Simple rules for ranking and optimally managing metapopulations

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We present two ‘rules of thumb’ for metapopulation management. The first identifies an explicit formula for the persistence time of the population, and thus enables the population manager to form a priority species ranking by identifying those species most at risk of extinction. The second identifies an optimal management strategy that gives direction on how to alter the colonisation rate (creation or improvement of habitat corridors) and local extinction rate (restoring habitat quality or expanding habitat) in order to maximise the persistence time under a budgetary constraint. We employ a simple stochastic version of Levins (1969) metapopulation model, which is first calibrated to a more realistic spatial model. Our rules are tested on computer-generated patch networks and a model for malleefowl (Leipoa ocellata) in the Bakara region of South Australia.

1. Introduction

The metapopulation paradigm has proved to be useful for studying species dynamics; many species exist naturally in a network of geographically separated patches, and many others have suffered modification of habitat, generally due to anthropogenic disturbance, resulting in their occupying a mosaic of patches (Levins, 1969; Gilpin and Hanski, 1991; Hanski, 1999; Dobson, 2003). Such habitat fragmentation, in combination with other factors such as climate change, is placing species at high risk of extinction. Ecologists and conservation biologists must attempt to limit this risk. With less funding than is required to protect all species, they must rank extinction risk in order to determine priority in allocating funding (Hobbs and Kristjanson, 2003), and determine the optimal way to invest available funding to minimise extinction threat.

This paper provides ‘rules of thumb’ for ranking metapopulation extinction risk, allowing a rapid evaluation of species priority rankings, and for determining optimal management strategies under constrained conservation funding. Their best feature is simplicity: the formulae can be evaluated quickly, yet they are sufficiently accurate to be of benefit to the conservation community.

We commence by determining ‘rules of thumb’ for ranking metapopulation extinction risk, and for determining the optimal management strategy, based upon a stochastic version of the classical metapopulation model Levins (1969). We then subsequently determine an explicit procedure for calibrating this simple model to a more realistic spatial metapopulation model, and investigate the accuracy by testing our rules on computer-generated patch networks for a spatially realistic metapopulation model, and data for an Australian species of concern to conservationists.

2. Rules of thumb

We will use a stochastic formulation of the classical Verhulst (2009) model for population growth, which first appeared in the metapopulation context in the much-cited paper of Levins (1969). There are N patches, which are always suitable for occupancy. Propagules (individuals) emanate from each occupied patch (and survive to reach another patch) at rate c (commonly called the colonisation rate) and each occupied patch becomes vacant (through extinction and migration) at rate e (commonly called the local extinction rate). If n(t) denotes the number of occupied patches at time t, then n(t) = c(n/N)(N − n) − en. Our stochastic formulation is a continuous-time Markov chain whose transition rates are given in Table 1. The spatially realistic model we use as our gold-standard (for the purposes of this paper) models individual patch positions, affecting migration rate between patches, and patch areas, affecting the local extinction rate; the precise transition rates are given in Table 2.

In our spatially realistic model the state is n = (n1, n2, . . . , nN), where the ith entry equals 1 if patch i is occupied, and 0 otherwise, 1, is used to denote a vector with a 1 in the ith entry and 0 s elsewhere, g is the base migration rate, β is the exponential dispersion parameter, d ij is the distance between patches i and j, x is the
is expected time to extinction starting from our simple model. It is a frequently used measure of persistence, which we now evaluate. The expected time to extinction is a wide variety of species to be compared, then either of the approximation (A1) or (A2) provides a criterion upon which to determine if more precise evaluation using (R1) (and subsequently, perhaps via simulation of a spatially realistic model) is required. We emphasise the simplicity of our rule—the formulae may be evaluated rapidly for a host of species.

Whilst (R1) provides rapid species priority ranking, it tells us nothing about optimal strategies for those species most at risk. This is addressed by our second rule of thumb (R2).

Optimal management strategy (R2). The management options available are to increase the colonisation rate $c$, say via creation or improvement of habitat corridors, or decrease the extinction rate $e$, say by restoring habitat or expanding patches (Etienne and Heesterbeek, 2001). The budgetary constraint can be expressed in terms of $e$, numbers of patches $N$, and initial numbers of occupied patches $n(0) = i$, aids species priority ranking.

