

# On a species survival model

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## Abstract

In this paper we provide some sharp asymptotic results for a stochastic model of species survival recently proposed by Guiol, Machado, and Schinazi.

## 1 Introduction and statement of results

Recently, Guiol, Machado, and Schinazi [7] proposed a new mathematical framework for modeling species survival which is closely related to the discrete Bak-Sneppen evolution model. In the original Bak-Sneppen model [3] a finite number of species are arranged in a circle, each species being characterized by its location and a parameter representing the *fitness* of the species, taking values between zero and one. The number of species and the sites occupied by them on the circle remain fixed throughout the evolution of the system. At discrete times  $n = 0, 1, \dots$ , the species with the lowest fitness and its two immediate neighbors, one from the left and one from the right, update their fitnesses simultaneously at random. An alternative interpretation is that the three species are eliminated and then replaced by new species with new independent random fitnesses. The Bak-Sneppen evolution model is often referred to as an “ecosystem” because of the local interaction between different species. The distinguishing feature of the model, shown through numerical simulations, is the emergence of self-organized criticality [1, 2, 6, 8] from these simple dynamics, as well as robustness of this under perturbations of the system. The Bak-Sneppen model has attracted significant attention over the past few decades, but it has also been proven to be difficult for analytical study. See for instance [6] for a relatively recent survey of the model.

The asymptotic behavior of the Bak-Sneppen model, as the number of species gets arbitrarily large, was conjectured on the basis of computer simulations in [3]. It appears that the distribution of the fitness is asymptotically uniform on an interval  $(f_c, 1)$  for some critical parameter  $f_c$ , the value of which is close to  $2/3$  [1, 8].

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Guiol, Machado, and Schinazi [7] were able to prove a similar result for a closely related model with a stochastically growing number of species. Their analysis is based on a reduction to the study of a certain random walk, which allows them to build a proof using well-known results from the theory of random walks. The main result of [7] is thus based on general properties of Markov chains, and suitable variations of the result can in principle be carried out to other similar models.

In this paper we focus on the model introduced in [7] as is. Our aim is to elucidate the underlying mechanism responsible for the phenomenon described in [7] by refining the estimates that lead to the major qualitative statement therein. We proceed with a description of the Guiol, Machado, and Schinazi (GMS) model.

In contrast to the Bak-Sneppen model, the number of species in the GMS model is random and changes in time, and only the species with the lowest fitness is randomly replaced. The local interaction between species is not considered in the GMS model, and therefore the spatial structure of the population is of no importance. Let  $p > \frac{1}{2}$  be given and denote  $q = 1 - p$ . Let  $\mathbb{Z}_+$  denote the set of non-negative integers and let  $X = (X_n : n \in \mathbb{Z}_+)$  be a discrete-time birth and death process with the following transition probabilities: from each site,  $X_n$  increases by 1 with probability  $p$ ; from each site different than 0,  $X_n$  decreases by 1 with probability  $q = (1 - p)$ ; finally, at 0,  $X_n$  stays put with probability  $q$ . Thus  $X$  is a nearest-neighbor transient random walk on the integer lattice  $\mathbb{Z}_+$  with holding times and reflection barrier at zero. For convenience, throughout the paper we assume that  $X_0 = 0$  with probability one.

The model describes the evolution of a population of species. The population size or the number of species *alive* at time  $n$  is given by  $X_n$ . At each birth, that is a jump to the right of  $X$ , the newborn species is given “equal opportunity” by assigning is a random *fitness*, sampled from the uniform distribution on  $[0, 1]$ , independently of the past. At each death, that is a jump to the left of  $X$ , the least fit species is eliminated. We comment that a similar model in a different context was considered by Liggett and Schinazi in [9].

