $m > \mu$, infinite if $m < \mu$, but can be either one if $m = \mu$.

THEOREM 1. *Let $(X_n, Y_n)_{n\geq 0}$ be a GWPPP with $\mu > 1$, $m > 1$ and $\alpha > 0$. Let $\gamma = \sum_{n\geq 1} c_n/d_n$.*

(a) *If $\gamma = \infty$, then $q(x, y) = 1$ for all $x, y \in \mathbb{N}$.*

(b) *If $\gamma < \infty$ and $\eta^* = \infty$, or if $\gamma < \infty$, $\eta^* < \infty$ and $p_0(\nu) > 0$, then $q(x, y) < 1$ for all $x, y \in \mathbb{N}$.*

(c) *If $\gamma < \infty$, $\eta^* < \infty$, $p_0(\nu) = 0$ and $p_0(\xi) > 0$, then $q(x, y) < 1$ if and only if $x \geq 1$ and $y > \nu_* \xi_* /(\eta^* - 1)$.*

(d) *If $\gamma < \infty$, $\eta^* < \infty$ and $p_0(\nu) = p_0(\xi) = 0$, then $q(x, y) < 1$ if and only if $x \geq 1$ and $y > \nu_* \xi_* x/(\eta^* - \xi_*)$, or $x \geq 1$, $y = \nu_* \xi_* x/(\eta^* - \xi_*)$ and $\operatorname{Var}(\xi + \eta + \nu) = 0$ (i.e., $\xi_* = \mu$, $\eta^* = m$ and $\nu_* = \alpha$).*

Under the additional assumption that ξ, η and ν have finite variances, Coffey and Bühler (1991) proved $q(x, y) = 1$ for all $x, y \in \mathbb{N}$ if $m \leq \mu$ and $q(x,y) < 1$ for all $x \geq 1$ and sufficiently large $y > y(x)$ if $m > \mu$. For the latter case they also gave an example where $q(x, y) = 1$ for some $x, y \in \mathbb{N}$. Theorem 1 shows that one can dispense with finite variances and furthermore completely answer the question when $q(x, y) = 1$, respectively, less than 1 holds. Its proof is based on rather different arguments than in the aforementioned paper, especially on a suitable construction of $(X_n, Y_n)_{n\geq 0}$ in Section 2. Let us note for the case $m = \mu$ that $\sum_{n\geq 1} c_n/d_n < \infty$ and thus $q(x, y) < 1$ for all $x, y \in \mathbb{N}$ can only hold when $E\xi \log(1 + \xi) = \infty$.

Our second theorem considers the case where $q(x, y) < 1$ and shows that the d_n from (1.4) are the right normalizing constants in the sense that Y_n/d_n tends $P_{x,y}$-a.s. to a nondegenerate limit.

THEOREM 2. *Let $(X_n, Y_n)_{n \geq 0}$ be a GWPPP with $m, \mu > 1$, $\alpha > 0$ and* $\mathrm{Var}(\xi + \eta + \nu) > 0$. *Let $(d_n)_{n \geq 0}$ be as previously defined. Then*

$$\frac{Y_n}{d_n} \to Y \qquad P_{x,y}\text{-}a.s., \tag{1.6}$$

for some random variable Y which satisfies $P_{x,y}(Y = 0 | X_n \to \infty) = q(x, y)$ for all $x, y \in \mathbb{N}$.

A prey process thus shows the same dichotomy as a simple GWP. It either explodes at an exponential rate given by its reproduction mean or it dies out. A further discussion of this as well as the proof of Theorem 2 are given in Section 4.

The paper is organized as follows. The next section contains a number of prerequisites for the proofs of Theorem 1 and 2, in particular a two-district migration model which in a certain sense is a reformulation of the predator–prey model described before. Section 3 gives the proof of Theorem 1 and Section 4 that of Theorem 2 as already stated.

2. A two-district migration model and other prerequisites. We begin with a general strong law of large numbers for double arrays which will be used several times later on.

LEMMA 1. *Let $(S_n)_{n \geq 1}$ be a sequence and $(\zeta_{n,j})_{j,n \geq 1}$ be a double array of nonnegative, integer-valued random variables such that S_n and $(\zeta_{n,j})_{j \geq 1}$ are independent for all n, and the $\zeta_{n,j}$ are all i.i.d. with possibly infinite mean β. Then*

$$\lim_{n \to \infty} \frac{1}{S_n} \sum_{j=1}^{S_n} \zeta_{n,j} = \beta \quad a.s. \text{ on } \left\{ \liminf_{n \to \infty} \frac{S_{n+1}}{S_n} > 1 \right\}. \tag{2.1}$$

The proof is a simple adaptation of those of Lemma 5.2 and 5.3 in Asmussen and Hering [(1983), Chapter II] and can be omitted.

