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# Proximity among protected area networks promotes functional connectivity for wintering waterfowl

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**The equilibrium theorem provided a fundamental framework for understanding species' distributions and movement in fragmented ecosystems. Wetland-dependent avian species are model organisms to test insular predictions within protected area networks because their mobility allows surveillance of isolated patches without landscape barriers. We hypothesized size and isolation would influence functional connectivity of sanctuaries by GPS-marked wintering mallards (*Anas platyrhynchos*) within a mesocosm protected sanctuary area network. We evaluated functional connectivity and sanctuary use, measured by movements between sanctuaries, using a multistate modeling framework. Proximity drove connectivity, underscoring that patch isolation—not size—influenced connectivity, even for an avian species with no ascertainable landscape resistance or barriers. We also found that sanctuary use increased overwintering survival by reducing harvest mortality. Our test of equilibrium theory predictions demonstrated that isolation of protected sanctuary areas supersedes their size in determining functional connectivity for mallards and access to these areas may have direct fitness consequences. Our findings could refine land acquisition, restoration, and management practices with equal or greater emphasis on adjacency in protected area network design, especially for wetland-dependent migratory gamebirds.**

**Keywords** *Anas platyrhynchos*, GPS telemetry, Functional connectivity, Island biogeography, Multistate modeling, National Wildlife Refuge System, Protected area networks, Sanctuary, Wintering waterfowl

The theory of island biogeography laid the foundation for critical insights across the fields of ecology, evolution, and conservation biology[1–3]. In particular, the equilibrium model offered the first conceptual framework describing connectivity between discrete patches where bi-directional movement jointly depended on patch size and isolation[4,5]. The model predicted increased colonization of larger and closer patches and emigration from smaller isolated patches[6,7]. A key insight was its application to non-island environments where protected areas (i.e., "reserves", "refuges", "sanctuaries") become functional islands as land use change fragmented natural ecosystems[8–11]. Conservation practitioners embraced these general principles for optimal design of protected area networks[12].

The influential single large versus several small (SLOSS) debate posited that a single large protected area promoted greatest species abundance, richness, and immigration than several smaller reserves[13–17] (i.e., SL > SS). While global protected areas effectively conserve species diversity, abundance, and demography[18–20], the relative importance of size and connectivity are context-dependent. Conservation planners recognize influential factors of protected areas such as their authorized purposes (e.g., endangered species recovery vs. biodiversity goals), target organism(s) and traits (e.g., dispersal ability), and the surrounding landscape matrix[2,21–24]. For instance, connectivity becomes more vital for recovery of endangered species or those with limited dispersal ability[25,26]. Thus, protected area networks require case-specific evaluations based on the species and ecosystems they are designed to serve[27–29].

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Despite the contextual nature of protected area network design, large contiguous habitat is nearly always prioritized for protection over smaller areas[30,31], implying lower conservation value of small patches, which may undermine conservation or budgetary objectives[32,33]. For example, megafauna require large protected areas but smaller connected patches may be as effective as large ones if they facilitate movement and dispersal (e.g., habitat corridors)[22,34]. Likewise, conservation values of large marine protected areas are well-established (e.g., less sensitive to environmental perturbations)[35] but smaller marine protected area networks (i.e., stepping stones) may be equally effective depending on site characteristics, target taxonomic groups, and limiting consumptive use and other human disturbance[36,37]. Smaller protected areas can also harbor substantial biodiversity, enhance landscape connectivity, are more cost-effective to acquire and maintain, and likely complement larger protected areas[38]. Therefore, their potential conservation value should not be dismissed and may be especially important in the Anthropocene as natural ecosystems are increasingly fragmented and fiscal resources limited[32,33,38].

Wetland-dependent birds are notable models to evaluate protected area connectivity under the equilibrium framework because their mobility allows individuals to assess isolated patches without landscape barriers or resistance[39–41]. Furthermore, wetland-dependent birds rely on severely threatened and fragmented ecosystems throughout their life-cycle[42]. Protected area wetlands provide resting and foraging areas during non-breeding seasons[18,43], migratory stopover and refueling sites[43–47], and nesting and brood-rearing habitat[48,49]. Ultimately, these sites are stepping stones that fulfil annual cycle requirements, and their connectivity is a prerequisite to the vitality and long-term viability of wetland-dependent migratory bird populations[50–52]. Indeed, evaluations have emphasized a need for a greater number of integrated wetlands (i.e., complexes or networks) rather than larger contiguous wetland habitats to connect wetland-dependent bird movements at local and landscape scales and during different stages of their annual life cycle[43–48].

Historically, global protected areas were established as sanctuaries (i.e., prohibited or very limited human access) for threatened or iconic species, landscapes, and seascapes to restore declining wildlife populations or promote biodiversity[53,54]. Protected areas are increasing, but public support hinges on their utility to people and thus broader objectives are required to satisfy growing demands of increasingly diverse stakeholders[55,56]. For example, the U.S. National Wildlife Refuge (NWR) System is the premiere example of a protected area network for wildlife conservation[57]. In its infancy, the NWR System's mission was to protect land as inviolate sanctuary for at-risk and iconic wildlife[53] (e.g., brown pelican [*Pelicanus occidentalis*] and bald eagle [*Haliaeetus leucocephalus*]). However, NWRs now have unique designations (e.g., sanctuary, waterfowl production areas, human recreation) and subsequently, their authorized purposes change to meet public demand[57,58]. One such directive for midcontinental NWR networks is to provide spatial sanctuary, free from hunting and other human disturbance, for migrating and wintering waterfowl with goals to: (1) provide rest areas and promulgate foraging resource requirements that promote population persistence; (2) serve as stepping stones that facilitate migratory and local wintering movements and connectivity; and (3) influence local–regional distributions of waterfowl[59–61]. State agencies also establish smaller waterfowl sanctuaries to enhance disturbance-free wetland connectivity and waterfowl movement within sanctuary networks with implicit assumptions that protected sanctuary complexes enhance local waterfowl harvest opportunities and sustain abundant waterfowl populations regionally throughout autumn and winter[60–62].

