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Stability of patch-turnover relationships under equilibrium and nonequilibrium metapopulation dynamics driven by biogeography

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Abstract

Two controversial tenets of metapopulation biology are whether patch quality and the surrounding matrix are more important to turnover (colonisation and extinction) than biogeography (patch area and isolation) and whether factors governing turnover during equilibrium also dominate nonequilibrium dynamics. We tested both tenets using 18 years of surveys for two secretive wetland birds, black and Virginia rails, during (1) a period of equilibrium with stable occupancy and (2) after drought and arrival of West Nile Virus (WNV), which resulted in WNV infections in rails, increased extinction and decreased colonisation probabilities modified by WNV, nonequilibrium dynamics for both species and occupancy decline for black rails. Area (primarily) and isolation (secondarily) drove turnover during both stable and unstable metapopulation dynamics, greatly exceeding the effects of patch quality and matrix conditions. Moreover, slopes between turnover and patch characteristics changed little between equilibrium and nonequilibrium, confirming the overriding influences of biogeographic factors on turnover.

KEYWORDS
biogeography, black rail, equilibrium dynamics, matrix, metapopulation, nonequilibrium dynamics, patch quality, Virginia rail, West Nile virus, wetland

INTRODUCTION

Metapopulation biology has been undergoing a reexamination of its basic tenets. A key area of contention concerns the importance of different kinds of patch characteristics to turnover and whether their influence shifts under nonequilibrium conditions. Metapopulation theory, which was originally based on biogeographic relationships of patch area and isolation (Hanski, 1999), has been challenged by the roles of patch habitat quality (Armstrong, 2005; Armstrong et al., 2022; Ovaskainen & Saastamoinen, 2018; Schooley & Branch, 2009) and the surrounding matrix (Gebauer et al., 2013; Matthews, 2021; Ricketts, 2001). In addition, an important criticism of metapopulation theory in general, and the incidence function model in particular (Hanski, 1994; Risk et al., 2011; Thomas & Hanski, 2004), is that they assume equilibrium conditions or "quasi-stationarity," with little change in patch number, size or quality (Baguette, 2004; Holyoak & Ray, 1999). Yet, habitat destruction, climate change and succession are widespread processes and many landscapes may be far from equilibrium. Moreover, disturbances from abiotic (e.g. heat waves or drought) or biotic (arrival of diseases, predators or competitors) processes can result in local population extinction (Chesson, 2013). Thus, patch characteristics affecting turnover under equilibrium may have different effects during nonequilibrium conditions, reducing the ability of models to project future dynamics. As a result, the incorporation of habitat and disturbance dynamics into metapopulation models has been an area of active theoretical development (Hastings, 2003; Mestre et al., 2021; Ovaskainen & Saastamoinen, 2018) and application (Howell et al., 2018; Ruete et al., 2014; Van Schmidt et al., 2019). Nevertheless, field studies that examine the factors affecting turnover during equilibrium and nonequilibrium conditions are lacking.

We tested whether the processes that govern patch occupancy and turnover during equilibrium operate similarly during nonequilibrium, and quantified the relative importance of biogeography, patch quality and matrix conditions to metapopulation dynamics using 18 years of field surveys for two secretive wetland birds at 307 wetland patches (Figure S1). The California black rail (*Laterallus jamaicensis corturniculus*) and Virginia rail (*Rallus limicola*) metapopulations provide an ideal test of metapopulation processes due to the high habitat specialisation of rails, the large study area (2000 km^2), numerous small patches in which rails reside year-round, a moderate turnover rate, and a high probability of detecting rails using playback of their vocalisations (Richmond et al., 2008; Van Schmidt et al., 2019; Van Schmidt & Beissinger, 2020). Moreover, following a period of relative stability, the black rail suffered a large decline in occupancy due apparently to climatic variation and the arrival of a nonendemic disease, West Nile Virus (WNV), which is a potent source of mortality for birds (LaDeau et al., 2007). We took advantage of this unusual opportunity to: (1) examine metapopulation dynamics during a shift from equilibrium to nonequilibrium, (2) quantify the regional processes that caused the shift, (3) test the relative importance of biogeography, patch quality and matrix condition on colonisation and extinction and (4) determine whether important patch covariates affecting turnover differed between equilibrium and nonequilibrium conditions.

METHODS

Study species and study area

The black rail is the smallest rail in North America, has a highly disjunct distribution, and is rarely observed. The California subspecies *(L. j. coturniculus)* is state-listed as threatened and occurs as metapopulations in three small, isolated regions (Sierra Nevada Foothills, San Francisco Bay and Sacramento-San Joaquin Delta, and lower Colorado River). Connectivity between these three metapopulations is limited or nil (Girard et al., 2010; Hall & Beissinger, 2017). Within the Sierra Nevada Foothills (hereafter "Sierra Foothills"), the median dispersal distance between parent-offspring pairs was 0.18 km, with occasional long-distance movements to 28 km (Hall et al., 2018). Virginia rails are common and widespread across North America. Compared to black rails, Virginia rails are larger (90 vs. 30 g), have larger home ranges (1.6 vs. 0.4 ha), are stronger flyers and can colonize isolated patches (Risk et al., 2011; Van Schmidt & Beissinger, 2020). The two species have similar breeding biology and diets and co-occur as year-round residents in the Sierra Foothills (Richmond, Hines, & Beissinger, 2010; Van Schmidt et al., 2019).

