



Isolating the roles of movement and reproduction on effective connectivity alters conservation priorities for an endangered bird

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Movement is important for ecological and evolutionary theory as well as connectivity conservation, which is increasingly critical for species responding to environmental change. Key ecological and evolutionary outcomes of movement, such as population growth and gene flow, require effective dispersal: movement that is followed by successful reproduction. However, the relative roles of movement and postmovement reproduction for effective dispersal and connectivity remain unclear. Here we isolate the contributions of movement and immigrant reproduction to effective dispersal and connectivity across the entire breeding range of an endangered raptor, the snail kite (*Rostrhamus sociabilis plumbeus*). To do so, we unite mark–resight data on movement and reproduction across 9 years and 27 breeding patches with an integrated model that decomposes effective dispersal into its hierarchical levels of movement, postmovement breeding attempt, and postmovement reproductive success. We found that immigrant reproduction limits effective dispersal more than movement for this endangered species, demonstrating that even highly mobile species may have limited effective connectivity due to reduced immigrant reproduction. We found different environmental limitations for the reproductive component of effective dispersal compared with movement, indicating that different conservation strategies may be needed when promoting effective dispersal rather than movement alone. We also demonstrate that considering immigrant reproduction, rather than movement alone, alters which patches are the most essential for connectivity, thereby changing conservation priorities. These results challenge the assumption that understanding movement alone is sufficient to infer connectivity and highlight that connectivity conservation may require not only fostering movement but also successful reproduction of immigrants.

connectivity | dispersal | gene flow | immigrant | network

Movement underlies many key processes in ecology and evolution (1–3). Consequently, movement has been at the core of a wide range of ecological and evolutionary theories, including the equilibrium theory of island biogeography, metapopulation and metacommunity theories, and population genetics theory (1, 4–6). Understanding the movement of organisms across populations and landscapes, often referred to as population or landscape connectivity, informs many conservation strategies, such as building corridors, designing and restoring protected areas, and translocations—all of which are becoming more critical over time with environmental change (7–10). Although movement is undoubtedly important to ecology, evolution, and conservation, in many cases it has the greatest effects if immigrants successfully reproduce upon arrival to new locations, what has been termed effective dispersal (11, 12).

Effective dispersal can have important effects on populations and communities, such as increasing immigrant fitness and gene flow, thereby shaping the ecological and evolutionary outcomes of movement across landscapes (5, 13, 14). Some of the earliest ideas on effective dispersal stem from plant ecology, such as understanding not only whether seeds are dispersed across a landscape

but also whether there is successful establishment of new individuals after arrival (15). In marine ecology, there is an increasing emphasis on how movement and subsequent recruitment may limit populations and the efficacy of marine protected areas (16, 17). In evolutionary biology, if both movement and successful immigrant reproduction occur, a major outcome of effective dispersal is gene flow (5), and it is this outcome that is increasingly emphasized in dispersal biology (2). Despite this widespread interest, isolating the roles of movement relative to immigrant reproduction on effective dispersal has remained challenging.

This challenge is particularly relevant for the problem of connectivity (17, 18). Metapopulation theory has long emphasized that connectivity and metapopulation persistence depend on colonization, which is the product of movement and population establishment (and thus successful immigrant reproduction; ref. 19). Demographic population models have also illustrated that appropriately interpreting connectivity requires understanding the roles of both movement and immigrant reproduction (12, 16, 17, 18). However, isolating the effects of movement and immigrant reproduction on connectivity in nature has been largely absent. Isolating these effects is needed for at least two reasons. First, isolating these effects could reveal separate mechanisms that may be influencing connectivity. For instance, habitat fragmentation can stimulate avian movement (20), yet it can also reduce reproductive output for many species of birds (21). Second, conservation strategies aimed at promoting connectivity to date have primarily focused on increasing movement (9, 22). However, if immigrant

Significance

Animal movement has captured the interest of biologists over the past century. Although animal movement is increasingly well understood, it is unclear how postmovement reproduction varies across landscapes despite its important role in many ecological and evolutionary processes. We address this problem by isolating the roles of movement and postmovement reproduction for connecting local populations using 9 years of data on an endangered bird across its entire geographic range. Our findings highlight the important role that postmovement reproduction can play for connecting animal populations across landscapes.