Evaluating the effectiveness of protected area networks in meeting conservation objectives is challenging, especially for highly mobile species that occupy large geographic ranges and dynamic spatiotemporal distributions[63,64]. Nevertheless, periodic and critical assessments are needed for effective management, restoration, or prioritization of new areas within or beyond established networks[18,43,50,65]. Traditional evaluations of protected areas that span large spatial extents have recorded wildlife vital rates (e.g., abundance) or diversity indices[18,66,67], but they are historically limited by temporal frequency and therefore, an inability to directly measure connectivity among protected areas (*but see*[68]). Emerging tracking technology allows practitioners to monitor movements among protected sanctuary areas directly, while removing spatial and temporal biases associated with resighting marked birds[68], thereby assessing functional connectivity and influential site characteristics (i.e., size, isolation) at biologically relevant spatial scales[69–71].

Our aim was to evaluate functional connectivity within a protected sanctuary network by wintering mallards (*Anas platyrhynchos*) by modeling daily movement transition probabilities to (i.e., immigration) and from (i.e., emigration) sanctuary "nodes"[72,73]. Wintering mallards serve as an informative model species to test equilibrium predictions because their mobility allows aerial assessment of habitat patches with no landscape resistance[74]. Yet, they rely on protected wetlands as suitable "islands" because of an otherwise inhospitable landscape matrix (i.e. intensive hunting). We hypothesized sanctuary size and isolation (i.e., distances) would influence movement transition probabilities among sanctuary nodes[6]. We predicted larger sanctuaries were local source populations and thus immigration transitions to larger sanctuaries were more likely, emigration transitions from larger sanctuaries were less likely, and the opposite immigration-emigration relationships for smaller sanctuaries. Likewise, we predicted mallards were more likely to transition to sanctuaries closer to one another compared to more distant sanctuaries. We also evaluated sanctuary use by mallards relative to capture-year and years after capture to ensure inferences were robust against transmitter marking biases (i.e., different sanctuary use behaviors in the first year compared to following winters). We predicted similar rates of sanctuary use between capture-year and return mallards and thus no or minimal marking biases. Last, we estimated overwintering survival for mallards that had access and used sanctuary compared to those that did not following capture. We hypothesized use of and access to protected sanctuary areas may confer fitness consequences; therefore, we predicted overwintering survival would be greater for mallards that used sanctuary because those that did not would experience greater harvest mortality. Our findings refine consequences of the equilibrium model, illustrating application and geographic generalizability for local, regional, and international sanctuary network design that promotes functional connectivity for a hunted gamebird during winter.

## Results

We removed 3 mallards that migrated through but did not stay within our sanctuary network. We tracked 421 mallards (41% females, 24% juveniles) from 2019 to 2023, and 22 individuals had 2 or more winter seasons within the study region. Sixty-nine percent of mallards used 1 sanctuary node during winter, 19% used 2 nodes, and 12% used 3 or more (maximum = 8).

The probability of daily sanctuary transitions decreased as distance increased ($\beta = -0.11$; 90% CRI = $-0.12$ to $-0.10$; Table 1). For every 10 km of spatial separation, mallards were 3.06 (90% CRI = 2.84–3.28; Fig. 1a) times less likely to transition from one sanctuary to another. Increased size of the "departure" (i.e., emigration) and "arrival" (i.e., immigration) sanctuaries increased the probability of sanctuary transitions ($\beta$s = 0.019 and 0.033; 90% CRIs = 0.009–0.032 and 0.021–0.045, respectively; Table 1); however, the magnitude of these effects were small (Fig. 1c,d). For example, given 10 km$^2$ (i.e., $\bar{x}$ size) increase in emigration sanctuary, mallards were 1.22 (90% CRI = 1.09–1.38) times more likely to transition from one sanctuary to another ($\psi$ range = 0.0002–0.006; Fig. 1c). Adults ($\beta = 0.44$; 90% CRI = 0.19–0.72) and males ($\beta = 0.61$; 90% CRI = 0.40 – 0.81) had greater transition probabilities than juveniles and females, respectively (Table 1). Adults were 1.56 (90% CRI = 1.21–2.05) times more likely to transition than juveniles, and males were 1.84 (90% CRI = 1.49–2.25) times more likely to transition than females (Fig. 1b). Probability of an adult male mallard making one or more transitions across the entire 120-day study period was 46.1% (90% CRI = 42.1–50.5%) when sanctuaries were 21.1 km apart ($\bar{x}$ distance − 1 SD), 3.4% (90% CRI = 2.9–4.5%) when sanctuaries were 46.9 km apart ($\bar{x}$), and 0.2% (90% CRI = 0.1–0.3%) when sanctuaries were 72.7 km apart ($\bar{x}$ + 1 SD).

Daily transition probabilities between sanctuary nodes was ≤ 6% (Fig. 1; Table S1). The greatest probability of daily sanctuary transitions was between Reelfoot Lake NWR north to south and south to north units for adult males ($\psi = 0.057$ and 0.056; 90% CRIs = 0.049–0.065 and 0.048–0.064, respectively; Fig. 2). Adult male daily transitions were relatively high from Phillipy Refuge to Reelfoot Lake NWR north and south units ($\psi = 0.044$ and 0.036; 90% CRIs = 0.038–0.051 and 0.032–0.041, respectively) and Black Bayou Refuge to Reelfoot Lake NWR north and south units ($\psi = 0.033$ and 0.044; 90% CRIs = 0.029–0.037 and 0.039–0.050, respectively). In fact, most emigration-immigration combinations among sanctuaries with the greatest daily transition probabilities were within the "Reelfoot Wetlands Complex" because of the proximity of these sanctuaries to one another (Fig. 2). The "Upper Obion Wetland Complex", which included Bean Switch Refuge, Maness Swamp Refuge, and Hop-In Refuge, were also relatively well connected (Fig. 2). Among these, the greatest transition probabilities were from Hop-In Refuge to Maness Swamp Refuge ($\psi = 0.021$; 90% CRI = 0.019–0.024), from Maness to Hop-In ($\psi = 0.020$; 90% CRI = 0.018–0.023), from Bean Switch Refuge to Maness ($\psi = 0.016$; 90% CRI = 0.014–0.018) and from Maness to Bean Switch ($\psi = 0.015$; 90% CRI = 0.013–0.017). Although, farther away from the "Reelfoot Wetlands Complex", Lake Isom NWR was weakly connected with greatest connectivity from Lake Isom NWR to Reelfoot Lake NWR south unit ($\psi = 0.021$; 90% CRI = 0.019–0.023), to Black Bayou Refuge ($\psi = 0.012$; 90% CRI = 0.011–0.013), and to Reelfoot Lake NWR north ($\psi = 0.010$; 90% CRI = 0.008–0.013). In other words, Lake Isom NWR was an apparent source for the "Reelfoot Wetlands Complex". All other daily sanctuary transition probabilities were < 1% (Table S1; Fig. 2).

