



Equilibrium population dynamics of site-dependent species

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Abstract

Adults of site-dependent species require a discrete structure, e.g., a cavity, for breeding, which they are unable to construct and must locate and occupy. The environment provides only a limited number of such sites, which may vary in overall quality due to their environmental context. Heterogeneity of site quality can result in population equilibrium, often construed as source-sink dynamics. Rodenhouse et al. (*Ecology* 78:2025-2042, 1997) proposed a mechanism of site-dependent equilibrium that they claimed was more general than source-sink dynamics. After defining notions of source and sink, I use explicit dynamical models for a site-dependent population, based on the life history of golden eagles (*Aquila chrysaetos*), with two levels of site quality, to investigate the existence of population equilibria under several scenarios: source-source, source-sink, and source-floater. The life history traits I employ are not overly restrictive and serve the purpose only of providing models explicit enough to be treated analytically. I use a generalized notion of “golden eagle” since site dependency is often discussed in the literature on raptors, and I have exploited details from Hunt et al. (*PLoS ONE* 12:e0172232, 2017) for numerical simulations. The crucial features of the modeling, however, are those of site dependency. The modeling emphasizes that equilibrium results from the limited supply of source sites and that vital rates averaged across site qualities do not provide a compelling explanation of equilibria, contra Rodenhouse et al. Counterintuitively, equilibria are theoretically possible, even when both site qualities are intrinsically source sites.

Keywords Equilibria · Floaters · Population dynamics · Site-dependent species · Source-sink dynamics

Introduction

Pulliam (1988) discussed the dynamics and consequences of the existence of source and sink habitats. His demographic analysis assumed that the source habitat contained a finite, fixed number of breeding sites. Dhondt et al. (1992) reported a study of *Parus* (tits) species in which nesting was controlled with nest boxes. Their results suggested that clutch size of breeding pairs occupying a fixed nest box did not vary with increasing population size, but might if the pair changed nest box, i.e., a pair's reproductive performance depended on the site quality of the box occupied, but not population density. On the other hand, average clutch size did vary with increasing population size, reflecting habitat heterogeneity; in particular, mean clutch size decreased with

increasing population size after all nest boxes in good habitat were occupied and further occupancy occurred in nest boxes located in poorer habitat.

Pulliam and Danielson (1991) proposed the notion of “ideal pre-emptive site selection,” i.e., that individuals correctly judge site quality and once a site is occupied by a pair, it is unavailable to any other individuals. Combining with Pulliam's (1988) theoretical consideration and Dhondt et al.'s (1992) study suggested the concept of a *site-dependent* species, i.e., a species for which breeding pairs require a territory containing a pre-existing breeding site, such that any territory is pre-emptively occupied by a breeding pair, its quality is unaffected by the presence of other individuals, and there is a fixed number of breeding sites in any given habitat, this number also unaffected by population size. Examples of site dependence involve some form of discrete structure in the habitat necessary for breeding purposes, which cannot be created by members of the species. Obligate, non-excavating cavity nesters provide an obvious example (e.g., *Parus caeruleus* and *major* of Dhondt et al.'s 1992 study; Newton 1998:192–204).

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While cavity nesting provides a good example of site dependence, non-cavity nesters may also be site dependent (Newton 1998:204 – 209), e.g., raptors such as peregrine falcons (*Falco peregrinus*) (Hunt 1988; Newton 1988), northern aplomado falcons (*Falco femoralis septentrionalis*) (McClure et al. 2016), European red kites (*Milvus milvus*) (Katzenberger et al. 2021), golden eagles (*Aquila chrysaetos*) (Hunt 1998; Hunt et al. 2017), and Spanish imperial eagles (*Aquila adalberti*) (Ferrer and Donazar 1996). There are likely non-avian examples, including insects requiring an oviposition site, and cavity-nesting mammals such as the greater glider (*Petauroides volans*) (Strahen 1998), but I will restrict my presentation to the avian context.

That heterogeneity of habitat can play a role in establishing population equilibrium, or “regulating” population size, was not novel to Pulliam’s notion of source-sink dynamics (e.g., Brown 1969). Nor is the idea that a fixed number of available sites, or territories, limits population size (Moffat 1903). Adopting the notion that “a regulatory process involves some negative feedback mechanism that increases demographic rates when population size declines (and vice versa), relative to some equilibrium” (p. 2025), Rodenhouse et al. (1997) characterized the change in mean per capita vital rates due to occupation of sites of varying suitability as the mechanism resulting in equilibrium for site-dependent species, which they argued was more general than Pulliam’s notion of source-sink dynamics. Rodenhouse et al. (1997) discussed at length aspects of site dependency and habitat heterogeneity, and I refer the reader to their useful discussion for an extensive list of literature on these topics.

In this paper, I employ explicit matrix models, refining Pulliam’s (1988) demographic analysis, to explore the equilibrium population dynamics of a site-dependent model species in idealized scenarios. Although not universally applicable, their specificity permits detailed calculations which suffice, I believe, to challenge Rodenhouse et al.’s (1997) proposed explanation for such equilibria. I will contend that there is in fact no “regulatory mechanism,” in their sense, necessarily at work in the occurrence of population equilibrium for site-dependent species. As “site-dependent

regulation” has been the subject of subsequent studies (e.g., Kokko et al. 2004; Nevoux et al. 2011; Bennett et al. 2022) and Rodenhouse et al. (1997) has been cited some 491 times (Google Scholar, 6 March 2023), as recently as Rockweit et al. (2023), I believe clarification is warranted and is necessary for ecological understanding of site-dependent species and applications to their conservation.

For a site-dependent species, and continuing the terminology of Pulliam (1988), for an adult that cannot obtain a source site, an alternative to occupying a sink site is to float until a source site becomes available. I will show that the model is readily adapted to accommodate floating as an alternative strategy and how that informs site-dependent population dynamics. Finally, I will indicate how the model can be made more realistic for modeling actual populations, including how to generalize the model to incorporate both floating and sink-occupation strategies in a single model in which, rather than being mutually exclusive alternatives, these two strategies become age-dependent. In the “Discussion,” I will employ the modeling results obtained here to show Rodenhouse et al.’s (1997) proposed explanation of site-dependent, equilibrium dynamics as resulting from demographic parameters averaged over sites is inadequate and that equilibrium results rather from the limited number of source sites. I will also comment on some earlier reactions to Rodenhouse et al. that have appeared in the literature. Tables 1 and 2 record the notation employed in this article.

Model species’ site demography, site quality, sources, and sinks

I consider a population in which breeding is an annual synchronized event followed by synchronized fledging of the offspring of that year. Age is measured from fledging, and survival from conception to fledging is incorporated into fecundity. I employ the following female-only, single-sex, stage-based matrix model to describe the demography of a site occupant, modeled on a post-fledging census.