All notation from the previous section is kept throughout. In addition we define

$$S_n = \sum_{j=1}^{Y_{n-1}} \eta_{n,j} \quad \text{and} \quad U_n = \sum_{j=1}^{X_n} \nu_{n,j} \quad \text{for } n \geq 1, \tag{2.2}$$

thus $Y_n = (S_n - U_n)^+$. Since $X_{n+1}/X_n \to \mu$ $P_{x,\cdot}$-a.s. on $\{X_n \to \infty\}$, Lemma 1 implies

$$(2.3)\qquad \lim_{n\to\infty}\frac{U_n}{X_n}=\alpha \quad\text{and}\quad \lim_{n\to\infty}\frac{U_n}{c_n}=\alpha X \qquad P_{x,\cdot}\text{-a.s. on } \{X_n\to\infty\}$$

for all $x \in \mathbb{N}$. Similarly,

$$(2.4)\quad \lim_{n\to\infty}\frac{S_n}{Y_{n-1}}=\lim_{n\to\infty}\frac{1}{Y_{n-1}}\sum_{j=1}^{Y_{n-1}}\eta_{n,j}=m \quad P_{x,y}\text{-a.s. on } \left\{\liminf_{n\to\infty}\frac{Y_{n+1}}{Y_n}>1\right\}$$

for all $x, y \in \mathbb{N}$. We will see in Section 4 that the latter event coincides $P_{x,y}$-a.s. with $\{Y_n \nrightarrow 0\}$.

An important tool for proving our results will be the construction of a suitable a.s. convergent martingale. Define $Y_0^* = Y_0$, and for $n \ge 1$,

$$(2.5)\qquad Y_n^* = H(Y_{n-1}^*)\sum_{j=1}^{|Y_{n-1}^*|}\eta_{n,j} - U_n,$$

where H is the ordinary sign function, that is, $H(0) = 0$ and $H(x) = x/|x|$ for $x \neq 0$. Observe that $Y_n^* = Y_n$ if $Y_n > 0$, and that $Y_n^* \le 0$ whenever $Y_n = 0$, that is, $Y_n = (Y_n^*)^+$. Coffey and Bühler (1990) considered the martingale

$$(2.6)\qquad m^{-n}\left(Y_n^* + \sum_{j=1}^{n} m^{n-j}U_j\right), \qquad n \ge 0,$$

which is L_2 bounded if ξ, η and ν have finite variances. In the absence of the latter condition, however, this martingale does not appear to be appropriate, because we cannot prove its L_1 boundedness which would be required for an application of the martingale convergence theorem. Moreover, the normalizing constants m^{-n} need not be the appropriate ones if only first moments are supposed to be finite. Instead, the following construction will lead us to another procedure of proving a.s. convergence. It will be of great importance for the proofs of our theorems.

A two district migration model. In order to better understand this construction we drop the predator–prey interpretation and replace it by the following one: Let $Z_0, Z_1, \dots$ as defined in (1.2) be the successive generation sizes of a population which colonizes two districts A and B and the members of which we call natives. During the first time period all Z_0 ancestors live in district A and nobody lives in B. Beginning with the first generation members can migrate from A to B and settle there. In addition, further individuals can immigrate from the outer world into B. Let us call these individuals as well as all their descendants aliens. Migration into A is not possible, neither from B nor the outer world. So A can only be left whereas B can only be entered. Aliens reproduce according to the same distribution (that of η) as all natives and also independent of them and each other. Let $Y_0 = Z_0, Y_1, \dots$ be the successive numbers of natives which stay at A until death, that is, until next reproduction, and let $\hat{Y}_{k+1} = \sum_{j=1}^{Y_k}\eta_{k+1,j}$, $k \ge 0$ denote their numbers of offspring. The sequence $U_1, U_2, \dots$ in (2.2) governs the number of migrating individuals for the successive generations with priority always given to native immigrants. More precisely, at each time $k \geq 1$, just after reproduction has taken place, $\hat{Y}_k \wedge U_k$ natives migrate from A to B first and are followed by $U_k - Z_k$ aliens only if $\hat{Y}_k < U_k$. We denote by $(Z_n^{(k)})_{n \geq 0}$ the GWP originating from them, natives as well as aliens. The total number of individuals colonizing B at time k is thus given by

$$Z_k^* =_{\text{def}} \sum_{j=1}^{k} Z_{k-j}^{(j)} \quad \text{for all } k \geq 0, \tag{2.7}$$

the total population size including aliens by

$$\hat{Z}_k =_{\text{def}} Y_k + Z_k^* \quad \text{for all } k \geq 0. \tag{2.8}$$

It is obvious and underlined by the choice of notation that the number Y_n of natives of the nth generation who stay and therefore reproduce in A corresponds to the number of surviving prey of this generation in the original model. The predator process $(X_n)_{n \geq 0}$ still appears as a control sequence hidden in the sequence $U_1, U_2, \dots$ which governs the number of individuals who enter district B in successive time periods and originate simple GWP.

Now consider the sequence $(Y_n^*)_{n \geq 0}$ defined in (2.5). Recall that $Y_n = (Y_n^*)^+$ for all $n \geq 0$. Let τ denote the first entrance time of aliens, obviously given by

$$\begin{aligned} \tau &= \inf\{n \geq 0 \colon Y_n = 0\} = \inf\{n \geq 0 \colon Y_n^* \leq 0\} \\ &= \inf\{n \geq 0 \colon \hat{Z}_n = Z_n^*\}. \end{aligned} \tag{2.9}$$

Since $Z_n = \hat{Z}_n$ for $0 \leq n < \tau$, we infer from (2.8) that

$$Z_n = Y_n^* + Z_n^* = Y_n + Z_n^* \quad \text{for all } 0 \leq n < \tau. \tag{2.10}$$

