On valuing patches: estimating contributions to metapopulation growth with reverse-time capture–recapture modelling

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Metapopulation ecology has historically been rich in theory, yet analytical approaches for inferring demographic relationships among local populations have been few. We show how reverse-time multi-state capture–recapture models can be used to estimate the importance of local recruitment and inter-population dispersal to metapopulation growth. We use ‘contribution metrics’ to infer demographic connectedness among eight local populations of banner-tailed kangaroo rats, to assess their demographic closure, and to investigate sources of variation in these contributions. Using a 7 year dataset, we show that: (i) local populations are relatively independent demographically, and contributions to local population growth via dispersal within the system decline with distance; (ii) growth contributions via local survival and recruitment are greater for adults than juveniles, while contributions involving dispersal are greater for juveniles; (iii) central populations rely more on local recruitment and survival than peripheral populations; (iv) contributions involving dispersal are not clearly related to overall metapopulation density; and (v) estimated contributions from outside the system are unexpectedly large. Our analytical framework can classify metapopulations on a continuum between demographic independence and panmixia, detect hidden population growth contributions, and make inference about other population linkage forms, including rescue effects and source–sink structures. Finally, we discuss differences between demographic and genetic population linkage patterns for our system.

Keywords: contribution metrics; density effects; dispersal; kangaroo rat; seniority; source–sink

1. INTRODUCTION

The metapopulation concept has produced substantial theory and discussion [1–3], and has been used as the basis for management and conservation of various species [4–6]. The concept includes local populations at least partially linked via dispersal. Local populations that comprise a metapopulation typically exhibit variation in contributions they make to, and receive from, other system components. Incidence function approaches to modelling metapopulation dynamics focus on variation among local populations with respect to sizes of the patches that they inhabit and isolation of these patches from potential sources of colonists [7]. Source–sink approaches focus on internal dynamics of local populations, specifically, their abilities to provide emigrants to other local populations and to sustain themselves in the absence of immigration [8,9]. We propose a comprehensive framework that considers the relative contributions of each local population to every other local population and to overall metapopulation growth [9–11].

While the value of this comprehensive framework is intuitive, we have little knowledge of the magnitude or sources of variation in contributions among local populations within any metapopulation. The ability to estimate for each local population the relative contributions to adult population growth from both internal processes (survival, in situ recruitment) and external processes (immigration from other sites and from outside the metapopulation) is relevant in understanding and managing any metapopulation system. For example, the ability to assign values to local populations with respect to their contributions to other local populations is relevant to patch selection for reserve design [5,6]. Estimating rates of immigration is also crucial for understanding the genetic structure of metapopulations [12]. For our study, we had specific questions involving hypothesized sources of variation in these contributions to and from local populations, including local population location (central versus peripheral; distance from other local populations), overall metapopulation density and animal age. These hypothesized sources of variation include factors emphasized in both incidence function and source–sink approaches to metapopulation modelling (e.g. density effects [13,14], distance between local populations [3]).

Despite the appeal of this comprehensive framework for metapopulation understanding and management, we agree with Kawecki’s [9, p. 413] statement about metapopulations that ‘the development of theory has outpaced the accumulation of empirical data’. Fortunately, recent years have brought important methodological advances for drawing inferences about metapopulation dynamics.
from field data (e.g. [15,16]). Estimates from these methods can be used to assign values to local populations with respect to their metapopulation contributions, viewed either asymptotically or time-specifically. The most useful asymptotic approach is the concept of spatial reproductive value developed by Willekens & Rogers [17] as an extension of Fisher’s [18] reproductive value. Reproductive value quantifies the expected long-term contribution of an individual from any local population to metapopulation size at some time in the distant future. This metric has been suggested as a way to assess local population value in the context of sources and sinks (e.g. [9,10]). Alternatively, Runge et al. [11] present an approach for assigning value to local populations based on their contributions over specified periods of ecological time.

In this paper, we apply the conceptual framework of Runge et al. [11] in combination with reverse-time modelling [19] to draw inferences about a metapopulation of banner-tailed kangaroo rats (Dipodomys spectabilis). Specifically, we investigate the contributions of local population dynamics and dispersal between local populations to metapopulation growth. Because studies of real-world systems seldom include every possible local population, we consider contributions from outside the system, in addition to those from within. After defining the relevant contribution metrics, we estimate them by applying reverse-time models to 7 years of capture-recapture data. Although reverse-time methods were proposed a decade ago, to our knowledge this is their first usage within a metapopulation.