Rails in the Sierra Foothills inhabit small (median = 0.45 ha, range: 0.02–16.27 ha), perennial, shallow wetland patches dominated by dense emergent vegetation that range in elevation from 25 to 825 masl (Figure S1). Water sources for these wetlands include natural springs, creeks and ponds and leaks from irrigation canals (Richmond, Chen, et al., 2010). Wetland patches are surrounded by open grasslands, oak or pine forests, agriculture and sparse development. They are situated on a nearly even mix of private and public lands and differ greatly in size, isolation and other characteristics (Richmond, Chen, et al., 2010; Van Schmidt et al., 2019).

Quantifying rail turnover and metapopulation dynamics

Although both rails rarely emerge from dense vegetative cover, they readily respond to playbacks of their

vocalizations, so systematic surveys comprised of repeated visits effectively estimate patch occupancy and turnover. We annually surveyed an average of 203 of the 307 wetland patches (range: 110–255) during the breeding season (late May to early August) for black rails from 2002 to 2019 and Virginia rails from 2005 to 2019. New patches were added when discovered, whilst some previously surveyed patches on private lands were eliminated if access was revoked by landowners. Wetlands were surveyed using call-playback methods, with up to 3 visits each summer (5 in 2002) to allow estimation of annual detection probabilities using a removal model, where sites were not revisited once both species were detected in that year (MacKenzie et al., 2018). Our survey methods are described in detail elsewhere (Richmond et al., 2008; Richmond, Hines, & Beissinger, 2010).

We employed a dynamic multi-season occupancy model (MacKenzie et al., 2003) to jointly estimate probabilities of colonisation (γ), extinction (ε) and occupancy (ψ), whilst accounting for imperfect detection (p), from the annual rail survey data using Program Presence v13.17 (Hines, 2006). It takes the general recursive form of:

$$\psi_t = \psi_{t-1}\left(1 - \varepsilon_t\right) + \left(1 - \psi_{t-1}\right)\gamma_t \qquad (1)$$

We found no evidence of competitive exclusion at patches (Richmond, Hines, & Beissinger, 2010; Risk et al., 2011), so we modelled the species separately. Models were fit with annual detection terms, which greatly improved Akaike's information criterion (AIC) compared to null models. For Virginia rails, an extra term was added for the first survey year to distinguish visit 1, which used call-playbacks, from visits 2 and 3, which did not employ playbacks.

We tested for equilibrium and nonequilibrium dynamics by modelling colonisation and extinction for various groupings of years prior to and after the arrival of WNV (Table 1), and compared fit with AIC. An equilibrium period was represented by fitting a single term across multiple years for γ and another for ε, which results in a relatively stable value for occupancy. In contrast, we identified nonequilibrium periods as consecutive years where yearly estimates for γ and ε were required, which results in occupancy fluctuating annually. We compared mean occupancy during years of equilibrium to equilibrium occupancy (ψ^*) expected from theory (Hanski, 1999):

$$\psi^* = \gamma / (\gamma + \varepsilon) \qquad (2)$$

We calculated the metapopulation growth rate or finite rate of change in occupancy (λ_t) as λ_{t+1}/λ_t (MacKenzie et al., 2018). We compared annual fluctuations in γ, ε, ψ, and λ between black and Virginia rails using Pearson correlations and Deming regression, which explicitly incorporates uncertainty of x and y estimates using the package *deming* (Therneau, 2018) in R version 4.1.2 (R Core Team, 2020).

Determining drivers of turnover leading to nonequilibrium conditions

We identified three environmental conditions that changed annually and could have caused a shift from equilibrium to nonequilibrium and explored their influence on turnover using the dynamic multi-season occupancy model. They included WNV and two factors related to climatic variation (annual precipitation and number of days below freezing). Sensitivity analyses of coupled human and natural systems models found annual precipitation and WNV play key roles in rail metapopulation dynamics (Van Schmidt et al., 2019).

To confirm that rails are frequently infected with WNV, we collected blood samples from 199 black rails and 103 Virginia rails that we captured throughout the Sierra Foothills and tested them for WNV antibodies (SI Methods).

We developed a model set consisting of annual measures of precipitation, WNV vector index, freeze days, and their two-way and three-way interactions, and tested their impacts on rail turnover throughout the entire study period using the multi-season occupancy model (Table S3). Annual precipitation and freeze days were calculated based on water years (October of the previous year through September of the target year), which aligned with annual rail surveys because most precipitation and freezing conditions occur between November and April. The WNV vector index measured the density of WNV-infected mosquitoes, which is the product of the minimum infection rate within tested mosquito pools and mosquito abundance (number per trap night). Further justification for the choice of these annual covariates, their measurement and their expected interactions on turnover are provided in the SI Methods. Annual covariates were centred and scaled by one standard deviation prior to analysis. We used AIC to compare the ability of models to describe turnover. We explain the rationale for constructing the model set and determining the most parsimonious model in the SI Methods. Covariate relationships from the best model were graphed using the delta method to estimate standard errors with the R package msm v1.6.9 (Jackson, 2011).

Patch and matrix characterization

We quantified patch characteristics likely to influence metapopulation dynamics using published methods and criteria (Richmond et al., 2012; Richmond, Hines, & Beissinger, 2010; Van Schmidt et al., 2019; Van Schmidt & Beissinger, 2020). Biogeographic covariates included: patch area (calculated from digital imagery and ground-truthed annually); isolation (natural log of the geometric mean distance to the nearest three occupied patches), which described turnover better than indices based on occupancy and site area (Van Schmidt & Beissinger, 2020);

per cent of wetland within 500 m of a patch (a mesoscale measure of isolation); and elevation (masl).