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Data deposition: Data for these analyses, as well as code and documentation for running the model, are available at figshare, <https://doi.org/10.6084/m9.figshare.6247619.v1>.

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reproduction plays a crucial role for effective dispersal, fostering immigrant reproduction and preserving key breeding locations may be necessary for promoting effective connectivity over time.

We link 9 y of data on individual movement and reproduction to understand effective dispersal and connectivity for the federally endangered snail kite (*Rostrhamus sociabilis*) across its entire geographic range in the United States. To do so, we focus on outcomes of connectivity that can lead to gene flow, given its prominent focus in dispersal biology and connectivity science (2), by examining the emergence of effective dispersal across a landscape, what we term “effective connectivity.” We derive a hierarchical model that provides predictions of effective connectivity and decomposes the components of effective dispersal: movement from natal patches to nonnatal patches, the likelihood of breeding given movement, and the likelihood of reproductive success given a postmovement breeding attempt. We ask several important questions. First, is effective dispersal across a landscape more limited by movement or reproduction? Second, are there different environmental limitations for the movement or reproductive components of effective dispersal? Third, does incorporating immigrant reproduction into our evaluation of connectivity change conservation prioritization?

Results

Using a hierarchical modeling approach, we combined mark-resight data on movement and reproduction to estimate movement (from natal patches to nonnatal patches), dispersal (movement followed by a breeding attempt; ref. 23), and effective dispersal (movement followed by successful reproduction; refs. 11 and 12), while accounting for imperfect detection of these processes and associated uncertainty (Fig. 1). We fit this model to data collected across nine breeding seasons (2007–2015) and 27 patches

throughout the breeding range of snail kites. We found that movement away from the natal patch was common because 55% of resightings of marked individuals during the breeding season occurred in nonnatal patches. However, 90% of movements did not result in effective dispersal. Thirty-two percent of immigrants (705/2,223) attempted breeding, and only 10% (221/2,223) of immigrants successfully reproduced. The fact that movement was common and yet successful immigrant reproduction was rare indicates that reproduction limits effective dispersal more than movement in this species. Immigrant reproduction was also important for explaining the spatial variability in effective dispersal, where 43% of the spatial variation in effective dispersal was explained by immigrant reproduction (36% by immigrant breeding probability, 7% by immigrant reproductive success, and 57% by movement; marginal R^2). Moreover, several pairs of sites that were connected through movements were not connected through effective dispersal due to a lack of successful immigrant reproduction (Fig. 1).

Geographic isolation commonly affects connectivity (1, 3), and here we found that geographic distance between natal and nonnatal patches was an important factor limiting effective dispersal (Fig. 2D). However, the effect of geographic isolation differed for movement and immigrant reproduction. We found that movement declined sharply with geographic distance from natal patches (Fig. 24). However, breeding probability of immigrants had a nonlinear relationship with distance, where breeding probability was high only for moderate distances from natal patches (Fig. 2B). This pattern appears to be driven primarily by males rather than females (SI Appendix, Fig. S1). There was no effect of distance on the reproductive success of breeding immigrants (Fig. 2C). Area of the breeding patch, a factor that frequently influences movement and reproduction (24–27), had no effects on movement [$\beta_2^m = 0.13$,