Fix  $f \in (0, 1)$ . We examine the model by considering two coupled random processes,  $L = (L_n : n \in \mathbb{Z}_+)$  (for *lower or left*) and  $R = (R_n : n \in \mathbb{Z}_+)$  (respectively, for *right*), where  $L_n$  denotes the number of species alive at time  $n$  whose fitness is less than  $f$  while  $R_n$  denotes the number of the remaining species alive at time  $n$ ,  $R_n = X_n - L_n$ .

We observe that  $L$  is itself a birth and death process, with the following transition probabilities. At each site it jumps one step to the right if  $X$  does and if the newborn species has fitness  $< f$ . This occurs with probability  $pf$ . At each site different than 0,  $L$  jumps one step to the left if  $X$  does, and this occurs with probability  $q$ . Therefore from any site different than 0,  $L$  stays put with probability  $1 - pf - q$ , while from 0,  $L$  stays put with probability  $1 - pf$ . Since  $p > q$ , it is positive recurrent if  $pf < q$ , null-recurrent if  $pf = q$ , and is otherwise transient. In what follows we will denote the critical value  $q/p$  of the parameter  $f$  by  $f_c$ .

Next consider the process  $B = (B_n : n \in \mathbb{Z}_+)$ , where  $B_n$  is the total number of species born by time  $n$  with fitness at least  $f$ . Observe that  $B_n$  is the partial sum of the first  $n$  random variables in an sequence of IID Bernoulli random variables with mean  $p(1 - f)$ . Finally we define the process  $\Delta = (\Delta_n : n \in \mathbb{Z}_+)$ , where  $\Delta_n$  is the number of species with fitness  $\geq f$  eliminated up to time  $n$ . That is,  $\Delta_n = B_n - R_n$ .

The key result of [7] is the following. Let  $f = f_c = \frac{q}{p}$ . Then for any  $\varepsilon > 0$

$$\lim_{n \rightarrow \infty} \frac{\Delta_n}{n^{1/2+\varepsilon}} = 0 \text{ a.s.} \quad (1)$$

Since by the law of large numbers  $\lim_{n \rightarrow \infty} B_n/n = p(1 - f_c)$ , a.s., it follows from (1) that  $\lim_{n \rightarrow \infty} \Delta_n/B_n = 0$  a.s. That is, the proportion of species eliminated from those born with fitness  $\geq f_c$  is asymptotically vanishing. On the other hand, as mentioned above, with the same choice of  $f = f_c$ , the process  $L$  representing the number of species alive with fitness  $< f_c$ , is recurrent. In particular, since  $X$  is transient, it follows that the proportion of species with fitness  $< f_c$  is asymptotically vanishing as well. From these two observations and the fact that the distribution of newborn species is uniform on  $[0, 1]$ , it follows that the empirical distribution of the fitnesses converges to a uniform law on  $[f_c, 1]$  as  $n \rightarrow \infty$ .

We sharpen (1) by proving the following limit theorem.

**Theorem 1.** *Suppose that  $f = f_c = \frac{q}{p}$ . Then*

1.  $\limsup_{n \rightarrow \infty} \frac{\Delta_n}{\sqrt{4qn \ln \ln n}} = 1$ , a.s.
2.  $\frac{\Delta_n}{\sqrt{2qn}} \Rightarrow |N(0, 1)|$ , where  $N(0, 1)$  denotes a mean-zero Gaussian random variable with variance one, and  $\Rightarrow$  stands for convergence in distribution.