For $n \geq \tau$, Y_n^* is negative with absolute value just giving the total number of aliens in the nth generation. Subtracting this number from the total population size at time n, given by $\hat{Z}_n = Z_n^*$, yields the number of natives at this time, given by Z_n. Consequently, the first equality in (2.10) remains true for $n \geq \tau$ and we have proved:

LEMMA 2. *Let Y_n^*, $n \geq 0$ be as in* (2.5). *Then $Z_n = Y_n^* + Z_n^*$ for all $n \geq 0$.*

The importance of Lemma 2 relies on the fact that $(Y_n^*)_{n \geq 0}$ and thus $(Y_n)_{n \geq 0}$ on $\{\tau = \infty\}$ have now been constructed as the difference of two "nice" processes, namely, the simple GWP $(Z_n)_{n \geq 0}$ and the GWP with immigration $Z_n^* =_{\text{def}} \sum_{j=1}^{n} Z_{n-j}^{(j)}$. Note also that the $P_{x,y}$-distribution of $(Z_n)_{n \geq 0}$ does not depend on x, whereas that of $(Z_n^*)_{n \geq 0}$ does not depend on y.

Our final prerequisite is an a.s. convergence result for Z_n^*/d_n which combined with (1.4) and Lemma 2 trivially implies a.s. convergence of Y_n^*/d_n. For each $j \geq 1$, we denote by $Z^{(j)}$ the a.s. limit of $Z_n^{(j)}/d_n$, as $n \to \infty$, with respect to each $P_{x,\cdot}$. Note that, given $(X_n, U_n)_{n \geq 0}$, the $Z^{(j)}$, $j \geq 1$ are conditionally independent under each $P_{x,\cdot}$ with

$$(2.11)\qquad P_{x,\cdot}\big(Z^{(j)}\in\cdot\,|(X_n,U_n)_{n\ge 0}\big)=P_{\cdot,1}(Z\in\cdot)^{*(U_j)}\qquad P_{x,\cdot}\text{-a.s.},$$

where $*(k)$ denotes k-fold convolution and Z is given in (1.4).

LEMMA 3. *For all $x,y\in\mathbb{N}$, Z_n^*/d_n and Y_n^*/d_n converge $P_{x,y}$-a.s. to random variables Z^* and Y^*, respectively, which satisfy $Y^*=Z-Z^*$ and*

$$(2.12)\qquad P_{x,\cdot}(Z^*<\infty|X_n\to\infty)=P_{x,y}(Y^*>-\infty|X_n\to\infty)=\begin{cases}1, & \text{if } \gamma<\infty,\\ 0, & \text{if } \gamma=\infty.\end{cases}$$

If $m>\mu$ and $E\eta\log(1+\eta)<\infty$, then $Z^*=\sum_{j\ge 1}m^{-j}Z^{(j)}$ and $E_{x,\cdot}Z^*=\alpha xm/(m-\mu)$.

PROOF. As already stated above, we must only consider the sequence Z_n^*/d_n, $n\ge 0$, and it clearly suffices then to prove the assertions under $P_{1,\cdot}$. Furthermore it is no loss of generality to assume $P_{1,\cdot}(X_n\to 0)=0$. Put $c_n=-\log g_n^{(\xi)}(s_0)$ and $d_n=-\log g_n^{(\eta)}(s_0)$ for some s_0 sufficiently close to 1.

It is easily verified that $g_n^{(\eta)}(s)^{Z_n^*}$, $n\ge 0$ forms a bounded, nonnegative supermartingale under $P_{1,\cdot}$ and thus converges a.s. Taking the logarithm yields that Z_n^*/d_n a.s. has a limit which, of course, may be infinite.

Next, observe that c_n/d_n always converges to some $\rho\in[0,\infty]$, as $n\to\infty$. This is trivial if $m\ne\mu$ and follows by rather straightforward analytic arguments if $m=\mu$. We omit further details. As a consequence, U_n/d_n converges $P_{x,\cdot}$-a.s. to the limit $U=\rho\alpha X$ where (2.3) should be recalled. If $\rho=\infty$, we have thus already proved the assertion of the lemma because $Z_n^*\ge U_n$ for all $n\ge 1$. In the following ρ is therefore always supposed to be finite.

Let h_n be the generating function of Z_n^* for each $n\ge 1$ and let ψ and φ denote the Laplace transforms of Z^* under $P_{1,\cdot}$ and of $Z=\lim_{n\to\infty}Z_n/d_n$ under $P_{\cdot,1}$, respectively. Note that φ satisfies $\varphi(t/m)=g^{(\eta)}\circ\varphi(t)$ for all $t\ge 0$ such that $\varphi(t)\in[q_{(\eta)},1]$; see Jagers [(1975), Theorem (2.7.2)]. Hence $\varphi(t/m^n)=g_n^{(\eta)}\circ\varphi(t)$ for all such $t\ge 0$ and all $n\ge 1$. Note further that $\phi(0)=1$ because $\rho=\lim_n c_n/d_n<\infty$.