<table>
<thead>
<tr>
<th>Event</th>
<th>Transition from $n$ to Rate</th>
</tr>
</thead>
<tbody>
<tr>
<td>Colonisation</td>
<td>$n + 1$, $c_1 \sum_i n_i \exp(-e \sqrt{A_i})$</td>
</tr>
<tr>
<td>Extinction</td>
<td>$n - 1$, $\alpha n_i / A_i$</td>
</tr>
</tbody>
</table>

Table 2 Transition rates: spatially realistic model.
as $K_c(c' - c) + K_e(e - e') \leq B$, where $K_e$ and $K_c$ are the respective costs for changes in $c$ and $e$ with $B$, the total budget, fixed (all evaluated over the same management period) and $(c', e')$ is the optimal choice of $c$ and $e$ we seek to determine. Since any increase in $c$ or decrease in $e$ will always increase the expected extinction time, we will always expend our entire budget. Thus, the inequality in our budget constraint will be satisfied with equality: $\delta c = (B - K_e \delta e)/K_c$, where $\delta c = c' - c$ and $\delta e = e - e'$. We therefore choose the $(c', e')$ combination that maximises the expected extinction time. From the exact formula (R1) it can be seen that we must choose $\rho$ as small as possible, being equivalent to maximising the expected (quasi-)equilibrium number of occupied patches in the metapopulation network. Thus, assuming there is a minimum level that the extinction rate can be reduced to, our rule of thumb is:

Invest in reducing $e$ to its allowable minimum, unless $B < K_c e - K_c c$, in which case invest in increasing $c$.

**Spatially realistic models.** To use our rules for spatially realistic models, we need to calibrate our simple model (Table 1) to the more complex model (Table 2). We propose and adopt the following calibration, obtained by matching the colonisation and extinction rates (weighted by area in the spatially realistic model, which is a good proxy for occupancy probability) when there is only a single patch occupied:

$$c := \frac{g N^N}{(N - 1)!} \sum_{i=1}^{N} A_i \sum_{j=1}^{N} \exp(-\beta \sqrt{\bar{d}_j}), \quad e := \frac{k N}{\sum_{i=1}^{N} A_i}.$$  \hfill (1)

For testing this calibration in concert with (R1) and (R2) we randomly generated, in each case, 100 metapopulation networks and species parameters. In all cases $N = 8$, a size chosen so that the exact expected time to extinction may be evaluated (as opposed to requiring simulation to estimate it), and because it corresponds to the size of our application species. Furthermore, for each simulation and patch $i = 1, 2, \ldots, 8$, we sampled as follows: $A_i \sim \text{U}(10, 500)$ (km²), $\bar{d}_i \sim \text{U}(0.02, 0.20)$ (km), $g \sim \text{U}(0.05, 1)$, $\beta \sim \text{U}(1/5, 3/5)$, $\kappa \sim \text{U}(15, 50)$ and $n(0) \sim \text{Bern}(1/2)$, $\ldots, \text{Bern}(1/2)$, where $U(a, b)$ is the uniform distribution on the interval $(a, b)$ and $\text{Ber}(p)$ is the Bernoulli distribution with success probability $p$.

For evaluating Rule (R1) we accepted only those generated networks for which the exact expected time to extinction was less than 500 years (and also with the calibrated $\rho = e/c$ less than or equal to 1, corresponding to a species of (some) conservation concern, but needing to be assessed to determine the extinction risk). Additionally, we restricted attention to species with $\rho > 1/5$, noting that $\rho \leq 1/5$ typically corresponded to species near the upper limit of extinction time equalling 500 years, as our approximation method was found to consistently over estimate the expected time to extinction by a sizeable margin when $\rho \leq 1/5$; we note that this condition may be determined simply from $c$ and $e$, and thus poses no impediment to use of our methodology. Finally, we also ensured that at least two patches were initially occupied. Our results are presented in Table 3, in the form of mean, median and variance of the Relative Error (RE) between the exact and approximated extinction time, and also the mean and median of the Absolute value of the Relative Error (ARE).

The statistic of most interest from Table 3 is the median absolute relative error (0.0748), which demonstrates that the approximation method typically performs well, with an over- or under-estimate of typically around 7.5%. From the median relative error, of 0.0512, we can see that typically we over estimate the extinction time.