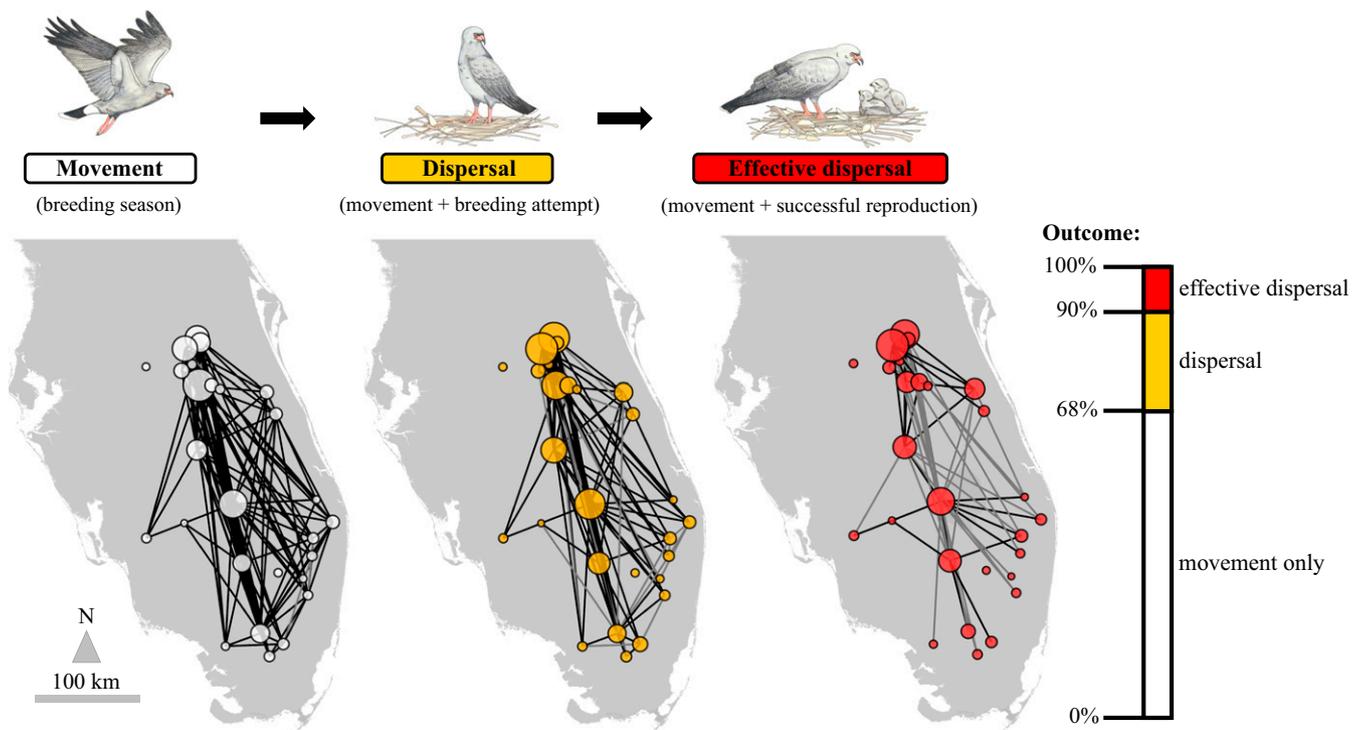


Fig. 1. Effective dispersal is limited despite frequent movement across the geographic breeding range of snail kites from 2007 to 2015. Effective dispersal contains three hierarchical processes: movement from the natal patch to a nonnatal patch during the breeding season, postmovement breeding attempt, and postmovement successful reproduction. Shown are maps of Florida with breeding patches ($n = 27$) as points, where point size corresponds to the amount of flow (either the number of movement, dispersal, or effective dispersal events) coming into the patch (in-strength) (larger point = larger in-strength). Links between patches correspond to the estimated amount of flow between patches, where a gray link indicates a single event and a black link indicates at least two events. The rightmost bar plot shows the outcomes of all movements across the breeding range where 68% of movements were not followed by a breeding attempt (movement only), 22% of movements were followed by a breeding attempt (dispersal) that resulted in nest failure, and only 10% of movements were followed by successful reproduction (effective dispersal).