## 2 Proof of Theorem 1

We begin with a formal definition of the processes involved in our analysis, constructed from sequences of IID Bernoulli random variables. We construct  $X$  in terms of an IID sequence of Bernoulli random variables with mean  $q$ ,  $J = (J_n : n \in \mathbb{Z}_+)$ , where the event  $\{J_n = 0\}$  represents one birth at time  $n$ , and  $\{J_n = 1\}$  represents an attempt to eliminate one species at time  $n$ , an attempt which succeeds if and only if the population size is strictly positive. That is, letting  $s_n = \mathbf{1}_{\{0\}}(X_n)$  we obtain:

$$\begin{aligned} X_0 &= 0; \\ X_{n+1} &= X_n + (1 - J_n) - J_n(1 - s_n) \end{aligned}$$

We now incorporate the fitness into the system in a similar fashion. Let  $F = (F_n : n \in \mathbb{Z}_+)$  be an IID sequence of Bernoulli random variables with mean  $f_c$ . The random variable  $F_n$  is the indicator of the event that a species born at time  $n$  has fitness  $< f_c$ . This allows us to define  $B_n, L_n$  and  $R_n$  inductively as follows:

$$\begin{aligned} B_0 &= 0; B_{n+1} = B_n + (1 - J_n)(1 - F_n) \\ L_0 &= 0; L_{n+1} = (1 - J_n)F_n - J_n(1 - \mathbf{1}_{\{0\}}(L_n)) \\ R_n &= X_n - L_n \end{aligned}$$

Finally we define a Markov chain  $G = (G_n : n \in \mathbb{Z}_+)$  on  $\mathbb{Z}_+ \times \{0, 1\}$  by letting  $G_n = (L_n, J_n)$ . That is, the first component of  $G_n$ ,  $L_n$ , represents the number of

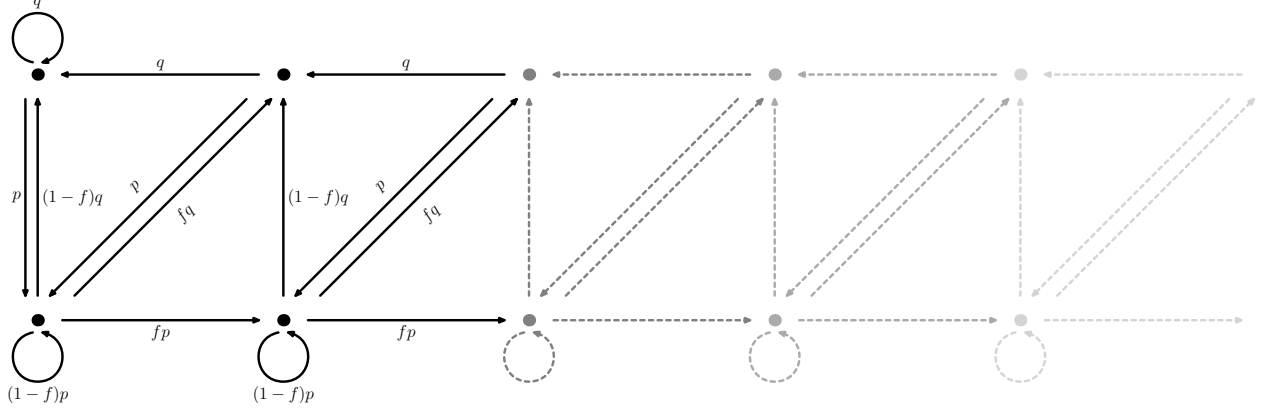


Figure 1: Transition probabilities for  $G$

species with fitness  $< f_c$  alive at time  $n$ , and the second component of  $G_n$  indicates whether at time  $n$  an attempt to eliminate or a birth occurs at time  $n$ . Figure 1 illustrates the transition mechanism of  $G$ .

## 2.1 Reduction from $\Delta$ to Number of Excursions of $G$

Observe that at each time  $n$ ,  $\Delta$  either stays put or increases by 1. The latter occurs if and only if  $X$  decreases by 1 by eliminating a species with fitness  $\geq f_c$ , which can occur only if  $L$  is equal to 0. This gives:

$$\Delta_{n+1} - \Delta_n = J_n(1 - s_n)\mathbf{1}_{\{0\}}(L_n).$$

Let  $\eta = (\eta_n : n \in \mathbb{Z}_+)$  denote the occupation time of  $G$  at state  $(0,1)$ ,  $\eta_n = \sum_{i=0}^n J_i \mathbf{1}_{\{0\}}(L_i)$ . Since  $\Delta_0 = 0$ , we have that

$$\Delta_n = \eta_{n-1} - \underbrace{\sum_{i=0}^{n-1} J_i s_i \mathbf{1}_{\{0\}}(L_i)}_{(*)}.$$