For evaluating Rule (R2) we set $B = 1$ (without loss of generality) and then randomly generated changes, $\delta c$ and $\delta e$, to the colonisation rate and local extinction rate (so both were less than the minimum of $c$ and $e$); these were then used to determine the cost parameters $K_e = 1/\delta e$ and $K_c = 1/\delta c$. We then evaluated the optimal policy using (R2), and compared this to the true optimal policy by evaluating the exact expected extinction times with colonisation rate increased by $\delta c$ and local extinction rates decreased by $\delta e$. Rule (R2) was found to give the correct policy 90% of the time. We note that out of the 100 randomly generated metapopulation systems, the optimal policy was to increase the colonisation rate in only 13 systems, and our procedure correctly identified these cases in all instances. Thus, in 10 of the remaining 87 cases our procedure incorrectly recommended increasing the colonisation rate when in fact decreasing the local extinction rate was optimal.

Finally, we considered a species of conservation concern in Australia: malleefowl (*Leipoa ocellata*) in the Bakara region of South Australia. The species occupies an 8-patch network with patch areas and positions as detailed in Table 4. We assume parameter values used in an earlier study (Day and Possingham, 1995): $g = 0.005$, $\beta = 1/5$ and $\kappa = 13$. We calibrated our simple model to this spatially realistic model using (1), thus giving $c = 0.0216$ and $e = 0.0168$. The exact expected time to extinction for this malleefowl population, starting from all patches initially occupied, is 327.5 years, and our estimate using (R1) is (an impressively accurate) 323.3 years. Obviously from Fig. 1 we can see that with $N = 8$ patches the approximations (A1) and (A2) should clearly not be used; for interests sake, the estimated expected time to extinction using (A1) and (A2), respectively, are 529.5 and 791.3 years. Note that the error in these estimates is close to those for similar sized patches as illustrated in Fig. 1.

### Table 3
Spatially realistic extinction time test results.

<table>
<thead>
<tr>
<th>Statistic</th>
<th>Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean (RE)</td>
<td>0.0747</td>
</tr>
<tr>
<td>Median (RE)</td>
<td>0.0512</td>
</tr>
<tr>
<td>Var (RE)</td>
<td>0.0234</td>
</tr>
<tr>
<td>Mean (ARE)</td>
<td>0.1159</td>
</tr>
<tr>
<td>Median (ARE)</td>
<td>0.0748</td>
</tr>
</tbody>
</table>

### Table 4
Patch areas and positions for malleefowl habitat in the Bakara region of South Australia.

<table>
<thead>
<tr>
<th>Patch</th>
<th>Area (km²)</th>
<th>x-Coordinate (km)</th>
<th>y-Coordinate (km)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>2700</td>
<td>6</td>
<td>17</td>
</tr>
<tr>
<td>2</td>
<td>100</td>
<td>14</td>
<td>16</td>
</tr>
<tr>
<td>3</td>
<td>750</td>
<td>18</td>
<td>14</td>
</tr>
<tr>
<td>4</td>
<td>550</td>
<td>11</td>
<td>13</td>
</tr>
<tr>
<td>5</td>
<td>100</td>
<td>19</td>
<td>10</td>
</tr>
<tr>
<td>6</td>
<td>400</td>
<td>6</td>
<td>8</td>
</tr>
<tr>
<td>7</td>
<td>1200</td>
<td>14</td>
<td>7</td>
</tr>
<tr>
<td>8</td>
<td>400</td>
<td>3</td>
<td>5</td>
</tr>
</tbody>
</table>

3. Method

For a general Markov chain with transition rates $Q = (q(i, m, n), m, n \in S)$, whose state space $S$ includes a subset $A$, which is reached with probability 1, the expected time $\tau_i$ it takes to reach $A$ starting in state $i$ is the minimal non-negative solution to $\sum_{j \in A} q(i, j) \tau_j + 1 = 0$ ($i \notin A$), with $\tau_i = 0$ ($i \in A$). This result, which can be found in most texts on Markov chains, reduces the problem of computing persistence times to that of solving a system of linear equations, for which there is a host of numerical methods available. For any stochastic birth-and-death process, with sets of (population-size dependent) birth rates $\{b_j\}$ and death rates $\{d_j\}$, $\tau_i$...
is given by \( \tau_0 = 0 \) and

\[
\tau_i = \sum_{j=1}^{i-1} \frac{1}{\mu_j} \sum_{k=j}^{N} \pi_k \quad (1 \leq i \leq N),
\]

(2)

where the “potential coefficients” \( \pi_i \) are given by \( \pi_1 = 1 \) and

\[
\pi_i = \prod_{k=2}^{i} \frac{\lambda_k - 1}{\mu_k} \quad (j \geq 2),
\]

valid in the infinite state case, replacing \( N \) by \( \infty \) (see Norden (1982)).