Table 1 Life-stage notation^f

Symbol	Life stage and abundance thereof	Survival rate	fecundity
S_j	j -year old subadults; $j=0, \dots, m$	$\sigma_{j+1}, j=0, \dots, m$	0
A	Adult	σ_A	f_A
PA	Primary adult	σ_P	f_P
SA	Secondary adults	σ_S	f_S
F	Floaters	σ_F	0
B	Breeders, i.e., PA in source-floater dynamics	σ_P	f_P
F_i	Floaters of age $m+1+i, i=1, \dots, n-1$	σ_F	0
S_{m+1}	First-year adult, not yet old enough to breed, in source-floater-sink dynamics	σ_F	0

Table 2 Miscellaneous symbols

Symbol	Definition	Symbol	Definition
N	Number of primary sites	M	Number of secondary sites
m	The number of years individuals spend as subadults	σ	$\sigma_{m+1} \dots \sigma_1$
P_s	Projection matrix for sites of one quality (1)	λ_s	Dominant eigenvalue of P_s ; site growth rate
R_0	Net reproductive rate	\mathbf{w}	Right eigenvector of λ_s ; stable stage distribution
P_{SS}	Projection matrix for sites of two qualities (5) or (9)	\mathbf{u}	Left eigenvector of λ_s ; reproductive value vector
τ_{t+1}	Proportion of secondary adults surviving from time t that occupy primary sites at time $t+1$ (6cc)	τ	Equilibrium value of τ_{t+1}
R_0^P	Net reproductive rate of primary sites	R_0^S	Net reproductive rate of secondary sites
PB	Primary breeder; breeding adult occupying a primary site, distinct from PA only in model (9)	x	$= \frac{s}{1-s}$, for any survival parameter s
BP_m	The m 'th birth pulse, $m = 1, \dots$	$V(k)$	Reproductive value for k years of site occupancy
n	Maximum number of birth pulses an adult can breed at before dying of old age	$V^{P(k)}$	Reproductive value for k years of primary site occupancy
τ_i	The probability of a floater of age $m+1+i$ occupying a primary site, $i = 1, \dots, n-1$	$V^S(k)$	Reproductive value for k years of secondary site occupancy
ν_i	The probability of a floater of age $m+1+i$ occupying a secondary site, $i = 1, \dots, n-1$		

$$P_s = \begin{pmatrix} 0 & 0 & \dots & 0 & f_A \sigma_A \\ \sigma_1 & 0 & \dots & 0 & 0 \\ 0 & \sigma_2 & \dots & 0 & 0 \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & \dots & \sigma_{m+1} & \sigma_A \end{pmatrix} \quad (1)$$

The life stages are $S_j, j = 0, \dots, m$, subadults of age j at the census and adult A (where I will use these symbols to denote both the stage and the number in the stage). By allowing age dependence of “subadult” survival, I incorporate into this single life stage both juvenile and subadult ages as a notational convenience. Then, the projection matrix P_s encodes the following dynamics:

$$S_0(t+1) = f_A \sigma_A A(t) \quad (2a)$$

where σ_A is the survival rate of adults and f_A is their fecundity (the number of fledglings produced per capita);

$$S_{j+1}(t+1) = \sigma_{j+1} S_j(t) \quad (2b)$$

where σ_{j+1} is the rate at which subadults aged j years survive to age $j+1$ years, $j = 0, \dots, m-1$;

$$A(t+1) = \sigma_{m+1} S_m(t) + \sigma_A A(t) \quad (2c)$$

where σ_{m+1} is the rate at which subadults aged $m+1$ survive to become adults at age $m+1$.

Combining (2a–2c) yields.

$$A(t+1) = \sigma f_A \sigma_A A(t-m-1) + \sigma_A A(t), \text{ where } \sigma = \sigma_{m+1} \dots \sigma_1 \quad (2d)$$

Note that on becoming an adult, an individual must survive a year, at rate σ_A , before reproducing. Model (1)

is not the only possibility; it reflects the demography of golden eagles, for which $m=3$ (Hunt et al. 2017), but will illustrate that the equilibrium population dynamics of site-limited populations with more than one quality of site are more subtle than might appear at first sight. An alternative is mentioned at the end of this section. Nevertheless, the life history I employ here is not overly restrictive and is applicable to stage-based accounts of a variety of avian and mammalian species. The life history assumptions provide a context for analyzing site dependency, but it is the features of site-dependent demography that are crucial.

This matrix model (1) also represents the performance of an occupant on a site with the given vital rates. This standard life-cycle projection matrix is irreducible (there are not two disjunct life cycles within the overall life cycle of the population) and primitive (the adult stage constitutes a self-loop) (Caswell 2001:81). As is well known, in these circumstances, there is a unique eigenvalue λ of maximum magnitude, called the dominant eigenvalue, which is real and positive, and possesses unique right and left eigenvectors (up to scalar multiples), each of which is real and strictly positive (Caswell 2001:84) For a population whose dynamics are governed by P_s , the dominant eigenvalue yields the asymptotic growth rate of such a population. The right eigenvector \mathbf{w} is called the stable stage distribution (SSD) (Caswell 2001:84–86). The left eigenvector \mathbf{v} is called the reproductive value vector (Caswell 2001:92–94). One usually fixes the scale of \mathbf{w} by requiring its components to sum to one; whence the components give the proportion of the stable-stage population in each stage. One then fixes the scale of \mathbf{v} by requiring $\mathbf{v} \cdot \mathbf{w} = 1$ (i.e., the sum of products of corresponding components of \mathbf{w} and \mathbf{v} is one). The asymptotic

dynamics can be expressed as *strong ergodicity*, i.e., for any population vector \mathbf{X} (i.e., with nonnegative components), $(P_s / \lambda_s)^t \mathbf{X} \rightarrow (\mathbf{v} \cdot \mathbf{X}) \mathbf{w}$, as $t \rightarrow \infty$ (Cohen 1979).

All females are considered identical at this stage, and sites are judged by the demographic performance of any occupant. I call the resulting dominant eigenvalue λ_s , the site λ . It is the rate at which a SSD of descendants occupying an unlimited supply of identical sites would increase. Also, for an individual with a mutant genotype that results in that individual bearing the vital rates of (1) in the context of a background population with different vital rates, λ_s is the relevant measure of fitness for determining whether this mutant genotype can invade the background population (Caswell 2001, § 11.3).

For such a stage-based projection matrix P_s , there is a well-defined notion of net reproductive rate R_0 (Caswell 2001 § 5.3.4), which in the present circumstances measures the expected number of offspring produced by an individual during its life on this site (Caswell 2001:128). In the Appendix, it is shown that λ_s is greater than/equal to/less than one iff R_0 is greater than/equal to/less than one, respectively. I define a site to be a *source* site if and only if

$$R_0 > 1 \quad (3)$$

which by the result quoted above from the Appendix, equivalently, is one for which λ_s is greater than one. By (A2), this condition is

$$\frac{\sigma \sigma_A f_A}{1 - \sigma_A} > 1 \quad (4)$$

Replacing $>$ by equality in the definition yields a *maintenance site*, while replacing $>$ by $<$ defines a *sink* site.