Reverse-time modelling focuses on the ‘seniority’ parameter, γ, the probability that an individual in a particular state on sampling occasion t was present in that state on sampling occasion t − 1. Pradel ([20]; cf. [21]) discussed the relationship of seniority to recruitment in a single population with no age-specificity. Nichols et al. ([19]; cf. [22]) generalized the idea of seniority to multiple ‘strata’, where γ becomes the probability that an individual present in a specific stratum represents a transition from that or another stratum (strata may be defined as age classes, local populations or via other state variables) in the previous sampling period. These authors noted that γ’s can be used to compute proportional contributions of various components to population growth rate, λ, and the method is increasingly used to examine the impact of variation in recruitment and age-specific survival rates on growth of individual populations [23,24]. Reverse-time modelling has equal promise in describing the demographic importance of population-specific vital rates (survival, in situ reproductive recruitment, dispersal) to specific local populations and to overall metapopulation growth. This is the focal application in our analyses.

Banner-tailed kangaroo rats build and live in conspicuous dirt mounds occupied by a single adult or female with juveniles. This ensures high capture probability and unambiguous location of individual residences during sample periods. Patterns of within-population dispersal [25–27] and between-population dispersal [28] have been documented in this study system, as has been some degree of genetic connectivity among the local populations [12,29,30]. We previously investigated impacts of age, sex, distance between populations and the nature of the habitat matrix on interpopulation dispersal, and demonstrated the importance of age and distance between populations within our system to interpopulation dispersal [28]. Within the study system, mounds occur in eight clusters, each separated from other clusters by hundreds of metres (median 600 m, range 100–1600 m) of unoccupied land. Some populations of similar size exist outside of the study system (minimum distance 500 m, figure 1), and may influence dynamics of peripheral populations within the system. Because kangaroo rats can disperse between these mound clusters, we refer to them as ‘local populations’ and the eight-cluster system as a ‘metapopulation’, without meaning to imply any particular demographic relationship among populations other than they are linked. During our study, the overall metapopulation density and local population abundances fluctuated, possibly influencing local population contributions to the metapopulation. We expect that larger populations will contribute more to metapopulation growth than smaller populations.

We ask four general questions with the reverse-time multi-state approach: (i) what are the relative contributions of survival, in situ recruitment and immigration to adult population growth for local populations and the entire metapopulation? (ii) how ‘closed’ is the set of local populations—is there an important component of immigration from outside? (iii) does the importance of survival, in situ recruitment and immigration vary substantially among local populations? and (iv) do the following factors represent important sources of variation among local populations in their contributions to each other and the entire metapopulation: local population abundance, local population location (central versus peripheral, distance between pairs of local populations), overall
metapopulation density (number of animals per unit area within the metapopulation, i.e. the group of local populations) and animal age. Our approach provides a useful way to detect hidden (possibly extra-system) contributions to population growth, and to make inferences about a possible rescue effect [31], presence of sources and sinks [8] and degree to which local populations are demographically independent [11]. Finally, we comment on the differences between demographic patterns of interpolation connectivity revealed here and genetic patterns of connectivity described elsewhere for this same system [12,29,30].

2. MATERIAL AND METHODS

(a) Field data collection

We applied our approach to data from annual trapping surveys (late July/early August) in desert grassland, Cochise County, southeast Arizona, USA (31°37'N, 109°15'W), from 1994 through to 2000. We placed three Sherman live traps at entrances to each active (based on signs of fresh excava- tion or sandbathing) mound, baited traps with birdseed in late afternoon and checked them before dawn the following morning. Each survey consisted of, on average, three trap nights (range two to five). We marked each animal with two individually numbered ear tags, and recorded trapping location, sex and age ('juvenile' for animals born the same year, 'adult' for animals that were at least 1 year old; juveniles graduated to the adult age class during the winter following their birth). Animals first captured as adults were identifiable from their size (more than 110 g) and reproductive criteria (visible nipples in females, descended testes in males).