Mallards returning to the study region did not differ in number of sanctuaries used compared to those captured during winter ($\beta = 0.05$; SE = 0.28). Likewise, arrival or capture month did not affect sanctuary use by mallards (December: $\beta = -0.16$; SE = 0.003, January: $\beta = -0.33$; SE = 0.21, February: $\beta = -0.05$; SE = 0.34). However, the number of sanctuaries used increased with increasing time spent in the study region ($\beta = 0.015$; SE = 0.003). Specifically, mallards used 1.59 (90% CI 1.36–1.85) times as many sanctuaries for every 30 days in the region (Fig. 3).

Mallards that did not use sanctuary nodes following capture (11% or 45 individuals) had reduced overwintering survival compared to individuals that established winter ranges near and thus, had access to sanctuaries (Fig. S2). Specifically, individuals that used sanctuary had 3.06 (95% CI 1.77–5.31) times reduced hazard of death compared to individuals that never used sanctuary following capture. For 30 days within the sanctuary network, survival was 0.91 (95% CI 0.88–0.94) for mallards that had access and used sanctuary and 0.72 (95% CI 0.59–0.87) for mallards that did not use sanctuary. For 60 days, survival was 0.83 (95% CI 0.77–0.87) and 0.55

| Hypothesis | Variable | β | 90% credible intervals | |
|---|---|---|---|---|
| | | | Lower | Upper |
| System-specific | Intercept (sanctuary) | − 4.48 | − 4.88 | − 4.18 |
| Individual characteristics | Age | 0.44 | 0.19 | 0.72 |
| | Sex | 0.61 | 0.40 | 0.81 |
| Island biogeography | Distance | − 0.11 | − 0.12 | − 0.10 |
| | Size (emigration) | 0.02 | 0.01 | 0.03 |
| | Size (immigration) | 0.03 | 0.02 | 0.05 |

**Table 1.** Parameter estimates on the logit scale (β) and associated 95% credible intervals from the multistate model evaluating daily sanctuary transition probabilities for system-specific (i.e., specific sanctuaries or the intercept), individual characteristic variables including age and sex, and island biogeography covariates including distance between sanctuaries and their sizes, including the departure or "emigration" sanctuary the individual left and the arrival or "immigration" sanctuary the individual transitioned to.