Patch quality covariates included key characteristics affecting inundation and vegetation of patches: (1) wetland geomorphology—categorised following Richmond, Chen, et al. (2010) as slope (gently sloping and flowing, non-channelised), fringe (around ponds edges) and fluvial (flowing water on edges of creeks or streams). We excluded impoundments associated with rice fields because few were surveyed during the equilibrium period and they are poor rail habitats; (2) water source—natural, irrigated or both sources, which was determined from site visits and aerial imagery collected prior to the 1950s. Irrigated wetlands have more consistent and stable inundation than natural spring- or stream-fed wetlands (Van Schmidt et al., 2021); (3) vegetative cover—wetlands with >25% ground cover of *Juncus* spp. (preferred by black rails) or *Typha* spp. (preferred by Virginia rails), estimated during site visits; (4) land ownership (public versus private)—wetlands on private lands may be more likely to dry out, depending on landowner motivations (Van Schmidt et al., 2021); (5) grazing—whether sites were actively or recently grazed by cattle or goats. Heavily grazed sites have less vegetative cover and are less likely to support rails (Richmond et al., 2012); (6) presence of surface water—dry sites rarely support rails (Richmond, Chen, et al., 2010); and (7) enhanced vegetation index (EVI), which is a 30-m resolution Landsat product that quantifies vegetation greenness whilst correcting for atmospheric conditions and canopy background noise (Huete et al., 1994). EVI is a sensitive indicator for areas with dense vegetation (Huete et al., 1997), which characterises rail wetlands.

Matrix composition included the per cent of open, forest and developed land cover within a 100 m buffer around each patch. The surrounding matrix could influence extinction through spillover of predators (e.g. developed), or affect colonisation by making wetlands more difficult for dispersing rails to discover or reach (e.g. forest). We used the 30-m resolution 2011 National Land Cover Dataset (NLCD; Homer et al. 2011) and the 1-m resolution Sierra Foothills Emergent Wetland (NVS) dataset (Van Schmidt et al., 2019), which had ground-truthed polygons of rice fields, open water and emergent wetlands, favouring the latter when datasets overlapped. We categorised pixels as wetland (NVS wetland dataset; NLCD open water, woody wetlands, emergent herbaceous wetlands classes), forest (NLCD deciduous, evergreen and mixed forest classes), developed (NLCD developed open space and low, medium and high-intensity classes) and open (NLCD barren land, shrub/scrub, grassland/herbaceous and pasture/hay classes).

We modelled the effects of biogeographic, patch quality and matrix covariates on rail turnover with a dynamic multi-season occupancy model using the *colext* function in the R package *unmarked* v1.1.1 (Fiske & Chandler, 2011). For this analysis, continuous covariates were centred and scaled by two standard deviations for comparing slopes with dichotomous categorical covariates (Gelman, 2008). Two model structures were used. First, to determine if the relative importance of patch covariates changed with the shift from equilibrium to nonequilibrium period for black rails, we created a model set comprised of the independent effect of each patch covariate and fit it separately for each period. The best combination of covariates was determined separately for biogeographic, patch quality and matrix covariates within each period using the *dredge* function in the *MuMIn* R package (Bartoń, 2022). Detection was modelled by year and initial occupancy covariates included area, slope, and isolation, key factors affecting rail occupancy (Richmond, Hines, & Beissinger, 2010; Van Schmidt et al., 2019). Second, to test if the slopes of covariates changed with the shift from equilibrium to nonequilibrium dynamics (*period*) for black rails, we modelled colonisation and extinction as a function

TABLE 1 Multi-season occupancy models comparing annual variation in turnover to test for periods of equilibrium and nonequilibrium metapopulation dynamics for the black (BLRA) and Virginia (VIRA) rails in relation to the arrival of West Nile virus (WNV) in 2006

Species	No.	Rationale for year groupings	Year groupings	ΔAIC	AIC wt	*k*
BLRA	1	Pre-WNV, WNV, Post-WNV by year	2002–06; 2007, 2008, …, 2019	0.00	0.661	47
	2	By year	2002, 2003, 2004, …, 2019	1.34	0.338	53
	3	Pre-WNV, WNV, Post-WNV	2002–2006, 2007, 2008–2019	12.06	0.002	25
	4	Pre-WNV, WNV+Post-WNV	2002–2006, 2007–2019	22.55	0.000	23
	5	Constant	(.)	60.21	0.000	21
VIRA	6	By year	2006, 2007, …, 2019	0.00	0.642	45
	7	Pre-WNV, WNV, Post-WNV	2006; 2007; 2008–2019	1.79	0.262	23
	8	Pre-WNV, WNV+Post-WNV	2006, 2007–2019	4.75	0.060	21
	9	Constant	(.)	6.68	0.023	19