An alternative to model (1) allows maturing adults to reproduce immediately, i.e., the penultimate entry in the first row of the matrix (1) is replaced by the nonzero entry $f_A \sigma_{m+1}$. For this alternative model, $R_0 = f_A \sigma (1 - \sigma_A)^{-1}$, i.e., differs from (1) by the absence of σ_A in the numerator as one might expect as individuals do not wait an extra year with survival rate σ_A before reproducing. When $\sigma_{m+1} = \sigma_A$, one can pool S_m individuals with adults into a single life stage and then the alternative model reduces to model (1), with m replaced by $m - 1$. Thus, one can view the essential difference between the two models as the rate at which individuals survive during the year ending with their first reproduction.

Founding of a population occupying source sites

Consider a habitat consisting of N unoccupied source sites, of identical quality. Assuming the population dynamics is modeled by (1–2), since $R_0 > 1$, then, as shown in the Appendix, $\lambda_s > 1$. Thus, no number of occupied source sites can

constitute a self-sustaining equilibrium; any initial population will grow. This mathematical result ignores a biological constraint, however, as it allows abundances less than one in a life stage to grow, which veils an issue for establishment of a population.

Suppose $n \leq N$ breeding pairs occupy sites in year labeled zero to breed first in year one. Projecting the population via (1), $f_A \sigma_A n$ female fledglings result from the first breeding season, which takes $m + 1$ years to become adults and a further year to become reproductively active adults (breeders) occupying sites. During these $m + 3$ years, attrition of adults leaves $k = (\sigma_A)^{m+3} n$ sites occupied by breeders. If $k \geq 1$, the first cohort of new breeders supplements the k remaining founders and the number of occupied sites increases. The following year, $(1 - \sigma_A)k$ of those occupying the k sites die and a new cohort of breeders, derived from the founders that survived to year two (namely $(\sigma_A)^2 n$), is available to occupy sites. Since $(\sigma_A)^2 n \geq k = (\sigma_A)^{m+3} n$, by the definition of a source site, this new cohort is sufficient to compensate the $(1 - \sigma_A)k$ sites that became vacant due to adult attrition, i.e., site occupancy remains at least k . Likewise, since each subsequent cohort of new breeders always derives from at least k sites, then site occupancy remains at least k by assumption that sites are sources. Since there can be no self-sustaining equilibrium on source sites, this population must grow and eventually occupy all N sites.

On the other hand, if $k < 1$, then in year $m + 3$, the founders have effectively died out (even if the model projects a nonzero number of surviving founders) and only new breeders occupy sites. These in turn suffer attrition and are supplemented the following year by the cohort of new breeders derived from the founders still alive in year two. In this scenario, there exists an actual possibility of population extinction, dependent on the size n of the founding population, the time m to maturity, and the survival and fecundity rates. For a real population, m will not be very large so the lag in production of the first cohort of maturing fledglings will not be too great and the factor most important for whether an actual founding population achieves success in establishing itself is likely n , the size of the founding population. For example, the vital rates, with anthropogenic mortality censored, of the golden eagle population of Hunt et al. (2017) are: $m = 3$; $f_A = 0.2313$ (female fledglings per pair); $\sigma_1 = 0.893$; $\sigma_2 = \sigma_3 = \sigma_4 = 0.978$; $\sigma_A = 0.935$, $R_0 = 2.78$. Simulation 1 (all simulations, i.e., numerical instances of the models, are displayed in Supplement.xlsx, with additional text in Supplement.pdf) provides an example of how a population increases with this regime of vital rates when sites are unlimited in number. Using (1) to project a founding population of n breeding pairs and, at each census, setting any abundances less than one to zero, for $n \leq 5$, the population goes extinct within 24 years (simulation 2a), while for $n \geq 6$, the population grows indefinitely. A more realistic

approach to modeling these circumstances would be an individual-based model in which survival rates are interpreted as probabilities and fecundities replaced by a probability distribution for possible numbers fledged.

Of course, founding of a population can be aided by multiple immigration events to sustain site occupancy during the initial $m + 1$ years before a cohort of fledglings mature. Also, subadults may occupy vacant sites and attempt to breed (Steenhof et al. 1983; Balbontin et al. 2003; Ferrer et al. 2003). My concern, however, is with the dynamics of an established population and the theoretical possibility of equilibrium.

Dynamics with two distinct site qualities

Now consider a habitat consisting of N identical source sites (hereafter *primary sites*) and M identical sites of lower quality (hereafter *secondary sites*), but for the moment, I leave unspecified whether the latter are source or sink sites. Denote the net reproductive rate on the former by R_0^P and on the latter by R_0^S . I assume a founding population has grown to occupy all N primary sites and that these sites are now always occupied by breeders. Model (1) is replaced by.

$$P_{SS} = \begin{pmatrix} 0 & 0 & \dots & 0 & f_S(1 - \tau)\sigma_S & f_P \\ \sigma_1 & 0 & \dots & 0 & 0 & 0 \\ 0 & \sigma_2 & \dots & 0 & 0 & 0 \\ \vdots & \vdots & \ddots & \vdots & \vdots & \vdots \\ 0 & 0 & \dots & \sigma_{m+1} & (1 - \tau)\sigma_S & 0 \\ 0 & 0 & 0 & 0 & \tau\sigma_S & \sigma_P \end{pmatrix} \quad (5)$$

Occupants of primary sites will be called *primary adults* (denoted PA) and occupants of secondary sites *secondary adults* (denoted SA). The subadults maturing to adult status are included initially within the secondary adults and become breeders the following year, as either primary or secondary adults. (This assumption reflects an aspect of site dependence and plays a delicate role in the dynamics and resulting equilibria, as these individuals may experience reduced survival during their first year as adults compared to primary adults.) Thus, τ is the proportion of secondary adults that survived the previous year and transition to become primary adults (i.e., occupy a primary site) in the current year. Note that by assumption, there are always N primary adults at breeding/fledging (the projection via the last row always sums to N) so there is no survival factor in the final entry of the first row. I assume here that M is large enough to accommodate all secondary adults so that all adults acquire a site. Equation 2a is modified to become.

$$S_0(t + 1) = f_S(1 - \tau_{t+1})\sigma_S SA(t) + f_P N \quad (6a)$$

and Eq. 2c is replaced by two equations:

$$SA(t + 1) = \sigma_{m+1} S_m(t) + (1 - \tau_{t+1})\sigma_S SA(t) \quad (6b)$$

$$N = \tau_{t+1}\sigma_S SA(t) + \sigma_P N \quad (6c)$$

Note the transition rate τ is time-dependent. Combining (6a), (2b), and (6b) yields.