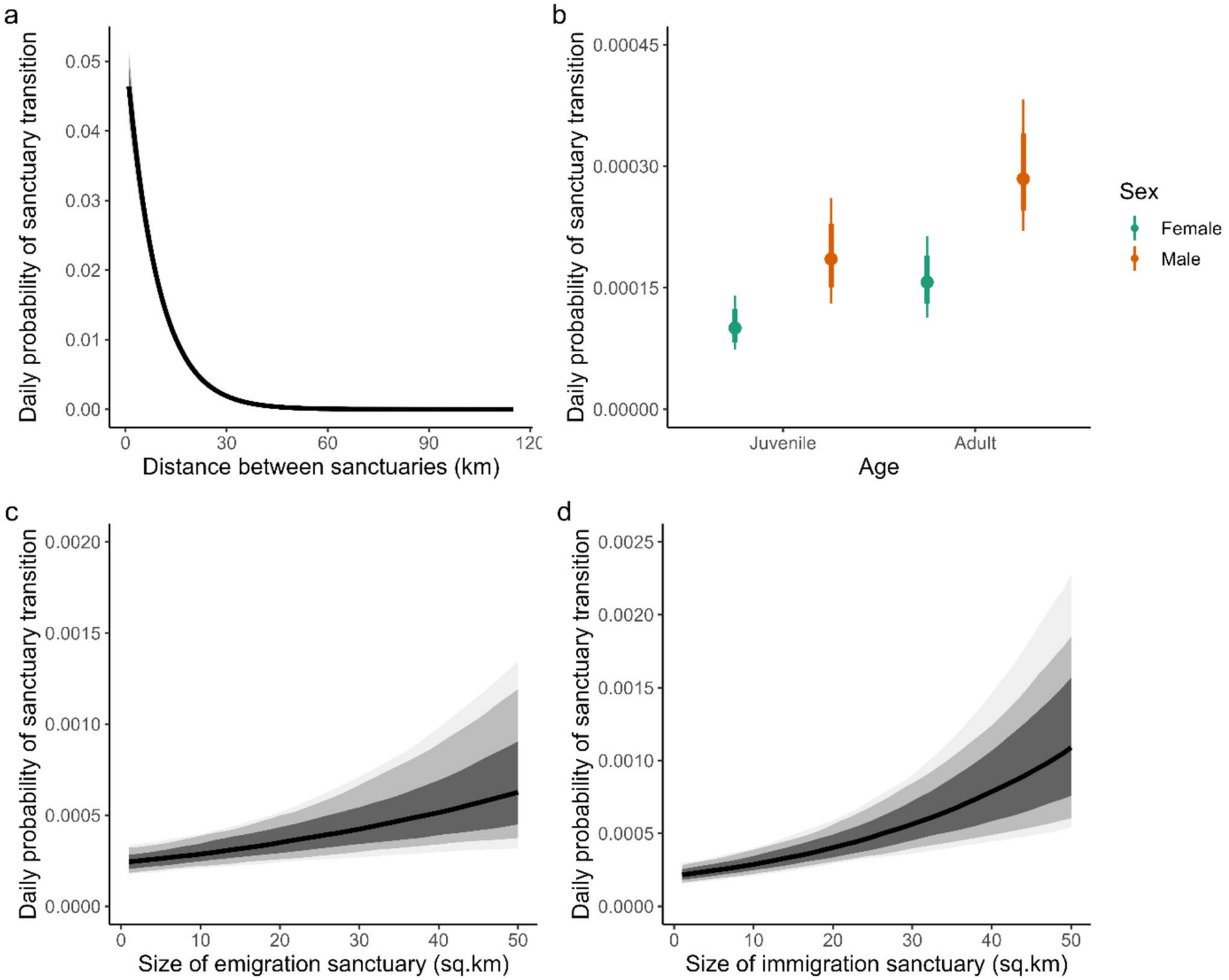

**Figure 1.** The daily transition probabilities ($\psi$) from one waterfowl sanctuary to another by a wintering mallard (*Anas platyrhynchos*) captured or arriving in the west Tennessee and surrounding sanctuary complexes (November through February 2019–2023) relative to distance between sanctuaries (**a**), individual characteristics including female or male (green and orange, respectively) and age (juvenile or adult; **b**), and sanctuary sizes including the size of the sanctuary an individual left (emigration; **c**) and the size the individual transitioned to (immigration; **d**). Transition probabilities are associated with 68%, 90%, and 95% credible intervals for (**a**), (**c**), and (**d**) (dark to light gray) and 68% and 90% credible intervals for (**b**) (thick and skinny line, respectively). Predictions are generated from posterior distributions with all other values held constant at their mean value. Predictions for (**a**), (**c**), and (**d**) are for juvenile males because these were categorical indicator variables. Note different *y*-axes for visual aesthetics; despite increases or differences visually, distance between sanctuary nodes (**a**) was the only biologically meaningful effect. All Figures were produced in R version 4.3.3. https://www.r-project.org/.

(95% CI 0.39–0.77) for individuals that used and did not use sanctuary, respectively (Supplementary Context, Methods, and Results 2; Fig. S2).

## Discussion

We evaluated functional connectivity of a highly mobile gamebird species within a mesocosm protected area network to refine applications of equilibrium theory. Proximity between sanctuary nodes promoted inter-patch movements more than area size, even for an avian species that is, theoretically, unimpeded by the matrix[2]. Our findings align with previous research demonstrating isolation overrides patch size for connectivity outcomes, including for flying taxa[27,75–78]. This highlights the equilibrium theory's assumption that landscape matrices impose dispersal costs, which may apply differentially to highly vagile or hunted species[79]. For such mobile organisms, structural connectivity, facilitated by adjacent protected areas, can enhance functional connectivity without sole reliance on intervening habitat patches of lesser quality[80,81]. Consequently, we suggest maximizing adjacency should be as much a focus as size for protected area networks aimed at increasing connectivity, especially for overwintering gamebirds and other wildlife that can transit above a hostile matrix to more suitable patches.