Note: All models included initial occupancy modelled without covariates and the best detection model for each species (BLRA: Year; VIRA: Year except for year 1 (visit 1, visit 2+3)). For each species, models are numbered (no.) from best to worst based on ΔAIC (the difference between the model and the best model) and AIC weight (wt) is given relative to other models in the species' set. *k* is the number of model parameters.
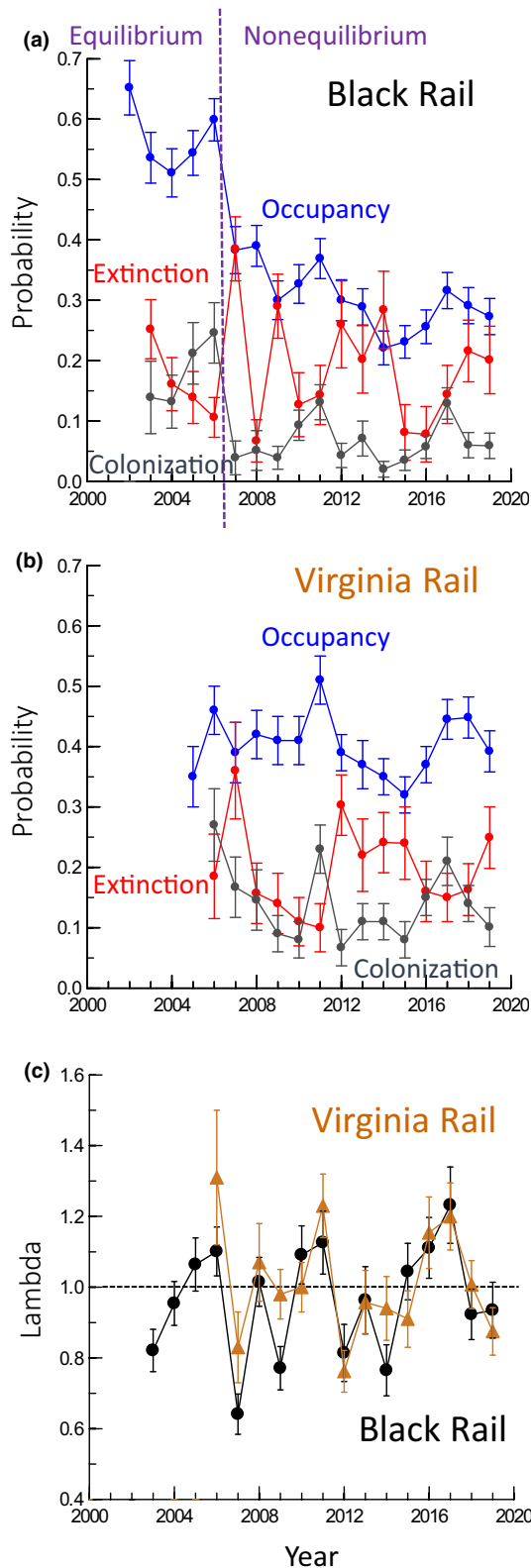
FIGURE 1 Metapopulation dynamics of (a) black and (b) Virginia rails. Periods of equilibrium and nonequilibrium dynamics for black rails were determined by occupancy modelling (Table 1). (c) Metapopulation lambda indicates the growth rate or finite rate of change in occupancy (λ_{t+1}/λ_t).

of each covariate (x), *period* and *x*period*, using the *p*-values of the later term to test for significance after controlling the false discovery rate of 0.1 from multiple comparisons with the Benjamini–Hochberg procedure (Benjamini & Hochberg, 1995). A similar model set of biogeographic, patch quality and matrix covariates was fit for Virginia rail surveys from 2007 to 2019 to compare with black rails for the same period.

RESULTS

Metapopulation dynamics of rails

The black rail metapopulation was in dynamic equilibrium from 2002 to 2006 prior to the spread of WNV and then shifted to nonequilibrium dynamics from 2007 to 2019 (Table 1, Figure 1a). The best-performing temporal model (Table 1, model #1) had single estimates for colonisation and extinction from 2003 to 2006, and annual estimates thereafter. This temporal structure received twice the support (AIC weight) as model #2 with annual colonisation and extinction estimates. Models with other combinations of years prior to and after 2007 (#3, #4) were not competitive (ΔAIC >12).

During dynamic equilibrium (2002–2006), the probability of colonisation for black rails averaged 0.190 ± 0.025 (SE) and extinction averaged 0.163 ± 0.020 (Figure 1a). Mean occupancy during this period was 0.590 ± 0.030—a value similar to the expected equilibrium occupancy ($\psi^* = 0.539$). Occupancy plummeted in 2007 by more than one-third to 0.362 ± 0.037, as extinction jumped to 0.385 ± 0.053 and colonisation fell to 0.043 ± 0.029. Over the next decade, black rail occupancy exhibited a declining trend, reaching a low of 0.219 ± 0.028 in 2014 and ending at 0.272 ± 0.030 in 2019, less than half of the equilibrium value 13 to 17 years earlier. Occupancy changes during nonequilibrium reflected a relatively low rate of colonisation coupled with a highly fluctuating extinction probability (Figure 1b).

Systematic monitoring of Virginia rails began in 2005 3 years after the onset of black rail surveys. Thus, there was little opportunity to detect if turnover probabilities for Virginia rails were in dynamic equilibrium prior to 2007. The best-performing temporal occupancy model (#6) featured annual colonisation and extinction estimates (Table 1). It received nearly twice as much AIC support as a model (#7) that produced estimates for 2006, 2007, and 2008–2019 and 10 times more support than a model (#8) with an estimate for 2006 and another for all subsequent years.