Since the $Z^{(j)}$, $j\ge 1$ are conditionally independent, given $(X_n,U_n)_{n\ge 0}$, and (2.11) holds, we obtain for all $n\ge 1$ and $s\in[0,1]$,

$$(2.13)\qquad \begin{aligned} h_n(s)&=E_{1,\cdot}\left(\prod_{j=1}^{n}f_{n-j}^{(\eta)}(s)^{U_j}\right)=E_{1,\cdot}\left(\prod_{j=1}^{n}f^{(\nu)}\circ f_{n-j}^{(\eta)}(s)^{X_j}\right)\\ &=E_{1,\cdot}\left(f^{(\nu)}\circ f_{n-1}^{(\eta)}(s)^{X_1}E_{1,\cdot}\left(\prod_{j=1}^{n-1}f^{(\nu)}\circ f_{n-1-j}^{(\eta)}(s)^{X_{j+1}}\middle|X_1\right)\right)\\ &=E_{1,\cdot}\left(f^{(\nu)}\circ f_{n-1}^{(\eta)}(s)^{X_1}E_{X_1,\cdot}\left(\prod_{j=1}^{n-1}f^{(\nu)}\circ f_{n-1-j}^{(\eta)}(s)^{X_j'}\right)\right)\\ &=E_{1,\cdot}\left(\left[f^{(\nu)}\circ f_{n-1}^{(\eta)}(s)\cdot h_{n-1}(s)\right]^{X_1}\right)\\ &=f^{(\xi)}\left[f^{(\nu)}\circ f_{n-1}^{(\eta)}(s)\cdot h_{n-1}(s)\right],\end{aligned}$$

where $(X'_n)_{n\geq 0}$ is an independent copy of $(X_n)_{n\geq 0}$ satisfying $P_{x,\cdot}(X_0 = X'_0 = x) = 1$ for all $x \in \mathbb{N}$. We then further obtain for all $t \geq 0$:

$$\begin{aligned}\psi(t) &= \lim_{n\to\infty} E_{1,\cdot}\big(\exp\big(tZ_n^* \log g_n^{(\eta)}(s_0)\big)\big) = \lim_{n\to\infty} h_n\big(g_n^{(\eta)}(s_0)^t\big)\\ &= \lim_{n\to\infty} f^{(\xi)}\big[f^{(\nu)} \circ f_{n-1}^{(\eta)}\big(g_n^{(\eta)}(s_0)^t\big) \cdot h_{n-1}\big(g_n^{(\eta)}(s_0)^t\big)\big]\\ &= \lim_{n\to\infty} f^{(\xi)}\left[f^{(\nu)}\left[E_{\cdot,1}\left(\exp\left(-\frac{tZ_{n-1}}{d_n}\right)\right)\right] \cdot E_{1,\cdot}\left(\exp\left(-\frac{tZ_{n-1}^*}{d_n}\right)\right)\right]\\ &= f^{(\xi)}\left[f^{(\nu)} \circ \varphi\left(\frac{t}{m}\right) \cdot \psi\left(\frac{t}{m}\right)\right].\end{aligned} \tag{2.14}$$

For $t = 0$, (2.14) gives $\psi(0) = f^{(\xi)}(\psi(0))$, hence $\psi(0) = P_{1,\cdot}(X_n \to 0) = 0$ or $\psi(0) = 1$. In the first case $\psi \equiv 0$, in the second one $\psi > 0$. Now consider $t = 1$. Equation (2.13) yields

$$\begin{aligned}\psi(1) &= \lim_{n\to\infty} h_n\big(g_n^{(\eta)}(s_0)\big) = \lim_{n\to\infty} E_{1,\cdot}\left(\prod_{j=1}^{n} g_j^{(\eta)}(s_0)^{U_j}\right)\\ &= E_{1,\cdot}\left(\prod_{j\geq 1} g_j^{(\eta)}(s_0)^{U_j}\right) = E_{1,\cdot}\left(\exp\left(-\sum_{j\geq 1}\frac{U_j}{d_j}\right)\right)\end{aligned} \tag{2.15}$$

and the last expression is obviously positive if and only if $\sum_{j\geq 1} U_j/d_j < \infty$ $P_{1,\cdot}$-a.s., which in turn holds if and only if $\sum_{n\geq 1} c_n/d_n < \infty$, because $\lim_{n\to\infty} U_n/c_n = \alpha X > 0$ $P_{1,\cdot}$-a.s. We have thus proved (2.12).

In order to prove the final assertions of the lemma, note that under the stated conditions we can choose $d_n = m^n$ and that $Z_{n-j}^{(j)}/m^n \to Z^{(j)}/m^j$ $P_{x,\cdot}$-a.s. Moreover, $\sup_{n\geq 0} m^{-n} Z_n$ is integrable w.r.t. $P_{\cdot,1}$ by the Kesten–Stigum theorem; see, for example, Asmussen and Hering [(1983), Chapter II, Theorem 2.1], whence by $P_{x,\cdot}((Z_n^{(j)})_{n\geq 0} \in \cdot \mid U_j = u) = P_{\cdot,u}((Z_n)_{n\geq 0} \in \cdot)$ and a simple estimate,

$$E_{x,\cdot}\left(\sup_{n\geq 0}\frac{Z_n^{(j)}}{m^n}\right) \leq E_{x,\cdot}(U_j) E_{\cdot,1}\left(\sup_{n\geq 0}\frac{Z_n}{m^n}\right) = \alpha x \mu^j E_{\cdot,1}\left(\sup_{n\geq 0}\frac{Z_n}{m^n}\right) < \infty,$$

follows for all $x, j \in \mathbb{N}$. We conclude that $\sum_{j\geq 1} m^{-j} \sup_{n\geq 0} m^{-n} Z_n^{(j)}$ is integrable and a.s. finite w.r.t. each $P_{x,\cdot}$, and then by dominated convergence

$$Z^* = \lim_{n\to\infty}\sum_{j=1}^{n} m^{-j}\frac{Z_{n-j}^{(j)}}{m^{n-j}} = \sum_{j\geq 1}\frac{Z^{(j)}}{m^j} \qquad P_{x,\cdot}\text{-a.s.},$$

which is the asserted identity for Z^*. If we finally observe that $E_{x,\cdot}Z^j = E_{x,\cdot}U_j = \alpha x \mu^j$ for all $j \geq 1$, then also the assertion on $E_{x,\cdot}Z^*$ follows. □