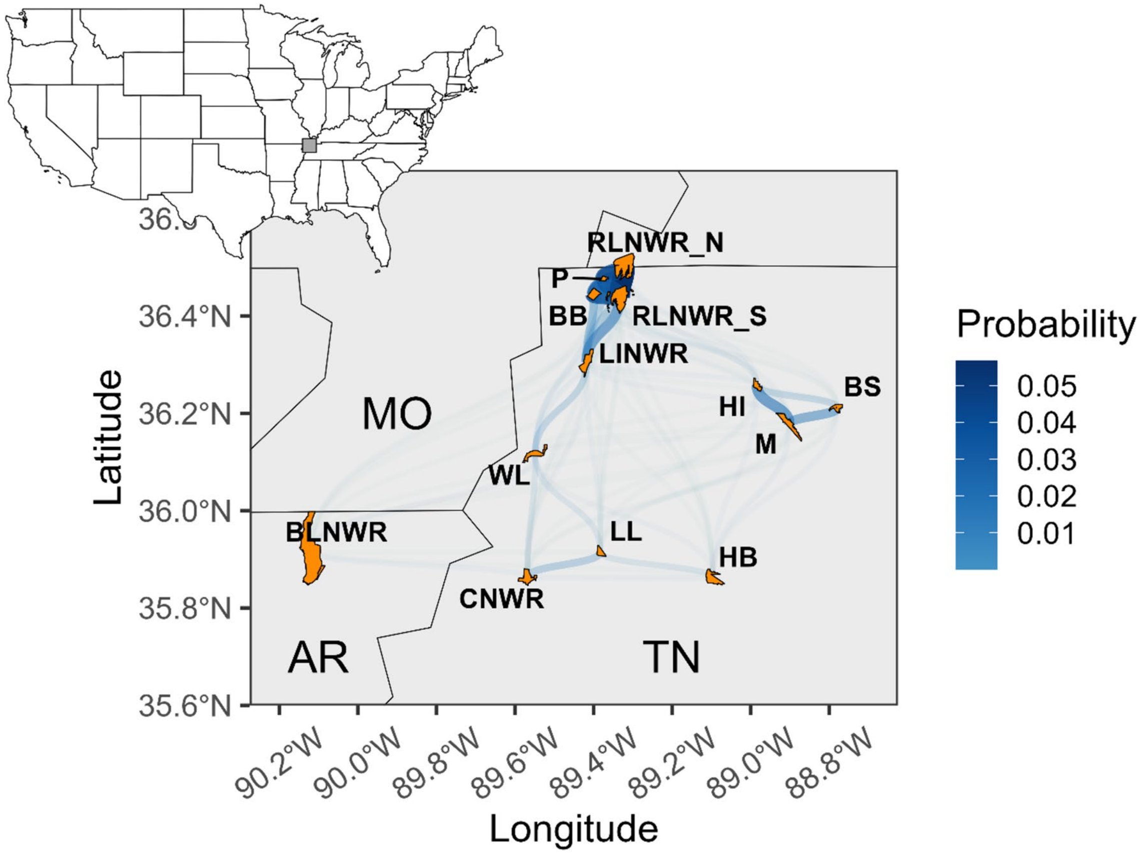

**Figure 2.** Predicted functional connectivity of mallards (Anas *platyrhynchos*) represented as daily sanctuary transition probabilities (*p*) among sanctuary nodes within the west Tennessee and surrounding sanctuary network of Arkansas, Kentucky, and Missouri. Individual mallards were captured and monitored with GPS transmitters from November through February 2019–2023. Sanctuary nodes included 4 National Wildlife Refuges: Big Lake National Wildlife Refuge (BLNWR) in Arkansas, Reelfoot Lake NWR north unit (RLNWR_N) in Kentucky and Tennessee, and Reelfoot Lake NWR south unit (RLNWR_S), Lake Isom NWR (LINWR), and Chickasaw NWRs in Tennessee. Additional smaller sanctuary nodes included state-owned waterfowl sanctuaries: Lake Lauderdale (LL), Horns Bluff (HB), White Lake (WL), Bean Switch (BS), Maness Swamp (M), Hop-in (HI), Black Bayou (BB), and Phillipy Waterfowl Refuges (P). Greatest functional connectivity was clearly within the Reelfoot Lake sanctuary complexes that included Black Bayou, Phillipy, and Reelfoot NWR north and south units. State sanctuary nodes in the upper Obion River Complex including Hop-in, Bean Switch, and Maness Swamp Waterfowl Refuges also were more connected nodes illustrating distance, not size, as a primary driver of functional connectivity for wintering mallards. Figure was produced in R version 4.3.3. https://www.r-project.org/.

Measuring connectivity outcomes remains challenging and relies on indirect measures of genetic diversity, occupancy, or abundance[81–83]. However, tracking individual movements provides a direct evaluation of network connectivity and possible barriers[71,84,85]. Here, we used GPS tracks of mallards to estimate functional connectivity of protected sanctuary areas which revealed that individuals rarely transitioned between protected sanctuary nodes, despite the ability to fly above and avoid hunting risk when relocating (*cf.*[86]), thereby implying some unknown costs. Critical to island biogeography is the assumption that the landscape matrix between suitable patches is inhospitable[7,11]. While some wetlands beyond sanctuary borders may provide temporary refugia[87,88], our most connected area was also the most hunted (Table S1; Fig. S1). Instead, resource tracking and abundance theories predict reduced movement when resources are plentiful[89–92]. Mallards likely foraged outside sanctuaries nocturnally when these patches were suitable and returned to sanctuary nodes diurnally[93–96].

Few and proximity-biased transitions could be interpreted as energy conservation decision-making[97–99]. Indeed, waterfowl and other taxa minimize travel distances to foraging patches during winter unless payoffs at distant patches outweigh travel costs[95,100–104]. However, food resources surrounding sanctuary nodes remained throughout winter precluding any need to conserve energy[105,106]. Instead, few sanctuary transitions—predominantly to closer nodes—suggests adequate food resources within and around nodes, that translated into a single sanctuary being suitable the entire winter[96,107]. A more likely cost of transitioning between sanctuaries is the immediate mortality risk by hunters[18,60,108] (Fig. S2); that is, chronic hunting likely impeded connectivity. Mallards returning to the same sanctuary indicates a cognitive map of locally suitable patches[109–111]. Waterfowl in our region have only a short period to develop search images (i.e., pre-hunting season from arrival to ~ 5 December) and cognitive maps decay with time, in turn promoting shorter movement distances to areas frequently visited,