Virginia rail occupancy showed no clear trend (Figure 1b). In 2006, the proportion of patches occupied was 0.461 ± 0.042, about 0.13 less than for black rails
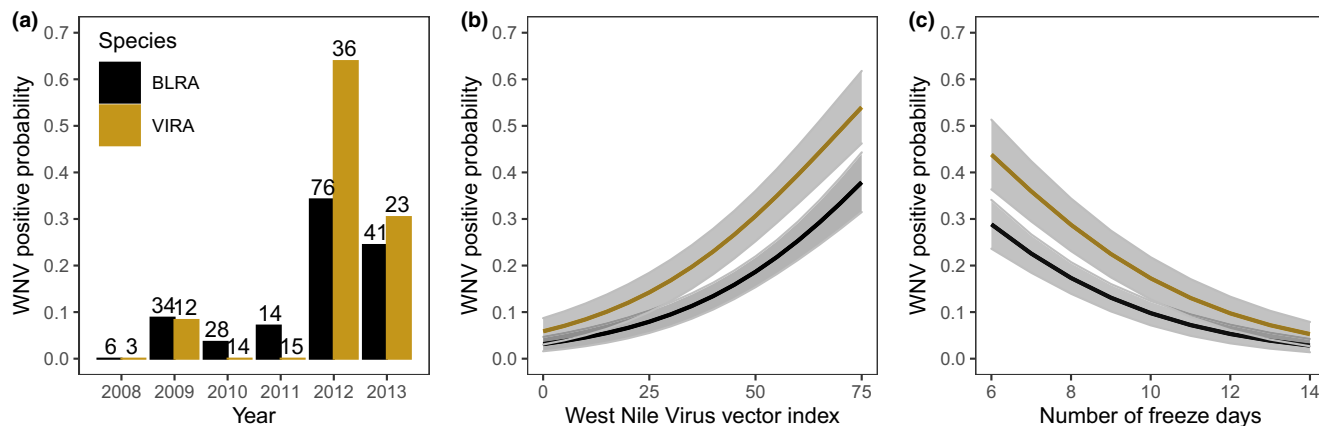
FIGURE 2 (a) The proportion of black rails (BLRA) and Virginia rails (VIRA) captured in the Sierra Foothills metapopulation that tested seropositive for West Nile virus from 2008 to 2013. The number of rails sampled is indicated above each bar. (b, c) The relationship between the West Nile virus positivity rate and West Nile virus vector index (b) and the number of days below freezing (c) for black rails (black lines) and Virginia rails (brown lines) ±1 standard error (grey).

during equilibrium. In 2007 extinction rose and colonisation fell, resulting in a moderate decline in Virginia rail occupancy to 0.385 ± 0.046, a value similar to black rails. Thereafter, Virginia rail occupancy fluctuated annually, with extinction probabilities typically lower and colonisation probabilities typically higher than black rails (Figure 1a,b). Occupancy reached a high of 0.508 ± 0.038 in 2011 and a low of 0.320 ± 0.031 in 2015. When surveys concluded in 2019, Virginia rail occupancy was similar to the start of monitoring 13 years earlier (0.392 ± 0.034) and 0.12 higher than black rail occupancy.

Metapopulation dynamics of black and Virginia rails were strongly related, despite differences in their overall trajectories. Annual fluctuations of metapopulation lambda (Figure 1c) for the two rails were strongly correlated ($r = 0.750$, $p = 0.002$), as were their probabilities of colonisation ($r = 0.798$, $p = 0.001$) and extinction ($r = 0.604$, $p = 0.022$). These significant correlations were supported by slopes and 95% CIs of Deming regressions, which did not overlap zero. Nevertheless, annual fluctuations in occupancy of the two rails were not significantly related ($r = 0.336$, $p = 0.221$).

Drivers of nonequilibrium dynamics

Captured rails frequently had antibodies indicating exposure to WNV and the proportion of seropositive rails varied greatly over the years (Figure 2a). Seroprevalence was much higher in 2012 and 2013 compared to 2008–2011. Virginia rail seroprevalence was higher than black rails in 2012 and 2013, but not in earlier years. Seroprevalence was best described by a model that included the WNV vector index in the year of capture, freeze days, and species (Table S2), but not precipitation (likelihood ratio test to drop from the full model $\chi^2 = 1.210$, $p = 0.271$). The probability of WNV infection increased strongly with

the WNV vector index and decreased with freeze days (Figure 2b,c).

WNV, low precipitation and cold temperatures—acting alone and in concert—pushed the black rail metapopulation from equilibrium to nonequilibrium (Table S3). Precipitation was the best single covariate model describing turnover (model #22), outperforming the WNV vector index (#25) and freeze days (#26) by 18 and 30 AIC points, respectively. However, two-factor models with precipitation and WNV vector index (#18) or freeze days (#21) outperformed precipitation alone by more than 11 and 3 AIC points, respectively. Moreover, a model with all three covariates (#13) improved on the best two-covariate model (#18) by >6 AIC points. It performed only slightly less well (ΔAIC = 0.7) than a model with all three covariates and their two-way interactions (#10), which greatly outperformed (ΔAIC = 3.9) the full model that also included a 3-way interaction (#16). Exploring models with combinations of two-way interactions on colonisation and extinction yielded the best model (#1) that contained only the three main effects for colonisation and those main effects plus all two-way interactions for extinction. It had an AIC weight ~2.4 times greater than its closest competitor (#2), which contained the same covariates except for the interaction between precipitation and freeze days on extinction.