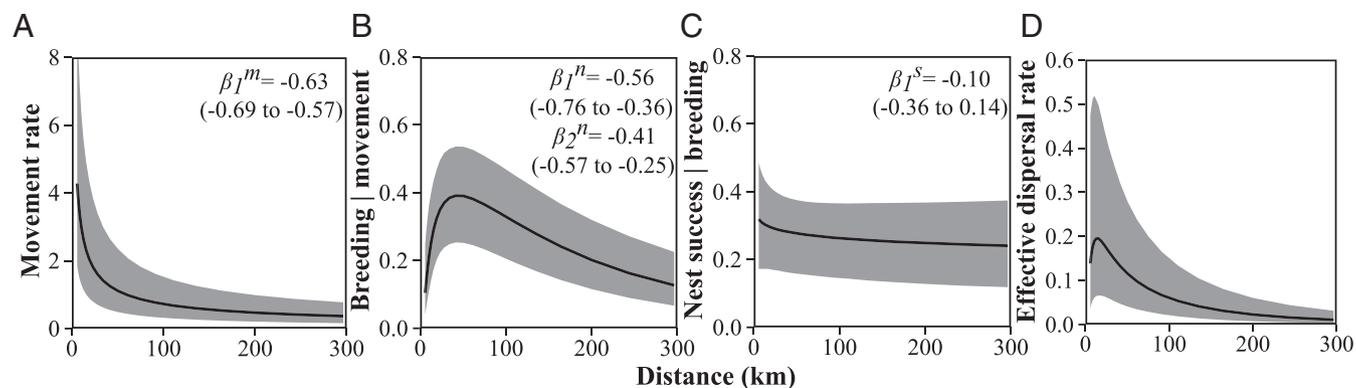


Fig. 2. Effective dispersal (movement that is followed by successful reproduction) between patches is limited by geographic distance differently from movement alone for snail kites. (A) Individuals are less likely to move to patches far from their natal patch although (B) those that do move (i.e., immigrants) are more likely to breed at intermediate distances from their natal patch with (C) no effect of distance on immigrant nest success. These three processes combine such that (D) effective dispersal shows a slightly quadratic but mostly declining pattern with distance from the natal patch. Black lines represent mean values, and shaded areas represent 95% credible intervals (CI). The slope parameters for distance (β) and 95% CI (values in parentheses) are provided. Note that effective dispersal is a derived parameter such that the slope is not reported.

95% credible interval (CI) = -0.27 – 0.54], breeding probability ($\beta_3^n = 0.08$, 95% CI = -0.25 – 0.43), or reproductive success ($\beta_2^s = -0.27$, 95% CI = -0.62 – 0.03) in this system.

Patches of habitat are often prioritized for conservation based on patch connectivity metrics that quantify each patch's relative importance for promoting connectivity across the landscape (8, 28). We considered two patch connectivity metrics that focus on the relative importance of patches for receiving immigrants (in-strength) and for acting as stepping-stones for promoting connectivity across the landscape (betweenness centrality) (29–32). For each of these metrics, we quantified these aspects of connectivity based on movement, dispersal, and effective dispersal. We found that patch prioritization for connectivity conservation changed when considering effective dispersal rather than movement alone. Patches that had the most immigrants, and were ranked the highest for movement-based connectivity, tended to have relatively low breeding probabilities by immigrants, leading to lower conservation importance in terms of effective dispersal (Figs. 1 and 3A). Similarly, sites that functioned as important stepping-stones did not necessarily act as strong effective dispersal stepping-stones (Fig. 3B and *SI Appendix, Fig. S2*). The lack of consistency in patch rankings indicates that these data types (movement and effective dispersal) are not equivalent for conservation decision-making.

Discussion

A crucial but largely neglected topic for ecology, evolution, and conservation is whether and how immigrant reproduction hinders the effects of movement in wild populations. We found that immigrant reproduction hindered effective dispersal and connectivity, despite frequent movement across the breeding geographic range of an endangered bird. Species with high movement rates are typically not considered connectivity-limited (12), yet we show that even highly mobile species may be connectivity-limited due to low immigrant reproduction. Furthermore, our results emphasize that information on movement may not always be an appropriate surrogate for understanding effective dispersal: each had different limitations and patterns across the landscape, resulting in notable changes for conservation prioritization.

Although it is well known that several factors can limit movement (e.g., physical barriers and certain land uses; ref. 2) and that movement rates tend to decline with distance (33), less is known about how movement distances can affect immigrant reproduction. There is some empirical evidence for reduced reproductive success for immigrants compared with residents (34, 35), although it is usually unknown how far the immigrants have traveled (36). Theory has posited positive, negative, or nonlinear mating preferences for immigrants, but there is little empirical evidence (12). Our results

demonstrate a nonlinear effect of movement distances on the probability of breeding. This pattern is consistent with a reproductive cost of moving far distances but also indicates that individuals may have decreased breeding probabilities at short distances. The latter effect has sometimes been attributed to inbreeding avoidance or female choice for less similar phenotypes (37). The spatial pattern of breeding probability by immigrants was above and beyond patch-level variation in breeding that was accounted for in our model structure (*Materials and Methods*). Our results highlight that there can be different environmental limitations for the reproductive component of effective dispersal compared with movement, suggesting that different conservation strategies may be needed when promoting effective dispersal rather than movement alone.