Banner-tailed kangaroo rat mounds on our 2 x 3 km site were mapped with a theodolite. We determined edge-to-edge distances between each pair of local populations by measuring the distance between the closest mounds in each member of the pair. Since other mound clusters occurred outside the metapopulation, we classified six of the eight local populations as ‘peripheral’, because they were interposed between local populations outside the study system and our two ‘central’ populations. Sizes of all local populations fluctuated from year to year. Compared with trends since 1980, population density was relatively high (two to three animals per hectare) between 1994 and 1998, and lower (approx. one animal per hectare) in 1999 and 2000 [32].

(b) Hypotheses and predictions

We compared models examining several hypotheses regarding sources of variation in relative contributions of local populations to the metapopulation. First, components of population growth might differ between central and peripheral local populations. Connectivity with other local populations of the system should be higher for central populations [3], leading to the expectation of greater dispersal to and from central sites relative to peripheral locations. Immigration from outside the study area might be more likely to contribute to dynamics of peripheral populations. Also, some attributes of our set of local populations suggest a possible source–sink structure: two peripheral populations are adjacent to dirt roads, potentially subjecting kangaroo rats to additional mortality. Another two peripheral populations suffered periods of local extinction during the late 1980s and early 1990s. Thus, it seems that peripheral populations may contribute less to the overall system than central popu- lations. Moreover, when we originally selected the two

central populations for study 30 years ago [25], we naturally chose an area with a conspicuously high rate of mound occupancy, and thus might have chosen local populations that contribute more to the overall system.

Second, we constructed models designed to ask whether overall metapopulation density, defined by number of animals per unit area within the metapopulation, influences patterns of demographic interaction among local populations. Relative contributions of immigration, local recruitment and survival might depend on system-level density. Emigration from high-density populations is often predicted to be greater than from low-density populations [13,14], and if survival of emigrants is density-independent, demographic contribution of immigrants to a local population should be greater when density is high within the metapopulation. Possible mechanisms of positive density-dependence of dispersal include increased competition for resources in natal populations [33] or increased social interactions [34]. However, juvenile kangaroo rats that disperse within populations survive better at low density [35], suggesting the opposite prediction: immigration might be more important when overall metapopulation density is low [14]. Possible mechanisms for negative density-dependence include increased aggression towards immigrants [13] or conspecific attraction [36]. Hypotheses about system-level population density effects were based on our expectation of considerable synchrony among the local populations [37]. Because our local populations are close to each other, they experience similar exposure to environmental variation and densities are highly correlated among local populations (median Spearman’s r among dyads of our eight local populations 0.62, range −0.12 to 0.91). In addition to this specific question about overall metapopulation density, our analysis included local populations that differed greatly in abundance. Without evidence of substantial variation among local populations in rates of survival, in situ recruitment and emigration [28], we hypothesized that larger local populations would tend to contribute more to overall metapopulation growth than smaller populations.

Third, our previous results included best forward-time models of both survival and dispersal that incorporated age [28], so we modelled seniority as a function of age (i.e. \(y^{(1)} = y^{(0)}\)). Because juveniles and adults occur in similar numbers, and because juveniles disperse more frequently than adults [28], we expected greater contributions of juveniles than adults to other populations. However, we predicted that overall contributions to the entire metapopulation would typically be larger for adults, based on the tendency for adult survival rates to be higher than those of juvenile ani- mals [28]. Previous forward-time results also provided strong evidence that dispersal between local populations depended on distance between them [28]. Distance was thus incor- porated into all of our models, providing direct inference about the strength of the relationship between distance and between-population contributions for both ages.

To assess whether centrality or density substantially influences demographic interaction patterns, we compared models that included these factors with models that did not. In all models, we allowed contributions to population growth that incorporate dispersal to depend on age and dis- tance [28], while contributions to growth from within the same local population depended only on age (i.e. adults pre- sent could include both surviving adults from the same population in the previous year, or recruited juveniles from the same population the previous year).
(c) Inference methods