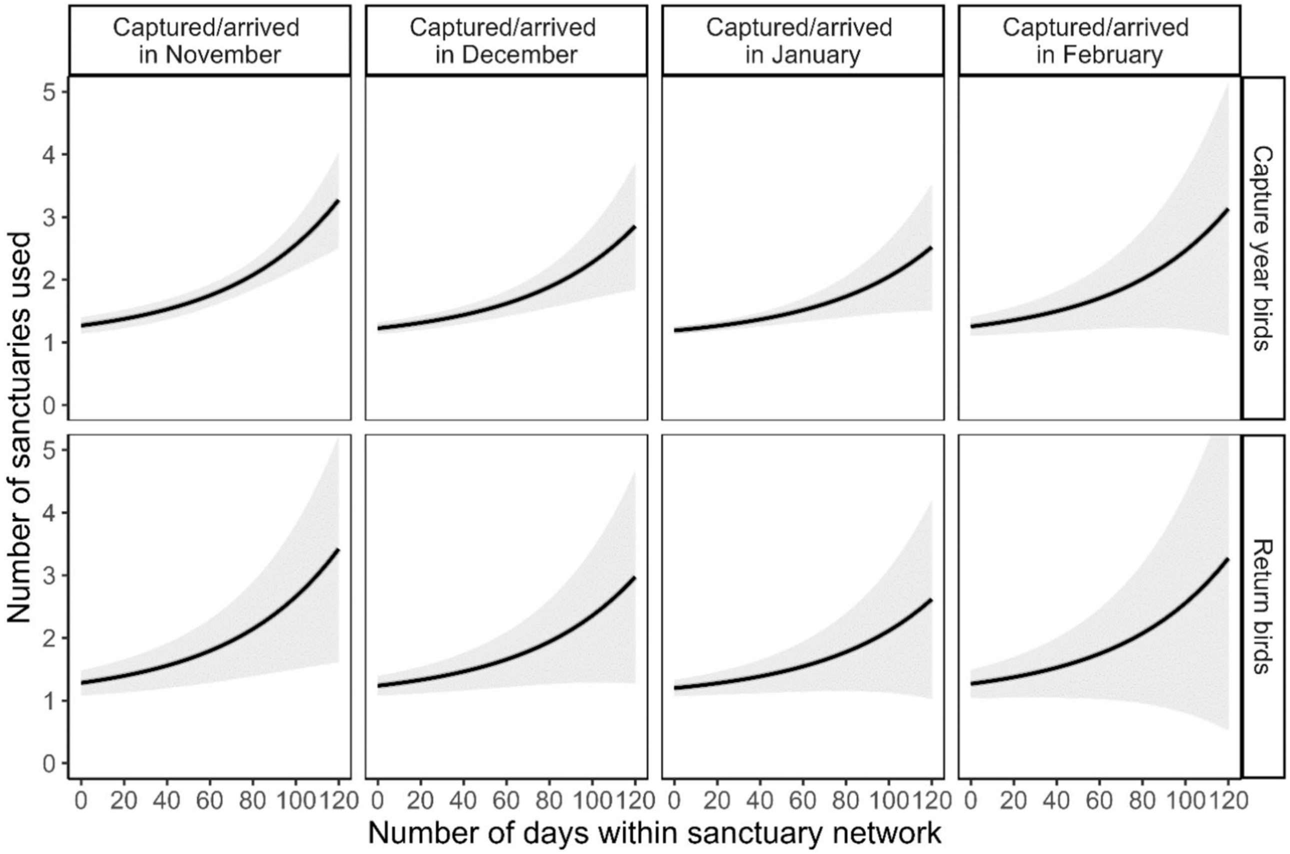

**Figure 3.** Predicted number of waterfowl sanctuary nodes used by wintering mallards (*Anas platyrhynchos*) within the west Tennessee and surrounding wetland complex protected sanctuary network relative to the number of days in the study area. Plots are faceted by the month (columns) and by individuals using sanctuaries during the same winter they were captured and individuals returning to the study area (rows). Figure was produced in R version 4.3.3. https://www.r-project.org/.

especially given diurnal movement constraints during hunting season[96,100,109]. In other words, transitions to distant and unvisited sanctuaries would require exploratory behaviors that may increase hunter encounters[108,112,113]. In concert, forage availability and abundance, spatial memory, and the negative fitness consequences for exploratory behavior (Supplementary Context, Methods, & Results) may explain why sanctuary proximity and not size promoted functional connectivity.

Authorized purposes for waterfowl spatial sanctuaries vary regionally, nationally, and internationally[54,58]. Within our region, state-owned sanctuaries are intended to bolster or maintain local waterfowl abundance and facilitate movements among sanctuaries to improve waterfowl hunting and hunter satisfaction[60,114]. National Wildlife Refuges in the region serve similar purposes but are six times the size of state-owned sanctuaries; therefore, they are better equipped to support biodiversity, population persistence, and host large abundances of waterfowl as local "source" populations to surrounding areas[53]. However, our data indicate larger NWRs do not necessarily serve as local source populations that facilitate movement of mallards across our region, but we suggest they could if they were better connected to smaller state-owned sanctuary nodes within the network. Therefore, state conservation agencies that aim to increase waterfowl movements and connectivity should consider acquiring or leasing land that serves as stepping-stone sanctuaries to connect larger existing nodes, such as NWRs[115,116]. A similar strategy was implemented in Louisiana, USA for northern pintails (*A. acuta*) with mixed results[117,118]. Success or failure of attempts to improve wintering waterfowl connectivity undoubtedly depend on regional landscape matrices and sanctuary patch habitat quality[39]. If food resources within and beyond sanctuary boundaries are abundant and hunting mortality risk in the surrounding matrix is high, waterfowl should minimize exploration to the extent physiologically possible, especially to distant nodes, making stepping-stone sanctuaries even more critical to improve functional connectivity[102,107,115]. Additionally, smaller connecting sanctuaries must be disturbance-free[87,119]. Hunting and other human disturbances within small sanctuaries would likely negate any positive connectivity benefits[37,59,115].

Private lands are crucial to wildlife conservation delivery worldwide[120–122] and can influence waterfowl resource selection and movement when protected legally[18,43,123]. Protected private lands provide critical habitat and potential connectivity benefits among sanctuaries; however, single ownership parcels are often small and landowners typically recreate and disturb these areas, which likely limits their conservation value as stepping-stone sanctuaries. Private land cooperative partnerships may resolve this scalar problem as an effective mechanism for connecting waterfowl habitat while simultaneously improving recreational opportunities[124]. Voluntary partnerships among neighboring private landowners that collectively improve habitat quality and hunting experiences have proven effective at promoting connectivity for terrestrial wildlife species[124–126], but seldom has this model been translated to wetlands and waterfowl management. We suggest a similar model of private land conservation partnerships[127] to enhance waterfowl movement, landscape connectivity, and recreational opportunities. Private landowners may consider wetland management cooperatives (WMCs) that regulate waterfowl hunting temporally[88] and establish spatial sanctuary shared among the WMCs. This waterfowl management strategy has potential to enhance recreational opportunities by reducing isolation effects among state- and federally-owned sanctuary nodes thereby improving connectivity within the network.

Our findings refine applications of the equilibrium theory predictions for highly mobile and hunted species using protected area networks. Proximity promoted connectivity more than area, even for an unfettered avian migrant[2]. Empirical studies like ours rarely support single large over several small reserves[21,128,129], yet conservation planners prioritize larger reserves, which may undermine landscape structural connectivity and disincentivize movement[30,31]. For locally wintering waterfowl, numerous small sanctuaries could act as stepping stones to connect large reserves harboring source populations[4,7,130]. In other words, "mainlands" likely already exist (e.g., National Wildlife Refuges) within established sanctuary networks for locally wintering waterfowl but functional connectivity may not. Conservation planners should consider the landscape matrix and species' movement transitions, distances, and range sizes when prioritizing areas for protection within pre-existing waterfowl or other protected area network designs[43,69,70,131]. Publicly-funded programs to lease private lands as spatial sanctuaries or voluntary private land wetland management cooperatives (WMCs) that incorporate spatial sanctuary and limit hunting disturbance may enhance connectivity as stepping-stones within a sanctuary network. For example, if two 10 km$^2$ (3.9 mi$^2$) sanctuaries were separated by 20 km (12.4 mi), a male mallard only had a 46% chance to transition to or from each sanctuary across the entire 120-day winter period. Hypothetically, should another 10 km$^2$ (3.9 mi$^2$) stepping-stone sanctuary be established in the middle of the two existing sanctuaries (i.e., now 10 km or 6.2 mi between nodes), mallard functional connectivity would increase threefold, with a 88% probability of transitioning during the winter period.