Conservation focused specifically on the issue of connectivity (connectivity conservation) often seeks to identify locations that

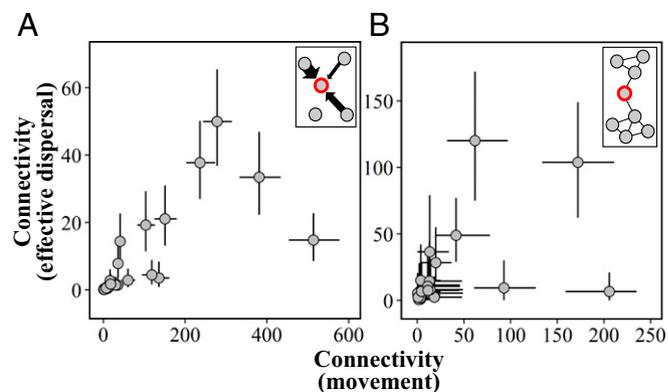


Fig. 3. Conservation prioritization changes when considering effective dispersal (movement that is followed by successful reproduction) rather than movement alone. When ranking patches (circles) using two network measures of patch connectivity representing (A) the amount of flow coming into a patch (in-strength) and (B) the role of a patch for acting as a stepping-stone for promoting connectivity across the landscape (betweenness centrality), the most connected patches for movement were not necessarily those that were most connected for effective dispersal. Circles are mean values, and horizontal and vertical lines represent 95% credible intervals for each patch connectivity metric. Both metrics are illustrated with examples in *Insets* where (A) in-strength is the sum of all flow (either the total amount of movement or effective dispersal) from all natal patches (black circles) into a focal patch (red, bold circle), where a thicker arrow indicates more flow. In *B*, *Inset* illustrates a focal patch (red, bold circle) with high betweenness centrality due to its critical role for acting as an intermediary (stepping-stone) connecting all other patches in the network (black circles).

are either in need of increased connectivity (e.g., isolated patches) or critical for existing connectivity (e.g., well-connected patches) (22). It is well established in network theory that certain patches are often more important than others for promoting flow throughout networks (38, 39). Patch connectivity rankings based on network analyses are often taken into account when designing nature reserves and making the important decision of which locations to preserve given limited conservation resources (32). Our results emphasize that prioritizing patches for conservation using movement-based connectivity can lead to omission of the best patches for promoting effective dispersal. The degree that movement and effective dispersal differ for conservation prioritization will likely depend on species' life histories, where high reproductive failure rates and/or spatial variation in reproduction should lead to greater discrepancies in these processes.

In most systems, it is not feasible to resight individuals as they move and reproduce across the landscape. However, two general alternatives can provide some understanding of effective connectivity and its importance for populations. First, some approaches can provide indirect information without isolating effects of movement and immigration reproduction. For instance, genetic distance measures and colonization rates in metapopulations may provide some indirect information on effective dispersal (40, 41). Such approaches are useful for understanding the outcome of effective dispersal but may be limited for isolating the roles of movement relative to reproduction. Simulation models could help in this regard (42, 43). Second, a variety of approaches could link independent information on movement and reproduction to make predictions of effective connectivity. For example, simulations of dispersal (biophysical dispersal models) and linkages with population demographic models in marine systems have demonstrated that both reproduction and movement can potentially limit connectivity and genetic structure across seascapes (16, 17, 44). Although synergistic effects of movement on reproductive outcomes might be missed (e.g., Fig. 2B), such approaches could account for other issues such as environmental limitations to movement (e.g., matrix resistance; ref. 45). Finally, we note that other methods, rather than the mark-resight data used here, may be available for tracking individuals and isolating the components of effective connectivity. Some types of genetic analyses (46, 47) and new advances in radio-tracking (48, 49) may help track both movement and reproductive components of effective dispersal across landscapes. We argue that more work is needed on harnessing different sources of information and modeling approaches to understand the causes and consequences of effective connectivity.