We first define a metric reflecting the contribution of each of our local study populations to the metapopulation. This metric is defined for the eight-population study system and does not include emigrants that may contribute to extra-system locations. We can, however, estimate contributions to the system via immigration from outside it. We define the seniority parameter $\gamma^{s(0)}$ as the probability that an adult present in local population $r$ at time $t$ was an animal of age $l(0 = \text{juvenile}, 1 = \text{adult})$ in local population $s$ at time $t - 1$. Seniorities over all time periods, $\gamma^{s(t)}$, provide estimates of the contributions of juveniles and adults from every population to each focal population in the metapopulation. Growth rate of the entire metapopulation, $\lambda^s$, is:

$$
\lambda^s = \frac{\sum_s N^s_i}{\sum_s N^s_i}
$$

(2.1)

where $N^s_i$ is the number of adults in local population $r$ at time $t$. The contribution of local population 1 to growth of the system involves both individuals that remained in local population 1 between $t$ and $t + 1$, with expectation $N^s_{r(1)}(Y^s_{r+1} + Y^s_{r+1})$, and individuals that moved from local population 1 to local populations 2 to 8 between $t$ and $t + 1$, with expectation $\sum_s N^s_{r(1)}(Y^s_{r+1} + Y^s_{r+1})$. The proportional contribution of local population 1 to the numerator of equation (2.1), and hence to growth of the metapopulation, is:

$$
c^s_1 = \frac{\sum_s N^s_{r(1)}(Y^s_{r+1} + Y^s_{r+1})}{\sum_s N^s_{r(1)}}
$$

(2.2)

The numerator of equation (2.2) expresses the number of animals in the system at time $t + 1$ that were either surviving adults from local population 1 that remained in the system between times $t$ and $t + 1$, or new recruits at $t + 1$ to all other local populations that were produced in local population 1 at $t$. A similar expression can be written for the relative contribution of each local population. More generally, $\hat{c}^s$ estimates the average overall contribution of each local population, $s$, to the growth of the entire metapopulation over all time periods.

If the study system is closed (i.e. dispersers from any local population emigrate to one of the eight component local populations and no immigrants from outside the metapopulation contribute to any component local populations), then the sum of expression (2.2) over all eight local populations equals 1, $\sum_s c^s_1 = 1$. More generally, the proportional contribution of immigrants from outside the study system (denoted with superscript 0) to population growth between $t$ and $t + 1$ is:

$$
c^s_0 = 1 - \frac{\sum_s \sum_s N^s_{r(1)}(Y^s_{r+1} + Y^s_{r+1})}{\sum_s N^s_{r(1)}}
$$

(2.3)

When $c^s_0 = 0$, the system is closed and all contributions to growth come from system components. Similarly, for any specific local population, $r$, proportional contribution to growth of that local population attributed to immigration from outside the study system is:

$$
\gamma^{s(0)}_r = 1 - \sum_r \gamma^{s(0)}_r
$$

(2.4)

We obtained estimates required to compute the contribution metrics of expressions (2.2)–(2.4) from kangaroo capture–recapture data using reverse-time multi-state modelling [19], with state defined by both age and local population. We estimated seniority parameters, $\gamma^{s(t)}$, and time- and state-specific capture probabilities, $p^{r(t)}$, using this approach. We used estimates of capture probability to estimate time- and state-specific adult abundance:

$$
N^s_r = \frac{n^{r(1)}}{p^{r(1)}},
$$

(2.5)

where $n^{r(1)}$ is the number of adults captured at time $t$ in local population $r$.

All expressions are time-specific to this point, but we were interested in overall metrics associated with contributions of local populations over the entire study duration. Therefore, we computed expressions identical to (2.2) and (2.3), except that we substituted average estimated local population abundance ($\bar{N}^s$) for time-specific abundance and time-constant seniority parameter estimates ($\gamma^{s(0)}$) for time-specific values. We computed average relative contribution of local population $s$ to growth of the metapopulation as:

$$
\bar{c}^s = \frac{\sum_s \bar{N}^s(\gamma^{s(1)} + \gamma^{s(0)})}{\sum_s \bar{N}^s}, \quad s = 1, \ldots, 8,
$$

(2.6)

where the average relative contribution of immigrants from outside the metapopulation to metapopulation growth is estimated as:

$$
\bar{c}^0 = 1 - \sum_s \bar{c}^s.
$$

(2.7)