$$\begin{aligned} SA(t + 1) &= \sigma S_0(t - m) + (1 - \tau_{t+1})\sigma_S SA(t) \\ &= \sigma [f_S(1 - \tau_{t+m})\sigma_S SA(t - m - 1) + f_P N] + (1 - \tau_{t+1})\sigma_S SA(t) \\ &= \sigma f_S(1 - \tau_{t-m})\sigma_S SA(t - m - 1) + (1 - \tau_{t+1})\sigma_S SA(t) + \sigma f_P N \end{aligned} \quad (6d)$$

Observe that (6d) is a modified version of (2d), in which SA survival is $(1 - \tau_{t+1})\sigma_S$ and there is a constant annual immigration of $\sigma f_P N$ individuals. Rewriting (6c) as

$$\tau_{t+1} SA(t) = \frac{(1 - \sigma_P)N}{\sigma_S} \quad (6e)$$

shows that time dependence of τ can be regarded as an inverse density dependence. Thus, the population dynamics on secondary sites can be interpreted as the intrinsic dynamics of secondary sites modified by an inverse density dependence of adult survival combined with a constant annual influx of immigrants from primary sites. While the latter aids the growth of the population of secondary adults, the former suggests that at low numbers, the modified survival rate may reduce the effective net reproductive rate R_0^S of secondary sites.

Removing the time dependence from (6d and (6e) gives the conditions on the secondary adult population for equilibrium:

$$SA = \sigma f_S(1 - \tau)\sigma_S SA + (1 - \tau)\sigma_S SA + \sigma f_P N \quad \tau\sigma_S SA = (1 - \sigma_P)N \quad (7)$$

Using the second equation of (7) to eliminate τ from the first equation of (7), one can write the equilibrium condition for SA as:

$$0 = (1 - \sigma_S)(R_0^S - 1)SA + (1 - \sigma_P)N \left[\frac{\sigma f_P}{(1 - \sigma_P)} - 1 \right] - f_S \sigma (1 - \sigma_P)N \quad (8)$$

where R_0^P is the net reproductive rate of primary sites.

Model (5) will not be valid if there are insufficient numbers of SAs to fill all vacancies in primary sites; (6c), e.g., would imply $\tau > 1$, an illegitimate value. I will assume that primary sites not occupied by adults of breeding age can be occupied by individuals of age $m + 1$, i.e., by non-breeding adults. Since the primary sites are source sites, there will always be enough such individuals to fully occupy the N primary sites. Such $(m + 1)$ -aged individuals enjoy the adult survival rate of primary sites but must survive a further year to breed.

(If one did not allow such individuals to occupy vacant primary sites, all $(m + 1)$ -aged individuals would experience the adult survival rate of secondary sites during their first year of adulthood. In that case, there are scenarios in which the number of both SAs and PAs decline to extinction. I do not treat this possibility here.) While the number of PAs at each census is still N , not all of these are breeding adults, denoted PB, though those that survive to the next census have bred just prior to that census. Since all surviving SAs from the previous census have filled primary sites that have become vacant, $\tau = 1$ at each census. In place of (5), the projection matrix is now.

$$P_{SS} = \begin{pmatrix} 0 & 0 & \dots & 0 & f_p \sigma_S & f_p \sigma_P \\ \sigma_1 & 0 & \dots & 0 & 0 & 0 \\ 0 & \sigma_2 & \dots & 0 & 0 & 0 \\ \vdots & \vdots & \ddots & \vdots & \vdots & \vdots \\ 0 & 0 & \dots & (1 - \mu) \sigma_{m+1} & 0 & 0 \\ 0 & 0 & 0 & \mu \sigma_{m+1} & \sigma_S & \sigma_P \end{pmatrix} \tag{9}$$

(6a) is replaced by.

$$S_0(t + 1) = f_p \sigma_S SA(t) + f_p \sigma_P PA(t) = f_p PB(t) \tag{10a}$$

(6b) by.

$$SA(t + 1) = (1 - \mu_{t+1}) \sigma_{m+1} S_m(t) \tag{10b}$$

(6c) by.

$$PB(t + 1) = \sigma_S SA(t) + \sigma_P N \tag{10c}$$

and there is the new equation.

$$N = PA(t + 1) = \mu \sigma_{m+1} S_m(t) + \sigma_S SA(t) + \sigma_P N \tag{10d}$$

Imposing the equilibrium conditions on Eq. 10, Eqs. 10a, 10b, and 10c become.

$$S_0 = f_p (\sigma_S SA + \sigma_P N) \quad \mu \sigma S_0 = \sigma S_0 - SA \quad PB = \sigma_S SA + \sigma_P N \tag{11}$$

and (10d) becomes, after eliminating μ via (11),

$$0 = (1 - \sigma_S) \left[\frac{\sigma f_p \sigma_S}{(1 - \sigma_S)} - 1 \right] SA + (1 - \sigma_P) [R_0^P - 1] N \tag{12}$$

The ratio of SAs to PAs of possible equilibria is readily obtained from (8) and (12).

Scenarios in which the number of SAs is sometimes adequate to fill vacancies in primary sites and at other times not adequate require the utilization of both projection matrices (5) and (9), but at different time steps, e.g., simulation 5.

Source-source dynamics

Simulation 3 consists of 50 primary sites with the vital rate regime of Hunt et al. (2017) and an unlimited number of secondary source sites, with slightly lower adult survival and fecundity, exhibiting the expected result of unbounded growth on secondary sites. Equations 6d and 6e, however, suggest the possibility of an equilibrium, even if the secondary sites are intrinsically source sites. Assuming $R_0^S > 1$, a positive value for SA occurs in (8) if and only if.

$$f_S \sigma (1 - \sigma_P) N > (1 - \sigma_P) N \left[\frac{\sigma f_P}{1 - \sigma_P} - 1 \right], \text{ i.e.,} \\ f_S \sigma > \left[\frac{\sigma f_P}{(1 - \sigma_P)} - 1 \right] \tag{13}$$

Note that $R_0^P > 1$ implies the term in square brackets in (13) is positive. Inequality (13) will hold if $f_S \sigma > \frac{\sigma f_P}{(1 - \sigma_P)}$, which in turn is greater than $f_P \sigma$, which implies $f_S > f_P$. The last inequality then requires $\sigma_S < \sigma_P$ to preserve $R_0^P > R_0^S$. Simulation 4 provides an explicit example of a nontrivial equilibrium with 50 primary source sites, an unlimited availability of secondary source sites, of which a fixed finite number (125.68) is occupied each year. The equilibrium transition rate $\tau = 0.85$ in this example, and the intrinsic survival rate σ_S is reduced to an effective survival rate for SAs of $(1 - \tau) \sigma_S = 0.04$, which entails an effective net reproductive rate of 0.12 for the secondary sites. Note that these effective rates are not averages over site quality but reflect the dynamics of site dependence in that SAs prefer vacant primary sites to secondary sites. If they did not, the population of SAs would grow to fill all available secondary sites. Thus, despite the constant annual influx of immigrants from the production on primary sites, the loss of secondary adults to fill annually occurring vacancies on primary sites converts the secondary sites effectively into sink sites even though the intrinsic quality of the secondary sites has not changed. Recall that it is secondary adults, not maturing adults from primary sites, that first fill vacancies on primary sites. The limited number of primary sites is also essential for an equilibrium. For simulation 4, the mean site quality is 1.19, the mean adult fecundity is 7.43, the mean adult survival rate is 0.31, and the latter two imply a net reproductive rate of 1.20 (simulation 4). Thus, these mean values do not explain the existence of the equilibrium.