3. Proof of Theorem 1. We keep the notation of the previous sections. The proof of Theorem 1(a) is trivial now because we infer from Lemma 3 that $\gamma = \infty$ implies $1 = P_{x,y}(Y^* = -\infty | X_n \to \infty) \le q(x,y)$ for all $x, y \in \mathbb{N}$.

The proof of Theorem 1(b)–(d) is based on the following.

LEMMA 4. *If $\gamma < \infty$, there is $k \in \mathbb{N}$ such that $q(x,y) < 1$ for all $x \in \mathbb{N}$ and $y/x \ge k$.*

PROOF. Put $r(x,y) = P_{x,y}(\tau = \infty,\ X_n \to \infty)$ with τ given in (2.9). Clearly, $q(x,y) < 1$ if and only if $r(x,y) > 0$.

We show first $q(1,y) < 1$ for all sufficiently large y. Recall that $Y^* = Z - Z^*$ with

$$P_{x,y}(Z \in \cdot) = P_{\cdot,y}(Z \in \cdot) = P_{\cdot,1}(Z \in \cdot)^{*(y)}$$

and

$$P_{x,y}(Z^* \in \cdot) = P_{x,\cdot}(Z^* \in \cdot) = P_{1,\cdot}(Z^* \in \cdot)^{*(x)}$$

for all $x, y \in \mathbb{N}$. Recall further $E_{\cdot,1}Z = 1$ or $= \infty$. Hence by the law of large numbers,

$$\lim_{y \to \infty} P_{\cdot,y}(Z > \varepsilon y) = 1 \quad \text{for all } \varepsilon \in (0,1)$$

and

$$\lim_{y \to \infty} P_{x,\cdot}(Z^* > \varepsilon y) = 0 \quad \text{for all } \varepsilon > 0 \text{ and } x \in \mathbb{N}.$$

We obtain for each $\varepsilon \in (0, 1/2)$,

$$\begin{aligned} r(x,y) &\ge P_{1,y}(Y^* > 0,\ X_n \to \infty) \ge P_{1,y}(Z - Z^* > \varepsilon y) \\ &= P_{\cdot,y}(Z > 2\varepsilon y) - P_{1,\cdot}(Z^* > \varepsilon y), \end{aligned}$$

and the last expression is obviously positive for all $y \ge k$, k sufficiently large.

In order to complete the proof of the lemma, consider $(Y_n^*, X_n)_{n \ge 0}$ under $P_{x,mx}$ for arbitrary $x, m \in \mathbb{N}$. Observe that

$$P_{x,mx}((Y_n^*, X_n)_{n\ge 0} \in \cdot) = P_{1,m}((Y_n^*, X_n)_{n \ge 0} \in \cdot)^{*(x)},$$

from which $r(x, mx) \ge r(1,m)^x$ easily follows and thus $r(x, mx) > 0$ for all $m \ge k$. Finally, for arbitrary $x \in \mathbb{N}$ and $y \ge kx$ we conclude $r(x,y) \ge r(x, kx) > 0$ because $r(x, \cdot)$ is obviously increasing. □

With the help of Lemma 4 we will now prove Theorem 1(b)–(d). Indeed, since $(X_n, Y_n)_{n\ge 0}$ is a Markov chain, Lemma 4 implies that $q(x,y) < 1$ if for all $t > 0$,

$$\sup_{n \ge 0} P_{x,y}\left(\frac{Y_n}{X_n} > t,\ X_n > 0\right) > 0. \tag{3.1}$$

CASE 1. $\gamma < \infty$, $\eta^* = \infty$. There is nothing to prove because $\eta^* = \infty$ obviously implies $P_{x,y}(Y_1 > tX_1) > 0$ for all $x, y \in \mathbb{N}$ and $t > 0$ which is stronger than (3.1).

CASE 2. $\gamma < \infty$, $\eta^* < \infty$, $p_0(\nu) > 0$. In this case it is enough to note that, given any $x, y \in \mathbb{N}$, for sufficiently large $n \in \mathbb{N}$ and $t > 0$,

$$P_{x,y}\left(\frac{Y_n}{X_n} \geq t\frac{d_n}{c_n}, X_n > 0\right) \geq P_{x,y}\left(Y_n = y\eta^{*n}, \max_{0 \leq j \leq n} U_j = 0, 0 < X_n \leq tyc_n\right) > 0,$$

that $\eta^{*n} \geq m^n \geq d_n$ and that $d_n/c_n \to \infty$.