For the present static landscape model we arrive at (R1). Whilst (R1) does not pose any significant numerical problems, a simpler (asymptotic) expression can be derived. Using (R1) we obtain the explicit asymptotic (large-\( N \)) formula (A1), which is valid when \( \rho < 1 \). Further approximation can be made to obtain formula (A2) (full details can be found in Appendix A). The optimal management strategy rule of thumb (R2) was derived by simply choosing the option that maximised the expected number of occupied patches in quasi equilibrium. As reported above, to apply our rules to spatially realistic models we adopted the calibration detailed in the previous section (definitions given in (1)). They were obtain by matching the colonisation and extinction rates (weighted by area in the spatially realistic model) when there is only a single patch occupied. We emphasise that this provides an explicit procedure for approximating the spatially realistic model by way of the simple model.

Finally, the 200 metapopulation systems were generated by sampling, for each simulation and patch \( i = 1, 2, \ldots, 8 \), as: \( \lambda_i \sim U[10, 500] \text{ (km)}^2 \), Position \( \sim U[0,20] \text{ (km)} \), \( \mu_i \sim U[3,5] \), \( \kappa \sim U[1,5, 50] \) and \( n(0) \sim \text{Ber}(1/2, \ldots, \text{Ber}(1/2)) \). We then used the exact expected time to extinction, and policy, to compare with our rules using the above mentioned calibration (1) in concert with (R1) and (R2), respectively.

4. Discussion

We note that in assuming equal costs of increasing \( c \) and decreasing \( e \), that is \( K_e = K_c \) (and in fact whenever \( K_e \geq K_c \)), it is always optimal to invest in decreasing the extinction rate (first) if \( c > e \) (Rule (R2)). This conclusion broadly supports the conclusion of Etienne and Heesterbeek (2001). Our result advances their finding by incorporating the costs of the two management strategies, meaning that for certain costs it may be optimal to invest in increasing the colonisation rate first.

We have assumed here that costs are linear in the relevant variables. In reality it is likely that increasing costs will be associated with increasing changes in parameter values—small changes can be made cheaply, but further changes cost substantially more. Additionally, we have assumed that all patches are equally modified, that is, all colonisation and extinction rates are varied. With a limited budget, we may wish to target only a subset of the patches, or it might be optimal to spread the changes across patches in a weighted manner. Future research should consider these realistic modifications.

The approach to approximating the expected time to extinction of a metapopulation is similar to that adopted by Frank and Wissel (2002). We start by considering the exact expected time to extinction formula for the stochastic version of the classical Levens (1969) model calibrated to a more realistic spatial model. However, our approximations (A1) and (A2) account for the current (initial) number of occupied patches, whereas Frank and Wissel (2002) assume full metapopulation occupancy. The ability to account for the number of patches currently occupied may be an important component in determining an accurate ranking of metapopulation extinction risk, in particular when ranking species that vary significantly in their total patch sizes in comparison to the variation in the current numbers of patches occupied. In contrast, Frank and Wissel (2002) incorporate correlated local population extinction between pairs of patches, which has not been considered here.

Our results provide encouragement for using rules of thumb based on simple models calibrated to more complex ones, particularly in light of previous studies reporting similar findings, for example, Etienne and Heesterbeek (2001); Keeling (2002); Frank and Wissel (2002) and Ovaskainen (2002). However, the robustness of our calibration methodology and our rules need to be explored fully, for larger metapopulation systems and for other spatially realistic models. Despite this, it appears that our methods can be used, at the very least, to greatly reduce the number of species requiring more detailed analysis, and can provide a rapid indication of the optimal management policy. We recommend that whenever feasible exact methodology be used.