We developed a nested set of a priori capture–recapture models designed for inference about potential sources of variation in the local population contributions. In all models, we modelled capture probability $p$ as a function of age and time (year), based on previous modelling results [28]. Because prior investigation showed few differences between sexes in survival or dispersal patterns, and because the absolute number of dispersers was small [28,38], we combined sexes in all analyses. In prior forward-time modelling [28], the best dispersal models incorporated edge-to-edge distance between local populations (modelled in a linear-logistic fashion); therefore, we modelled seniority parameters that incorporated dispersal the same way. Our most general model allowed contributions to growth of survival and immigration to vary with age ($A$, adults versus juveniles), location ($C$, central versus peripheral), distance between local populations ($D$) and overall metapopulation density ($D_0$, relatively high versus low years). We denote this model as $\gamma^{(A \times C \times D)_0}$. $\gamma^{(D + A + C + D_0)}$, where the notation $\gamma^{(A \times C \times D)}$ indicates that we modelled effects of age, centrality and density on transitions within a local population in a multiplicative fashion (all interactions included; i.e. a different parameter for each age, location and density combination). For transitions involving dispersal between local populations, notation $\gamma^{(D + A + C + D_0)}$ indicates that we modelled effects of distance between local populations, age, centrality and density in an additive manner (without interaction terms). The additive structure was dictated by sample size (dispersal rates are small), but also seems reasonable on ecological grounds.

Inferences about the above hypotheses were obtained using a model selection approach [39,40]. We assessed goodness-of-fit by computing the corresponding variance inflation factor, $\hat{c}$, for the most general model in the model set. We used a parametric
Table 1. Candidate model set and model selection statistics for reverse-time analysis of our kangaroo rat metapopulation in Cochise County, southeast Arizona, USA. We modelled capture probability \( p \) as a function of age and time (year) for all models. Seniority parameters, representing the probability that an animal present in local population \( r \) at time \( t \) was in local population \( s \) at time \( t - 1 \), were modelled as functions of age class of kangaroo rats \( (A) \), centrality \( (C) \), overall metapopulation density \( (D) \) and/or distance between local populations \( (D) \). For each model, we report the log-likelihood (log lik), number of parameters (np), quasi-likelihood Akaike's information criterion, adjusted for small sample size \((\Delta QAIC_c)\), \( QAIC_c \) and \( QAIC_c \) weight.

<table>
<thead>
<tr>
<th>model</th>
<th>log lik</th>
<th>np</th>
<th>QAIC_c</th>
<th>( \Delta QAIC_c )</th>
<th>QAIC_c weight</th>
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<td>( \gamma''(A) \gamma''(D + A) )</td>
<td>-1232.950</td>
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<td>1777.261</td>
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<td>0.361</td>
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<td>55</td>
<td>1777.949</td>
<td>0.668</td>
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<td>( \gamma''(A \times D) \gamma''(D + A) )</td>
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<td>1778.638</td>
<td>1.377</td>
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<td>( \gamma''(A \times C \times D) \gamma''(D + A + C) )</td>
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<td>1779.393</td>
<td>2.132</td>
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<td>1780.839</td>
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</table>

bootstrapping approach by generating data as random variables governed by parameter estimates from our analysis. We computed a Pearson goodness-of-fit statistic for the actual dataset and for each bootstrap replicate. We estimated \( \tilde{c} \) as the ratio of the fit statistic computed for the actual dataset to the average fit statistic computed over all bootstrap replicates (1000). The fit of the most general model, \( \gamma''(A \times C \times D) \gamma''(D + A + C + D) \), provided some evidence of overdispersion, \( \tilde{c} = 1.48 \). We used \( \tilde{c} \) to compute quasi-likelihood Akaike's information criterion, adjusted for small sample size \((QAI C_c)\) for model selection and to inflate model-based variance estimates [40]. All model-fitting and model-specific estimation was accomplished using software developed by J.E.H. to implement the multi-state, robust design, reverse-time modelling.

Because of model selection uncertainty, we computed all estimates of \( \gamma'' \) and \( p'' \) using model averaging across all models in the model set [40]. We calculated estimates of overall contributions, \( \tilde{c} \), using model-averaged estimates in conjunction with equation (2.5). Finally, we approximated estimates of variances for derived parameters, \( \hat{\mathbf{N}} \) and \( \tilde{c} \), using the delta method [41] but ignoring covariance terms.

3. RESULTS

Our effective sample size (total number of releases) was 2614. The low-QAI C, model for seniority was the simplest in the model set, \( \gamma''(A) \gamma''(D + A) \) (table 1). Under this model, the contribution of a focal population to itself was a function of age. The contributions to a focal population involving dispersal were a function of age and distance. Models incorporating centrality have considerable support (summed QAI C, weight \( \approx 0.40 \)). Models incorporating population density have weaker support (summed QAI C, weight \( \approx 0.25 \)), and those incorporating both density and centrality have almost no support.