CASE 3. $\gamma < \infty$, $\eta^* < \infty$, $p_0(\nu) = 0$, $p_0(\xi) > 0$. Fix $x, y \in \mathbb{N}$ and define for $n \geq 1$:

$$\begin{aligned} \bar{y}_n &= \sup\{k \geq 0: P_{x,y}(Y_n = k, X_n > 0) > 0\}, \\ \underline{x}_n &= \inf\{k \geq 1: P_{x,y}(X_n = k, Y_n = \bar{y}_n) > 0\}, \\ \underline{u}_n &= \inf\{k \geq 0: P_{x,y}(U_n = k, Y_n = \bar{y}_n) > 0\}. \end{aligned} \tag{3.2}$$

It is then easily verified by using (1.1) that under the preceding assumptions $\underline{x}_n = \xi_*$, $\underline{u}_n = \nu_*\xi_*$ and

$$\bar{y}_n = \left(\eta^{*n}y - \frac{\eta^{*n} - 1}{\eta^* - 1}\xi_*\nu_*\right)^+ = \eta^{*n}\left(y - \frac{\nu_*\xi_*}{\eta^* - 1}(1 - \eta^{*-n})\right)^+ \tag{3.3}$$

for all $n \geq 1$.

If $y > \nu_*\xi_*/(\eta^* - 1)$, then $\bar{y}_n/\underline{x}_n \uparrow \infty$ as $n \to \infty$, so that (3.1) and thus $q(x, y) < 1$ follows.

If $y < \nu_*\xi_*/(\eta^* - 1)$, then $\bar{y}_n = 0$ for sufficiently large n, implying $Y_n = 0$ on $\{X_n > 0\}$ for sufficiently large n, that is, $q(x, y) = 1$.

Finally, if $y = \nu_*\xi_*/(\eta^* - 1)$, then (3.3) shows that $\bar{y}_n = y$ for all $n \geq 1$. But together with $U_k \to \infty$ $P_{x,y}$-a.s. on $\{X_k \to \infty\}$, this implies $Y_n \leq (y - U_n)^+ = 0$ on this event for sufficiently large n, that is, again $q(x, y) = 1$.

CASE 4. $\gamma < \infty$, $\eta^* < \infty$, $p_0(\nu) = p_0(\xi) = 0$. Note first that $p_0(\xi) = 0$ implies $P_{x,y}(X_n \to \infty) = 1$ for all $x, y \in \mathbb{N}$. If x, y are now again fixed, we obtain here for $\bar{y}_n$, $\underline{x}_n$ and $\underline{u}_n$ in (3.2),

$$\begin{aligned} &\underline{x}_n = x\xi_*^n, \qquad \underline{u}_n = x\nu_*\xi_*^n \quad \text{and} \\ &\bar{y}_n = \eta^{*n}\left(y - \frac{x\nu_*\xi_*}{\eta^* - \xi_*}\left(1 - \left(\frac{\xi_*}{\eta^*}\right)^n\right)\right)^+ \end{aligned} \tag{3.4}$$

for all $n \geq 1$. Similar arguments as in the previous case show $q(x, y) < 1$, respectively, $q(x, y) = 1$ according to whether $y > x\nu_*\xi_*/(\eta^* - \xi_*)$ or $y < x\nu_*\xi_*/(\eta^* - \xi_*)$.

If $y = x\nu_*\xi_*/(\eta^* - \xi_*)$, then (3.4) implies $\bar{y}_n = x\nu_*\xi_*^{n+1} = \underline{x}_n\nu_*\xi_*/(\eta^* - \xi_*)$ for all $n \geq 1$. Furthermore we infer from the definition of η^*, ξ_* and ν_* that

$$\left\{Y_n = \frac{X_n\nu_*\xi_*}{\eta^* - \xi_*}\right\} = \{Y_j = \bar{y}_j,\ X_j = \underline{x}_j,\ U_j = \underline{u}_j \text{ for all } 1 \leq j \leq n\}$$

$$=_{\text{def}} D_n \qquad P_{x,y}\text{-a.s.}$$

for all $n \geq 1$, whereas $Y_n < X_n\nu_*\xi_*/(\eta^* - \xi_*)$ on D_n^c $P_{x,y}$-a.s. Now put

$$T = \inf\{n \geq 1: \mathbf{1}(D_n) = 0\}.$$

If $\mathrm{Var}(\xi + \eta + \nu) = 0$, that is, in the purely deterministic case, we clearly have $T = \infty$ and thus $q(x,y) = 0$. But if the latter variance is positive, then $T < \infty$ $P_{x,y}$-a.s. which together with the strong Markov property and $Y_T < X_T\nu_*\xi_*/(\eta^* - \xi_*)$ implies

$$r(x,y) = E_{x,y}r(X_T, Y_T) = 0, \quad \text{thus } q(x,y) = 1.$$

The proof of Theorem 1 is herewith complete. □

4. Proof of Theorem 2. In the following we fix any $x, y \in \mathbb{N}$, suppose $\gamma < \infty$, $q(x,y) < 1$ and define $A = \{Y_n \nrightarrow 0,\ X_n \to \infty\} = \{Y_n \nrightarrow 0,\ U_n \to \infty\}$. We infer immediately from the definition of Y_n that $\sum_{j=1}^{Y_{n-1}}\eta_{n,j} > U_n \to \infty$ and thus $Y_n \to \infty$ $P_{x,y}$-a.s. on A, that is, $A = \{Y_n \to \infty,\ X_n \to \infty\}$. Since Lemma 3 already implies $P_{x,y}$-a.s. convergence of Y_n/d_n to some random variable Y, namely $Y = (Z - Z^*)^+$, it remains to prove for Theorem 2 that $P_{x,y}(Y = 0 | X_n \to \infty) = q(x,y)$, or equivalently that $P_{x,y}(Y > 0,\ X_n \to \infty) = r(x,y)$.