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Appendix A

Our static landscape model is a birth–death process \( (n(t), t \geq 0) \) taking values in \( S = \{0, 1, \ldots, N\} \) with birth- and death rates \( \lambda_n = (c/N)n - \mu_n = en \), where \( e > 0 \) and \( c > 0 \). Thus, \( S \) consists of an irreducible class \( C = \{1, \ldots, N\} \) and an absorbing state 0 which is accessible from C. It is well known that if \( e > c \) the process is absorbed quickly, but, as noted earlier, if \( e < c \) the population settles down to a quasi equilibrium that may persist for a long period. In this latter case, the carrying capacity is \( (1 - \rho)N \), where \( \rho = e/c \).

We are interested in the expected time \( \tau_i(N) \) it takes for the process to reach 0 starting in state \( S \) for a given ceiling \( N \). For a general birth–death processes on \( S \) with birth rates \( \lambda_n \) and death rates \( \mu_n \), \( \tau_1 = \tau_1(N) \), for \( i \geq 1 \), is given by (2). For our model, it is given by (R1).

Several authors have derived asymptotic expansions like those given in Theorem A.1 below. Kryscio and Lefèvre’s (1989) formula (labelled (2.4) in their paper) for the case \( \rho < 1 \), which is apparently due to Oppenheim et al. (1977), is at variance with our formula (A1). We note that Norden (1982, p. 698) went some way towards deriving a \( \rho > 1 \) approximation. Kryscio and Lefèvre (1989, Page 689) also derived an asymptotic formula for this case, but we have not attempted to compare ours with theirs.

In what follows, \( a_n - b_n \) means \( a_n/b_n \rightarrow 1 \) as \( N \rightarrow \infty \).

Theorem 1. The following hold in the limit as \( N \rightarrow \infty \). If \( \rho > 1 \),

\[
\tau_1(N) = \frac{1}{c} \log \left( \frac{\rho}{\rho - 1} \right)
\]

and, for \( i \geq 2 \),

\[
\tau_i(N) = \frac{1}{c(\rho - 1)} \left( (\rho - 1) \log \left( \frac{\rho}{\rho - 1} \right) - \sum_{k=1}^{i-1} \frac{(\rho^k - 1)}{k} \right).
\]

If \( \rho < 1 \),

\[
\tau_i(N) = \frac{1}{c(1 - \rho)} \left( \frac{1}{1 - \rho} \left( 1 - \frac{e^{-(1 - \rho)}}{\rho} \right)^N \right)^{\frac{1}{2N}} - \sum_{k=1}^{i-1} \frac{(1 - \rho^k - 1)}{k}
\]

(A.1)
Proof. The plan is to evaluate the factorials implicit in (R1) as gamma integrals and then invoke standard asymptotic results. We use Laplace’s method (see Section 12.2.5 of Olver (1983)) to estimate the integrals. Let \( \sigma_j \) be the expected first-passage time to state \( j - 1 \) from state \( j \), so that \( \tau_j(N) = \sum_{j=1}^{N} \sigma_j \). Then,

\[
\sigma_j = \frac{1}{\mu_j \mu_j^T} \sum_{k=j}^{N} \pi_k = \frac{(N-j)!}{e} \sum_{k=0}^{N} \frac{1}{k![N-k]!} w^k
\]

\[
= \frac{w(N-j)!}{eN!} \sum_{k=j}^{N} \left( \frac{N}{k} \right) (k-1)! w^k
\]

where \( w = \rho N \), this being true for \( j = 1, \ldots, N \). Now, evaluating the factorial as a gamma integral gives

\[
\sigma_j = \frac{w(N-j)!}{eN!} \sum_{k=j}^{N} \left( \frac{N}{k} \right) (k-1)! w^k
\]

where \( w = \rho N \), this being true for \( j = 1, \ldots, N \). Now, evaluating the factorial as a gamma integral gives

\[
\sigma_j = \frac{w(N-j)!}{eN!} \sum_{k=j}^{N} \left( \frac{N}{k} \right) (k-1)! w^k
\]

First suppose that \( \rho > 1 \). Then, since \( \frac{N!}{(N-j)!} \sim (N-j)^{-1} \) as \( N \to \infty \),

we have, for \( N \) large,

\[
\sigma_j \sim \frac{\rho^j}{e} \int_0^\infty \frac{e^{-s/s}}{s} \left( e^{s/s} - \sum_{k=0}^{j-1} (s/s)^k \right) ds.
\]

(Since \( (1+s/(\rho N))^N \) is increasing, the interchange of limit and integral is justified by the Monotone Convergence Theorem.) The right-hand side is well defined because the integral is dominated by

\[
\int_0^\infty \frac{e^{-s/s}}{s} (e^{s/s} - 1) ds = \log \left( \frac{\rho}{\rho-1} \right).
\]