Model-averaged contribution estimates \( \hat{\gamma}'' \) are presented for the two sets of years reflecting relatively high (electronic supplementary material, table S1) and low (electronic supplementary material, table S2) density and together (figure 2). At both high and low overall metapopulation densities, self-contributions to each local population are greater for adults than juveniles \( \gamma''(A \geq \gamma''(A) \gamma''(r \neq A) \). By contrast, contributions from each local population to others are greater for juveniles than adults \( \gamma''(A \geq \gamma''(A) \gamma''(r \neq A) \). Demographically, local populations are largely independent of others within the system: self-contributions are one to two orders of magnitude larger than contributions via dispersal.

Within each overall metapopulation density level and for each age, estimated self-contributions are large for central populations 1 and 2, than for peripheral populations 3–8. As a corollary, estimates of immigration from outside the study system are always larger for peripheral (range 0.23–0.29) than for central populations (range 0.18–0.25) (figure 2a, electronic supplementary material, tables S1 and S2). Estimates of slope parameters \( (b) \) associated with the relationship between distance and \( \gamma''(D) \) are negative for all candidate models, reflecting reduced contributions from dispersal with increasing distance; populations separated by more than 0.25 km contribute essentially nothing to each other (figure 2c).

Estimates of relative self-contributions are larger for both age classes in the central populations during years of low overall metapopulation density than during years of high density (figure 2a; electronic supplementary material, tables S1 and S2). This is true of juveniles in peripheral populations as well, but not for adults.

Point estimates of overall relative contributions of local populations to metapopulation growth ranged from 0.02 to 0.19 (electronic supplementary material, table S3 and figure 3). Thus, some local populations contributed roughly 10 times more animals to the metapopulation than others. This variation among local populations was positively associated with local population adult abundance (figure 3). Average adult abundance for the entire system during relatively high-density years was 115.6 \((\pm 3.6)\) animals; abundance during low-density years was 71.5 \((\pm 1.4)\) animals. Estimated extra-system contribution to metapopulation growth was larger during higher density years, \( \hat{\gamma}''(D) = 0.27(\pm 0.009) \), compared with lower density years, \( \hat{\gamma}''(D) = 0.23(\pm 0.05) \). However, estimated contributions from within-system dispersal, \( \hat{\gamma}''(D) \), were slightly larger during low-density years (electronic supplementary material, tables S1 and S2).

4. DISCUSSION

The reverse-time approach provides a compact and complete description of the roles of recruitment and dispersal within our kangaroo rat system, and has wide potential for inferring demographic contributions of local populations in metapopulations. Our capture-recapture models allowed...
us to make inferences about important sources of variation in the contributions of each local population to every local population in the metapopulation, $\gamma^{rs}$. These estimates are unique within the metapopulation literature, and provide important details about location-specific processes contributing to this metapopulation. Inferences about these processes and extra-system immigration can further be used to make inference about the contributions of each local population to the entire system. Contribution metrics provide a currency by which values can be assigned to local populations for conservation prioritization. Similarly, potential management actions directed at local populations can be assessed by the degrees to which they are expected to increase overall metapopulation growth. Finally, we believe this decomposition of metapopulation change into components associated with local populations represents an important step towards developing a general theory of metapopulation dynamics applicable to many taxa.

As predicted, estimates of adult self-contributions were greater than those of juveniles, whereas estimates of contributions involving interpopulation dispersal were greater for juveniles. Juveniles are more likely to disperse than adults in many vertebrates [42], so asymmetry in age-specific contributions involving interpopulation dispersal may be a general phenomenon. Estimated contributions to the entire system were greater for adults. Contributions via dispersal to the growth of each local population were greater from other local populations that were nearby. Although this result was expected and is widely claimed in metapopulation ecology literature [3], our estimates are among the first to quantify it.

Population ‘centrality’ was a relatively important source of variation in the contribution metrics, as inferred from model selection. Based on estimates of $\gamma^{rs}$, central populations relied less on immigration from outside the study system than peripheral populations. Estimated contributions of central populations to the entire system were large, but did not always exceed estimated contributions of peripheral populations. If centrality is an important determinant of local population contributions in other metapopulations, this feature would have direct implications for reserve design [5,6], where central populations may be more important. We note that the ideas tested here for a specific metapopulation could have implications for larger scales, such as species’ geographical ranges. Populations located in the interior of a species range are typically characterized by higher abundances and lower probabilities of local extinction and turnover than local populations near range edges (e.g. [43]).