The idea to prove the latter assertion can be intuitively described as follows: Given $Y_n \to \infty$, we show the existence of a (random) time point τ such that the prey generation at this time can be reduced by one individual and still originates a prey process which does not become extinct. Moreover, the separated individual originates an ordinary GWP which will not die out. One may think of this individual as being brought to a district where inhabitants are no longer exposed to predators. If we look at the branching tree of the whole prey population, this means that on the set of nonextinction we may extract a full subtree of an ordinary GWP with one ancestor. The theory of ordinary GWP, more precisely the Heyde–Seneta theorem, ensures that the subpulation size divided by d_n has a positive limit on its set of nonextinction, whence this must also hold for the total population size divided by d_n.

In order to make the previous argument rigorous we give a number of lemmas.

Lemma 5. *For all $x, y \in \mathbb{N}$, $\lim_{n\to\infty} r(X_n, Y_n) = \mathbf{1}(A)$ $P_{x,y}$-a.s.*

Proof. Note that $(r(X_n, Y_n))_{n\geq 0}$ is a nonnegative, bounded martingale w.r.t. each $P_{x,y}$ and thus converges a.s. to a limit r, say. Clearly, $r = 0$ on A^c

so that

$$P_{x,y}(A) = r(x,y) = \lim_{n\to\infty} E_{x,y} r(X_n, Y_n) = \int_A r\, dP_{x,y}$$

forces r to be a.s. 1 on A. □

LEMMA 6. *If* $\operatorname{Var}(\xi + \eta + \nu) > 0$, *then* $\liminf_{n\to\infty} r(X_n, Y_n - 1) \geq 1/2$ $P_{x,y}$-*a.s. on* A *for all* $x, y \in \mathbb{N}$.

PROOF. Without loss of generality fix $x, y \in \mathbb{N}$ such that $r(x,y) > 0$. Suppose $\operatorname{Var}\eta > 0$. In the following we use a simple coupling-type argument. Let $(\tilde{\eta}_{1,j})_{j\geq 1}$ be a sequence of random variables with the following properties:

(a) $(\eta_{1,j}, \tilde{\eta}_{1,j})$, $j \geq 1$ are i.i.d. and independent of $(\eta_{n+1,j}, \xi_{n,j}, \nu_{n,j})_{j,n\geq 1}$;
(b) $\eta_{1,j}$ and $\tilde{\eta}_{1,j}$ have the same distribution;
(c) $\eta_{1,j} - \tilde{\eta}_{1,j}$ is symmetric with positive, finite variance.

The existence of such a sequence is easily verified, possibly after an enlargement of the underlying probability space $(\Omega, \mathscr{A}, P_{x,y})$. Now define

$$\tilde{Y}_0 = y - 1, \qquad \tilde{Y}_1 = \sum_{j=1}^{y-1} \tilde{\eta}_{1,j} - U_1 \quad \text{and} \quad \tilde{Y}_n = \sum_{j=1}^{\tilde{Y}_{n-1}} \eta_{n,j} - U_n \quad \text{for } n \geq 2.$$

Obviously, $P_{x,y}((X_n, \tilde{Y}_n)_{n\geq 0} \in \cdot) = P_{x,y-1}((X_n, Y_n) \in \cdot)$. Moreover, $\tilde{Y}_n \geq Y_n$ for all $n \geq 1$ if this is true for $n = 1$. The central limit theorem implies

$$\lim_{y\to\infty} P_{x,y}\big(\tilde{Y}_1 \geq Y_1\big) = \lim_{y\to\infty} P_{\cdot,y}\left(\frac{1}{(y-1)^{1/2}} \sum_{j=1}^{y-1} \big(\tilde{\eta}_{1,j} - \eta_{1,j}\big) \geq \frac{\eta_{1,y}}{(y-1)^{1/2}}\right)$$
$$= \frac{1}{2}.$$

Consequently, for $x_k, y_k \to \infty$ such that $\lim_{k\to\infty} r(x_k, y_k) = 1$ we conclude

$$\begin{aligned}\liminf_{k\to\infty} r(x_k, y_k - 1) &\geq \liminf_{k\to\infty} \lim_{n\to\infty} \int_{\{\tilde{Y}_1 \geq Y_1 > 0\}} r(X_n, Y_n)\, dP_{x_k,y_k} \\ &= \lim_{k\to\infty} P_{x_k,y_k}\big(\{\tilde{Y}_1 \geq Y_1\} \cap A\big) \\ &= \lim_{k\to\infty} \big(r(x_k, y_k) - P_{\cdot,y_k}(\tilde{Y}_1 \geq Y_1)\big) = \frac{1}{2},\end{aligned}$$

which together with Lemma 5 yields the assertion.