Assuming model (5) describes small perturbations of this equilibrium, local stability analysis (Caswell 2001, §16.4) indicates that this equilibrium is unstable (Supplement.pdf). Before examining this instability further, consider possible equilibria of model (9). An equilibrium with positive SA in (12) requires, (recall that $f_P < f_S$ in this context)

$$\frac{\sigma f_p \sigma_S}{(1 - \sigma_S)} < 1 \tag{14}$$

The vital rates of simulation 4 that permit an equilibrium of (5) also satisfy (14) and thus allow an equilibrium of model (9) too, for which SA = 96.91, PB = 47.13, and $\mu = 0.03$. Once again, the mean vital rates do not explain this equilibrium (Supplement.xlsx). In simulation 4, perturbing the equilibrium value of SA to exactly 125, one observes that after 270 time steps, model (5) is no longer satisfied with a value of $\tau \leq 1$. Thus, a simulation that applies model (5) or (9), as appropriate at each time step, is necessary to explore the dynamics. Simulation 5 encodes this scenario for the data of simulation 4. One now observes that when perturbing the value of SA lower than the equilibrium value for model (5), the population now converges on the equilibrium of model (9). Perturbing the value of SA higher than the equilibrium value for model (5), the population of SAs grows without bound. These simulation results are consistent with instability of the equilibrium of model (5). Simulation 6 encodes both models (5) and (9) again, but for the equilibrium of (9). Local stability analysis (Caswell 2001, §16.4) implies that, assuming (9) is valid for small perturbations x of its equilibrium, the equilibrium is asymptotically stable (Supplement.pdf). Perturbing SA in simulation 6 is consistent with asymptotic stability.

While the mathematical existence of such equilibria is the focus of this paper, it is a separate issue to the ecological question of whether such an equilibrium would arise in nature. The vital rates in the simulations are unrealistic for raptors, though perhaps not for insects. The theoretical model also assumes that abundances take real, rather than whole number, values.

I note in passing that model (5) admits an equilibrium with $R_0^S = 1$ if the inequality (13) is replaced by an equality, for any value of SA.

Source-sink dynamics

Now suppose the secondary sites are sinks: $R_0^S < 1$. Equation (8) then requires the reverse inequality to (13) to obtain a positive value of SA at equilibrium, which is a less severe constraint. Simulation 7 exhibits a solution for which 50 primary source sites are parametrized by Hunt et al. (2017), while secondary sink sites have lower fecundity (0.1) and slightly lower adult survival (0.9), resulting in $R_0^S = 0.75$ and an equilibrium with SA = 247.37. Local stability analysis demonstrates that the equilibrium is asymptotically stable (provided model (5) describes small perturbations; Supplement.pdf). Perturbing SA in simulation 7 is consistent with asymptotic stability.

Secondary sites with lower survival may be insufficient to fill all annual vacant primary sites, thus requiring model (9).

In simulation 7, reducing survival of SAs results at first in equilibria with fewer SAs and higher τ . But for $\sigma_S = 0.33$, the equilibrium of model (5) can no longer be achieved, model (9) comes into play, and an equilibrium with nonzero μ occurs, for which (12) describes the equilibrium SA value rather than (8). The condition for an equilibrium with positive SA is still (14). Since $R_0^S < 1$, (14) makes clear that σ_S must be small enough that even with the fecundity of primary sites, secondary sites would still be sinks. Simulation 8 exhibits the equilibrium of model (9) for the same data as simulation 7 except that $\sigma_S = 0.33$. Note that for σ_S at least 0.34, simulation 8 converges on the equilibrium of model (5) described by simulation 7 with that value for σ_S . Local stability analysis of the equilibrium of model (9) demonstrates that the equilibrium is asymptotically stable (provided model (9) describes small perturbations; Supplement.pdf). Perturbing SA in simulation 8 is consistent with asymptotic stability.

For neither equilibrium do the mean vital rates provide a compelling explanation for the existence of these equilibria. In simulations 7 and 8, mean net reproductive rates are greater than one but net reproductive rates implied by mean fecundity and adult survival are less than one, neither of which by itself implies a nontrivial equilibrium. While there is an ongoing injection of individuals into secondary sites from the excess production of primary breeders, these individuals cannot, by the nature of sink sites, create permanent lineages on sink sites. The equilibrium results from the limited supply, each year, from primary sites to secondary sites that can balance the intrinsic winnowing on sink sites. One would therefore expect that an equilibrium always results from source-sink dynamics. Failure of an equilibrium to occur would require $R_0^P > 1$, $R_0^S < 1$, inequality (13), and the converse inequality to (14). But these conditions are incompatible. For convenience, write $x = \zeta / (1 - \zeta)$, for any survival parameter ζ , whence $1 / (1 - \zeta) = x + 1$. Now $R_0^S < 1$ is $\sigma f_S x_S < 1$, whence $1 / x_S > \sigma f_S > \sigma f_P (x_P + 1) - 1$, by (13), i.e., $1 > \sigma f_P x_S (x_P + 1) - x_S$. The converse of (14) is $\sigma f_P x_S > 1$, so combining with the previous inequality yields $1 > 1 \cdot (x_P + 1) - x_S$, i.e., $x_S > x_P$.

Since $\sigma f_P x_P = R_0^P > R_0^S = \sigma f_S x_S$, then one must have $f_P > f_S$. Hence, $\sigma f_P > \sigma f_S > \frac{\sigma f_P}{1 - \sigma_P} - 1$, by (13). Therefore, $\sigma f_P (1 - \sigma_P) > \sigma f_P - (1 - \sigma_P)$, which, upon expanding the left-hand side, canceling the σf_P 's and rearranging is equivalent to $1 > R_0^P$, a contradiction.

Source-floater dynamics

“Floating” is an alternative strategy to occupation of a secondary site in which an adult refuses secondary sites, preferring to wait for a vacancy in a primary site (Kokko and Sutherland 1998; or possibly evict an occupant of a primary site, although I do not consider that possibility in these

models). Presumably, in populations that adopt the floating strategy, floaters enjoy greater survival than they would by occupying secondary sites.