A widespread debate in conservation is whether securing habitat or promoting connectivity is more valuable for the persistence of species and communities (50). Central to this debate are the relative benefits of improving within-patch characteristics (e.g., habitat quality of the patch) versus between-patch characteristics (e.g., quality of habitat between patches, or "the matrix") for conservation. Effective connectivity connects these two perspectives by linking a key between-patch metric (movement) with a key within-patch demographic parameter (reproduction). It is frequently assumed that movement is the greatest limiting factor for connectivity (51, 52), although simulations have demonstrated that within-patch characteristics could potentially have strong influence as well (53). Nonetheless, within-patch processes have been less emphasized than between-patch processes for understanding connectivity (54). Our results suggest that although conservation strategies designed to encourage movement may be useful (e.g., creating corridors and improving matrix habitat), it may prove more beneficial in some instances, such as when reproductive rates are low and variable across the landscape, to also focus efforts on providing high-quality breeding habitat for promoting effective dispersal. Maintaining effective dispersal across landscapes, rather than movement alone, will be essential for fostering population persistence with ongoing environmental change.

Materials and Methods

Focal Species and Study Area. The snail kite is a critically endangered bird with a distribution in the United States that is limited to freshwater wetlands in central and south Florida. We define patches ($n = 27$) similar to previous studies where patch borders were delineated based on physical barriers separating contiguous wetland habitat or hydrologic management units used by state agencies (55–57). Dynamic hydrologic conditions from water management activities, extreme climatic events, and variations in prey availability can lead to high spatial variation in snail kite reproduction (57–59).

Snail kites are long-lived, iteroparous raptors with the potential to breed in multiple patches throughout their lifetime (60). Movement, similar to reproduction, can also be highly variable in this species. Although individuals are highly mobile and can traverse the entire range in short periods of time, movement is structured, leading to variation in connectivity across the range (55, 56, 61, 62).

Measuring Dispersal and Nesting. We collected data using standardized mark-resight and nest monitoring surveys conducted at all known breeding patches across the snail kite's entire geographic range between 2007 and 2015 (58, 63, 64). We focused on this time period because it was after the invasion of an exotic prey species (*Pomacea maculata*) that has had major effects on the demography and movement patterns of snail kites (59). Mark-resight surveys were conducted by airboat during the peak breeding season (1 March to 30 June) every 18–21 d (typically six surveys each year), and nest monitoring extended between approximately January and October each year. During surveys, we identified all observed banded birds and attempted to find all nests. Nests were monitored every 2–3 wk until the young successfully fledged or the nest failed (successful nests are active for ~56 d; refs. 59 and 60). At each nest visit, we identified parents observed at the nests (63). All birds in our study were banded as nestlings just before fledging (~24 d old); thus, the natal patch for each banded bird was also known. Having information on natal and breeding patches of banded birds allowed assessments of effective dispersal.

Connectivity Analysis. We used a network approach to interpret connectivity. Network analyses of connectivity (sometimes referred to as graph-theoretic analyses of connectivity; refs. 65 and 66) represent patches as nodes and movement between nodes as links (or edges/arcs), such that the network is a landscape representation of habitat patches and movement between them. These approaches can provide an understanding of connectivity at different scales, as well as the incorporation of potential indirect linkages, such as stepping-stones (67). These approaches also allow for consideration of more patches than is traditionally considered in multistate mark-recapture models (68). We summarized our data across years (2007–2015), rather than in yearly time steps (as in multistate models) to focus entirely on movement from natal patches to potential breeding patches that may allow for gene flow.