If $\operatorname{Var}\eta = 0$ but $\operatorname{Var}\xi > 0$ or $\operatorname{Var}\nu > 0$, then use a similar construction with the $\xi_{1,j}$'s or $\nu_{1,j}$'s replaced by appropriate copies in the definition of $\tilde{Y}_1$, respectively. The details can be omitted. □

We are now ready for the intrinsic step towards the proof of Theorem 2, which is basically a geometric trial argument. We fix any $x, y \in \mathbb{N}$ such that

$r(x,y) > 0$. Define

$$\tau_1 = \inf\{n \geq 0: r(X_n, Y_n - 1) > \tfrac{1}{4}\}$$

which is a.s. finite on A (w.r.t. $P_{x,y}$). Using the definition of Y_n^* we have the decomposition

$$Y^*_{\tau_1+n} = \mathscr{Y}_n^*(\tau_1) + \mathscr{Z}_n(\tau_1), \qquad n \geq 0,$$

where, w.r.t. $P_{x,y}(\cdot\,|X_{\tau_1} = x_1, Y_{\tau_1} = y_1)$, $(\mathscr{Y}_n(\tau_1), X_{\tau_1+n})_{n\geq 0}$ has the same distribution as $(X_n, Y_n)_{n\geq 1}$ under P_{x_1, y_1-1}, and $(\mathscr{Z}_n(\tau_1))_{n\geq 0}$ is an ordinary GWP with one ancestor, the same distribution as $(Z_n)_{n\geq 0}$ under $P_{\cdot,1}$ and independent of the previous process. Let

$$T_1 = \inf\{n > \tau_1: \mathscr{Y}_n^*(\tau_1) \leq 0 \text{ or } \mathscr{Z}_n(\tau_1) = 0\},$$

with the usual convention $\inf\varnothing = \infty$.

For $k \geq 2$, we now define recursively

$$\tau_k = \inf\{n \geq T_{k-1}: r(X_n, Y_n - 1) > \tfrac{1}{4}\},$$

decompose $Y^*_{\tau_k+n}$ into $\mathscr{Y}_n^*(\tau_k)$ and $\mathscr{Z}_n(\tau_k)$ in the obvious manner and put

$$T_k = \inf\{n > \tau_k: \mathscr{Y}_n^*(\tau_k) \leq 0 \text{ or } \mathscr{Z}_n(\tau_k) = 0\}.$$

Note that $\tau_k < \infty$ $P_{x,y}$-a.s. on $A \cap \{T_{k-1} < \infty\}$ by Lemma 6. Recall further for the next lemma that $q_{(\eta)} = P_{\cdot,1}(Z_n \to 0)$ is strictly less than 1 because $(Z_n)_{n\geq 0}$ is supercritical.

LEMMA 7. *The first occurrence time* $\sigma = \inf\{k \geq 1: T_k = \infty\}$ *is* $P_{x,y}$-*a.s. finite.*

PROOF. We will prove $P_{x,y}(T_k < \infty) = P_{x,y}(\sigma > k) \to 0$ as $k \to \infty$. It follows by using the strong Markov property that

$$\begin{aligned}
P_{x,y}(T_k < \infty) &= \int_{\{\tau_k<\infty\}} P_{X_{\tau_k}, Y_{\tau_k}}(T_1 < \infty)\, dP_{x,y}\\
&= \int_{\{\tau_k<\infty\}} \Big(1 - P_{X_{\tau_k}, Y_{\tau_k}}\big(\mathscr{Y}_n^*(\tau_1) \to \infty, \mathscr{Z}_n(\tau_1) \to \infty\big)\Big)\, dP_{x,y}\\
&= \int_{\{\tau_k<\infty\}} \big(1 - r(X_{\tau_k}, Y_{\tau_k})(1 - q_{(\eta)})\big)\, dP_{x,y}\\
&\leq \left(1 - \frac{1 - q_{(\eta)}}{4}\right) P_{x,y}(T_{k-1} < \infty)
\end{aligned}$$

and hence upon induction,

$$P_{x,y}(T_k < \infty) \leq \left(1 - \frac{1-q_{(\eta)}}{4}\right)^k \to 0 \quad \text{as } k \to \infty. \qquad \square$$

PROOF OF THEOREM 2. Let $x, y \in \mathbb{N}$ such that $r(x,y) > 0$, that is, $q(x,y) < 1$. On A we obviously have $\tau_\sigma < \infty$, $T_\sigma = \infty$. Denote by $\mathscr{Y}(k)$ the $P_{x,y}$-a.s. limit of $\mathscr{Y}_n(\tau_k)/d_n$ and observe that $\mathscr{Y}(\sigma) > 0$ $P_{x,y}$-a.s. on A by construction. Consequently, the desired result follows from

$$\lim_{n\to\infty} \frac{Y_n}{d_n} \geq \lim_{n\to\infty} \frac{\mathscr{Y}_{n-\sigma}(\tau_\sigma)}{d_n} = m^{-\sigma}\mathscr{Y}(\sigma) > 0 \qquad P_{x,y}\text{-a.s. on } A.$$

If $\mathrm{Var}(\xi + \eta + \nu) > 0$, then Theorem 2 ensures that Y_n essentially behaves the same as the associated GWP Z_n where no predators occur: It either dies out or it explodes at the same order of magnitude d_n as Z_n. In the deterministic case, that is, when $\mathrm{Var}(\xi + \eta + \nu) = 0$, the situation is equal unless $m > \mu$ and $Y_0 = \alpha\mu X_0/(m - \mu)$. Whereas $q(X_0, Y_0) = 1$ in the nondeterministic case, $q(X_0, Y_0)$ equals 0 here and one can easily verify that Y_n grows like μ^n instead of m^n, a situation which never occurs otherwise. □

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