Mathematically, source-floater dynamics can be considered the extreme case of source-sink dynamics in which f_S , whence R_0^S , is zero. (I am ignoring here any subtleties involving when floaters transition to breeders such as contemplated in Hunt et al. 2017, Appendix 3 as they are not germane to the purpose of this paper.) For model (5), the condition for an equilibrium is, thus, from the reverse inequality of (13),

$$\frac{\sigma f_P}{1 - \sigma_P} > 1 \quad (15)$$

and, since the left-hand side is at least R_0^P , this inequality is satisfied. The floater-to-breeder ratio for this equilibrium is from (8)

$$\frac{F}{B} = \frac{\sigma f_P - (1 - \sigma_P)}{1 - \sigma_F}$$

where F replaces SA, B replaces PA, and σ_F replaces σ_S . The survival rate of floaters, with anthropogenic mortalities censored, in Hunt et al.'s (2017) study of a golden eagle population was 0.924. Simulation 9 exhibits this equilibrium, which is asymptotically stable as for source-sink dynamics, for the data of Hunt et al. (2017). A reduction of floater survival below 0.337 in this simulation is required to entail a value of $\tau > 1$, indicating that model (9) now describes an equilibrium, which is exhibited in simulation 10. The condition for an equilibrium of model (9) is again (14), which entails a survival rate of floaters that in effect reduces the net reproductive rate they would have with fecundity f_P below one. The floater-to-breeder ratio for this equilibrium is readily obtained from (12).

Once again, the mean vital rates do not suggest explanations for the occurrence of equilibrium. For source-floater dynamics, there is in fact a simple conceptual explanation, assuming that all primary sites are fully occupied at each breeding event by breeders (i.e., neglecting any subtleties in the establishment of such a breeding population). Let F_1 denote the youngest cohort of floaters at a birth pulse (BP₁) old enough to breed. This cohort is reduced by loss to fill vacant (primary) sites (for simplicity assume the cohort is large enough to replace all breeder deaths) at BP₁ and then survival over a further year. A new cohort F_2 occurs at the next birth pulse, BP₂, equal in number to F_1 at BP₁. Numerically, one can assume the members of F_2 fill site vacancies at BP₂. This pattern now repeats, with a new cohort added at each birth pulse, and each pre-existing cohort suffering attrition due to mortality. When the remaining survivors of F_1 die of old age after finitely many years, the remaining floaters consist of a distribution of, say, n floater cohorts that is now unchanging. Since there are only finitely many

cohorts, there are only finitely many floaters, and an equilibrium is established. This argument illustrates that it is the limited number of breeders that results in a limited number of floaters and an equilibrium (dubbed ‘‘Moffat’s equilibrium’’ by Hunt 1998).

Summary of modeling results

The crucial assumptions underlying the modeling results are those of site-dependent dynamics, namely, preference for the highest-quality site available and pre-emptive occupation, combined with the limited number N of primary sites. The life history assumptions were chosen to model birth-pulse site-dependent species, similarly to Rodenhouse et al. (1997) but more general.

Equations 1 and 2 characterize a population with a single kind of site. For an unlimited number of source sites, the population grows without bound, a well-known scenario. Table 3 provides a summary of the three modeling scenarios with two kinds of site. In each case, to investigate equilibrium, it is assumed that all N primary (source) sites are occupied at census. The number M of secondary sites is allowed to be as large as necessary to accommodate the number occupied at equilibrium so that M itself does not impose constraints. In each scenario, model (5) applies when there are sufficient adults of breeding age to occupy all N primary sites. Model (9) applies when there are insufficient adults of breeding age to occupy all N primary sites so that the shortfall is filled by first-year adults (of age $m + 1$), who nevertheless must wait a year before breeding.

Generically, source-source dynamics result in an expanding population that occupies as many secondary sites as are available. Under certain circumstances, however, an equilibrium is possible for source-source dynamics resulting in a limited number of secondary sites occupied, as indicated in the table. Equilibrium always results from source-sink dynamics and from the special case of source-floater dynamics.

For each equilibrium, the number of secondary sites occupied and the population size are determined by N and the individual demographic parameters of the relevant model, not the vital rates averaged over sites. The numerical examples provided by the simulations show that the average of demographic parameters over site quality does not explain the existence of equilibrium or the size of the equilibrium population.

Source-floater-sink dynamics and further considerations

The previous sections constitute the evidence for my explanation for equilibria in the population dynamics of site-dependent species, to be elaborated in the ‘‘Discussion.’’

Table 3 Summary of model results

Model scenario	Model equations	Equilibrium equations	Stability
Source-source $R_0^p > R_0^s > 1$	(5)	(8) ^a	Unstable
Source-source $R_0^p > R_0^s > 1$	(9)	(12) ^b	Asymptotically stable
Source-sink $R_0^p > 1 > R_0^s > 0$	(5) or (9)	(8) or (12), respectively	Asymptotically stable
Source-floater $R_0^p > 1 > R_0^s = 0$	(5) or (9)	(8) or (12), respectively	Asymptotically stable

Source-floater-sink dynamics and further generalizations $\frac{\sigma_f \sigma_s}{(1-\sigma_s)} < 1$

^aFor certain values of the demographic parameters satisfying, e.g., $f_p < f_s$ and $\sigma_p > \sigma_s$

^bFor certain values of the demographic parameters satisfying $f_p < f_s$ and $\frac{\sigma_f \sigma_s}{(1-\sigma_s)} < 1$

Here, I sketch generalizations of the basic models that are more ecologically realistic, although more difficult to analyze. For populations that adopt the floating strategy, it may be that as floaters age, secondary sites become attractive due to diminishing potential reproductive value on primary sites (Zack and Stutchbury 1992). If a floater occupies a site at a breeding pulse and has further k years of lifespan, one can take as a measure of its future reproductive value on a site with fecundity f and annual survival rate ζ :

$$V(k) = f + \zeta f + \zeta^2 f + \dots + \zeta^k f = f \left(\frac{1 - \zeta^{k+1}}{1 - \zeta} \right)$$

assuming the population is at equilibrium (Caswell 2001:188). To incorporate $V(k)$ into the dynamical model, one must model the floaters as age-based. Suppose an individual has final breeding opportunity at age $m + 1 + n$, dying after fledging the young of that birth pulse. To replace (5), consider