We define three observed linkage types that we measured for all banded snail kites, describing the link between natal patch i , for an individual, and patch j that is defined for each linkage type as either (i) movement resight, an individual's resight patch during the height of the breeding season (March–June); (ii) dispersal resight, an individual's resight patch as a parent of an attempted nest (i.e., an individual resighted at an active nest, which may or may not have been successful); or (iii) effective dispersal resight, an individual's resight patch as a parent of a successful nest. In some instances, individuals were seen at multiple patches (~21% of cases) or multiple nests (~24% of cases) within a given breeding season and we retained all of these instances. We note that we also ran the model retaining only the most frequent resight patch and a single, randomly selected nest per individual per year, and results were similar. We also note that the temporal scale of our linkages (i.e., the time to go from patch i to patch j) varies because links are between an individual's natal patch and their nonnatal movement, dispersal, or effective dispersal patch rather than over a set time interval. We used this format because gene exchange, and thus effective dispersal, occurs during the year that successful reproduction occurs regardless of when a parent was born. Here we consider all linkages where events at patch j occurred from 2007 to 2015, although individuals moving and/or reproducing in these years may have been born before 2007.

We summarized these three observed linkage types as three weighted, directed adjacency matrices (\mathbf{A}). Entries \mathbf{A}_{ij} in these matrices consisted of the total number of observed movements (or observed dispersal or effective dispersal events) between patch i and patch j between 2007 and 2015. Because we were interested in effective dispersal, rather than philopatry, we excluded all information on natal site fidelity (i.e., no self-links; $\mathbf{A}_{ii} = 0$), although we note that site fidelity can be highly important for population dynamics and

metapopulation persistence (17, 69) despite not contributing to effective dispersal and gene flow. These three observed connectivity networks were used as data within the hierarchical model (described below) for predicting latent (unobserved) movement, dispersal, and effective dispersal networks that accounted for imperfect detection of these processes and associated uncertainty.

We coupled our three observed networks by deriving a three-level hierarchical model, analyzed in a Bayesian framework, that modeled movement from natal patches to nonnatal patches, breeding attempts conditional on movements, and reproductive success conditional on breeding attempts. The first level of this model was similar to hierarchical social network models (70), but we extended this approach to better account for sparse data on movements and imperfect detection. We considered two landscape structure covariates (distance between patches and area of patches) that might influence movement, breeding probability, and reproductive success (20, 21). We expected all relationships with distance and area to be linear within the model (on the link scale; see below), although we also tested for quadratic effects of distance on immigrant breeding probability because this relationship has been hypothesized by some theory (12). Our three-level model makes two advances for connectivity modeling by (i) capturing hierarchical biological processes that are commonly assumed in connectivity yet rarely separated and (ii) formally incorporating uncertainty for connectivity, which is a largely neglected aspect for connectivity science (71).

For the first level of the model that focused on movement, we assumed that the observed number of movements between the natal patch i and nonnatal patch j , Y^m_{ij} , came from a binomial distribution:

$$Y^m_{ij} \sim \text{Binomial}(p^m_{ij}, z^m_{ij}),$$

where p^m_{ij} is the detection probability and z^m_{ij} is the latent number of movements. We assigned an informative prior for the detection probability p^m_{ij} , given by

$$p^m_{ij} \sim \text{Beta}(\alpha^m_{ij}, \beta^m_{ij}),$$

where α^m_{ij} and β^m_{ij} are the shape and scale parameters from the beta distribution and are based on our previous work (SI Appendix). We then modeled the latent number of movements z^m_{ij} with a zero-inflated Poisson distribution, given by

$$z^m_{ij} \sim \text{Poisson}(\lambda_{ij}^{\text{Eff}}),$$

$$\lambda_{ij}^{\text{Eff}} = w_{ij} \lambda_{ij},$$

$$w_{ij} \sim \text{Bernoulli}(\psi),$$

where the expected count $\lambda_{ij}^{\text{Eff}}$ is given by λ_{ij} multiplied by a binary value (w_{ij}) to account for extra zeros in the data. We modeled the expected number of movements λ_{ij} as a function of distance between the natal and breeding patch (d_{ij}), area of the breeding patch (a_j), and a random effect of the breeding patch (γ^m_j):

$$\log(\lambda_{ij}) = \beta_0^m + \beta_1^m d_{ij} + \beta_2^m a_j + \gamma^m_j.$$