The best model for black rails (Table S3) showed expected relationships of annual covariates with colonisation and the role that WNV played as a modifier for extinction (Figure 3). Colonisation was strongly positively related to annual precipitation and negatively related to the WNV vector index, as predicted (Figure 3a,b). Slopes for these two relationships were similar in magnitude, but in opposite directions. Colonisation also increased with freeze days, but the slope was much shallower (Figure 3c).
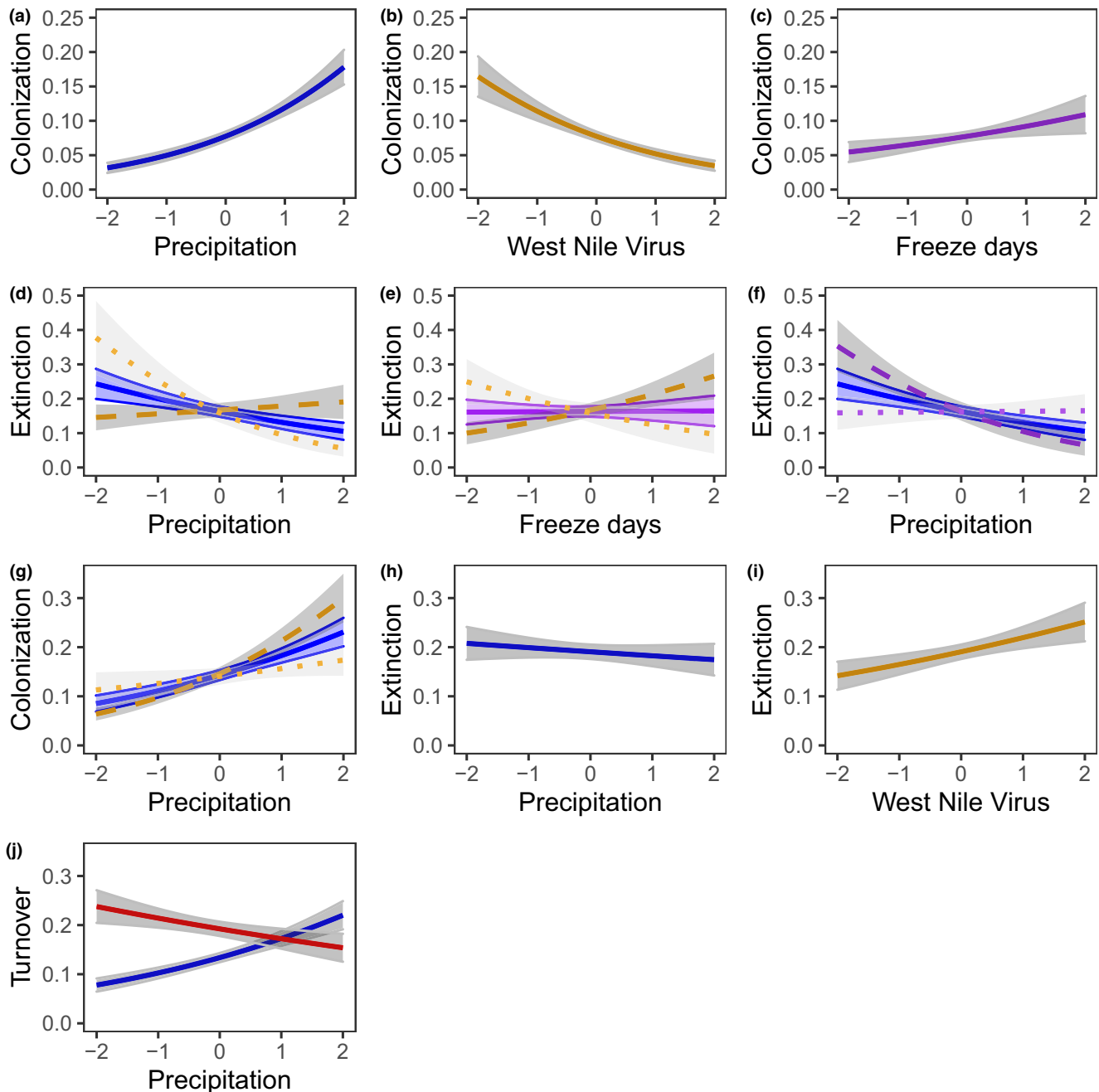
FIGURE 3 Relationships (±1 standard error) for annual factors affecting the probability of colonisation and extinction of black (a–f) and Virginia (g–j) rails from the best-supported models (Tables S3, S4). Two-way interactions are depicted for the modifying covariate values of 0 (solid line and coloured confidence intervals), +1 (dashed and dark grey confidence intervals) and −1 standard units (dotted and light grey confidence intervals) for the West Nile virus vector index on precipitation (d, g) and freeze days (e) and for freeze days on precipitation (f). Turnover for the second-best Virginia rail model depicts colonisation (blue) and extinction (red).

Extinction exhibited complex, crossover interactions. It was negatively related to precipitation and freeze days as expected, but the relationships were strongly modified in years of high WNV to become positive (Figure 3d,e). Freeze days also had a weak moderating effect on the negative relationship between precipitation and extinction (Figure 3f).

Important turnover covariates for Virginia Rails were similar to black rails, but simpler models ranked higher

(Table S4). Like black rails, precipitation was the best single-covariate describing Virginia rail colonisation and extinction (model #2). It outperformed the WNV vector index (#9) and freeze days (#15) by more than 7 and 16 AIC points, respectively. In contrast to black rails, two-factor models with precipitation and the WNV vector index (#4) or freeze days (#5) did not outperform precipitation alone (ΔAIC = 1.15 and ΔAIC = 1.23, respectively). Precipitation also outperformed models that

TABLE 2 The roles of biogeography (biogeo), patch quality, and the surrounding matrix (matrix) on colonisation (γ) and extinction (ε) of black rails during equilibrium and nonequilibrium conditions

Period	Category	Turnover covariates	k	AIC	ΔAIC	AIC wt
Equilibrium	Biogeo	γ: Area, Isolation, Elevation ε: Area, Isolation, Elevation, Wetland	18	1074.0	0.0	1
	Patch quality	γ: Irrigation, Fringe, Fluvial, Public, *Juncus*, Grazing, Surface water ε: Fringe, Fluvial, *Juncus*, Grazing	22	1120.5	46.5	0
	Matrix	γ: Open ε: Open	13	1142.9	68.9	0
Nonequilibrium	Biogeo	γ: Area, Isolation ε: Area, Isolation, Wetland	24	3546.3	0.0	1
	Patch quality	γ: Irrigation, Natural, Fringe, Surface water ε: Irrigation, Natural, Fringe, *Juncus*, Surface water, Grazing	29	3694.4	148.1	0
	Matrix	γ: Developed, Forest ε: Developed, Open	23	3752.4	206.1	0