It now simplifies to

\[
\frac{\rho^j}{e} \int_0^\infty \frac{e^{-s/s}}{s} \left( \sum_{k=0}^{j-1} (s/s)^k \right) ds = \frac{\rho^j}{e} \sum_{k=0}^{j-1} \frac{s/s}{k!} \int_0^\infty e^{-s/s} s^k ds
\]

\[
= \frac{\rho^j}{e} \sum_{k=0}^{j-1} \frac{\rho^{-k}}{k!} = \frac{\rho^j}{e} \left( \log \left( \frac{\rho}{\rho-1} \right) - \sum_{k=1}^{j-1} \frac{\rho^{-k}}{k} \right).
\]

with the interpretation that the empty sum is 0 when \( j = 1 \). Notice the infinite sum converges because \( \rho^{-1} < 1 \). Therefore, as \( N \to \infty \),

\[
\tau_i(N) = \sum_{j=1}^{i} \sigma_j \sim \frac{\rho^j}{e} \log \left( \frac{\rho}{\rho-1} \right) \sum_{j=1}^{i} \rho^{-j} - \sum_{j=2}^{i} \frac{\rho^j}{e} \sum_{k=1}^{j-1} \rho^{-k}
\]

After a modicum of algebra, we get the result stated.

For \( \rho < 1 \) we use Laplace’s method to estimate the integral in (A.2), which can be written

\[
\int_0^\infty e^{-\rho Nx} x \left( 1 + x \right)^N - \sum_{k=0}^{j-1} \frac{N^k}{k!} x^k \right) dx = \int_0^\infty e^{\rho Nx} q(x) dx,
\]

where \( q(x) = 1/x \) and

\[
r_N(x) = -\rho x + \frac{1}{N} \log \left( x + (1 + x)^N - \sum_{k=0}^{j-1} \frac{N^k}{k!} \right).
\]

For all \( x > 0 \) and \( j \geq 1 \),

\[
\lim_{N \to \infty} \left( 1 + x \right)^N - \sum_{k=0}^{j-1} \frac{N^k}{k!} \right) x^k = 1 + x,
\]

and so \( r_N(x) \to r(x) \), where \( r(x) = -\rho x + \log(1 + x) \). However, we get no useful information if we base our approximation on estimating \( \int_0^\infty e^{\rho Nx} q(x) dx \), because this integral is divergent for any \( N \). Instead, we estimate

\[
\int_0^\infty e^{-\rho Nx} x \left( 1 + x \right)^N - 1 \right) dx = \int_0^\infty e^{\rho Nx} q(x) dx,
\]

where

\[
s_N(x) = -\rho x + \frac{1}{N} \log \left( (1 + x)^N - 1 \right).
\]

First, since \( r(x) = 1/(1+x) - \rho \) and \( r'(x) = -1/(1+x)^2 \), it is clear that \( r \) achieves its maximum at \( x = 1/\rho - 1 \). We deduce that \( s_N(x) \) achieves its maximum near \( x = 1/\rho - 1 \). So, employing Laplace’s method, we get in the limit as \( N \to \infty \),

\[
\int_0^\infty e^{\rho Nx} q(x) dx \approx q(a) = \frac{1}{1-\rho} \left( e^{(1-\rho)/\rho} \right)^N \sqrt{\frac{2\pi}{N}}.
\]

Therefore,

\[
\sigma_j \sim \frac{\rho^j}{c(1-\rho)} \left( \frac{e^{(1-\rho)/\rho}}{\rho} \right)^N \sqrt{\frac{2\pi}{N}} \sum_{k=1}^{j-1} \rho^{-k}.
\]

Summing over \( j \) from 1 to \( i \), and using an earlier calculation, gives the stated result. □

Approximation (A2) is then achieved using

\[
\sum_{k=1}^{j-1} \frac{1 - \rho^{-k}}{k(1-\rho)} = \gamma + \ln(i-1),
\]

by taking the ratio \( (1 - \rho^{-k})/(1 - \rho) \) \( \approx 1 \) (noting that this ratio is in fact less than or equal to 1) and taking a first-order approximation to the digamma function in the resulting \( (i-1) \) th harmonic number.

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