Now

$$(*) \leq \sum_{i=0}^{\infty} s_i < \infty \text{ a.s.},$$

because  $X$  is transient. Therefore it suffices to prove that Theorem 1 holds with  $\Delta_n$  replaced by  $\eta_n$  in its statement.

**Excursion decomposition for the path of  $L$ .** We decompose the path of  $L$  to *excursions* away from 0. Each excursion begins at 0 and ends at the last time before the next return to 0 from 1. Formally, let  $V_0 = -1$  and define inductively

$$V_{k+1} = \inf\{n > V_k : L_n = 1, L_{n+1} = 0\}.$$

The first excursion is the path restricted to the time interval  $\{0, \dots, V_1\}$ , the second excursion is the path restricted to  $\{V_1+1, V_1+2, \dots, V_2\}$ , and in general the  $k$ -th excursion begins at time  $V_{k-1}+1$  and ends at time  $V_k$ . Note that an excursion begins with some holding time at 0, then jumps to one, never returning again to 0 and eventually ending at 1. From the definition of  $L$ , the holding time at 0 during the  $k$ -th excursion, which we denote by  $h_k$ , is geometric with parameter  $E((1 - J_0)F_0) = pf_c = q$ . The sequence  $(h_k : k \in \mathbb{N})$  is an IID sequence. Let  $\mu_k$  denote the occupation time of  $G$  at  $(0, 1)$  during the  $k$ -excursion of  $L$ . That is:

$$\mu_k = \eta_{V_k} - \eta_{V_{k-1}} = \sum_{i=V_{k-1}+1}^{V_k} J_i \mathbf{1}_{\{0\}}(L_i) = \sum_{i=V_{k-1}+1}^{V_{k-1}+1+h_k} J_i.$$

Then  $(\mu_k : k \in \mathbb{N})$  is again an IID sequence. For  $n \in \mathbb{Z}_+$ , let  $N_n = \sup\{k \in \mathbb{Z}_+ : V_k \leq n\}$ , where here we define  $\sup \emptyset = 0$ . Then clearly

$$\sum_{1 \leq k \leq N_n} \mu_k \leq \eta_n < \sum_{1 \leq k \leq N_{n+1}} \mu_k. \quad (2)$$

We now compute  $\mu = E(\mu_k)$ . Note that  $E(\mu_k) \leq E(h_k) < \infty$ , by embedding the excursions of  $L$  in paths of  $G$ . When embedded in  $G$ , an excursion has initial distribution  $q\delta_{(0,1)} + p\delta_{(0,0)}$ , representing the different possible states for the second coordinate along with the respective probabilities. The excursion lasts until the first exit of  $G$  from  $\{(0, 0), (0, 1)\}$ . Using the transition probabilities of  $G$  given in Figure 1 and first step analysis we have:

$$\begin{aligned} \mu &= P(J_0 = 1)(1 + \mu) + P(J_0 = 0, L_1 = 0)\mu + P(J_0 = 0, L_1 = 1) \cdot 0 \\ &= q(1 + \mu) + p(1 - f_c)\mu + pf_c \cdot 0 = q + \mu(1 - pf_c) = q + \mu p. \end{aligned}$$

Hence,  $\mu = 1$ . Now  $\lim_{n \rightarrow \infty} N_n = \infty$ , because  $N_n$  counts the number of excursions of the recurrent process  $L$  up to time  $n$ . Therefore by (2) and the law of large numbers, we obtain

$$\eta_n \sim N_n \text{ as } n \rightarrow \infty, \quad \text{a.s.} \quad (3)$$

Here and henceforth,  $a_n \sim b_n$  as  $n \rightarrow \infty$  for two sequences of real numbers  $(a_n : n \in \mathbb{N})$  and  $(b_n : n \in \mathbb{N})$  means, as usual,  $\lim_{n \rightarrow \infty} a_n/b_n = 1$ .