Note: Modelling was done separately for the equilibrium and nonequilibrium periods. We identified the best multi-season occupancy model (lowest AIC) within each category by dredging all possible covariate combinations within that category. Models are ranked within each period from best to worst based on ΔAIC and AIC weight (wt) relative to other models in the set. k is the number of model parameters.
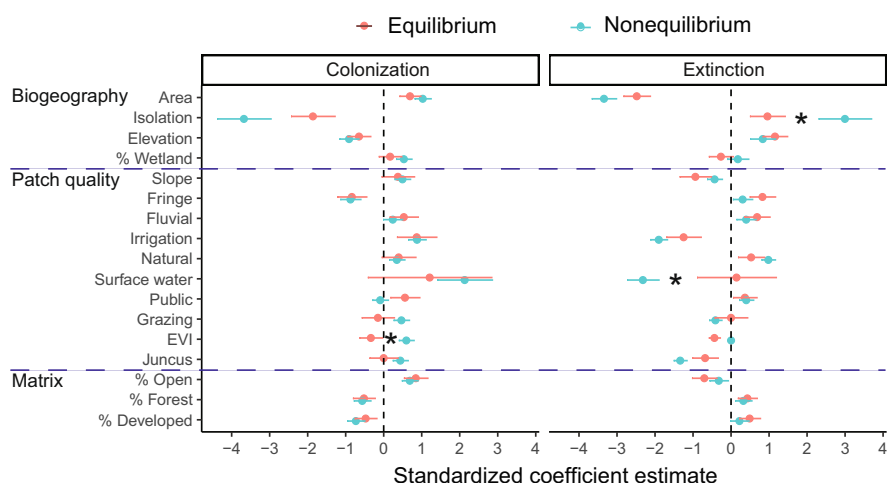
FIGURE 4 Slopes (±1 standard error) during equilibrium and nonequilibrium for black rail turnover in relation to patch characteristics categorised by biogeography, patch quality and the surrounding matrix. An "*" indicates slopes differed significantly between periods. Turnover relationships during equilibrium and nonequilibrium are presented in Figure S5.

added the interaction between precipitation and WNV vector index (#3) or freeze days (#8). The best model (#1) emerged when the interaction between precipitation and WNV vector index was only retained on colonisation. However, it differed from the second-best model with precipitation alone (#2) by only 0.74 AIC points. Thus, we present relationships from both models.

Turnover in Virginia rails exhibited relationships with precipitation that were similar to black rails, but the impact of WNV differed (Figure 3g–j). Colonisation was strongly positively related to annual precipitation in the top two Virginia rail models. The second-best model, which did not include the WNV vector index, featured a strong negative relationship between precipitation and extinction (Figure 3j). In the best model, however,

this relationship was dampened with the addition of the WNV vector index, which was strongly and positively related to extinction (Figure 3h) and acted as a weak moderator of precipitation on colonisation (Figure 3g). In Virginia rails, however, colonisation increased slightly in years with more WNV.

Patch characteristics, turnover, and equilibrium-nonequilibrium conditions

There was a consistent ranking of the most important patch characteristics affecting black rail turnover under equilibrium and nonequilibrium conditions, regardless of whether we sought the best combination of

characteristics by category (Table 2) or covariates were modelled individually (Table S5). By far, the greatest effects on colonisation and extinction were biogeographic, accounting for all the AIC weight by category (Table 2), whilst patch quality ranked a distant second followed by matrix condition. Patch area captured nearly all the AIC weight (>0.99) in single covariate models during both equilibrium and nonequilibrium, whilst isolation had a secondary role, outperforming the third best covariate in each period by a ΔAIC of 16 and 50. As expected, larger sites were less likely to go extinct and more likely to be colonised, whilst patch isolation was negatively related to colonisation and positively related to extinction (Figure S3). During equilibrium, only three other patch characteristics had lower AIC scores than a model with annual fluctuations (year). Geomorphology, a measure of patch quality that reflects a site's hydrological context (slope, fringe or fluvial), was the third most important covariate during equilibrium but fell to fifth during nonequilibrium. Elevation was fourth- and third-most important during equilibrium and nonequilibrium, respectively. Higher sites were less likely to be colonised and more likely to go extinct, perhaps because they are more likely to freeze. Per cent of open habitat surrounding patches was the only matrix condition in the top five. It was positively associated with colonisation and negatively associated with extinction. It ranked fifth during equilibrium and fourth during nonequilibrium.

The slope of the relationship between patch characteristics and turnover did not differ significantly between equilibrium and nonequilibrium periods for 12 of 15 patch characteristics evaluated (Figures 4, Figure S3). Colonisation and extinction coefficients for the area—the most influential patch characteristic related to turnover—were unchanged. The slope of the isolation-extinction relationship increased significantly during nonequilibrium as occupancy declined, which might be expected given the low vagility of black rails and the importance of rescue effects (Van Schmidt & Beissinger, 2020). Only two other measures of patch quality shifted slopes between periods, but neither was particularly influential on turnover (Table S5). The largest change was that of surface water, which became more negatively associated with extinction after the switch from equilibrium to nonequilibrium. A smaller shift occurred with EVI, a measure of vegetative cover, which became more positively associated with colonisation during nonequilibrium.

Virginia rails exhibited turnover relationships with patch characteristics during nonequilibrium that were similar to black rails (Figures S4, S5; Table S6), but with several notable differences. Like black rails, patch area completely dominated Virginia rail turnover dynamics. However, the role of isolation differed, likely due to the greater vagility of Virginia rails. Colonisation was much less negatively affected by isolation and isolation had little effect on extinction. Subtle differences in habitat associations were also revealed, as Virginia rails were less likely to colonise slope wetlands and more likely to colonise fringe wetlands than black rails. Extinction was less likely for Virginia than black rails at higher elevations, fluvial sites, natural wetlands and patches with a forested matrix. In contrast, patches that were irrigated and surrounded by open matrix habitats had a greater mitigating effect on extinction for black than Virginia rails.