Our second level of the model focused on the probability of breeding, conditional on movement. Similar to the movement model, we assumed that the observed number of dispersal events Y^n_{ij} from natal site i to breeding patch j was given by a binomial distribution:

$$Y^n_{ij} \sim \text{Binomial}(p^n_{ij}, z^n_{ij}),$$

where z^n_{ij} is the latent number of dispersal events and p^n_{ij} is the detection probability of nesting. We again assigned informative priors for p^n_{ij} :

$$p^n_{ij} \sim \text{Beta}(\alpha^n_{ij}, \beta^n_{ij}),$$

where α^n_{ij} and β^n_{ij} are based on our earlier work (SI Appendix). We link the dispersal and the movement models by assuming that the latent number of dispersal events z^n_{ij} comes from a binomial distribution based on the latent movement parameter z^m_{ij} and breeding probability b_{ij} :

$$z^n_{ij} \sim \text{Binomial}(b_{ij}, z^m_{ij}).$$

We modeled breeding probability as a quadratic function of distance and a linear function of area and a random effect of the breeding patch:

$$\text{logit}(b_{ij}) = \beta_0^n + \beta_1^n d_{ij} + \beta_2^n d_{ij}^2 + \beta_3^n a_j + \gamma^n_j.$$

Our third level of the model focused on reproductive success, conditional on breeding and movement. We modeled the observed number of effective dispersal events Y^s_{ij} using a binomial distribution based on the latent number of effective dispersal events z^s_{ij} and detection p^n_{ij} :

$$Y^s_{ij} \sim \text{Binomial}(p^n_{ij}, z^s_{ij}).$$

We link this model to the dispersal model by assuming that the latent number of effective dispersal events (z^s_{ij}) comes from a binomial distribution based on the latent number of dispersal events (z^n_{ij}) and the probability of reproductive success (s_{ij}):

$$z^s_{ij} \sim \text{Binomial}(s_{ij}, z^n_{ij}).$$

We then modeled probability of reproductive success as a function of distance, area, and a random effect of the breeding patch:

$$\text{logit}(s_{ij}) = \beta_0^s + \beta_1^s d_{ij} + \beta_2^s a_j + \gamma^s_j.$$

Because our data matrices are formatted pairwise between patches, rather than at the individual nest level, s represents apparent reproductive success (number of successful nests divided by the total number of nests) rather than daily nest survival, common in the avian literature, which considers variation in the amount of time between nest visits (72). Elsewhere we have shown that using daily nest survival in lieu of apparent success provides similar conclusions in the context of dispersal (57). We then derived latent network predictions of the number of movement ($\lambda_{ij}^{\text{Eff}}$), dispersal ($\lambda_{ij}^{\text{Eff}} b_{ij}$), and effective dispersal ($\lambda_{ij}^{\text{Eff}} b_{ij} s_{ij}$) events, along with their posterior distributions, between all patches across the landscape. See SI Appendix for additional information on model and simulations.

To examine the relative contributions of movement and reproduction to spatial variability in effective dispersal, we obtained marginal R -squared (R^2) values from linear mixed-effect models (LMMs; ref. 73) describing the latent amount of effective dispersal across the network as a function of either the latent amount of dispersal or movement. We included random effects for patch i and patch j in these LMMs.

Connectivity Metrics. We used the posterior distributions for each latent network (movement, dispersal, effective dispersal) to calculate the mean and 95% credible intervals of two patch-connectivity metrics: in-strength and betweenness centrality. In-strength quantifies, for each patch, the sum of all linkages directed into the patch (30, 31). Consequently, this metric equates to the number of individuals born elsewhere that used the patch during a breeding season (i.e., immigration) when parameterized with movement estimates, the number of immigrants nesting when parameterized from dispersal estimates, and the number of immigrants successfully nesting when parameterized from effective dispersal estimates. Betweenness centrality was also calculated per patch and is defined as the number of shortest paths between all pairs of patches that go through the focal patch, divided by the total number of shortest paths between each pair of patches and where path length is the inverse of the amount of flow along the path (30, 32). Biologically, it quantifies the relative importance of a patch for connecting flow among all other patches. This metric is frequently used in spatial ecology to represent a patch's role as a stepping-stone in promoting flow across the network (29, 32, 74).

Data Sharing. Snail kites are a listed federally endangered species, and the specific location data are sensitive and have not been made available. However, all other data for these analyses, as well as code and documentation for running the model, are available at figshare (75).

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