**Reduction to a simple random walk.** With each excursion of  $L$  away from zero we can associate a *skeleton*, which is the path obtained from the excursion by omitting all transitions from a state of  $L$  to itself. Let  $\tau_k$  denote the length of the skeleton of the  $k$ -th excursion. From any site different than 0,  $L$  jumps one step to the right with probability  $pf_c = q$  and one step to the left with probability  $q$  and otherwise stays put, which occurs with probability  $1 - 2q$ . In particular, the time spent at each visit to such a site before jumping to one of the neighbors is geometric with parameter  $2q$ . Furthermore, since probabilities of jumping to the right and to the left are the same, it follows that  $\tau_k$  has the same distribution as the time required for simple

symmetric random walk to complete an excursion away from 0. Consistently with our definition of excursion for  $L$ , an excursion for the simple symmetric random walk begins when the walk is at 0 and ends at the last step before the next visit to 0. It follows that the duration of the  $k$ -th excursion of  $L$  is equal to a sum of  $\tau_k$  independent geometric random variables :  $h_k$ , the holding time at 0, plus  $\tau_k - 1$  IID geometric random variables with parameter  $2q$ , each of which representing the time spent (or holding times) at one of the  $\tau_k - 1$  visits to sites other than 0 during the excursion. If we replace  $h_k$  with a  $h'_k$  where  $(h'_k : k \in \mathbb{N})$  is an IID sequence of geometric random variables with parameter  $2q$ , then the resulting modified “excursion time” becomes a sum of  $\tau_k$  IID geometric random variables with parameter  $2q$ . Let  $V'_k$  denote the total length of the first  $k$  excursions modified this way. Then by the law of large numbers,

$$\lim_{k \rightarrow \infty} \frac{V_k - V'_k}{k} = E(h_1) - E(h'_1) = \frac{1}{2q}, \text{ a.s.}, \quad (4)$$

Letting  $T_m = \sum_{k=1}^m \tau_k$ , we obtain

$$V'_m = \sum_{k=1}^{T_m} h''_k,$$

where  $(h''_k : k \in \mathbb{N})$  is an IID sequence geometric random variables with parameter  $2q$ . By the law of large numbers,

$$V'_m \sim \frac{T_m}{2q} \text{ as } m \rightarrow \infty, \text{ a.s.} \quad (5)$$

Notice that  $T_m$  is distributed the same as the total length of the first  $m$  excursions from zero of a simple (nearest neighbor) symmetric random walk.

## 2.2 Completion of the proof.

**LIL for  $\eta_n$ .** We need the following result. Although the claim is a “folk fact”, we give a short proof for the sake of completeness.

**Lemma 1.**

$$\liminf_{m \rightarrow \infty} \frac{T_m}{m^2/(2 \ln \ln m)} = 1, \text{ a.s.}$$

*Proof of Lemma 1.* Let  $S = (S_n : n \in \mathbb{Z}_+)$  denote the simple symmetric random walk on  $\mathbb{Z}$ . That is  $S_0 = 0$  and

$$S_{n+1} = S_n + \zeta_n, \quad n \in \mathbb{Z}_+,$$

where  $(\zeta_n : n \in \mathbb{Z}_+)$  is a sequence of IID random variables, taking values  $\pm 1$  with equal probabilities. Let  $\gamma_0 = 0$  and define inductively  $\gamma_{m+1} = \inf\{k > \gamma_m : S_k = m + 1\}$  for  $m \geq 0$ , with the usual convention that the infimum over an empty set is  $+\infty$ . Let  $\phi(x) = \sqrt{2x \ln \ln x}$  for  $x > 0$ . By the law of the iterated logarithm for  $S$ ,

$$\limsup_{n \rightarrow \infty} \frac{S_n}{\phi(n)} = \limsup_{n \rightarrow \infty} \frac{S_{\gamma_n}}{\phi(\gamma_n)} = \limsup_{n \rightarrow \infty} \frac{n}{\phi(\gamma_n)}, \text{ a.s.}$$