DISCUSSION

Our study produced two important findings for metapopulation biology: (1) The key patch covariates affecting turnover were the same during equilibrium and nonequilibrium conditions, and relationships between most patch characteristics and turnover remained unchanged; and (2) Biogeographic factors—area and isolation—were far more important than patch quality and matrix conditions in driving turnover. To the best of our knowledge, this study represents the first empirical and direct demonstration of the relative stability of patch-turnover relationships. The second finding – that area and isolation dominated metapopulation dynamics – conflicts with other studies (Armstrong, 2005; Prugh et al., 2008; Ricketts, 2001) but is expected from theory for a classical metapopulation that undergoes frequent colonisation and extinction (Hanski, 1999). For rails, patch quality had underwhelming effects and the matrix hardly mattered, performing far behind area and isolation during equilibrium and nonequilibrium conditions (Tables 2, Tables S5, S6).

Equilibrium and non-equilibrium states can sometimes be difficult to identify. For metapopulations, local equilibrium can be identified by time-invariant occupancy and turnover (MacKenzie et al., 2018). The dynamic multi-season occupancy model (MacKenzie et al., 2003) provided a straightforward way to test for equilibrium by examining the fit of annual changes in turnover versus constant probabilities across groups of years (Table 1), whilst accounting for imperfect detection. However, accurately identifying equilibrium and nonequilibrium conditions requires large-scale, long-term data and may not have been possible for rails without monitoring hundreds of patches over two decades.

The shift from equilibrium to nonequilibrium dynamics generated few changes in the magnitude or direction of patch-level covariates of turnover (Figure 4). The only important change was that the role of isolation grew as occupancy declined in black rails. In a metapopulation with declining occupancy, isolation should increase over time. This, in turn, could drive occupancy lower and lead to negative feedback on metapopulation dynamics that overwhelms other factors, depending upon the network structure, modularity of patches and role of patch quality (Dallas et al., 2021; Fletcher et al., 2013). However,

isolation had a much weaker effect on the turnover of Virginia than black rails, possibly due to the greater dispersal abilities of the former.

Nonequilibrium metapopulation dynamics can result from changes in landscape structure, which operate on slow and moderate time scales, and from rapid shifts in local population dynamics (Hanski, 1999) driven by climatic variation (Dallas et al., 2020) or disease (Hess, 1996). Patch-level extinctions due to disease have also occurred in other systems (Frick et al., 2015), and are expected for multi-host, frequency-dependent pathogens (De Castro & Bolker, 2005). For the California black rail, recurring dry years combined with the arrival of an emergent disease (WNV) interacted to push metapopulation dynamics from equilibrium to nonequilibrium (Figure 1a). Our study occurred during the driest conditions the region experienced in millennia (Williams et al., 2022). Precipitation and WNV had strong effects on black rail colonisation and interacted in unexpected ways to propel extinction (Figure 3). Wet years produced occupancy gains through increased colonisation and decreased extinction, but high WNV years reversed these effects, especially for extinction. Turnover probabilities of black and Virginia rails were highly correlated, which suggests that precipitation, WNV, and cold temperatures acted similarly on both species. However, their effects on Virginia rail occupancy and metapopulation growth rates were weaker and interactions amongst these factors were limited (Figure 3, Table S3). Moreover, whilst both species were frequently infected by WNV (Figure 2), seroprevalence was higher for Virginia rails. If exposure to WNV is similar, the higher seropositive rate could indicate lower mortality after exposure for Virginia than black rails. Perhaps, as a result, Virginia rails did not experience the large and sustained decline following the arrival of WNV that black rails exhibited, and their occupancies fluctuated semi-independently.

CONSERVATION IMPLICATIONS

Whether the California black rail will recover from WNV, as many other birds have done (Kilpatrick & Wheeler, 2019), remains to be seen. Our study area has some of the highest incidences of human infections in California (Snyder et al., 2020) and recovery from WNV has been elusive for another local endemic of this region, the yellow-billed magpie (*Pica nutalli*) (Kilpatrick & Wheeler, 2019). Nevertheless, our results suggest that place-based conservation actions should be robust to environmental variation and the impacts of WNV because the relative importance of patch covariates related to turnover did not change between equilibrium and nonequilibrium periods (Figure 4, Table S5).

Surprisingly, WNV has gone unrecognised as a threat to the eastern subspecies of black rail (*L. j. jamaicensis*), which was protected under the US Endangered Species Act in 2020. Its decline has been attributed primarily to sea-level rise (Stevens & Conway, 2021) in the absence of direct evidence of reproductive failure and adult mortality. The subspecies is thought to have declined by 75% over the last 10–20 years, which equates to a 7–12% decline per year—a very rapid rate for a widespread bird unless a factor like a fast-spreading disease was involved. In comparison, the decline of the California black rail in the Sierra Foothills averaged 5% per year over the same time period. Nearly all surveys for the eastern black rail (McGowan et al., 2020) began after the arrival of WNV on the east coast of the US in 1999 and its rapid spread across the continent (Kramer et al., 2019). Wetland creation has been recommended for recovering the eastern black rail but could produce sink habitats unless the research is undertaken to understand the complex factors affecting the prevalence of WNV and its vectors (Kovach & Kilpatrick, 2018; Paull et al., 2017).

PEER REVIEW

DATA AVAILABILITY STATEMENT

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.