Ranked contributions of each local population to growth of the entire system, $\gamma^{rs}$, were consistent with ranked average abundances during both low and high

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**Figure 2.** Model-averaged estimates (95% CI) of seniority parameters from our reverse-time analysis of a kangaroo rat metapopulation in Cochise County, southeast Arizona, USA for high and low overall metapopulation density years for juveniles (grey diamonds) and adults (black diamonds). These represent estimated contributions to growth of each focal population from $(a)$ themselves or self-contributions, $\gamma^{rr}$, $(b)$ outside system immigration, $\gamma^r$, and $(c)$ non-focal populations, $\gamma^c$, grouped by distance from the non-focal populations. We classified local populations 1 and 2 as central (labelled as ‘C’) and local populations 3–8 as peripheral (labelled as ‘P’).

**Figure 3.** Model-averaged parameter estimates (approx. 95% CI) from our reverse-time analysis of a kangaroo rat metapopulation in Cochise County, southeast Arizona, USA. For both high (black circles) and low (grey circles) overall metapopulation density years, we include: $(a)$ abundance estimates (95% CI) for each local population $r$, and $(b)$ relative contributions of each local population $r$ to growth of the entire metapopulation (95% CI).
overall metapopulation density years. This commonsense result, that larger local populations make larger contributions to the metapopulation, is predicted for this system because local populations have similar survival and reproductive rates. This result is likely to be a common feature of metapopulations and has clear implications for reserve design [5].

Surprisingly, our results do not suggest a strong relationship between metapopulation density and contributions resulting from immigration, counter to other species with density-dependent dispersal [44], and predictions that density-dependent dispersal should evolve in many metapopulation systems [45]. Estimated contributions from within-system dispersal were slightly larger in years of low overall metapopulation density, consistent with our previous result that juvenile kangaroos which disperse within local populations survive better at low density [35]. However, point estimates of extra-system contributions were greater in years of higher overall metapopulation density, and both effects of density were weak.

Small estimated contributions to growth of any local population by other local populations within the study system were consistent with the low rates of dispersal estimated for this system [28]. However, in the light of the low dispersal rate and the inverse relationship between dispersal probability and distance, we were surprised at the large estimated contributions of immigration from outside the study system. Four local populations exist just outside our study area (figure 1), and contributions from ‘outside’ are greater to peripheral than to central populations (figure 2b; electronic supplementary material, tables S1 and S2) by an amount comparable with that expected if peripheral populations gain immigrants from such populations. However, even central populations have large extra-system contributions. In Skvarla et al. [28], we found that fewer than one out of 100 animals dispersed the greater than or equal to 1 km needed to reach a central population from outside our study area.

We can think of two ways in which flawed assumptions in our analysis might contribute to unexpectedly large estimates of immigration from outside the study system. First, dispersal from far outside the system might be more common than that observed within the study site [28,46]. But the distribution of active kangaroo rat mounds outside our study site was not obviously different from that within it, i.e. we located no obvious ‘sources’ in the surrounding area. Estimates of immigration from ‘outside’ seem too large (nearly half the magnitude of contributions from juvenile recruitment in situ) to be accounted for by long-distance dispersal from an undiscovered source, and we believe that a second, more cryptic flaw in our assumptions is responsible. We assumed that all surviving young animals are available for sampling in July–August. If some late-born young are not independent and exposed to traps during this sample period, then these late entries would be ‘assigned’ to extra-system immigration.

Although not explicitly described with our application owing to ambiguity of the source of ‘outside immigration’, our approach can also be used to detect sources and sinks [8] in other ecological systems where extra-system contributions are negligible. For example, we can use a metric $C'_r$, defined in Runge et al. [11], to identify local population $r = 1$ as a source or a sink using contributions of local population 1 to all eight local populations at time $t + 1$ and the population size of local population 1 at time $t$:

$$C'_r = \sum_{r=1}^{8} N_{t+1}^{r} \frac{g_r^{l(1)} + g_r^{l(0)}}{N_{t}^{r}},$$

where $C'_r < 1$ indicates that local population $r$ is a ‘sink’ and $C'_r > 1$ indicates a ‘source’. $C'_r$ can be viewed as the per capita contribution of individuals in local population $r$ to the abundance of the metapopulation in the next time period.