Since  $\phi^{-1}(k) \sim k^2/(2 \ln \ln k)$  as  $k \rightarrow \infty$ , we obtain

$$\liminf_{n \rightarrow \infty} \frac{\gamma_n}{n^2/(2 \ln \ln n)} = 1, \text{ a.s.} \quad (6)$$

Of course,  $\gamma_k$  is the hitting time of  $S$  at  $k$ , that is the first time  $S$  is at  $k$ . From that time  $S$  begins a sequence of excursions away from  $k$ , defined similarly to excursions away from 0 above, but the holding time at each site is always 1, as  $S$  stays at a site exactly one unit of time per visit. This sequence of excursions ends at when  $S$  hits  $k+1$  for the first time, that is at the first step of an excursion which moves to the right on the first step. This, of course, occurs at time  $\gamma_{k+1}$ . All excursions in the sequence, but the last one (if any) begin with a step to the left, that is from  $k$  to  $k-1$ . As a result, the number of excursions, including the last, is a geometric random variable with parameter  $\frac{1}{2}$ , which we denote by  $\sigma_k$ . Thus,

$$\gamma_{k+1} - \gamma_k = 1 + \sum_{1 \leq l \leq \sigma_k - 1} (\tau'_l + 1) = \sigma_k + \sum_{1 \leq l \leq \sigma_k - 1} \tau'_l,$$

where  $(\tau'_l : l \in \mathbb{N})$  is a copy of the IID sequence  $(\tau_n : n \in \mathbb{N})$  defined above. The constant 1 after the first equality sign represents the single step in the last excursion, the summation is over the remaining first  $\sigma_k - 1$  excursions, and we add 1 to the duration of each excursion to include the “missing last step” from  $k-1$  back to  $k$ . Letting  $\Sigma_k = \sum_{1 \leq l \leq k} \sigma_l$ , it follows that  $\gamma_k$  is equal in distribution to  $\Sigma_k + \sum_{1 \leq l \leq \Sigma_k - k} \tau'_l$ . This is equal in distribution to  $\Sigma_k + T_{\Sigma_k - k}$ . However, by the law of large numbers  $\lim_{k \rightarrow \infty} \Sigma_k/k = E(\sigma_1) = 2$ , a.s. In particular,  $\Sigma_k - k \sim k$ , a.s., as  $k \rightarrow \infty$ . Applying the law of large numbers again, we obtain

$$\lim_{k \rightarrow \infty} \frac{T_{\Sigma_k - k}}{k} = E(\tau_1), \text{ a.s.}$$

Since also  $\lim_{k \rightarrow \infty} \frac{T_k}{k} = E(\tau_1)$ , a.s., it follows that  $T_{\Sigma_k - k} \sim T_k$ , a.s., as  $k \rightarrow \infty$ . As a result, we have

$$\liminf_{k \rightarrow \infty} \frac{T_k}{k^2/(2 \ln \ln k)} = \liminf_{k \rightarrow \infty} \frac{\Sigma_k + T_{\Sigma_k - k}}{k^2/(2 \ln \ln k)} = \liminf_{k \rightarrow \infty} \frac{\gamma_k}{k^2/(2 \ln \ln k)} = 1, \text{ a.s.}$$