$$\begin{pmatrix} 0 & 0 & \dots & 0 & f_s v_1 (1 - \tau_1) \sigma_F & \dots & f_s v_n (1 - \tau_n) \sigma_F & f_s (1 - \tau) \sigma_S & f_P \\ \sigma_1 & 0 & \dots & 0 & 0 & \dots & 0 & 0 & 0 \\ 0 & \sigma_2 & \dots & 0 & 0 & \dots & 0 & 0 & 0 \\ \vdots & \vdots & \ddots & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots \\ 0 & 0 & \dots & \sigma_{m+1} & 0 & \dots & 0 & 0 & 0 \\ 0 & 0 & \dots & 0 & (1 - v_1)(1 - \tau_1) \sigma_F & \dots & 0 & 0 & 0 \\ 0 & 0 & \dots & 0 & 0 & \ddots & \vdots & \vdots & \vdots \\ \vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots \\ 0 & 0 & \dots & 0 & 0 & (1 - v_n)(1 - \tau_n) \sigma_F & 0 & 0 & 0 \\ 0 & 0 & \dots & 0 & v_1 (1 - \tau_1) \sigma_F & \dots & v_n (1 - \tau_n) \sigma_F & (1 - \tau) \sigma_S & 0 \\ 0 & 0 & 0 & 0 & \tau_1 \sigma_F & \dots & \tau_n \sigma_F & \tau \sigma_S & \sigma_P \end{pmatrix}$$

acting on the population vector (in row form)

$$(S_0, \dots, S_{m+1}, F_1, \dots, F_{n-1}, SA, PA)$$

where, for equilibrium, one supposes $PA = N$ at each birth pulse, i.e., the bottom row always sums to N , F_i denotes floaters of age $m + 1 + i$, $i = 1, \dots, n - 1$. Note that floaters of age $m + 1 + n$ need not be included in the population vector

as they do not survive a further year. S_{m+1} denotes adults that are not yet old enough to breed and σ_F is the survival rate of floaters. The parameter τ_i denotes the probability of a floater of age $m + 1 + i$ occupying a primary site, $i = 1, \dots, n - 1$, while v_i denotes the probability of a floater of that age occupying a secondary site. An obvious challenge in utilizing such a model is assigning values to the τ_i and v_i . While the model allows SAs to fill vacant primary sites, it does not allow them to revert to floating. One might suppose, however, that an individual who has committed to occupying a secondary site cannot compete with floaters to fill vacant primary sites, i.e., $\tau = 0$.

If only floaters compete for sites, since there are a fixed number of vacancies each year and, at equilibrium, a fixed number of floaters, the probability of a given floater filling a vacancy is constant, unless it is age dependent, viz., τ_i . A floater that does not obtain a primary site at age $m + 1 + i$ has reproductive value $V^p(n - i)$ if it gains a primary site next year so its potential reproductive value on a primary site is currently $\sigma_F \tau_{i+1} V^p(n - i)$ while its current reproductive value if it occupies a secondary site at age $m + 1 + i$ is $V^s(n - i + 1)$. One might propose that $v_i = 0$ until the former quantity is less than the latter, at which time $v_i = 1$.

While this model is more interesting than (5), it is likely suitable only for numerical simulation studies and would be challenging to parametrize for any species of interest. The theoretical speculation of the previous paragraph suggests a line of research for a given species as regards the ability of individuals to assess their current and future (potential) reproductive value.

The quality of sites has, so far, been treated as intrinsic, in particular, unaffected by density (supported by Ferrer and Donazar 1996) but several modifications are plausible. Increasing density, especially of floaters, might result in negative density feedback interactions (Haller 1996; Nevoux et al. 2011; Katzenberger et al. 2021). Overall, site quality might depend on the fitness of the occupant (Reynolds et al. 2019), requiring individual-based models. Spatially explicit

models can include consequences of the distribution of heterogeneous sites, such as the cost of search effort (Forsman and Kivelä 2022) and interference from competing species (Rockweit et al. 2023). Demographic and environmental stochasticity can also be included in modeling (Monzón and Friedenberg 2018). All these refinements of the basic model pose considerable challenge as regards parameter estimation and analysis and are, most likely, profitably pursued in the context of a specific population.

Discussion

I have employed a dynamical model, based on the life history of golden eagles, to explore how equilibria arise in site-dependent dynamics. Rodenhouse et al. (1997) conducted simulations of a model involving pre-emptive use of sites of varying quality assuming that sites of highest available quality were filled preferentially and argued that (p. 2026) “Population size will not continue to grow indefinitely, even with continued use of sites of highest suitability, because breeding productivity on these sites will be balanced at some population size by low breeding productivity or survival on sites of lower suitability. Use of progressively less suitable sites reduces average demographic rates as a whole... which slows population growth.” These authors interpreted these simulations as indicating that the resulting equilibria were explained by the average of demographic rates over sites and argued this interpretation provided a new mechanism for site-dependent equilibrium.

But all their simulations assumed a finite number of sites and thus a limited number of sites above replacement level, i.e., source sites. As the models in this paper demonstrate, it is this limitation that is ultimately responsible for equilibria. Moreover, the mean demographic rates in the explicit simulations of these models do not provide explanations of the resulting equilibria. Indeed, the vital rates averaged over sites play no dynamical role and no individual experiences them. They are summary statistics only. Sites of lower quality, secondary sites, are only occupied, or floaters generated, due to the limited production of excess individuals from the limited number of source sites. Once all source sites are occupied, equilibrium is inevitable. The size of that equilibrium does depend on the quality of the sink sites or the option to float but these are consequences of the limited supply of source sites. An equilibrium is possible when both primary and secondary sites are source sites, in stark contrast to the expectation of Rodenhouse et al. “Of course, site dependence could not be regulatory if all sites produced recruits in excess of replacement level...” (p. 2028). The rates used in the explicit model for the source-source equilibrium are unrealistic for raptors, more generally birds, but do not undermine the theoretical significance of this result.

Namely, a limited supply of the best source sites can still result in an equilibrium when there is an unlimited supply of source sites of lower quality, and the primary sites impose a sufficient drain on the adults available for secondary sites. But again, in simulation 4 (Supplement.xlsx), the mean demographic parameters do not provide an explanation of this equilibrium.

When a species is site dependent, a limited number of primary source sites results in a limited number each year of offspring and thus a limited number of surplus adults for future occupation of secondary sites. If secondary sites are sink sites, the occupiers of secondary sites cannot generate an equilibrium themselves on those sites; any equilibrium must rely on the limited production of primary sites. This conclusion has been demonstrated explicitly with my models and appears robust to the life-history assumptions of my models. The surprising *theoretical* possibility of an equilibrium with source-source dynamics, however, may depend on my life-history assumptions, which, I emphasize, are realistic for a range of species (simple life-history and birth-pulse demography). Whether an actual equilibrium occurs in my models of source-source dynamics does depend on the vital rate regimes of both kinds of source sites. Note, however, that site-dependent dynamics are an essential feature of the equilibrium. If the individuals produced by occupied secondary source sites ignored the primary sites, contrary to site-dependent dynamics, their population would grow to accommodate whatever number of secondary sites is available, rather than establish an equilibrium involving the occupants of primary sites. It is an interesting question whether source-source equilibria are possible with different, but still biologically realistic, life-history assumptions for site-dependent species.