The main data requirements for our approach are capture–recapture or re-observation data collected at multiple local populations. Data from a single population permit inference on the contribution to growth of that population made by internal (survival, in situ recruitment) versus external (immigration) processes [19]. However, application to a single population does not permit inference about the value of locally produced individuals that emigrate to other locations. Our example depended on the ability to identify young as having been produced in the local population of capture. In cases where this is not possible, we might use data from other sources (e.g. genetic assignment tests [47]) to determine local population of origin for juveniles [48]. Our approach requires the ability to estimate juvenile capture probability, which can be provided by the robust design [49,50]. Applications to some species (e.g. seabirds [51]) will include juveniles that can be marked during the year of hatching but do not return to the breeding colony for possible re-observation until their first year as a breeder, which may be several years later [52]. We should be able to deal with this situation by expanding the state space of the reverse-time multi-state modelling to include breeding adults from the previous time step in each local population, as well as new breeders hatched in different years from the various local populations.

One potential limitation to our method is that our contribution metric does not include emigrants that may contribute to extra-system locations (see §2c). This could lead to underestimation of the population’s contribution to metapopulation growth if there is more dispersal to extra-system populations than to within-system populations, suggesting this approach is ideally applied to metapopulations completely closed to extra-system immigration. Otherwise, contributions of populations located peripherally within the metapopulation may be more prone to underestimation than those of central populations. Study design and scale are important considerations for use of these and any methods. The relevance of extra-system contributions can sometimes be inferred from ancillary data (e.g. radio-telemetry, tag-resight, tag-recovery [41,53]). In addition, inference about temporary emigration to extra-system locations should be possible using our robust design approach [54] and multi-state models that include unobservable states (e.g. [55]). When contributions from locations outside the study system are potentially important, such methodological extensions to our basic approach deserve consideration.

This analytical approach has clear use for identifying where a population lies on the ‘metapopulation continuum’ demographically, such that magnitudes of $g^{l(0)}$ provide information about the relative importance of
dispersal among local populations as determinants of population growth. For example, if \( \hat{r}^{sr} + \hat{r}^{gs} \to 1 \), then we would conclude that local population \( r \) is relatively independent and might be best viewed as a discrete population, whereas \( \hat{r}^{sr} \approx \hat{r}^{gs}, r \neq s \), would suggest that the entire system be viewed as a single population. Situations intermediate between these extremes would reflect more classic metapopulation structures. Assuming that estimated extra-system contributions are primarily owing to late-born young (thus rescaling all within-system contributions to sum to 1), the kangaroo rat system is much closer demographically to a set of independent populations than to a metapopulation (figure 4).

This latter result might appear to contrast with previously reported patterns of genetic connectivity in the same system. Despite their demographic insignificance, cases of dispersal are frequent enough to limit genetic differentiation among local populations \( (0.01 < F_{st} < 0.03 \text{ during the years of this study}) \) and to prevent the expected loss of alleles during demographic bottlenecks \( [29,30] \). This comparison supports the concept that different levels of immigration are needed for meaningful demographic connectivity compared with genetic connectivity \( [12] \). More specifically, the number of immigrants required to make important genetic contributions is much smaller than required to make substantive demographic contributions. The genetic and demographic consequences of dispersal are thus particularly likely to differ in species such as this one where overall dispersal rates are low. Ideally, we would combine genetic and demographic information, as alluded to by Lowe & Allendorf \( [12] \), to form an encompassing view of a metapopulation. Regardless of how a metapopulation is ultimately defined, our reverse-time approach improves the demographic assessment of connectivity and provides a framework for testing hypotheses about demographic structure.

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Figure 4. Population continuum using average seniority estimates from our central (unfilled triangle) and peripheral (filled triangle) populations located in a kangaroo rat metapopulation in Cochise County, southeast Arizona, USA. Average estimates from within-system contributions were rescaled to sum to 1 to remove ambiguity from outside system contributions. Self-contributions close to 1 indicate that local populations, \( r \), are discrete populations, whereas if self and non-focal population contributions are approximately equal, the entire system could be classified as a single population. Intermediate values indicate metapopulation structures.

\[ \hat{r}^{sr} \]