This completes the proof. □

Using the lemma along with (4) and (5), we obtain

$$\liminf_{m \rightarrow \infty} \frac{2qV_m}{m^2/(2 \ln \ln m)} = \liminf_{m \rightarrow \infty} \frac{2qV'_m}{m^2/(2 \ln \ln m)} = 1, \text{ a.s.}$$

Consequently, since  $N$  is the inverse sequence of  $V$  (that is,  $V_{N_k} \leq k < V_{N_{k+1}}$ ), one can deduce from it (in the same way as (6) is derived from the usual LIL) that

$$\limsup_{k \rightarrow \infty} \frac{N_k}{\sqrt{4qk \ln \ln k}} = 1, \text{ a.s.}$$

Combining this with (3) completes the proof of the law of iterated logarithm for  $\eta_n$ .

**CLT for  $\eta_n$ .** The proof relies on a well-known limit theorem for a (properly normalized) random sequence  $T_m$ . Note that the time of the  $m$ -th return of  $S$  to 0 is equal to  $T_m + m$ , for which we have (see for instance [5, p. 394]):

$$\lim_{m \rightarrow \infty} E(e^{-\theta(T_m+m)/m^2}) = e^{-\sqrt{2\theta}}, \quad \theta \geq 0.$$

(see for instance [5, p. 394]). Thus,  $\lim_{m \rightarrow \infty} E(e^{-\theta T_m/m^2}) = e^{-\sqrt{2\theta}}$ . It follows from (4) and (5) that

$$\lim_{m \rightarrow \infty} E(e^{-\theta V_m/m^2}) = \lim_{m \rightarrow \infty} E(e^{-\theta V'_m/m^2}) = e^{-\sqrt{\theta/q}}.$$

The function  $\Phi_c(\theta) = e^{-c\sqrt{2\theta}}$ ,  $\theta \geq 0$ , with  $c > 0$ , is the Laplace transform of a positive stable law with index  $1/2$  whose density function is given by (see for instance [5, p. 395])

$$\varphi_c(u) = \mathbf{1}_{\{u \geq 0\}} \frac{ce^{-c^2/2u}}{\sqrt{2\pi u^3}}.$$

We will use this formula with the parameter  $c$  equal to  $c_* := \frac{1}{\sqrt{2q}}$ . Observe that for all  $k \in \mathbb{N}$  and  $u > 0$ ,

$$P(N_k \leq u) = P_0(V_{\lfloor u \rfloor + 1} > k),$$

where  $\lfloor u \rfloor$  stands for the integer part of  $u$ , that is  $\lfloor u \rfloor = \max\{n \in \mathbb{Z}_+ : n \leq u\}$ . Fix  $s > 0$  and let  $u = \sqrt{ks}$ . Then, using the standard notation  $o(1)$  to denote a sequence converging to zero when the underlying index  $k$  goes to infinity,

$$\begin{aligned} P(N_k \leq \sqrt{ks}) &= P(V_{\lfloor \sqrt{ks} \rfloor + 1} > k) \\ &= P\left(\frac{V_{\lfloor \sqrt{ks} \rfloor + 1}}{(\lfloor \sqrt{ks} \rfloor + 1)^2} > \frac{1}{s^2}(1 + o(1))\right) \xrightarrow[k \rightarrow \infty]{} \int_{s^{-2}}^{\infty} \varphi_{c_*}(u) du. \end{aligned}$$

Changing variables from  $u$  to  $t = 1/\sqrt{u}$  in the last integral, we obtain

$$\lim_{k \rightarrow \infty} P(N_k \leq \sqrt{ks}) = \int_0^s \frac{2e^{-t^2/(2c_*^{-2})}}{\sqrt{2\pi c_*^{-2}}} dt.$$

Therefore, as  $k \rightarrow \infty$ , the random sequence  $N_k/\sqrt{k}$  converges weakly to the absolute value of a centered normal random variable with variance equal to  $c_*^{-2} = 2q$ . Combining this with (3) completes the proof of the central limit theorem for  $\eta_n$ .  $\square$

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