Pre-emptive occupation of sites of the highest quality is essential to the models presented here, as assumed also by Rodenhouse et al. On the other hand, Rodenhouse et al. would likely object to my definition of site quality as net reproductive success. They asserted (all quotations from p. 2037) “suitability, according to site dependence, can be assessed independently of reproductive success or survival (e.g., using food or predator abundance), avoiding the tautology of defining site suitability in the same demographic terms used to measure site suitability. According to site dependence, differences among sites are the consequences of environmental differences. In contrast, source and sink habitats are defined by net recruitment (i.e., the outcome of births, immigration, deaths, and emigration). Consequently, identifying a source or sink habitat provides no mechanistic understanding of sources or sinks.” I rejoinder that one identifies environmental contributions to suitability ultimately in terms of their effects on fitness, i.e., demography. Rodenhouse et al. further say their proposal would be rebutted “if differences in suitability, as measured by environmental

variables, failed to predict differences in demographic traits”; but surely, this result would only mean the measures of the environmental factors contributing to fitness were in error or missing some additional factor, e.g., competition, as with the presence of barred owls (*Strix varia*) impacting the quality of sites for northern spotted owls (*Strix occidentalis caurina*) (Rockweit et al. 2023). To quote Pulliam (2000) “...ecologists must measure habitat specific demography and quantify how demographic parameters vary in response to temporal and spatial variation in measurable niche dimensions.” i.e., site quality is ultimately determined by demographic performance on site. I contend that Pulliam’s assertion provides the path to a mechanistic understanding of sources and sinks.

In response to Rodenhouse et al. (1997), Hunt and Law (2000) employed a conceptual model of the production and fates of cohorts of site-dependent populations to argue that the decrease in mean demographic parameters as more sink sites become occupied (or the floater buffer grows) is a mere statistical effect, not an explanatory mechanism for equilibrium, which, they argued, results from the limited supply of source sites. The explicit dynamical models analyzed here reinforce their conclusion but also reveal subtleties in the equilibria of site-dependent dynamics.

Rodenhouse et al. (2000) rejected Hunt and Law’s contention that Rodenhouse et al. (1997) highlighted only a statistical effect by asserting that they “focus the operation of regulatory mechanism at the level of the individual.” But, by assumption of site-dependence dynamics, an occupant of a site is unaffected by the presence of other individuals, so in what mechanistic sense do mean demographic rates of the population affect any individual? An equilibrium is theoretically possible even with two kinds of source sites, albeit only with certain demographic rates, and perhaps life-history assumptions, highlighting that the dynamics on the secondary source sites are affected by the presence of the primary source sites but not

by assumption, sites of the highest quality are filled preferentially, and it is the limitation on the number of these sites that is necessary for any resulting equilibrium. That one of their equilibria involved the production of 2.15 fledglings per pair on the poorest site of the simulation only indicates that one must consider the net reproductive rate in assessing site quality, which involves survival beyond the fledgling state.

In conclusion, attributing a causal role to a statistical summary in the dynamics of site-dependent populations misdirects attention from the true nature of the dynamics, with consequences not only for understanding these dynamics but also for conservation efforts for such populations. According to the modeling presented in this paper, the most important factor in assessing the viability of a site-dependent population is the number of source sites. Any number can generate an equilibrium, the population size of which depends not only on the number of those sites but also on the vital rates of individuals that either float or occupy sink sites. A further complication is theoretically possible even for a habitat with only source sites but of differing quality, although perhaps unlikely for avian demographic parameters.

Appendix. Net reproductive rate R_0

One decomposes P_s as a sum of matrices T , which contains transition rates only, and F , which describes reproduction (Caswell 2001:110).

One forms the *fundamental matrix*:

$N = (1 - T)^{-1}$ and then the matrix $R := FN$. Since F has a single nonzero entry, R has nonzero entries only in its first row, which consists of the final row of N multiplied by the nonzero entry of F . It follows that the entry R_{11} of R is the only nonzero eigenvalue of R and this value is R_0 , namely.

$$\left(\begin{array}{cccccc} 1 & 0 & 0 & 0 & \dots & 0 \\ \sigma_1 & 1 & 0 & 0 & \dots & 0 \\ \sigma_2 \sigma_1 & \sigma_2 & 1 & 0 & \dots & 0 \\ \vdots & \vdots & \vdots & \vdots & \ddots & \vdots \\ \sigma_m \dots \sigma_1 & \sigma_m \dots \sigma_2 & \sigma_m \dots \sigma_3 & \sigma_m \dots \sigma_4 & \dots & 0 \\ (1 - \sigma_A)^{-1} \sigma_{m+1} \dots \sigma_1 & (1 - \sigma_A)^{-1} \sigma_{m+1} \dots \sigma_2 & (1 - \sigma_A)^{-1} \sigma_{m+1} \dots \sigma_3 & (1 - \sigma_A)^{-1} \sigma_{m+1} \dots \sigma_4 & \dots & (1 - \sigma_A)^{-1} \end{array} \right) \tag{A1}$$

simply through the mean demographic rates nor by altering intrinsic site quality. Moreover, the individual characteristics Rodenhouse et al. (1997: 2037) mention, the “ability to assess and compete for sites, their reproductive potential on specific sites, and their dispersal tendency” need be no less relevant to sources-sink dynamics as construed here.

Rodenhouse et al. (1997, 2000) also emphasized that the equilibria in their numerical simulations did not necessarily involve occupation of all sites, which they appear to believe was inconsistent with Hunt and Law’s argument. But, again

$$(1 - \sigma_A)^{-1} \sigma_{m+1} \dots \sigma_1 \sigma_A f_A = \frac{\sigma_A}{(1 - \sigma_A)} \sigma f_A \tag{A2}$$

The characteristic equation $0 = \det(P_s - \lambda I)$ for P_s is.

$$\lambda^{m+1} (\lambda - \sigma_A) = \sigma \sigma_A f_A \tag{A3}$$

whence.

$$(\lambda_s)^{m+1} (\lambda_s - \sigma_A) = (1 - \sigma_A) R_0 \tag{A4}$$

Since the right-hand side of (A4) is positive, it follows that $\lambda_s > \sigma_A$. When $\lambda_s = 1$, it follows that $R_0 = 1$. When $\lambda_s > 1$, $\lambda_s - \sigma_A > 1 - \sigma_A$, and $R_0 = (\lambda_s)^{m+1} (\lambda_s - \sigma_A) / (1 - \sigma_A) > 1$. Similarly, when $\lambda_s < 1$, it follows that R_0 is less than 1. It therefore follows that if, e.g., $R_0 = 1$, then, λ_s must equal one, for if not, λ_s must be greater than or less than one, which would imply that R_0 must be likewise. Hence, λ_s is less than/equal to/greater than 1 iff R_0 is less than/equal to/greater than 1, respectively. This result is a specific case of a general result (Caswell 2001:128).

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Declarations

Competing interests The author declares no competing interests.

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