Researchers should evaluate effectiveness (and nuances) of such programs aimed at increasing connectivity across waterfowl species and other wildlife. Simulations to reveal "optimal" connectivity thresholds are a logical extension to our work that would provide conservation planners with decision support for targeted land easements or acquisition[132]. Additionally, conservation agencies and their communication specialists may consider promoting potential benefits of private land cooperation to support wildlife connectivity in increasingly fragmented landscapes[120,133,134]. Last, researchers should investigate a minimum sanctuary size to inform establishment of stepping-stone sanctuary sizes, which we could not identify because our smallest sanctuary node (1.3 km$^2$) was well connected[59,135]. Spatially-explicit models of hunting and waterfowl response to "disturbed areas" may be useful to infer risk perception and subsequently, inform minimum sanctuary sizes[59,87,106] (Fig. S1).

## Methods

### Study system

Our study was conducted in west Tennessee and surrounding wetland complexes of west Kentucky, northeastern Arkansas, and southeastern Missouri, USA spanning 12,875 km$^2$ during autumn and winter 2019–2023. Waterfowl hunting is culturally and economically important to the region[136–138]. Mallards are abundant and harvested intensively within and near the study region relative to the entire Mississippi Flyway of North America[139]. Therefore, waterfowl sanctuaries provide needed spatially-defined and legally-designated safe and protected spaces for mallards and other waterfowl within an otherwise inhospitable landscape matrix (i.e., high hunter densities and activity across time and space[60,96,114] (Fig. S1). Another purpose of the region's waterfowl sanctuaries is to maintain or enhance local–regional waterfowl abundance and facilitate movement among them during the waterfowl hunting season; both are assumed to increase harvest opportunity and hunter satisfaction[60,140,141].

Within this important geography exist four U.S. NWRs and seven state-owned waterfowl sanctuaries that vary in size and distance from one another. These sanctuaries prohibit hunting and other human activities on or before 15 November through 31 March[60,96]. Intense hunting surrounding each waterfowl sanctuary in the region makes them functional "islands" among few other suitable habitats for waterfowl diurnally (Fig. S1)[60,96]. Therefore, the region's sanctuary network is a model system or landscape mesocosm[142] to test sanctuary network connectivity relative to sanctuary sizes and isolation (i.e., SL > SS) because it meets several criteria: (1) suitable patches (i.e., sanctuaries) are rare but with geographically[143] and biologically[95,96] representative size-distance variation; (2) sanctuary patches are relatively homogenous spatially; and (3) the landscape matrix surrounding sanctuaries is "hostile" due to chronic anthropogenic hunting pressure (Fig. S1; Supplementary Context, Methods, Results 1)[2,60,96].

### Animal capture and monitoring

We captured male and female mallards from October through February 2019–2022 on 9 of 11 waterfowl sanctuaries within our study region, thereby ensuring a spatially and temporally balanced sample. We banded ducks with U.S. Geological Survey aluminum tarsal bands and determined sex and age based on cloacal inversion, wing plumage, and bill color[144]. We attached 20 g OrniTrack Global Positioning System-Global System for Mobile transmitters (GPS-GSM; Ornitela, UAB Švitrigailos, Vilnius, Lithuania) to birds weighing ≥ 1000 g to ensure deployment packages remained below 3% of recommended body weights for unbiased monitoring[145]. We programmed GPS-GSM transmitters to record hourly locations throughout the study. For analyses, we treated first year captured ducks and return wintering ducks as independent sampling units. All animal capture, handling procedures, and experimental protocols were in accordance with Tennessee Technological University's

Institutional Animal Care and Use Committee protocol #19-20-002, authorized under Federal Banding Permit #05796, and adhered to ARRIVE guidelines (https://arriveguidelines.org).

## Spatial and individual covariates

We used the protected area database (PAD-US; U.S. Geological Survey (USGS) Gap Analysis Project (GAP) 2022) to acquire U.S. NWR and state waterfowl sanctuary boundaries from northwest Tennessee, western Kentucky, eastern Arkansas, and Missouri. The PAD-US is an inventory of property boundaries with legal protected status intended to conserve biological diversity, recreation, and cultural uses. We defined spatial sanctuaries as areas managed for waterfowl and prohibited human recreation and disturbance before, during, and after the waterfowl hunting season. Following consultation with local biologists, we modified NWR and state-managed boundaries from PAD-US to exclude areas that allowed human recreation or other access, thereby ensuring our database only included waterfowl spatial sanctuaries[43]. We also eliminated erroneous features from the analysis[18] (e.g., boat docks, office buildings). Importantly, if sanctuaries were geographically separated—despite being considered one contiguous sanctuary—we separated them into two or more sanctuary nodes because mallards theoretically perceived these boundaries separately given the huntable landscape matrix between nodes (i.e., 1.6 and 2.1 km apart, respectively). Our resulting sanctuary network included five NWR nodes (three in Tennessee, one in Tennessee and Kentucky, and one in Arkansas) and eight state-owned waterfowl sanctuary nodes in Tennessee ($n = 13$).

For all federal and state-owned waterfowl sanctuaries, we calculated area (km$^2$) and distance matrices (km) to and from each sanctuary using the *sf* package in R version 4.2.2[146,147]. Sanctuary area ranged from 1.3–45.7 km$^2$ ($\bar{x}$ = 9.7 ± 11.8 km$^2$; $n = 13$) and minimum distances between sanctuaries ranged from 1.3–120.0 km ($\bar{x}$ = 46.9 ± 25.8; $n = 78$). We used sanctuary area and distances as covariates to test predictions that movement transitions (i.e., sanctuary departure and arrival) varied depending on the size of the emigrated sanctuary (e.g., source populations), the size of the sanctuary the individual relocated to, and the distance between them[7]. We also included age and sex of each individual as covariates to test predictions that males relocated more in search of limited females and pair bonding opportunities[148,149] and juveniles relocated more because they were naïve to hunting risk implied by greater harvest rates[150,151].

## Sanctuary transition multistate capture-recapture model

We developed multistate mark-recapture models in a Bayesian framework to estimate movement transition probabilities among sanctuaries[152–154] (File S1, Table S1). We built daily encounter histories for each individual from 1 November through 29 February from 2019–2023 where we assigned categorical "states" (i.e., sanctuary node) for each mallard on each day during winter. We treated individuals with two or more winters as separate sampling units with separate encounter histories because individuals with > 1 year of data could begin their capture history at different sanctuary nodes (states) in winters $t + 1$[155]. The encounter history for each individual began with their first GPS location on a sanctuary node, defined for each day between 1000 and 1900, which represented a time when most individuals would be within sanctuary boundaries[94–96]. Additionally, we filtered the first 4 days of GPS locations following deployment to allow ducks to acclimate to GPS transmitters and harnesses[94]. Individuals were assigned 1 of 14 possible states which included 13 sanctuary nodes and an unobserved state (File S1, Table S3, Table S4). Individuals with unobserved states missed GPS fixes or were not within sanctuary boundaries during the 1000–1900 observation window. Although not all sanctuary node transition combinations were reflected in the data, we did not restrict analyses to only observed transitions because all were biologically possible based on mallard movement and dispersal ability[155] (File S1, Table S3).

We estimated daily movement transition probabilities ($\psi$) from sanctuary node ($i$) to every other sanctuary ($j$), including the probability of staying on the current sanctuary, for a total of 169 transition probabilities ($\psi_{i,j}$), including "no transition". Specifically, we fitted generalized linear models with a multinomial link function to estimate movement probabilities on the logit scale for transitions from one sanctuary node ($s$) to any other node ($j$) for individual ($i$) relative to sanctuary sizes, distances, and age-sex demographics (1–13 possible transitions): $logit.\psi_{sji} = \beta_0 + \beta_{dist} \times Distance_{sj} + \beta_{size.s} \times Size_s + \beta_{size.j} \times Size_j + \beta_{sex} \times Sex_i + \beta_{age} \times Age_i$. We calculated the probability of staying on the current sanctuary node as $1 - \sum_{j=1}^{12} \psi_{s,j,i}$[154]. In other words, the probability of transitioning to another sanctuary was estimated conditionally relative to distance between sanctuaries (km), sizes of the emigration and immigration sanctuaries (km$^2$), and age and sex covariates. Conversely, the probability of staying (i.e., not transitioning) was calculated to ensure probabilities summed to 1[154]. We estimated movement transition probabilities with one intercept (i.e., transitions from one sanctuary to any other sanctuary), as opposed to 13 sanctuary-specific intercepts[154,156].

We fitted the multistate model using Markov Chain Monte Carlo (MCMC) simulation with the *jagsUI* package in R[147,157,158]. We specified vague priors for all model parameters[159]. We used a parallel processing framework for computational efficiency which ran 10 independent Markov chains for 100 iterations each, a 20 iteration burn-in, and a thinning rate of 3[160]. We proceeded with 100 iterations until models converged or until a priori maximum of 1000 iterations was reached. We monitored convergence based on visual inspection of the chains (Fig. 3) and the Gelman-Rubin statistic which converged $\widehat{R} \leq 1.01$[161]. We reported coefficients on a logit scale and odds ratios with 90% credible intervals (CRI)[162]. We illustrated predicted relationships with 68%, 90%, and 95% CRI bands graphically[163].

## Modeling sanctuary use and survival

We fitted a separate generalized linear model with a truncated Poisson error distribution and log-link function in a maximum likelihood framework using *glmmTMB* in R to estimate the effect of time spent in the study region (1–120 days), winter month (November, December, January, and February), and number of winters (1 winter = capture and > 1 winter = return) relative to the number of sanctuaries used[147,164]. Intuitively, we predicted the longer an individual remained within the study region, the greater number of sanctuaries used. We specified November as the categorical indicator and predicted individuals would use more sanctuaries during November and February and fewer sanctuaries during December and January to minimize risk of hunting mortality (i.e., less movement during hunting season). Importantly, we included the number of winters an individual was monitored (i.e., 1 or $>1$) to ascertain possible confounding sanctuary use behavior due to marker effects. Specifically, we assumed that an individual that returned to the region and thus survived the previous winter–fall migration was reasonably unaffected by their transmitter; therefore, no clear statistical difference of sanctuary use between capture-year wintering ducks compared to ducks that returned to the study region suggests no behavioral biases of sanctuary use as a result of external transmitters. We calculated Pearson's correlation ($r$) between pairs of continuous covariates but none were correlated ($|r| \leq 0.6$)[165]. We used the *DHARMa* package in R to ensure model assumptions were not violoted[166] (Fig. S4). We provided estimated coefficients and considered covariates statistically significant if 90% confidence intervals did not bound zero[167,168].

We identified 45 individuals (11%) that never used sanctuary following capture (Supplementary Context, Methods, Results 2). We assigned a binary independent variable of sanctuary use to each individual where "0" denoted individuals that never used a sanctuary node following capture and "1" was the opposite. We fitted a Cox proportional hazard model in the *survival* package in R to estimate known-fate Kaplan-Meir survival curves and hazard ratios[169,170]. We right-censored individuals that did not die by the end of winter (120-days from November–February) or stopped transmitting, assuming unbiased censoring[171,172]. We tested whether overwintering survival was different between sanctuary and non-sanctuary mallards using a log-rank $\chi^2$ test at an a priori $\alpha = 0.05$[173]. We reported a seasonal baseline hazard ratio, survival probabilities at 30 and 60 days and associated variance estimates for each GPS-marked cohort. Additional details are provided in Supplementary Context, Methods, Results 2.

## Animal ethics

Duck capture and handling procedures were in accordance with Tennessee Technological University's Institutional Animal Care and Use Committee protocol #19-20-002 and authorized under Federal Banding Permit #05796.

## Data availability

Relevant data and code are included in Supporting Information and are available in GitHub and published through Zenodo at https://doi.org/10.5281/zenodo.10150699.

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## Author contributions

*Conceptualization*: BSC, NMM, ACK, AGB, and CJH. *Data collection*: AGB, CJH, NMM, and HMH. *Data management, analysis, interpretation, and visualization*: ACK and NMM. *Writing*: NMM and ACK. *Review and editing*: BSC and CJH reviewed initial drafts; all authors contributed to final drafts. *Project administration and funding acquisition*: BSC, JCF, and HMH.

## Competing interests

The authors declare no competing interests.

## Additional information

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